

Intelligence in Corvids and Apes: A Case of Convergent Evolution?

Amanda Seed*, Nathan Emery† & Nicola Clayton‡

* Department of Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

† School of Biological & Chemical Sciences, Queen Mary University of London, London, UK

‡ Department of Experimental Psychology, University of Cambridge, Cambridge, UK

(Invited Review)

Correspondence

Nicola Clayton, Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB23EB, UK.
E-mail: nsc22@cam.ac.uk

Received: November 13, 2008

Initial acceptance: December 26, 2008

Final acceptance: February 15, 2009

(M. Taborsky)

doi: 10.1111/j.1439-0310.2009.01644.x

Abstract

Intelligence is suggested to have evolved in primates in response to complexities in the environment faced by their ancestors. Corvids, a large-brained group of birds, have been suggested to have undergone a convergent evolution of intelligence [Emery & Clayton (2004) *Science*, Vol. 306, pp. 1903–1907]. Here we review evidence for the proposal from both ultimate and proximate perspectives. While we show that many of the proposed hypotheses for the evolutionary origin of great ape intelligence also apply to corvids, further study is needed to reveal the selective pressures that resulted in the evolution of intelligent behaviour in both corvids and apes. For comparative proximate analyses we emphasize the need to be explicit about the level of analysis to reveal the type of convergence that has taken place. Although there is evidence that corvids and apes solve social and physical problems with similar speed and flexibility, there is a great deal more to be learned about the representations and algorithms underpinning these computations in both groups. We discuss recent comparative work that has addressed proximate questions at this level, and suggest directions for future research.

In the last few decades there has been a growing interest in the evolution of intelligence, and increasing evidence that it has evolved independently in several vertebrate groups other than primates, such as dolphins (Marino 2002), hyaenas (Holekamp et al. 2007) and canids (Miklosi et al. 2004; Hare & Tomasello 2005) (for a definition of ‘intelligence’, see Box 1). Perhaps most strikingly, there is evidence for impressive cognitive abilities in groups of large-brained birds, such as corvids and parrots (Emery & Clayton 2004). The discovery that these non-primate, non-mammalian animals are capable of feats thought until not long ago to be uniquely human, such as recalling specific past events (episodic-like memory; Clayton & Dickinson 1998), planning for the future (Raby et al. 2007), taking the visual perspective of conspecifics (Dally et al. 2006), coopera-

tive problem-solving (Seed et al. 2008) and creating novel tools to solve problems (Weir et al. 2002), has fascinated the scientific and non-scientific community alike, but it has also prompted questions. What exactly is it that has evolved convergently? Can these birds with walnut-sized brains really be using human-like reasoning to carry out these behaviours, and if not, what cognitive processes allow for their impressive flexibility? Did the same evolutionary processes that shaped the intelligence of primates (and ultimately humans) act upon corvid ancestors? What were they, and can the answer tell us anything about the evolution of the human mind? The notion that intelligence has evolved independently but convergently in corvids and apes has therefore prompted questions from all of Tinbergen’s four levels of explanation. In this review we will address the

Box 1 – What is Intelligence?

Ever since scholars began discussing animal intelligence it has been a highly divisive issue, and remains so today. At the poles of the debate are two opposite views concerning 'thinking' in animals. The first, the origin of which is attributed to Descartes, is that animals are essentially mindless machines, with their behaviour triggered wholly by external or internal stimuli. The other, most famously articulated by Darwin, is that 'the difference in mind between man and the higher animals...is one of degree and not of kind' (Darwin, 1882).

Both these views are to be found entrenched within the different historical approaches to the study of animal cognition (Dickinson 1980; Tomasello & Call 1997; Shettleworth 1998; Wasserman & Zentall 2006): the behaviourist school (Watson 1913) and that of cognitive ethology (Griffin 1978). The former illuminates in detail one powerful general mechanism by which animals acquire, process, store and act on environmental stimuli: associative learning. The latter is concerned with natural behaviours for which explanations based either on classical conditioning or hardwired predispositions seem to fall short, and seeks to explain them in mentalistic terms. Most contemporary accounts of animal cognition acknowledge the interplay between the two views (e.g. Dickinson & Shanks 1995).

Complex cognition or intelligence in animals is, therefore, usually defined by exclusion, rather than by some positive assessment of the mechanisms underpinning it. Identifying 'intelligence' in animals in practice typically amounts to observing animals performing complex behaviours in their environment, and looking for evidence for 'behavioural flexibility' or the appearance of novel solutions that are not part of the animal's repertoire (Roth & Dicke 2005). The relative size of the brain (or brain area) of the species or group in question is often used as a proxy for intelligence or 'cognitive potential', but as Healy & Rowe (2007) point out, 'considerable caution should be exercised when interpreting correlations between such multifunctional brain regions and complex behaviours, ... owing to the problems inherent in attributing a single function to such a region'.

What makes the evolution of intelligence so difficult to study is the fact that the feature itself is an unobservable property of an animal's psychology that has no positive definition; is unlikely to be unitary; and is held by some as not existing in most animals. Nevertheless, the seemingly 'intelligent' behaviours of animals are among the most fascinating. The emerging consensus is that the best way to address questions about the (possibly convergent) evolution of intelligence, and the fitness benefits it confers, is through carefully focused comparative experimentation (Reader et al. 2005; Healy & Rowe 2007).

hypothesis first from an ultimate and then a proximate perspective.

Why Would Intelligence Evolve? Surviving and Thriving in an Unpredictable Environment

Although we humans tend to see our complex cognition as one of the pinnacles of evolution, it is in many ways a costly and inefficient way of acting in the world. The more behaviour that is either fully intact from an animal's birth, or that can be acquired rapidly through simple associative learning, the faster the animal can get on with finding a mate and reproducing. In contrast, a cognitively complex strategy demands more time to be spent learning about the world and attaining the full complement of adult behaviours. As philosophers such as Godfrey-Smith and Sterelny have argued, the only sort of environment that could possibly favour the use of such a costly strategy is a complex and unpredictable one (Godfrey-Smith 2001;

Sterelny 2003). When the environment can change quickly, hardwired behaviours and rigid stimulus-response action patterns may become maladaptive, or less adaptive when compared with the flexible behaviour based on more abstract knowledge.

Potts (2004) has described the palaeoenvironmental conditions prevalent during the evolution of great apes, and the consequences they would have had for the evolution of cognition. Between the Late Miocene and the Late Pliocene, a diminished number of species of great apes became confined to the forests and woodlands of the tropical latitudes of Africa and Southeast Asia. During the following Pleistocene period, climatic instability led to sharp oscillations in these equatorial habitats. Unlike the cercopithecine primates, the great apes did not respond to these environmental challenges by changing their bodies, allowing for a reduction in the reliance on ripe fruits and an increase in the amount of plant material in the diet. Instead, the great apes continued to rely on

ripe-fruit frugivory, and Potts (2004) argues that this diet and habitat during such a period of instability would have exposed them to the environmental variability hypothesized to favour the evolution of advanced cognitive capacities.

Convergent Evolution

Environmental complexity and variability such as that faced by primates during the course of their evolution have also been faced by other groups of animals. Emery & Clayton (2004) argued that cognitive abilities of a level comparable with that of the great apes has evolved convergently in corvids, a relatively recently evolved group of passerine birds. Convergent evolution is defined as 'evolutionary change in two or more unrelated organisms that results in the independent development of similar adaptations to similar environmental conditions' (Keeton & Gould 1986). For similar traits to be shown to have evolved convergently, rather than being homologous, it must be demonstrated that the trait was not present in the common ancestor.

A useful analogy is the evolution of flapping flight in vertebrates. The forelimbs of birds, bats and pterosaurs have all evolved into wings. Knowledge of their divergent evolutionary history, and the discontinuity of such an adaptation in their ancestry, suggests that they must have arisen through a process of convergent evolution. Moreover, dissecting the wings reveals that they are in fact structured differently (Fig. 1). The bird wing is the result of an extension of all the bones of the forelimb, while the bats and pterosaurs support the wing through extended digits: the fifth digit for pterosaurs; while for bats it is the second, third, fourth and fifth.

Emery & Clayton (2004) pointed out that corvids, like apes, have evolved large brains relative to their body size, and that the areas of the brain thought to be functionally equivalent to the neocortex of primates, the nidopallium and mesopallium, are specifically enlarged. Behavioural hallmarks of intelligence

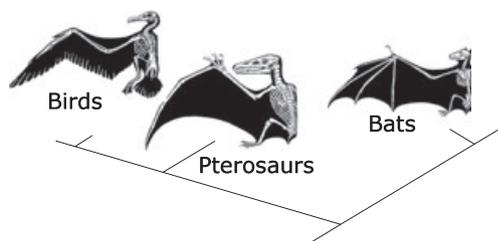


Fig. 1: The convergent evolution of wings in vertebrates.

in apes, such as the manufacture and use of tools and social strategizing, have also been documented for species of corvids, and laboratory experiments suggest that these are underpinned by a complex cognitive toolkit common to corvids and apes (Emery & Clayton 2004). This trait is likely to have arisen by convergent evolution, because the evolutionary lines that led to birds and mammals diverged around 280 million years ago, and have undergone very different evolutionary histories. In addition to the obvious differences in morphology, the avian brain is organized very differently from the mammalian brain. For example, while the mammalian brain is laminar, with the cells organized into layers, the avian brain is nuclear, and is comprised of clusters of cells. The difference in the structure of the brain between birds and mammals, much like the differences in the anatomical features of the different types of vertebrate wings, gives a good indication that if the intelligence of corvids and apes is indeed similar, the similarity must be the result of convergence. However, the hypothesis that intelligence in corvids and apes is the result of convergent evolution needs further testing: were similar environmental conditions responsible for the evolution of the trait in both groups, and is the trait really underpinned by independently evolved yet similar cognitive mechanisms?

Ultimate Perspectives – Hypotheses for the Evolution of Intelligence

Although many agree that the function of intelligence is to produce flexible adaptive behaviour in the face of environmental complexity and variability, different theories place different emphases on the challenges from the physical environment and those from the social environment. We describe the six predominant hypotheses for the evolution of great ape intelligence. These theories have received different degrees of support, but to date none has been wholly supported or refuted, and so we discuss the extent to which each one might apply to corvids. It is worth emphasizing that, while we are concerned with corvids and apes in this review, many of the hypotheses outlined above apply to other species of birds and mammals, including food-caching parids, omnivorous bears, tool-using Galapagos finches, extractive foraging parrots and monkeys, social carnivores such as hyaenas, wolves and meerkats to name but a few. Another point to stress at the outset is that these hypotheses are not mutually exclusive, and indeed it seems likely that more than one of

these evolutionary pressures has shaped the minds of corvids, apes, as well as other species.

Physical

Several aspects of the foraging strategies of primates have been linked to increased brain size. The different proposals place differing emphasis on where food is located, what food is eaten and how it is processed:

Where and when – Reliance on spatiotemporally dispersed food resources (Clutton-Brock & Harvey 1980; Milton 1981).

What – Omnivory and extractive foraging (Parker & Gibson 1977; Gibson 1986).

How – Complex foraging (Byrne 1996, 2004) and tool use (Goodall 1964; Parker & Gibson 1977).

Where and When can Food be Found?

Spatiotemporally Dispersed Food Resources

Milton (1981) suggested that the primate diet, in particular, the reliance on tropical plant foods, provided the evolutionary stimulus for the evolution of large brains. Tropical plants are patchily distributed throughout the forest, and plants may only provide edible ripe fruit at certain times of the year. However, this temporal and spatial patchiness is predictable; plants remain in the same place and ripen at predictable intervals. She proposed that those primate species feeding on the most patchily distributed plants would have evolved the largest brains in order to do so efficiently, perhaps through the use of a 'cognitive map', given the energetic expenditure of travelling long distances to find food. In support of this hypothesis, Clutton-Brock & Harvey (1980) found a positive correlation between range area and degree of frugivory, with the size of the brain relative to body size for primate species. However, two main problems with this finding have been raised; first, that the use of body size as a comparator may be inappropriate given the fact that foliovores have a larger gut than frugivores to extract enough nutriment from a diet of leaves, which lowers their brain:body ratio independently of the size of the brain (Deacon 1980; Byrne 2000). Secondly, Dunbar (1992, 1995) has argued that the absolute size of the range area may be an inappropriate measure, given that differences in body size will modulate the 'complexity' of any given range area. Dunbar instead correlated the 'neocortex ratio' (volume of the neocortex/volume of the rest of the brain) with range area corrected for body size, and found no relationship. A conceptual criticism is that although apes, including humans, are dependent

on ripe fruit, monkeys can in fact process unripe fruit and so the demand of locating the food within a narrow time window does not apply so strictly.

What about corvids?

While fruit features in the diet of many species of corvid, a reliance on ripe fruit does not, and rather most corvids are renowned for their ability to exploit a wide variety of food resources (Goodwin 1986). However, a conspicuous feature of corvid ecology worth mentioning here is the fact that many species cache foods during periods of seasonal abundance; indeed caching is likely to have been a trait present in the common ancestor (de Kort et al. 2006). Western scrub-jays not only remember where they have cached, but can also integrate information about what they cached and when, in order to recover perishable food when it is still edible (Clayton & Dickinson 1998, 1999; Clayton et al. 2001, 2003; de Kort et al. 2005). Remembering the location of thousands of caches, which vary in terms of their perishability, seems a comparable spatiotemporal challenge to locating ripe fruit.

What Food? Omnivory and Extractive Foraging

Parker & Gibson (1977) proposed two important elements of the primate diet for the evolution of intelligence: the degree of dietary generalism and reliance on foods that need to be extracted from a substrate. They suggested that the expansion of the neocortex was therefore favoured in order to exploit niches not readily available to others, because extractive foods tend to be high in nutritive value and available all year round. The main objection to this theory is the fact that extractive foraging per se does not help predict brain size. Dunbar (1995) found no relationship between extractive foraging and neocortex ratio. However, Parker and Gibson emphasized that it was the conjunction of omnivory and extractive foraging, and the consequent variety and complexity of the sensorimotor coordinations used in the finding and processing of food, that led to the evolution of intelligence. They support this notion with the observation that among primates, the species with the largest brain size relative to body size are omnivores that engage in extractive foraging, such as chimpanzees, orang-utans and capuchin monkeys.

What about corvids?

Some corvids such as crows, rooks and ravens are highly omnivorous. For example, from a review of

the available literature, Cramp & Perrins (1994) reported that rooks consume over 170 species of plants and animals, including many parts of the plant (roots, seeds, leaves and fruits); a number of insects both as larvae and adults; worms; seafood such as shrimps and mussels; the eggs and young of ground-living birds; and adult vertebrates, many as carrion, and also as small prey which are first caught and killed (mice, voles, frogs and even fish). They also rely on extractive foraging for a high percentage of their dietary requirements. Over 50% of their food is taken by digging in the soil for grain and invertebrates, particularly earthworms (Lockie 1955), and they also dig for roots and tubers such as potatoes and turnips. Other forms of extractive foraging among corvids include the dropping of mussels, limpets or bone from the air until the shell or enamel breaks. These foods are also accessed by hammering and prising with the beak, as are nuts such as walnuts and acorns. Many species feed on rubbish dumps, a feeding habit likely to involve both extraction and diversity (Cramp & Perrins 1994).

How is the Food Obtained? Complex Foraging and Tool-Use

The complexity of great ape feeding and tool-using behaviour has been linked to the evolution of intelligence by Byrne (1996, 2004). Byrne proposed that foraging and tool-use in the great apes is characterized by a complex organizational structure. In support of this notion he referred to the foraging skills of gorillas, and observations of great ape tool-use. Gorillas feed on a diet of plants with physical defences such as nettles, using a wide range of techniques, each involving the coordinated use of two hands in different roles. The techniques are comprised of a number of hierarchically organized steps (Byrne & Byrne 1991, 1993; Byrne 1996). Likewise, tool-use in chimpanzees and orang-utans is characterized by bimanual role differentiation, and the sequential use of different tools to achieve the same end (Byrne 1996, 2004). Several researchers have posited that tool-use may have been selected for advanced cognitive capacities, given the challenge of tracking events between objects outside the body (Goodall 1964). In support of the connection between tool-use and brain evolution is the correlation between relative 'executive brain' (neocortex and striatum) and amount of tool-use reported for a given species (Reader & Laland 2002).

What about corvids?

The foraging behaviour of corvids has not been studied in detail and so comparisons with apes are premature, but corvids (and other birds, such as raptors and parrots) use both beak and feet in the processing of foods (in Cramp & Perrins 1994). Hierarchically structured foraging techniques have been described for ravens by Heinrich (1999). There are reports of infrequent tool use by several species of corvids (Lefebvre et al. 2002), and New Caledonian crows are known to both manufacture and use tools routinely in the wild. They make two types of tools, and use them to obtain insect larvae from holes in living and dead wood, from the leaf litter, and from the base of plants (Hunt 2000). Stepped-cut tools are fashioned from pandanus and fern leaves in a series of steps, with the resulting tool retaining a thick base and tapering in steps to a narrow tip (Hunt & Gray 2004b). Hook tools are commonly made by trimming twigs of their branches, leaves and bark, in a complex series of steps (Hunt 1996; Hunt & Gray 2004a). They can also be fashioned from a variety of other substrates, including the midribs of leaves, bamboo stems, and thorny vines. This use of a range of materials and techniques to achieve the same end suggests flexibility (Hunt & Gray 2002).

However, some primate researchers have argued that the range of both the materials used to build tools and the uses to which they are put by New Caledonian crows is not as great as that described for chimpanzees and orang-utans (Mendes et al. 2007). Furthermore, while all species of great apes make and use tools, only one corvid has been reported to do so routinely (so the trait is unlikely to be the ancestral condition). However, it is not clear whether this reflects an absence of cognitively mediated foraging, or a lack of benefit to be gained from tool-mediated foraging in corvids. Corvids can use their beak for many of the sorts of tasks that apes use tools for, such as digging and cracking open nuts. Furthermore, the lack of hands and physical strength presents a limitation to the type of tool-using that a bird can perform; tasks such as smashing open insect nests could not conceivably be facilitated through tool-use. The ecological conditions favouring the use of tools in avian species might therefore be expected to be fairly uncommon, and perhaps these are not faced by most corvids. For example, in the Galapagos Islands, tool-use by woodpecker finches is common in some habitats but rare in others. It is most common in coastal zones, where harsh and unpredictable conditions are seen

Table 1: Comparison of corvids and chimpanzees

		Chimpanzees	Corvid examples
Physical			
When & where?	Spatiotemporally dispersed food	Fruits and leaves ¹	Arable crops, insects ²
*	Caching	Not reported	Yes
What?	Dietary diversity	High (328 foods, 198 plant species) ³	For example, rooks – high (>170 species) ²
	Extractive foraging	Habitual: fruits, nuts, nest-building insects ⁴ Opportunistic: e.g. bone marrow, honey ⁵	Habitual: ground living insects, seeds ^{2,6} Opportunistic: e.g. shellfish, nuts, fruit, rubbish ²
How?	Innovation	High levels ⁷	High levels ⁸
	Complex foraging	Bimanual, hierarchically organized manipulation ⁹	Not well studied, can involve coordination of beak and foot ²
*	Tool-use and manufacture	Extensive: e.g. ant-dipping, termite fishing, sponge making ¹⁰	Routine manufacture of hook tools by New Caledonian crows ¹¹
Social			
Competition	Group-size	Fairly large (19–106 individuals) ¹²	Rooks and jackdaws: large (50 to 1000 individuals) ²
	Alliance formation	Yes, with several individuals, 'tactical' ¹³	Rooks, ravens and jackdaws: yes, usually with 1 or 2 individuals ¹⁴
Cooperation	Post-conflict behaviour	Reconciliation, third-party affiliation, third-party punishment ¹⁵	Rooks: third-party affiliation ¹⁶
Social learning	Social facilitation of feeding	Yes, e.g. novel foods ¹⁷	Yes, e.g. crows, rooks, ravens ^{18,19,20}
	Social learning of foraging techniques	Yes, e.g. nut-cracking ¹⁷	Yes, e.g. Florida scrub-jays
Evolutionary legacy			
*	Reproductive biology	Viviparous, long gestation	Oviparous, altricial young
*	Mating system	Promiscuity	Varied, mostly long-term monogamy; cooperative breeding ²¹
*	Body size and locomotion	Large (50–80 kg), arboreal clambering	Relatively small (<1 kg), flight
*	Morphology	Hands	Wings, beaks

Asterisks denote clear differences between them.

¹Clutton-Brock & Harvey 1980; ²Cramp & Perrins 1994; ³Nishida & Uehara 1983; ⁴Parker & Gibson 1977; ⁵Brewer & McGrew, 1990; ⁶Lockie 1955; ⁷Reader & Laland 2002; ⁸Lefebvre et al. 1997; ⁹Byrne 2004; ¹⁰McGrew 1992; ¹¹Hunt 1996; ¹²Yamagiwa 2004; ¹³Harcourt 1992; ¹⁴Emery et al. 2007; ¹⁵de Waal 1982; ¹⁶Seed et al. 2007; ¹⁷Rapaport & Brown 2008; ¹⁸Sonerud et al. 2001; ¹⁹Waite 1981; ²⁰Marzluff et al. 1996; ²¹Clayton & Emery 2007.

in conjunction with the availability of particularly large grubs embedded in tree holes (Tebich et al. 2002). Tool-use may be the expression of a pre-existing physical intelligence rather than a necessary condition for it to evolve, but nevertheless the routine use of tools may provide selective pressure for further cognitive adaptation, a pressure not faced by most corvids. The similarities and differences between the challenges from the physical environment faced by apes and corvids, along with some relevant biological differences because of their divergent evolutionary history, are summarized in Table 1.

Social

The challenges and opportunities presented by the social environment can also be divided into three broad categories:

Competition – Machiavellian strategies for maximizing personal gain, resulting in social complexity (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Byrne & Whiten 1997).

Cooperation – Pro-social or mutually beneficial behavioural coordination (Strum et al. 1997; Boesch & Boesch-Achermann 2000; Barret & Henzi 2005; Connor 2007; Dunbar & Schultz 2007; Emery et al. 2007).

Social learning – Exploiting the opportunity to learn from others (Russon 1997; Whiten & van Schaik 2007).

Competition – Machiavellian Manoeuvring

Humphrey (1976) suggested that group-living primates could benefit from intelligent social strategies that circumvent the constraints of individual ability when competing for mates and resources. Though

not explicit in his proposal, emphasis has tended to be placed on exploitative aspects of social manoeuvring for the evolution of primate intelligence. It is in this competitive setting that Humphrey argued that an 'evolutionary ratchet' can be set up. When one individual gains a competitive advantage (and fitness benefits) through intelligent activity, such intelligence is likely to spread through the gene pool, and this effect will be iterated until an upper limit is set by natural selection, for example by the constraint of maximum daily calorific intake for use in fuelling brains. In primates, neocortex ratio correlates with group size, independently of other environmental variables such as home-range size (Dunbar 1992, 1995). More importantly for this hypothesis, neocortex size also correlates with indicators of social complexity, such as deception rate (Byrne & Corp 2004), mating system (Sawaguchi & Kudo 1990) and grooming-clique size (Kudo & Dunbar 2001). Interestingly, male rank predicts mating success less well for primate species with relatively larger neocortices (Pawolowski et al. 1998), which suggests that social strategizing is effective in circumventing individual competitive ability.

What about corvids?

Corvids display a variety of social organization, ranging from pair-living territorial species such as the Eurasian jay, to cooperative breeders such as the Florida scrub-jay, to communal-living species such as rooks and jackdaws (reviewed by Clayton & Emery 2007). Some corvids therefore fulfil the basic criteria for the evolution of social intelligence: 'living in large semi-permanent groups of long-lived individuals' (Byrne & Whiten 1997, pp. 14). Emery et al. (2007) argue that both rooks and jackdaws (in captivity) do indeed form long-term alliances with other group members, which are maintained through the use of affiliative behaviours, and employed in agonistic conflicts. They report preliminary evidence that rooks are sensitive to relationships between third parties, as they are seen to redirect aggression to the partner of an individual that they have received aggression from.

Food caching also provides a stimulant for group-living animals to maximize personal gain at the expense of others. In the wild, corvids' caches can be lost not just to degradation over time, but also to thieving conspecifics, which use observational spatial memory to accurately locate the caches of others (Bednekoff & Balda 1996a,b; Heinrich & Pepper 1998). A series of observations and experiments car-

ried out with western scrub-jays and ravens have shown that the strategies used by storing corvids to protect their caches are based not just on simple rules of thumb (e.g. by only hiding food when there is no competitor in sight), but are instead highly flexible, and may depend on an ability to take the visual perspective of the competitor into account (reviewed in Clayton et al. 2007).

However, living in a large group per se does not appear to have been an important selective pressure during the evolution of large brains in birds, for unlike primates and other mammals, there is no clear relationship between brain size and group size (reviewed in Emery et al. 2007; c.f. Iwaniuk & Arnold 2004). A fundamental difference between birds and mammals worth mentioning here is their divergent reproductive biology. Mammals are viviparous (give birth to live young, after an extended period of development in the womb), while birds are oviparous (lay eggs). The asymmetry between male and female mammals in the selective advantage to providing parental care means that in the majority of mammals, polygyny, and predominantly maternal care is seen. This asymmetry is smaller in birds (because the initial investment by the female is smaller), and for the majority of species, monogamy and biparental care are optimal. Competition for mates will occur at some point in the life cycle of birds (in birds such as rooks which pair for life, perhaps just once), but it is a continuous and critical feature in the social life of a polygamous primate (such as chimpanzees), because a dominant male has the potential to monopolize mating opportunities, leaving the female to care for the offspring. Such a mating system has obvious implications for social structure. Numerous species of primates are reported to maintain a network of valuable relationships: between males, for competition for alpha status and therefore mating rights; and between females, for protecting offspring from infanticidal males. Many of the advantages of such a network of relationships do not apply to a monogamous species, and as a consequence, neither does the need to track the changing relationships between different third parties.

Cooperation and Behavioural Coordination

In the Machiavellian framework, competition is central to animals that are 'forced' to live together, and cooperation functions largely in the accrual of individual benefits. However, other theorists have emphasized the inverse view: aggression is merely a

way for group-living animals to negotiate the terms of their peaceable co-existence, and adaptations that improve social cohesion are likely to be selected for. As Barret & Henzi (2005) explain, such adaptations may be the product of multi-level selection, wherein the individual has a stake in the well-being of the group (e.g. if large groups suffer less from predation). de Waal & van Roosmalen (1979) suggested that selective pressure exists for behaviours that minimize the likelihood of conflict occurring (behaviour reading, policing) or that ameliorate the costs of conflict after it has taken place, and repair threatened relationships (reconciliation, third-party affiliation). Group living may also provide a platform for animals to increase their fitness by combining their efforts, either as a group (e.g. group hunting, group defence), or as a smaller number of individuals (social grooming, pro-social helping). When animals start cooperating in this way, a situation which can be referred to as a 'biological market' is set up, and it would pay animals to select the most effective and/or reciprocal cooperative partners. Furthermore, adaptations that improve cooperative efficiency (such as coordinating with another's actions) are likely to have fitness benefits, not only because of the increased yield from cooperative action, but also because effective co-operators fare well in the biological market. At this point, a ratchet effect could conceivably be set up, much like the one described for effective competition by Humphrey (1976). There is evidence that conflict management, cooperation and biological markets (or 'score keeping') are important features of primate groups (Noe & van Hooff 2001). However, whether the pressure for such behaviours to evolve has been a driving force behind the evolution of primate brains is difficult to assess. Dunbar & Schultz (2007) report that species of primates that form coalitions have significantly higher neocortex ratios (Dunbar & Schultz 2007). However, there is no more consensus as to the cognitive requirements of these behaviours than there is for competitive behaviours such as 'tactical deception'.

What about corvids?

The difference between mammalian and avian reproductive biology and predominant mating system is also relevant to this discussion. In socially monogamous birds, increasing the quality of parental care may lead to increasing pay-offs, if more experienced pairs (that have paired for more than one breeding season) will raise more chicks. In such

cases, mate retention (long-term monogamy) may be favoured. Numerous studies indicate that 'divorce' in long-term monogamous species is more likely when the pairs' mating attempts have been relatively unsuccessful (Mock & Fujioka 1990), indicating that successful coordination is an important determining factor in the decision to remain paired. Interestingly, a recent analysis of brain size and mating system in birds found that the largest relative brain sizes are found in long-term monogamous species and cooperative breeders (Emery et al. 2007). This relationship may indicate that these mating systems set up a platform on which adaptations that increase coordination between pair mates (and helpers) are favoured. Most corvids form long-term monogamous pairs which associate throughout the year, and typically for life. Recent studies of captive rooks suggest that pair members do coordinate their actions, both during displays and outside this context (Emery et al. 2007). Furthermore, rooks engage in third-party affiliation with their partner, after one of them has been involved in a conflict with another group member (Seed et al. 2007). However, they do not reconcile these conflicts (with non-partnered individuals, they do not fight with their partners), a finding that is line with the notion that they do not form valuable relationships with group members outside their partnership. Therefore, while the pressure to increase the cooperative quality of social relationships may apply to both corvids and apes, the pressure to keep track of a number of collaborative partners in a 'biological market' may be a less relevant one for long-term monogamous corvids (although it may apply to species which spend an extended period of time in non-breeding flocks, such as ravens).

Social Learning – Exploiting the Opportunity to Learn from Others

Living socially also provides sources of information that it would pay an individual to be able to exploit, and this might select for intelligence (Byrne & Whiten 1997; Russon 1997; Whiten & van Schaik 2007). Individual learning is costly, in terms of time, and also risky (e.g. from eating poisonous foods). An ability to learn from the behaviours of others would therefore be beneficial, although not without potential costs, for example from copying an unreliable model, or employing a copied behaviour in the wrong context (Richardson & Boyd 1985). Furthermore, individual innovation may occur at a relatively low frequency if it depends on fortuitous

contingencies that happen rarely, and so learning from others might mean the difference between acquiring a useful behaviour and never doing so. Could the pressure to exploit this source of information have driven the evolution of large brains? Primates (as well as many other social vertebrates, including fish and birds) are known to take advantage of the opportunity to learn socially. Reader & Laland (2002) correlated the relative size of the 'executive brain' (neocortex and striatum) in primates with the number of reports of social learning, innovation and tool-use for a given species. They found a positive correlation for all three. This provides some indication that the pressure to learn from others may have played a role in primate brain evolution.

What about corvids?

Innovation rate correlates with brain size in birds, just as it does in primates (Lefebvre et al. 1997), with corvids emerging as one of the most innovative groups, along with parrots. However, no correlation has been performed with incidences of social learning, because only 72 cases of social learning were recorded (compared with 1796 observations of innovation). This contrasts with the ratio of 558 cases of innovation and 451 of social learning in Reader & Laland's (2002) study. Lefebvre & Bouchard (2003) suggest that the relative numbers indicate that feeding innovations do not spread as readily to other birds as they do in primates. However, Marler's (1996) cautionary note concerning the different research perspectives of ornithologists and primatologists should be remembered here, especially given the fact that all 76 avian experimental studies were positive accounts of social learning. Indeed, there are field studies indicating that corvids' foraging strategies are subject to social influence; for example, local enhancement accounted for the decision of rooks to forage near other birds (Waite 1981); Florida scrub-jays learned a novel foraging technique via social learning (Midford et al. 2000); and roosts function as information centres in ravens (Marzluff et al. 1996) and hooded crows (Sonerud et al. 2001).

Hunt & Gray (2002) suggest that the differing complexity of the stepped-cut tools made by New Caledonian crows may be a case for cumulative cultural evolution (increasing the number of steps required to make a more complex tool), analogous to minor technological innovations in humans. The geographical distribution of the use of tools with different numbers of steps varies across the island

in a way that is consistent with the idea that the behaviour has spread through social learning from a centre of innovation at the island's centre, where the tools are most complex (Hunt & Gray 2002). The authors report an absence of ecological variability that could explain this pattern. However, it is not yet clear whether or not the crows are capable of the sort of sophisticated social learning that could result in the manufacture of a three-stepped, rather than a two-stepped tool. Recent research has shown that the crows develop tool-use and manufacture in the absence of a model, and furthermore they do so as quickly as they do with a human demonstrator (Kenward et al. 2005). However, it should be noted that this study did not report the manufacture of stepped-cut tools, and only made use of human demonstrators. These researchers did report an effect of social influence; the hand-raised birds preferred to handle objects that their human demonstrators had handled previously (Kenward et al. 2006).

In summary, living in a complex social and physical environment creates both challenges and opportunities, and the pressure to respond to some or all of these may have selected for large brains and complex cognition in both apes and corvids. Table 1 summarizes these challenges and the evidence for an evolutionary response to them in apes (chimpanzees) and corvids, as well as the biological and morphological features that might facilitate or constrain such a response.

The challenges from the physical environment, while not identical (given the different geographic distributions of the two groups), can be seen to be comparable. However, the two groups face these challenges from a very different starting point, because of the 280 million years of divergent evolution that they have undergone. While the grasping hands and physical strength of great apes favour the use of tools in solving a great many problems, the beaks and small size of corvids make many of these uses unnecessary or impossible. Therefore, from the information on corvid foraging that is available, hypotheses citing omnivory and extractive foraging predict complex cognition in corvids, but those that emphasize tool-use do not to the same extent (only New Caledonian crows routinely make and use tools, and they use a smaller variety of tools than great apes such as chimpanzees and orang-utans). With regard to the pressures posed by social living, it can be seen that while qualitative changes might benefit species from both groups (the formation of alliances for competition, or increased coordination

for cooperative action), the challenges associated with employing and tracking such strategies within a complex and changing social network are relevant to promiscuous apes but probably not to the (largely) monogamous corvids.

It is clear that much further studies are needed before the function of intelligent behaviour in the two groups can be established. An extensive set of phylogenetically controlled comparisons, both within the corvids, within the primates, and across a larger range of avian and mammalian taxa, could reveal whether intelligence tends to go hand in hand with sociality, dietary generalism, tool use or some other variable. Extending the number of species studied within the corvids seems particularly important, because at present it is not clear whether or not intelligence is a corvid-wide trait, or rather is something seen in a few species that have been exposed to particular evolutionary pressures (e.g. social food-caching species such as scrub-jays and ravens, and tool-users such as New Caledonian crows). More studies of corvids are needed, not only of more species but also of several populations. Corvids show intra-species flexibility in their social and ecological habits; for example, carrion crows are largely territorial, but in harsh environments (such as northern Spain) they engage in cooperative breeding (Baglione et al. 2002). Social structure in Florida scrub-jays is similarly flexible (Woolfenden & Fitzpatrick 1984). Likewise, there is great variability in the feeding habits of corvid species across their range, and indeed corvids are known for high rates of feeding innovation (Lefebvre et al. 1998).

The evidence for the different hypotheses to date (largely correlational analyses with brain size) is difficult to interpret. The effects of different pressures are very difficult to disentangle, as is the direction of cause and effect, for example, if extractive foragers tend to have larger brains, was the pressure to exploit these hidden food resources the cause of increased brain size, or is the behaviour rather the expression of a general intelligence selected for in another domain? As Healy & Rowe (2007) have argued, it will also be important to develop a dependent variable other than relative brain size for measuring intelligence (Box 1). For that, we will need to have a better understanding of the proximate mechanisms underpinning intelligent behaviour, as well as techniques for measuring them across divergent species. The evidence that these mechanisms are indeed similar in corvids and apes is reviewed in the next section.

Proximate Mechanisms

In the case of morphological features such as wings in vertebrates, it is relatively easy to identify the level at which convergence has taken place: a simple dissection can reveal that the similarity is only skin-deep, and that different structures lie beneath (Fig. 1). When the feature is a psychological one, the task is not so simple, because it is that much less tangible. The difficulty is compounded in the case of 'intelligence' because there is no universally accepted definition of the term (Box 1). What does it mean to say that there has been a convergent evolution of a psychological feature such as intelligence? For example, both chimpanzees and New Caledonian crows can use a novel technique to obtain a food reward at the bottom of a transparent tube (Weir et al. 2002; Mendes et al. 2007). While both examples are clearly evidence of intelligent behaviour as defined by the principle of exclusion (the behaviour cannot easily be explained in terms of simple conditioning, or hard-wired action patterns, see Box 1), claims that the cognition underpinning the behaviour in the two species is the result of convergent evolution can lead to controversy. Some researchers have argued that the tool-using behaviour of the crows is likely to be an adaptive specialization and therefore not equivalent to that of apes, which is rather an expression of a generalized intelligence (Mendes et al. 2007). From another perspective, the case can also be made that the behaviour in both species is the outcome of conserved associative learning processes combined with exploratory behaviour, and therefore the result of homology or parallelism rather than convergence. However, Byrne & Bates (2006, 2007) have argued that setting associative accounts against such cognitive explanations for complex behaviours as, for example, an animal using a representation of another's mental states to determine what it can and cannot see, is really an unhelpful blurring of two different levels of description.

Finding the Level of Analysis

The notion that complex systems can be most usefully viewed at distinctly different levels of analysis is not a new one. Marr identified three kinds of questions that can be asked about psychological features from his study of vision (Marr 1982). The first level, the *computational*, is concerned with the goal of the cognitive process, and the logic by

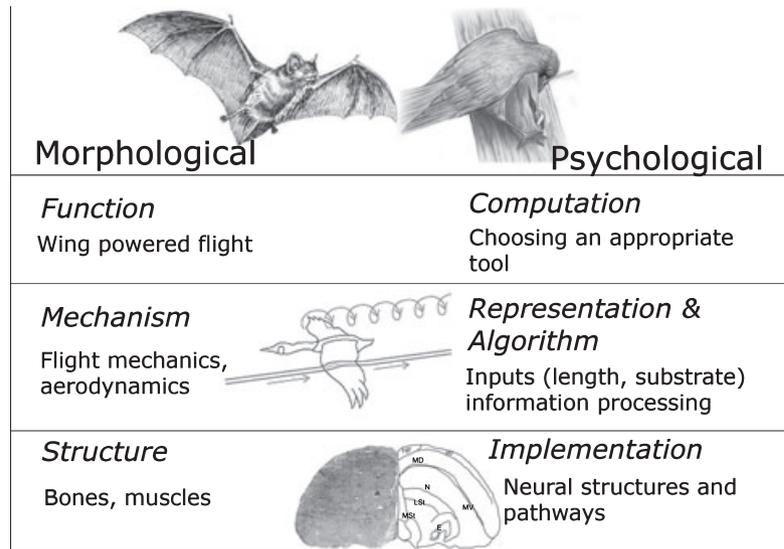


Fig. 2: Levels of analysis for viewing the convergent evolution of wing powered flight and tool selectivity. Images of New Caledonian crow tool use and rook brain taken from Emery & Clayton (2004). Reprinted with permission from AAAS.

which it is carried out. The second level, *representation and algorithm*, models the way in which stimuli are encoded and processed. The third level is the *implementation*, or the physical realization of these models. These three levels can be seen to be analogous to those that we use intuitively when describing the convergent evolution of a morphological feature such as the vertebrate wing. Comparing them side-by-side allows us to see the appropriateness of Marr’s levels for structuring our investigations into convergent psychological evolution (Fig. 2).

- The first level (*computation*) is basically concerned with the question ‘what?’ What do the forearms of birds, bats and pterosaurs do? What kinds of decisions can New Caledonian crows and apes make when choosing a tool?
- The second and third levels are concerned with the question ‘how?’ The second level (*representation and algorithm*) asks this question in the context of the mechanism, or algorithm that performs the function, and we can talk about the biomechanical processes by which species in the different groups power their flight, or the way in which certain stimuli (e.g. tool length, diameter and material) are represented in the mind of the animal, and the algorithms by which they are processed and fed into behaviour.
- The third level (*implementation*) asks how these processes are physically realized in terms of bones and muscles, or neural structures and pathways.

The challenge in the case of convergent evolution is first, to establish a level at which different features are similar in different species and secondly, to discover the differences at the other levels that reveal their divergent evolutionary history, and may explain limits to the similarities found.

McClamrock (1991) points out two important cautionary notes to bear in mind with the use of the three levels analogy. First, the three levels should not be seen as a model for the actual levels of organization that make up the complex feature in question; there may be more, and at each level there may be nested levels of organization. For example, beyond the third level described for the evolution of wings are the proteins and even the genes responsible for building them in the different vertebrate groups. In the case of cognition, there are probably sub-levels within *representation and algorithm*, for example, the algorithm could be modelled in terms of stimuli and associations, or using connectionist modelling (McClamrock 1991). Secondly, moving between levels of analysis can sometimes consist of ‘zooming in’ to a more fine-grained level of analysis, but it can sometimes consist of asking the question in a completely different contextual framework. As long as these points are held in consideration, several authors agree that Marr’s levels are a powerful tool for analysing complex systems (McClamrock 1991; Mitchell 2006), and we argue that they are especially useful for investigating convergent evolution (Box 2 – Why are Levels Useful?).

Box 2 – Why are Levels Useful?

1. Designing Appropriate Experiments

The field of animal cognition has experienced a great surge of interest since the cognitive revolution, and with it has come dozens of new discoveries concerning the computational abilities of animals, and their impressive complexity and flexibility. These findings have prompted research into all four of Tinbergen's questions (function, phylogeny, causation and development). Researchers focusing on causation (the proximate mechanisms underpinning behaviour) aim at designing ethologically valid experiments by considering Tinbergen's other three levels of explanation, for example by bearing in mind the role of individual experience over development on performance. Marr's three levels (computation, representation and algorithm, and implementation) further sub-divide Tinbergen's 'causation', and research at one level can inform that at the other two. The computational level is particularly important for two reasons. First, it is logical to know what a system is capable of before attempting to study how that is possible, in order to focus one's efforts on the right features of the system. Marr gives a useful example:

Trying to understand bird flight by studying only feathers...just cannot be done...we have to understand aerodynamics, only then do the structure of the feathers and the different shapes of the birds' wings make sense. (Marr 1982, p. 27)

Secondly, knowledge of a species' intelligence at the computational level can allow researchers to use paradigms that are most likely to tap into the animal's information-processing skills, and isolate

the variable under question without confounding it with other variables (e.g. the social cognition of primates might best be demonstrated in competitive contexts rather than cooperative ones, because competition features more widely in their social lives; Hare 2001). Being explicit about the level of analysis is particularly important when the aim is comparative. The chief reason for this is that different experimental approaches are appropriate for addressing convergence at different levels, because different task features need to be kept comparable depending on the type of question being asked.

2. Interpreting Results and Avoiding Needless Controversy

A common response to 'cognitive' descriptions of behaviour, such as describing a foraging chimpanzee or a caching scrub-jay as reasoning about mental states, is that these behaviours may be 'just the result of associative learning'. A dichotomy emerges between explanations based on the vocabulary used to describe the abilities of language-using animals (such as understanding, reasoning and rationalizing), and explanations based on associative models of animal learning. Byrne & Bates (2006) argue that different levels of description are being blurred in these debates, meaning that researchers are talking at cross purposes. They argue that the cognitive terms offer a useful framework with which to study the feats that animals such as corvids and apes are capable of (at what we have referred to as Marr's computational level). However, making the level of analysis explicit is important, especially when discussing convergent evolution, because the parallels being drawn can be misinterpreted.

Computational Convergence

The ethological validity of the studies that have been conducted in recent years with apes and with corvids (those capitalizing on naturally occurring behaviours such as food caching, tool-use and food competition) have allowed for insights into the ability of the animals to employ complex computations. However, little work has been done on both corvids and apes using paradigms that are directly comparable. Given the many possible sources of variation unrelated to cognition involved in comparing such

evolutionarily distant species (such as differences in perception, attention and motivation; Bitterman 1960, 1965), assessing results from different methodologies is especially problematic. Recent work both by ourselves and other groups has attempted to ford this gap by conducting experiments using comparative methodology. The aim is to go beyond broad comparisons (such as observing that species of both corvids and apes manufacture tools) to ask in more detail the range of problems that the animals are capable of solving (e.g. making or using a tool for a particular purpose).

Tool Use – Selectivity and Flexibility

Great ape and New Caledonian crow researchers have used some paradigms that allow for direct comparisons. In very similar tasks, both crows and apes have shown evidence for selectivity in their choice and manufacture of tools for a given problem. Two crows selected a tool of sufficient length to reach inaccessible food (Chappell & Kacelnik 2004), and they also manufactured a tool of the appropriate diameter (Chappell & Kacelnik 2002). Mulcahy et al. (2005) found that gorillas and orang-utans also choose a tool of sufficient length (Mulcahy et al. 2005), and similar to crows there was no evidence that their selectivity arose through trial-and-error learning over the course of the experiment. Meta-tool use, that is, using one tool to get another, is thought to be a steep cognitive challenge, and its emergence in the hominid tool-use record (in the form of stone-knapping) is an important landmark for anthropologists. Monkeys such as capuchins and Japanese macaques have performed poorly in tests requiring meta-tool use, often persistently directing their tool-using behaviour directly towards the food reward. Building on the earlier studies of Kohler (1927) and Rensch & Döhl (1968), Mulcahy et al. (2005) presented gorillas and orang-utans with a task in which they needed to use a small stick tool to get a longer one. Most apes displayed meta-tool use in the first trial when it was needed to get the food reward (Mulcahy et al. 2005). A recent study found that New Caledonian crows are also capable of spontaneously using a small tool to get a longer one (Taylor et al. 2007). Similar to the apes, most of the crows acted directly on the longer tool, instead of attempting to recover the food reward with the short tool. In addition to displaying tool selectivity, apes and corvids have also shown flexibility when faced with a similar problem (gaining access to a food reward at the bottom of a thin vertical tube). Betty the New Caledonian crow bent straight pieces of wire in order to hook out the reward, after her mate stole the hooked piece (Weir et al. 2002). Recently, orang-utans have also been reported to obtain food placed out of their reach at the bottom of a tube through spontaneous problem solving, by spitting their drinking water into the tube so that the food floats to the top (Mendes et al. 2007).

Using Social Cues to Solve Problems

Comparative work has also been done in the social domain. Two paradigms used to test primates' use of

social cues are gaze following, and the object choice test. Similar to all species of great apes (Brauer et al. 2005), ravens not only visually co-orient with the look-ups of a human experimenter but also reposition themselves to follow the experimenter's gaze around a visual barrier (Bugnyar et al. 2004). Apes have difficulty using a human gaze cue to locate a food item hidden under one of two cups, although they can use an iconic marker to do so (Call et al. 1998, 2000; Barth et al. 2005; Herrmann et al. 2006). Similarly, a few ravens can use a pointing gesture to locate food, but not a human gaze cue or the cues possibly given by a conspecific that could see the food (Schloegl et al. 2007). Both apes and ravens are suggested to have difficulty in this paradigm because of its cooperative nature; the location of a piece of food is not often pointed out by conspecifics in the competitive ecologies of these species (Hare 2001). Interestingly, jackdaws have recently been found capable of using the communicatory gestures of a familiar human (A. M. P. von Bayern & N. J. Emery, unpubl. data) and conspecific gaze cues in the object choice task, in the latter when paired with their social partner, but not with another group mate (A. M. P. von Bayern & N. J. Emery, unpubl. data). This makes sense in the light of the high levels of food sharing seen between affiliated pairs of jackdaws (von Bayern et al. 2007).

Corvids have also displayed primate-like social skills in competitive foraging paradigms. Jackdaws steal food more quickly from a human competitor who is either glancing away or has his/her eyes closed than one who is looking directly at the food (A. M. P. von Bayern and N. J. Emery, unpubl. data). Similarly, chimpanzees take into account the direction of a human competitor's gaze, and try to hide their approach to food (Hare et al. 2006). Interestingly, concealing auditory information (avoiding a noisy food or caching site) has also been documented for both chimpanzees (Melis et al. 2006a) and western scrub-jays (Stulp G., Emery N. J. & Clayton N. S., pers. obs.). Ravens lead conspecifics away from boxes baited with food (Bugnyar & Kotrschal 2004), just as chimpanzees were shown to do in the classic experiments of Menzel (1974). Ravens also rush to recover a piece of food that a dominant raven has seen being hidden, but delay their approach if the dominant raven's view of the baiting process was obstructed (Bugnyar & Heinrich 2005). Chimpanzees also differentiate between a dominant chimpanzee that has seen food being hidden and one that has not when deciding whether or not to approach, although unlike the ravens the chimpanzees

approached the food more often when the dominant chimpanzee had not seen the food (Hare et al. 2001).

Apes and corvids also attend to the actions of their conspecifics in order to coordinate with them to solve a problem. Seed et al. (2008) tested rooks on a task that has been used to test chimpanzees' ability to cooperate. The task requires the simultaneous pulling of both ends of a rope to bring in a platform containing food (Hirata & Fuwa 2007). Pulling just one end causes the rope to become unconnected from the platform. Tolerant pairs of chimpanzees (that would feed together) were able to spontaneously find the solution to the cooperative task (Melis et al. 2006a). Similarly, the eight rooks quickly solved the problem without training when paired with their social partner. However, although chimpanzees delayed acting on the apparatus while their partner gained access to the test room, and did so more often when two individuals were needed to solve the task than when one individual could prevail alone (Melis et al. 2006b), rooks did not delay acting on the apparatus over the course of 15 trials (Seed et al. 2008). Furthermore, given a choice between an apparatus that could be operated individually over one that required the action of two individuals, four of six individuals showed no preference. Further work is needed to support the idea that the difference between rooks and chimpanzees represents a real limitation in the computations that rooks are capable of in a cooperative setting. If this is the case, it remains to be seen what the limitations are (a failure to compute some of the requirements of the task, or the properties of the cooperative agent).

These experiments have shown that both corvids and apes are capable of selective and flexible problem-solving, and that their behaviour in very similar experiments can be strikingly convergent. Many of these experiments have also been able to give an indication of the representations and algorithms underpinning the behaviour (e.g. when the tests are novel to the animals and performance is good from the first trial, then associative learning of actions in response to task-specific stimuli and differential reinforcement cannot explain the results). However, for a positive assessment of the representations and algorithms at work further study is required. Have the animals acquired the knowledge needed to solve the tasks through past associative learning or do inborn predispositions play a role? Do they solve the novel tasks through a process of stimulus generalization, or do they have a representation of the abstract

properties at hand (such as object properties, animacy, or mental states such as seeing)? Are processes such as 'insight' or 'reasoning' involved, and what does this mean in algorithmic terms? Crucially for this discussion, are the answers to these questions similar for both corvids and apes? A few experiments have attempted to address this level of analysis, and those that have done so in a way that allows for direct comparisons between corvids and apes are described below.

Representation and Algorithm

When testing the cognition of a single species at the algorithmic level, it is difficult to find a paradigm that isolates the process under question, without confounding it with other variables. The problem becomes more difficult when the aim of the research is comparative, and an appropriate test of a given ability in one species is not necessarily suitable for another. There are two important ways in which this difficulty can be addressed: ascertaining task equivalence, and triangulation. Species do not need to be tested on the exact same piece of apparatus for meaningful comparisons to be drawn. It is more important that the same conceptual question is asked using tasks that the species can solve, or learn to solve, before investigations into the underlying cognition are made. Using a task that the majority of subjects can learn to solve should minimize the number of 'false-negatives' that occur because of limitations associated with perception and motivation. Once paradigms have been found, different conceptual features can be varied systematically in transfer tasks, in order to ascertain which of the possible features the subjects used to solve the task. This approach is referred to as 'triangulation', and has been advocated by Heyes (1993), among others.

We used this approach in a study of problem-solving in rooks. Visalberghi & Limongelli (1994) examined whether or not tool-users form representations about causal relations in a task which has since been widely employed: the trap-tube task. In this task, the subject must use a tool to push a food reward out from a horizontal tube, which has a trap along its length into which the food will drop if pushed over it. Seed et al. (2006) aimed to test the null hypothesis: 'a successful animal will use an arbitrary cue to solve the task'. Eight birds were tested on a version of the trap problem that featured two 'traps' along a horizontal tube. One of the traps was functional (sealed with a black disc at the bottom) and would trap the reward if the rooks pulled the food over it.

The other was non-functional; in Design A it had a black disc at the top, which the food could pass over; in Design B it had no black disc, so the food could fall through it. Seven of the eight birds learned to avoid the functional trap, in between 30 and 140 trials. This was evidence for convergence at the computational level; like capuchin monkeys and chimpanzees, rooks were able to learn to avoid the trap.

All seven rooks immediately solved task B once they had learned to solve A, and vice versa. However, both these tasks could have been solved by learning to avoid the trap with the black disc at the bottom, without anything about the properties of the objects being encoded. The seven birds were therefore given two transfer tasks, both featuring the two previously non-functional traps (pass-across or fall-through). In Design C both ends of the tube were blocked with bungs, so the food could not be recovered from the end of the tube, and the birds needed to pull away from the trap with the black disc at the top; in Design D the tube was lowered to the surface of the testing shelf, so that the food could not be recovered from beneath, and the rooks needed to pull towards the trap with the black disc at the top to be successful. Crucially, therefore, both tasks featured the same familiar cue, but each required the opposite response to it (pull away from the black disc in Task C, pull towards it in Task D). The birds were given 20 trials on both of these transfer tasks. Six of the subjects performed at chance on both tasks, but one bird was able to solve these transfers, suggesting that it did not solve the two-trap task simply by using the appearance of the functional trap as an arbitrary cue (Seed et al. 2006).

Seed et al. (in press) recently conducted a similar experiment with chimpanzees. Instead of having to use a tool to move the food, small holes cut into the front of the puzzle allowed them to use their fingers instead. All of the eight chimpanzees tested learned to avoid the trap. Furthermore, we found that one chimpanzee passed both Designs C and D. We compared the performance of these experienced chimpanzees with that of naïve ones on a new version of the task, which differed from the original task in size, shape, colour and material. Strikingly, the experienced subjects solved the task rapidly, but the inexperienced subjects failed to do so in 150 trials. Similarly, Taylor et al. (in press) recently found that New Caledonian crows can also learn to solve the two-trap problem, and that successful subjects were able to transfer to a version of the task that was as different from the original problem as the second task given to chimpanzees was. These results suggest

that rooks, chimpanzees and New Caledonian crows do not use a simple cue-based rule to solve the trap task. We propose that instead they extracted causally relevant functional information (such as surface continuity, or the solidity of barriers). However, further work is required to uncover the exact nature of their object representations, and the algorithms by which they are fed into behaviour.

Other comparative work has shown that corvids and apes are capable of solving problems by attending to a cue that is arbitrarily linked to the successful solution. Helme et al. tested rooks and bonobos on a task in which a disc attached to a stick needed to be pulled into contact with a food reward in order to get it out of a tube. Both rooks and bonobos learned to solve this task, and transfer tasks revealed that they did so by learning rules based on the relative length of the stick at either end, rather than using information about contact (Helme et al. 2006a,b).

Although it is arguably easier to manipulate the type of information given in physical tasks; this has also been done in experiments of visual perspective taking. Both western scrub-jays and chimpanzees behave differently when a competitor saw food hidden, and when they did not (Hare et al. 2000; Dally et al. 2005). What sorts of information are encoded for this differentiation to be made; is it done using an 'evil eye' strategy, by simply linking the presence of eyes to the hiding of the food? Both teams of researchers have ruled out this possibility, by swapping the dominant animal that witnessed the hiding event for another conspecific at the time of food recovery. Despite the fact that the food was observed at the time of hiding, western scrub-jays and chimpanzees treat this new observer as ignorant of food location. In the case of the scrub-jays, this new dominant had also seen a (different) hiding process, and so differential behavioural cuing cannot explain the results. Both species therefore encode not only the presence, but also the identity, of the observer (Hare et al. 2001; Dally et al. 2006).

Finding a paradigm which can reveal the content of mental representations that animals use to solve problems is a difficult task, and especially so in the case of comparative work. Triangulation is a powerful tool for establishing the sorts of information that are being used, and work so far has shown that corvids and apes seem to be capable of going beyond simple perceptual information and using more abstract representations, in both the social and the physical domain. This approach could be employed comparatively for a broad range of computational

problems. The question of algorithm is still more difficult. While the use of abstract representations may mean that a completely novel task can be solved in very few trials, does this mean that anything other than the learning of arbitrary associations was used to build the behaviour in the first context? Are corvids and apes capable of encoding information about the causal power of particular events or the animacy of their conspecifics? Penn et al. (2008) have argued that such 'unobservable' concepts are unavailable to non-human animals. This is undoubtedly an important area for future research in both corvids and apes, and our hope is that research will continue to use paradigms that allow for comparisons to be drawn between the two groups.

Conclusion

Convergent evolution is said to have occurred when distantly related organisms respond to similar evolutionary pressures by the development of similar traits. We have shown that corvids and apes have been exposed to similar evolutionary pressures during their evolutionary histories, but note that their divergent biologies may constrain an evolutionary response to some of them. However, the evidence for the effect of such pressures in both groups is restricted to correlational analyses with brain size, and we agree with Healy & Rowe (2007) that the next step for identifying the evolutionary pressures causing intelligence will be phylogenetically controlled comparative experimentation. At the proximate level, convergent evolution is characterized not only by similarities, but also by differences. We have argued that Marr's levels can help us to structure the study of convergence in a slippery and contentious feature: intelligence. In the case of intelligence in corvids and apes, while the similarities are fascinating, we should also celebrate the differences, because identifying both the similarities and differences in the cognition of corvids and apes, and assessing their life-history correlates, may enable us to pinpoint the features of ape cognition that served as crucial pre-adaptations for the evolution of human intelligence. Both of these can best be studied by being clear about the level of analysis being addressed.

Acknowledgements

We would like to thank Josep Call, Michael Tomasello and Anne Helme for useful discussion, and William McGrew and Juan Carlos Gomez for comments

on an earlier version of the manuscript. AMS was supported by a BBSRC studentship, a Royal Commission for the Exhibition of 1851 Fellowship and Clare College, Cambridge, and NJE was supported by a Royal Society University Research Fellowship.

Literature Cited

- Baglione, V., Marcos, J. M. & Canestrari, D. 2002: Cooperatively breeding groups of carrion crow, *Corvus corone corone* in northern Spain. *Auk* **119**, 325–343.
- Barth, J., Reaux, J. E. & Pivonelli, D. J. 2005: Chimpanzees' (*Pan troglodytes*) use of gaze cues in object-choice tasks: different methods yield different results. *Anim. Cogn.* **8**, 84–92.
- Barret, L. & Henzi, P. 2005: The social nature of primate cognition. *Proc. R. Soc. Lond. B* **272**, 1865–1875.
- von Bayern, A. M. P., de Kort, S. R., Clayton, N. S. & Emery, N. J. 2007: The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). *Behaviour* **144**, 711–733.
- Bednekoff, P. A. & Balda, R. P. 1996a: Observational spatial memory in Clark's nutcrackers and Mexican jays. *Anim. Behav.* **52**, 833–839.
- Bednekoff, P. A. & Balda, R. P. 1996b: Social caching and observational spatial memory in pinyon jays. *Behaviour* **133**, 807–826.
- Bitterman, M. E. 1960: Toward a comparative psychology of learning. *Am. Psychol.* **15**, 704–712.
- Bitterman, M. E. 1965: Phyletic differences in learning. *Am. Psychol.* **20**, 396–410.
- Boesch, C. & Boesch-Achermann, H. 2000: *The Chimpanzees of the Tai Forest*. Oxford Univ. Press, Oxford.
- Bräuer, J., Call, J. & Tomasello, M. 2005: All Great Ape species follow gaze to distant locations and around barriers. *J. Comp. Psychol.* **119**, 145–154.
- Brewer, S. M. & McGrew, W. C. 1990: Chimpanzee use of a tool-set to get honey. *Folia Primatol.* **54**, 100–104.
- Bugnyar, T. & Heinrich, B. 2005: Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proc. R. Soc. Lond. B* **272**, 1641–1646.
- Bugnyar, T. & Kotrschal, K. 2004: Leading a conspecific away from food in ravens (*Corvus corax*)? *Anim. Cogn.* **7**, 69–76.
- Bugnyar, T., Stöwe, M. & Heinrich, B. 2004: Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proc. R. Soc. Lond. B. Biol. Sci.* **271**, 1331–1336.
- Byrne, R. W. 1996: The misunderstood ape: Cognitive skills of the gorilla. In: *Reaching into Thought: The Minds of the Great Apes* (Russon, A. E., Bard, K. A. & Parker, S. T., eds). Cambridge Univ. Press, Cambridge, pp. 113–130.
- Byrne, R. W. 2000: Evolution of primate cognition. *Cogn. Sci.* **24**, 543–570.

- Byrne, R. W. 2004: The manual skills and cognition that lie behind hominid tool use. In: *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence* (Russon, A. E. & Begun, D. R., eds). Cambridge Univ. Press, Cambridge, pp. 31–44.
- Byrne, R. W. & Bates, L. A. 2006: Why are animals cognitive? *Curr. Biol.* **16**, R445–R448.
- Byrne, R. W. & Bates, L. A. 2007: Sociality, Evolution and Cognition. *Curr. Biol.* **17**, R714–R723.
- Byrne, R. W. & Byrne, J. M. E. 1991: Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). *Cortex* **27**, 521–546.
- Byrne, R. W. & Byrne, J. M. E. 1993: The complex leaf gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardisation. *Am. J. Primatol.* **31**, 241–261.
- Byrne, R. W. & Corp, N. 2004: Neocortex size predicts deception rate in primates. *Proc. R. Soc. Lond. B* **271**, 1693–1699.
- Byrne, R. W. & Whiten, A. 1997: Machiavellian Intelligence. In: *Machiavellian Intelligence. II. Extensions and Evaluations* (Whiten, A. & Byrne, R. W., eds). Cambridge Univ. Press, Cambridge, pp. 1–23.
- Byrne, R. W. & Whiten, A. 1988: Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans. Clarendon Press, Oxford.
- Call, J., Agnetta, B. & Tomasello, M. 2000: Cues that chimpanzees do and do not use to find hidden objects. *Anim. Cogn.* **3**, 23–24.
- Call, J., Hare, B. A. & Tomasello, M. 1998: Chimpanzee gaze following in an object-choice task. *Anim. Cogn.* **1**, 89–99.
- Chappell, J. & Kacelnik, A. 2002: Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Anim. Cogn.* **5**, 71–78.
- Chappell, J. & Kacelnik, A. 2004: Selection of tool diameter by New Caledonian crows *Corvus moneduloides*. *Animal Cognition* **7**, 121–127.
- Clayton, N. S. & Dickinson, A. 1998: Episodic-like memory during cache recovery by scrub jays. *Nature* **395**, 272–274.
- Clayton, N. S. & Dickinson, A. 1999: Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. *J. Comp. Psychol.* **113**, 403–416.
- Clayton, N. S. & Emery, N. J. 2007: The social life of corvids. *Curr. Biol.* **17**, R652–R656.
- Clayton, N. S., Yu, K. & Dickinson, A. 2001: Scrub-jays (*Aphelocoma coerulescens*) form integrated memory for multiple features of caching episodes. *J. Exp. Psychol. Anim. Behav. Process.* **27**, 17–29.
- Clayton, N. S., Yu, K. S. & Dickinson, A. 2003: Interacting cache memories: evidence for flexible memory use by scrub jays. *J. Exp. Psychol. Anim. Behav. Process.* **29**, 14–22.
- Clayton, N. S., Dally, J. M. & Emery, N. J. 2007: Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Phil. Trans. R. Soc. Lond. B* **362**, 507–522.
- Clutton-Brock, T. H. & Harvey, P. H. 1980: Primates, brain and ecology. *J. Zool.* **190**, 309–323.
- Connor, R. C. 2007: Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Phil. Trans. R. Soc. Lond. B* **362**, 587–602.
- Cramp, S. & Perrins, C. M. 1994: *The birds of the Western Palearctic*. Oxford University Press, New York.
- Dally, J. M., Emery, N. J. & Clayton, N. S. 2005: Cache protection strategies in western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Anim. Behav.* **70**, 1251–1263.
- Dally, J. M., Emery, N. J. & Clayton, N. S. 2006: Food-caching western scrub-jays keep track of who was watching when. *Science* **312**, 1662–1665.
- Darwin, C. 1882: *The descent of man and selection in relation to sex*, 2nd Edition. John Murray, London.
- Deacon, T. 1980: Fallacies of progression in theories of brain-size evolution. *International Journal of Primatology* **11**, 193–236.
- Dickinson, A. 1980: *Contemporary Animal Learning Theory*. Cambridge Univ. Press, Cambridge.
- Dickinson, A. & Shanks, D. 1995: Instrumental action and causal representation. In: *Causal Cognition: A Multidisciplinary Debate* (Sperber, D., Premack, D. & Premack, A., eds). Oxford Univ. Press, Oxford, pp. 5–25.
- Dunbar, R. I. M. 1992: Neocortex size as a constraint on group size in primates. *J. Human Evol.* **20**, 469–493.
- Dunbar, R. I. M. 1995: Neocortex size and group size in primates: a test of the hypothesis. *J. Human Evol.* **28**, 287–296.
- Dunbar, R. I. M. & Schultz, S. 2007: Understanding primate brain evolution. *Phil. Trans. R. Soc. Lond. B* **362**, 649–659.
- Emery, N. J. & Clayton, N. S. 2004: The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907.
- Emery, N. J., Seed, A. M., von Bayern, A. M. & Clayton, N. S. 2007: Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. Lond. B* **362**, 489–505.
- Gibson, K. R. 1986: Cognition, brain size and the extraction of embedded food resources. In: *Primate Ontogeny, Cognition and Social Behaviour* (Else, J. G. & Lee, P. c., eds). Cambridge Univ. Press, Cambridge, pp. 205–218.
- Godfrey-Smith, P. 2001: Environmental Complexity and the Evolution of Cognition. In: *The Evolution of Intelligence* (Sternberg, R. & Kaufman, J., eds). Lawrence Erlbaum Associates, Mahwah, pp. 233–249.
- Goodall, J. 1964: Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* **201**, 1264–1266.

- Goodwin, D. 1986: Crows of the World. British Museum (Natural History) Press, London.
- Griffin, D. R. 1978: Prospects for cognitive ethology. *Behav. Brain Sci.* **4**, 527—538.
- Harcourt, A. 1992: Coalitions and alliances: are primates more complex than non-primates. In: *Coalitions and Alliances in Humans and Other Animals* (Harcourt, A. & de Waal, F. B. M., eds). Oxford Univ. Press, Oxford, pp. 445—473.
- Hare, B. 2001: Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim. Cogn.* **4**, 269—280.
- Hare, B. & Tomasello, M. 2005: Human-like social skills in dogs? *Trends Cogn. Sci.* **9**, 439—444.
- Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000: Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* **59**, 771—785.
- Hare, B., Call, J. & Tomasello, M. 2001: Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**, 139—151.
- Hare, B., Call, J. & Tomasello, M. 2006: Chimpanzees deceive a human competitor by hiding. *Cognition* **101**, 495—514.
- Healy, S. D. & Rowe, C. 2007: A critique of comparative studies of brain size. *Proc. R. Soc. B: Biol. Sci.* **274**, 453—464.
- Heinrich, B. 1999: *Mind of the Raven*. Harper Collins Publishers, New York.
- Heinrich, B. & Pepper, J. W. 1998: Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Anim. Behav.* **56**, 1083—1090.
- Helme, A. E., Call, J., Clayton, N. S. & Emery, N. J. 2006a: What do bonobos (*Pan paniscus*) understand about physical contact? *J. Comp. Psychol.* **120**, 294—302.
- Helme, A. E., Clayton, N. S. & Emery, N. J. 2006b: What do rooks (*Corvus frugilegus*) understand about physical contact? *J. Comp. Psychol.* **120**, 288—293.
- Herrmann, E., Melis, A. P. & Tomasello, M. 2006: Apes' use of iconic cues in the object-choice task. *Anim. Cogn.* **9**, 118—130.
- Heyes, C. M. 1993: Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Anim. Behav.* **46**, 177—188.
- Hirata, S. & Fuwa, K. 2007: Chimpanzees learn to act with other individuals in a cooperative task. *Primates* **48**, 13—21.
- Holekamp, K. E., Sakai, S. T. & Lundrigan, B. L. 2007: The spotted hyaena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. *J. Mammal.* **88**, 545—554.
- Humphrey, N. K. 1976: The Social Function of Intellect. In: *Growing points in Ethology* (Bateson, P. P. G. & Hinde, R. A., eds). Cambridge Univ. Press, Cambridge, UK, pp. 303—317.
- Hunt, G. R. 1996: Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**, 249—251.
- Hunt, G. R. 2000: Tool use by the New Caledonian crow *Corvus moneduloides* to obtain cerambycidae from dead wood. *Emu* **100**, 109—114.
- Hunt, G. R. & Gray, R. D. 2002: Species-wide manufacture of stick-type tools by New Caledonian crows. *Emu* **102**, 349—353.
- Hunt, G. R. & Gray, R. D. 2004a: The crafting of hook tools by wild New Caledonian crows. *Proc. R. Soc. Lond.: Biol. Lett.* **271**, 88—90.
- Hunt, G. R. & Gray, R. D. 2004b: Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Anim. Cogn.* **7**, 114—120.
- Iwaniuk, A. N. & Arnold, K. E. 2004: Is cooperative breeding associated with bigger brains? A comparative test in the corvida (Passeriformes). *Ethology* **110**, 203—220.
- Jolly, A. 1966: Lemur social behavior and primate intelligence. *Science* **153**, 501—506.
- Keeton, W. T. & Gould, J. L. 1986: *Biological Science*, 4th edn. W.W. Norton & Co Ltd., New York.
- Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005: Tool manufacture in naive juvenile crows. *Nature* **433**, 121.
- Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. 2006: Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Anim. Behav.* **72**, 1329—1343.
- Kohler, W. 1927: *The Mentality of Apes*, 2nd edn. Vantage Books, New York.
- de Kort, S. R., Dickinson, A. & Clayton, N. S. 2005: Retrospective cognition by food-caching western scrub-jays. *Learning and Motivation* **36**, 159—176.
- de Kort, S. R., Tebbich, S., Dally, J. M., Emery, N. J. & Clayton, N. S. 2006: The comparative cognition of caching. In: *Comparative Cognition. Experimental Explorations of Animal Intelligence* (Wasserman, E. A. & Zentall, T. R., eds). Oxford Univ. Press, Oxford, pp. 602—619.
- Kudo, N. & Dunbar, R. I. M. 2001: Neocortex size and social network size in primates. *Anim. Behav.* **62**, 711—722.
- Lefebvre, L. & Bouchard, J. 2003: Social learning about food in birds. In: *The Biology of Traditions: Models and Evidence* (Fragaszy, D. M. & Perry, S., eds). Cambridge Univ. Press, Cambridge, pp. 94—126.
- Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997: Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549—560.
- Lefebvre, L., Gaxiola, A., Dawson, S., Timmermans, S., Rosza, L. & Kabai, P. 1998: Feeding innovations and forebrain size in Australasian birds. *Behaviour* **135**, 1077—1097.
- Lefebvre, L., Nicolakakis, N. & Boire, D. 2002: Tools and brains in birds. *Behaviour* **139**, 939—973.

- Lockie, J. D. 1955: The breeding and feeding of jackdaws and rooks with notes on carrion crows and other corvidae. *Ibis* **97**, 341–368.
- Marino, L. 2002: Convergence of complex cognitive abilities in cetaceans and primates. *Brain Behav. Evol.* **59**, 21–32.
- Marler, P. 1996: Social cognition: are primates smarter than birds? In: *Current Ornithology* (Nolan, V. & Ketterson, E. D., eds). Plenum Press, New York, pp. 1–32.
- Marr, D. 1982: *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. W. H. Freeman and Company, New York.
- Marzluff, J. M., Heinrich, B. & Marzluff, C. S. 1996: Roosts are mobile information centers. *Anim. Behav.* **51**, 89–103.
- McClamrock, R. 1991: Marr's three levels: a re-evaluation. *Mind. Mach.* **1**, 185–196.
- McGrew, W. C. 1992: *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge Univ. Press, Cambridge.
- Melis, A. P., Call, J. & Tomasello, M. 2006a: Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *J. Comp. Psychol.* **120**, 154–162.
- Melis, A. P., Hare, B. & Tomasello, M. 2006b: Chimpanzees recruit the best collaborators. *Science* **311**, 1297–1300.
- Mendes, N., Hanus, D. & Call, J. 2007: Raising the level: orangutans use water as a tool. *Proc. R. Soc. Lond. B: Biol. Lett.* **3**, 453–455.
- Menzel, E. W. Jr 1974: A Group of Young Chimpanzees in a One-Acre Field. In: *Behavior of Nonhuman Primates* (Schrier, A. & Stollnitz, F., eds). Academic Press, New York, pp. 83–153.
- Midford, P. E., Hailman, J. P. & Woolfenden, G. E. 2000: Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Anim. Behav.* **59**, 1199–1207.
- Miklosi, A., Topal, J. & Csanyi, V. 2004: Comparative social cognition: what dogs can teach us? *Anim. Behav.* **67**, 995–1004.
- Milton, K. 1981: Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *Am. Anthropol.* **83**, 534–548.
- Mitchell, J. P. 2006: Mentalizing and Marr: An information processing approach to the study of social cognition. *Brain Res.* **1079**, 66–75.
- Mock, D. W. & Fujioka, M. 1990: Monogamy and long-term pair bonding in vertebrates. *Trends Ecol. Evol.* **5**, 39–43.
- Mulcahy, N. J., Call, J. & Dunbar, R. I. M. 2005: Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *J. Comp. Psychol.* **119**, 23–32.
- Nishida, T. & Uehara, S. 1983: Natural diet of chimpanzees (*Pan troglodytes schwiinfurhii*): long term record from the Mahale Mountains, Tanzania. *Afr. Study Monogr.* **3**, 109–130.
- Noe, R. & van Hooff, J. A. R. A. M. 2001: *Economics in Nature. Social Dilemmas, Mate Choice and Biological Markets*. Cambridge Univ. Press, Cambridge.
- Parker, S. T. & Gibson, B. M. 1977: Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Human Evol.* **6**, 623–641.
- Pawolksi, B., Lowen, C. B. & Dunbar, R. I. M. 1998: Neocortex size, social skills and mating success in primates. *Behaviour* **135**, 357–368.
- Penn, D. C., Holyoak, K. J. & Povinelli, D. J. 2008: Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* **31**, 109–130.
- Potts, R. 2004: Paleoenvironmental basis of cognitive evolution in Great Apes. *Am. J. Primatol.* **62**, 209–228.
- Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007: Planning for the future by western scrub-jays. *Nature* **445**, 919–921.
- Rapaport, L. G. & Brown, G. R. 2008: Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evol. Anthropol. Issues News Rev.* **17**, 189–201.
- Reader, S. M. & Laland, K. N. 2002: Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441.
- Reader, S. M., Sol, D. & Lefebvre, L. 2005: Comparing cognition across species. *Trends Cogn. Sci.* **9**, 411–411.
- Rensch, B. & Döhl, J. 1968: Spontanes öffnen verschiedener Kistenverschlüsse durch einen Schimpanse. *Z. Tierpsychol.* **24**, 479–489.
- Richardson, P. J. & Boyd, R. 1985: *Culture and the Evolutionary Process*. Univ. Chicago Press, Chicago, IL; London.
- Roth, G. & Dicke, U. 2005: Evolution of the brain and intelligence. *Trends Cogn. Sci.* **9**, 250–257.
- Russon, A. E. 1997: Exploiting the expertise of others. In: *Machiavellian Intelligence. II. Extensions and Evaluations* (Whiten, A. & Byrne, R. W., eds). Cambridge Univ. Press, Cambridge, pp. 174–206.
- Sawaguchi, T. & Kudo, H. 1990: Neocortical development and social structure in primates. *Primates* **31**, 283–289.
- Schloegl, C., Kotrschal, K. & Bugnyar, T. 2007: Gaze following in common ravens, *Corvus corax*: Ontogeny and habituation. *Anim. Behav.* **74**, 769–778.
- Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S. 2006: Investigating physical cognition in rooks, *Corvus frugilegus*. *Curr. Biol.* **16**, 697–701.

- Seed, A. M., Clayton, N. S. & Emery, N. J. 2007: Third-party postconflict affiliation in rooks, *Corvus frugilegus*. *Curr. Biol.* **17**, 152–158.
- Seed, A. M., Clayton, N. S. & Emery, N. J. 2008: Cooperative problem solving in rooks (*Corvus frugilegus*). *Proc. R. Soc. B: Biol. Sci.* **275**, 1421–1429.
- Seed, A. M., Call, J., Emery, N. J. & Clayton, N. S. 2009: Chimpanzees solve the trap problem when the confound of tool use is removed. *J. Exp. Psychol. Anim. Behav. Process.* **35**, 23–24.
- Shettleworth, S. J. 1998: *Cognition, Evolution and Behavior*. Oxford Univ. Press, New York.
- Sonerud, G. A., Smedshaug, C. A. & Bråthen, O. 2001: Ignorant hooded crows follow knowledgeable roost-mates to food: support for the information centre hypothesis. *Proc. R. Soc. Lond. B* **268**, 827–831.
- Sterelny, K. 2003: *Thought in a Hostile World*. Blackwell Publishing, Oxford.
- Strum, S. C., Forster, D. & Hutchings, E. 1997: Why Machiavellian intelligence may not be Machiavellian. In: *Machiavellian Intelligence. II. Extensions and Evaluations* (Whiten, A. & Byrne, R. W., eds). Cambridge Univ. Press, Cambridge, pp. 50–85.
- Taylor, A. H., Hunt, G. R., Holzhaider, J. C. & Gray, R. D. 2007: Spontaneous metatool use New Caledonian crows. *Curr. Biol.* **17**, 1504–1507.
- Taylor, A. H., Hunt, G. R., Medina, F. S. & Gray, R. D. 2009: Do New Caledonian crows solve physical problems through causal reasoning? *Proc. R. Soc. B: Biol. Sci.* **267**, 247–254.
- Tebbich, S., Taborsky, M., Fessel, B. & Dvorak, M. 2002: The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecol. Lett.* **5**, 656–664.
- Tomasello, M. & Call, J. 1997: *Primate Cognition*. Oxford Univ. Press, New York.
- Visalberghi, E. & Limongelli, L. 1994: Lack of Comprehension of Cause-Effect Relations in Tool-Using Capuchin Monkeys (*Cebus apella*). *J. Comp. Psychol.* **108**, 15–22.
- de Waal, F. B. 1982: *Chimpanzee Politics: Power and Sex among Apes*. Harper & Row, New York.
- de Waal, F. B. M. & van Roosmalen, A. 1979: Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* **5**, 55–66.
- Waite, R. K. 1981: Local enhancement for food finding by rooks (*Corvus frugilegus*) foraging on grassland. *Zeitschrift für Tierpsychologie* **57**, 15–36.
- Wasserman, E. & Zentall, T. R. 2006: *Comparative Cognition. Experimental Explorations of Animal Intelligence*. Oxford Univ. Press, Oxford.
- Watson, J. B. 1913: Psychology as the behaviourist sees it. *Psychol. Rev.* **20**, 158–177.
- Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002: Shaping of hooks in New Caledonian crows. *Science* **297**, 981.
- Whiten, A. & van Schaik, C. P. 2007: The evolution of animal ‘cultures’ and social intelligence. *Phil. Trans. R. Soc. Lond. B.* **362**, 603–620.
- Woolfenden, G. E. & Fitzpatrick, J. W. 1984: *The Florida Scrub Jay: Demography of a Cooperatively Breeding Bird*. Princeton Univ. Press, Princeton, NJ.
- Yamagiwa, J. 2004: Diet and foraging of the great apes: ecological constraints on their social organisations and implications for their divergence. In: *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence* (Russon, A. E. & Begun, D. R., eds). Cambridge Univ. Press, Cambridge, pp. 210–233.