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Are Corvids ‘Feathered Apes’?

—Cognitive Evolution in Crows, Jays, Rooks and Jackdaws—

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“If men had wings and bore black feathers, few of them would be clever enough to be crows”
(Rev. Henry Ward Beecher, mid-1800s)

Although the common ancestor of birds and mammals lived over 280 million years ago, there are striking similarities in the cognitive abilities of members of the crow family (corvids) and primates; including tool manipulation, social reasoning and complex memory. Corvids are perhaps best known for their extraordinary feats of spatial memory. Clark’s nutcrackers, for example have been suggested to cache up to 33,000 seeds in thousands of different sites during a season, and to accurately recover a high percentage of those caches, even when critical features of the environment have changed, such as they are covered in snow (Balda & Kamil, 1992; Balda & Turek 1984; Vander Wall, 1982). There is more to the corvids, however, than just a sophisticated spatial memory. Folklore and legend, particularly in the Vikings and the North American Indians has long suggested that crows, magpies, rooks and ravens may be the most intelligent of birds (Savage, 1997) and recent research is beginning to investigate this long-held view in the laboratory.

In this chapter, I propose that corvids are not only amongst the most intelligent of birds, but that they may also rival the great apes in cognitive ability. I will review the evidence for this proposal in this chapter. By the end, I will conclude that corvids should perhaps be considered as 'feathered' apes. This proposal is, at first, a startling claim given that corvids have much smaller brains than the great apes, with the relative absence of cortical structures. This line of thinking has not been the result of deficits in great ape cognition in comparison to corvids, but rather to three points; the claim for 'special status' to the apes based on their evolutionary relationship to humans, a reluctance to embrace ecological validity in the design of primate experiments, and the relative lack of studies on avian cognition. First, a traditional doctrine that is still rife in comparative psychology is that intelligence fits with the 'scala naturae' (or ladder of life), with humans at the top, with the apes, monkeys and dolphins below them, then dogs and cats, rats, birds, reptiles, fish and amphibians, with the insects at the bottom. Although this idea was dispelled more than 30 years ago (Hodos & Cambell, 1969), it is surprising how prevalent this notion still is, particularly amongst primatologists (Emery & Clayton, in press). As such, there remains a distinct prejudice against any finding of complex cognition in non-primates or non-cetaceans. Second, there is still an absence of ethologically-based tasks for testing primate cognition. Some primate researchers have begun to incorporate a high degree of ethological validity into their studies, such as gaze following in rhesus monkeys and knowledge attribution in chimpanzees (Emery et al, 1997; Hare et al, 2000, 2001, Tomasello et al, 1998), and it is promising to note that these studies have demonstrated a number of feats that less naturalistic paradigms have not. As such, I certainly disagree with Heyes (1998) who has suggested that ecological validity is unimportant in the design of cognitive experiments in animals. Increasing the ecological validity is more than just placing a few branches into a cage, it is utilising specific information about an animal's natural history to design experiments in which animals should be more likely to succeed. Third, many ornithologists are behavioural ecologists, and although they use cognitive-laden terms, such as decision-making, strategies and tactics, they do not tend to think about the mechanisms involved (Marler, 1997). Therefore, the time is ripe for behavioural ecologists to collaborate with comparative psychologists (Yoerg, 1991).

Interestingly, although corvid and ape brains differ radically in their size and organization, they share many similar traits. As such, apes and corvids may reflect divergent evolution in relation to their neuroanatomy (i.e. the structure of their brains is very different), but convergent evolution in relation to mental processes (i.e. their cognitive abilities are similar). It is noted that other avian groups, particularly the parrots, may also qualify for the same treatment, however, I do not consider them further in this chapter (see Emery & Clayton, in press).

In the first section, I will discuss whether corvids have the appropriate neural machinery to sustain similar intelligence to the apes. This is an important issue, because if we find that there is nothing particularly special about the corvid brain compared to other birds, then perhaps our arguments about complex cognitive abilities in corvids should be re-evaluated, possibly as anomalous results. I will then go on to discuss some recent work on social knowledge in Old world corvids (rooks, ravens and jackdaws), including the formation of selective affiliative relationships (alliances), food sharing and tactical deception. Then, I discuss the mechanisms of social intelligence; social cognition ('theory of mind'), focusing on recent work in western scrub-jays. In the final section, I will discuss aspects of physical cognition, such as complex memory, insight, causal understanding, tool use and manufacture. I will conclude by providing an evolutionary reason for why corvids should be classed alongside the apes in terms of their intelligence.

1. Machiavellian Intelligence & the Evolution of Mind

The corvids are amongst the most social groups of birds (Goodwin, 1986). In primates, Humphrey (1976) proposed that successful living in a large, constantly changing social group should require more 'brainpower' than the most complex of technical problems. At the heart of this proposal, was the idea that conspecifics are animate beings; agents that have specific goals, intentions, beliefs and desires, agents which interact with other agents, agents that have special relationships with other agents, agents which deceive one another. In what has been named the 'social intelligence' (SI) hypothesis, Humphrey provided a theoretical framework for understanding the evolution of human intelligence which has overtaken all the main alternative hypotheses, such as tool use, hunting, enhanced spatial memory and extractive foraging. Indeed, there is very good evidence that social complexity was the driving force behind the evolution of the primate brain and intelligence (Byrne & Whiten, 1988; Dunbar, 1993; Whiten & Byrne, 1997). However, Humphrey's ideas were developed from the study of social behaviour in nonhuman primates. As I will describe below, corvids face many of the same social problems as primates, and possess many of the same neural and cognitive mechanisms for overcoming such social problems.

Do Corvids Have the Neural Machinery for Complex Cognition?

The great apes, including humans, have brains larger than would be predicted for their body size (*encephalization quotient;* K; Jerison, 1973). A closer examination of the regression lines on Jerison's classic figure reveals that the carrion crow (*Corvus corone*) also appears to be greatly encephalized, with a K value much higher than the regression line and higher than the chimpanzee. Jerison's data, however, were based on comparisons between whole brain size and body size. Body size has been criticized as an inaccurate scaling measure, as the brain stops developing sooner than the rest of the body, and external, ecological variables may have an undue influence on body size. Perhaps a better indication of the influence of the body on brain size is the size of the brainstem (Passingham, 1982). The primary function of the brainstem is to regulate visceral and somatic functions, such as breathing rate, and the control of blood pressure. These functions are largely dependent on body size, such as the force required to pump blood around a large body compared to a small body. Overall brain size has also been criticized as a poor measure of cognitive capacity. Many brain areas control primary sensory and motor functions that are not associated with 'intelligence' or cognition.

In mammals, the neocortex is the brain area most associated with cognitive processing (memory, reasoning, concept formation and social intelligence). Although, many areas of the neocortex are also important for basic sensory and motor functions, the available comparative data for neocortex size in primates is limited to the neocortex as a whole. Birds do not have a neocortex, but certain areas of the forebrain have been suggested to represent analogous structures to the mammalian neocortex, ones that may correlate with measures of higher cognition, such as feeding innovation and tool use (Lefebvre et al, 2003). Emery & Clayton (in press) performed a comparative analysis to investigate whether the primate neocortex represents a special case for dramatic expansion, or whether a similar pattern is seen in the avian forebrain. Portmann's (1947) data set of forebrain and brainstem volume for 140 avian species was used. The data were transformed from brain indices (using his basic unit; the brainstem of a Galliforme of comparable size to the chosen bird) to the actual weight of the forebrain (hemispheres) and brainstem. A forebrain: brainstem ratio (FBR) was therefore calculated for each species that was independent of phylogenetic anomalies. Stephan et al's (1981) data set of neocortex volume for 63 primates and insectivores was also used, and a neocortex: brainstem ratio was calculated. Within birds, the corvids (and parrots) were all located above the regression line (i.e. the forebrain volume was larger than predicted by brainstem volume; see Fig. 1). Interestingly, when the FBR of corvids was compared to other avian species, the pattern of difference closely resembles the difference of neocortex: brainstem ratio between the great apes and other primates and insectivores (except for parrots; Emery & Claytom, in press).

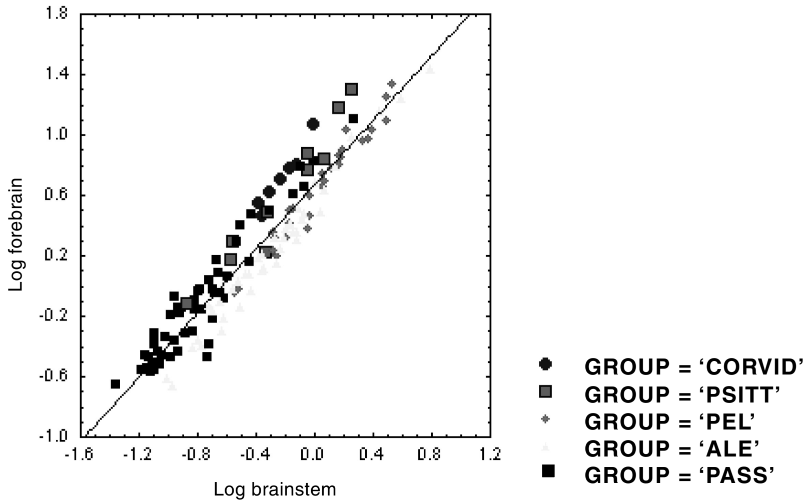

Figure 1. Scatter plot of 140 species of birds, with log10 brainstem size on the x-axis and log10 forebrain size on the y-axis. A regression line of the predicted forebrain to brainstem size has been drawn. The bird species are designated with different symbols based on super-order (Grey Diamond; PEL = *Pelargomorphae* & Light Diamond; ALE = *Alectoromorphae*), order (Black Square; PASS = *Passeriformes* & Grey Square; PSITT = *Psittaciformes*) and family (Grey circle; CORVID = *Corvidae*).

Social Intelligence & the Avian Brain

In primates, there is a strong correlation between the size of the brain or neocortex and mean group size (i.e. primate species with relatively large forebrains are usually found in larger social groups; Dunbar, 1992, Barton & Dunbar, 1997). It has been suggested that the larger the social group, the greater the number of potential relationships that may occur between individuals; therefore mean group size may provide a useful indication of the social complexity of a species. This idea has recently been refuted, however, as there is no correlation between social learning, innovation and group size in primates, although there is a significant correlation between social learning and neocortex size (Reader & Laland, 2002). No such relationship has been found between brain (or neocortex) size and various non-social, ecological variables, such as home range size or the percentage fruit eaten in the diet. This then appears to be a clear indication that social intellect may have been a significant factor in the evolution of brain and intelligence in primates.

If social intellect was also a driving force for the evolution of avian brain and intelligence, then we might predict some relationship between social complexity and forebrain size in birds, and more specifically in the corvids? I therefore split the birds in Portmann's data set into sub-categories based on a gross categorical measure of social complexity; social unit. Group size is extremely variable in birds and so an accurate measure could not be calculated. Six social units were identified for simplicity; Solitary (species which held a territory and remained alone except during the breeding season; Pairs (species which formed a selective pair-bond, but did not associate with conspecifics), Family Group (species which displayed an exclusive cooperative-breeding system, in which the adult male-female pair formed the core, and relatives helped during raising the young); Small Flocks (species with a group size between 10 and 50 individuals), Medium Flocks (species with a group size greater than 50) and Large Flocks (species with group sizes in the hundreds and thousands). In all cases, the largest possible social unit was used per species, as this represented the maximum possible social complexity that could be achieved in each species. For example, ravens form selective pair-bonds, but many pairs are located within the same territory, and juvenile ravens form small foraging flocks (Heinrich, 1999).

The average FBR was calculated for all birds of a particular social unit. Interestingly, there were no differences between any social unit (*ANOVA, F* (5, 133) = 1.17, p = 0.33; Fig. 2a). This suggests that either social complexity was not a significant factor in the evolution of avian cognition, or that it was only important for specific species which also fulfilled the other criteria for social intelligence, such as longevity, and extended development. Therefore, I split the species into their respective super-orders (*Coraciomophae, Pelargomorphae & Alectoromorphae*), orders (*Psittaciformes & Passeriformes*) and families (*Corvidae*). This classification followed Portmann (1947), and was largely based on the amount of available data. As can be seen in Figure 2b, the corvids for which data is available are found in small or medium flocks. In both cases, the FBR is larger in the Old world corvids than all other birds, except the parrots. Only *Alectoromorphae* species are found in large flocks, however, their FBR is significantly smaller than the corvids and parrots. It has been suggested that in humans there is an upper limit on the number of social partners and hence relationships, which an individual can successfully process (Dunbar, 1993). Individuals in flocks of hundreds or thousands of

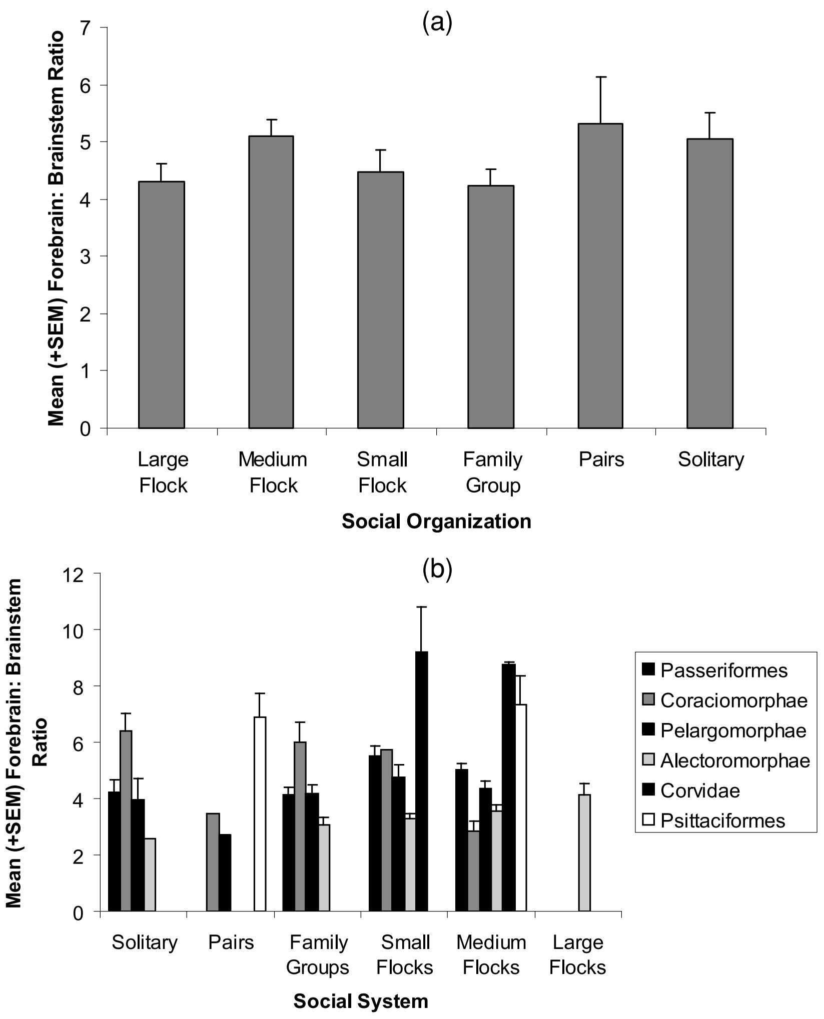

Figure 2. (a) Histogram displaying mean (+SEM) Forebrain: Brainstem Ratios (FBR) for 140 species divided by social unit (Solitary, Pairs, Family Group, Small Flock, Medium Flock and Large Flock). (b) Histogram displaying mean (+SEM) FBRs for 140 species divided by social unit (see above) and either super-order (*Coraciomorphae, Pelargomorphae & Alectoromorphae*), order (*Passeriformes & Psittaciformes*) and family (*Corvidae*).

group members may therefore be unable to process such relationships, and so not require larger brains. It is likely that such large flocks evolved as an antipredator mechanism, and so unrelated to social complexity.

Coalitions, Alliances and the Application of Social Knowledge

For individuals living within in a social group, it pays to develop selective relationships with others; to aid in the acquisition of resources and to receive protection against the threat of those who are aiming to acquire your resources. The techniques that monkeys, apes and dolphins employ tend to be the formation of temporary coalitions or occasionally more long-term alliances (sometimes referred to as ‘friendships’; Silk, 2002). It is assumed that these relationships are fostered through reciprocal altruism and tactical manipulation (Seyfarth & Cheney, 1984; de Waal & Luttrell, 1988), mechanisms that should require sophisticated cognitive processes. As many of the problems faced by mammals living in large social groups are also experienced by birds living in large flocks or colonies, then group-living, large-brained birds, such as corvids, should utilise many of the social tactics so far displayed in primates and dolphins.

Rooks (*Corvus frugilegus*) may be a strong candidate for social complexity as they demonstrate a fission-fusion society; congregating in large colonies during the breeding season, and then after the new young have become independent, the breeding pairs either disperse to forage, join other groups or migrate. After returning, the pairs re-join their original group for the next breeding season, often re-occupying the same nest as previous years (Roselaar, 1994). We therefore examined the development of social complexity in 11 hand-raised, mixed-sex & -kin, juvenile rooks, which were housed in an indoor aviary. *Ad lib* observations on the rooks’ social interactions were made in relation to a specific feeding event (food was distributed or clumped). We found that six rooks rapidly formed three alliance pairs during the initial round of the study (first 4 weeks), with individuals displaying significant levels of affiliative behaviour (preening, food sharing, dual-caching and bill-twining) with their partner (Emery et al, in prep). The choice of partner did not appear to follow a specific pattern (i.e. was not always with kin), and being in a partnership tended to increase the social status of both partners. Rooks in the alliances shared food reciprocally, which was either given without stimulation, in reaction to begging or as the result of tolerated theft. Food offering has also been seen in jackdaws and scrub-jays and so maybe a corvid-wide trait (de Kort et al, 2003; see next section). Food sharing had only been previously reported in primates, but at much lower frequencies than in the rooks, and largely as an outcome of begging and tolerated theft. Initiation of affiliative behaviours lead to an increase in the amount of aid given by a partner during agonistic interactions with other group members, and the alliance partners also acted together in the defence of resources. The rooks demonstrated a sophisticated understanding of ‘third-party’ relationships (i.e. those between other individuals) said to be one of the specialties of primate cognition (Tomasello & Call, 1997). This was demonstrated by ‘redirected aggression’ against the partners of those individuals that had attacked them or their own partner and intervention in the formation of new alliances. Finally, alliance partners consoled one another after heightened aggression, but this was independent of whether the partner was the aggressor or the victim.

Food Sharing

Food sharing is a primary example of altruistic behaviour, however evolutionary theory only goes as far as explaining the sharing of food between kin, parents to infants or as courtship feeding. Sharing food between nonrelated, same sex adults cannot be explained this way. Three main explanations for non-kin sharing have been proposed:

1) Reciprocal altruism – food (or other commodities) is shared on a like-for-like basis, for example, regurgitating blood to feed conspecifics, who will return the favour at a later date (Wilkinson, 1984). In the rooks, individuals within alliances shared food with their partner, and received food in return. The frequency of sharing was not equal, however.
2) Development of social relationships – food (or other commodities) is exchanged for a different type of commodity, such as grooming. For example, chimpanzees share food with conspecifics in return for help in fights (agonistic aid; Hemelrijk & Ek, 1991). This has been termed interchange. Such sharing may also form the basis for the development of long-term affiliative relationships, such as alliances. The rooks demonstrated high levels of food offering during the initial stages of the alliance, but this declined over time. Concurrently, the amount of preening given increased over time (Emery et al, in prep). Interestingly, food, preening and agonistic aid were exchanged with one another, and treated as having the same value (‘currency’, Emery et al, in prep).
3) Increase in social prestige – individuals which are seen to give food frequently to others may enhance their social status (Zahavi & Zahavi, 1997) or re-establish their dominance. Zahavi & Zahavi (1997) reported that high-ranking Arabian babblers would often feed low-ranking individuals, but the food was often refused and usually not reciprocated. In two of the three rook alliances, the dominant partner was the greatest provider of food, however, the subordinate partner also gave its partner food, and the act was also reciprocated (Emery et al, in prep).

Therefore, in rooks, food is given reciprocally between alliance partners, and it is often given in exchange for preening and help in aggressive encounters with a third party. Food sharing therefore appears to play a role in the development and maintenance of affiliative, long-term relationships in rooks. These explanations may also require the ability to ‘keep score’ of who has given to whom, what they gave, how long ago that they gave it and in what context (and as such may require complex memory, see later section).

We have also examined the mechanisms of food sharing in a pair of unrelated, male, juvenile jackdaws. Waxworms were presented to each jackdaw in turn, and what they did with the worm was recorded. Bird A was given a total of 1,112 worms, 16% of which he transferred to Bird B. Bird A actively gave Bird B 32% of these worms, responded to Bird B’s begging requests with 43% of these worms, and tolerated theft of 25% of the worms by Bird B. Bird B was given a total of 1,077 worms, 12% of which he transferred to Bird A. Bird B actively gave Bird A 30% of these worms, responded to Bird A’s begging requests with 27% of these worms, and tolerated theft of 43% of the worms by Bird A (de Kort et al, 2003; Fig. 3). The jackdaws did not appear to give worms because they were satiated, as they ate the majority of worms after they had transferred the first worm. This level of active giving (30-32% of total food given) is 100 times greater than a similar behaviour in capuchin monkeys (0.3%, de Waal, 1997). We suggest that in a similar fashion to the rooks, the jackdaws are using active food offering to establish and maintain an affiliative bond with a social partner.

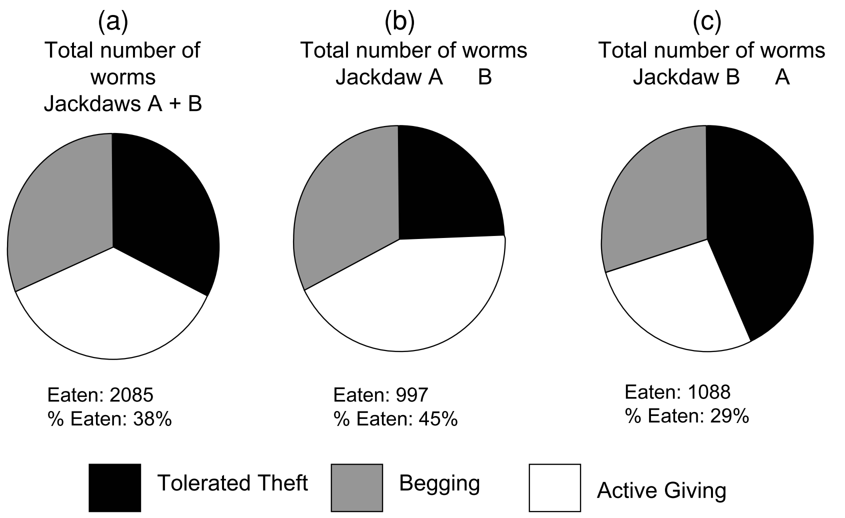

Figure 3. Pie-charts displaying the amount of food-offering between 2 male, un-related jackdaws. Wax worms were either actively given from one individual to another (White), one individual gave the other a worm in response to begging (Grey) or an individual tolerated theft of a worm from the other (Black). The 3 charts display (a). the total number of food transfers between the 2 jackdaws, (b). the total number of transfers from A to B, and (c). the total number of transfers from B to A. Data derived from de Kort et al (2003).

Tactical Deception

Tactical deception, or the intentional manipulation of another's beliefs leading to deception, has been proposed as another important indication of ToM (Whiten & Byrne, 1988). Very little experimental work has been performed on this cognitive capacity, with the predominant source of data compiled from a large number of anecdotes produced by primatologists (Whiten & Byrne, 1988). The use of anecdotes as a source of data has been criticized by Heyes (1998) and others, and very few experiments on tactical deception have been performed in any species (discussed in Tomasello & Call, 1997).

Many corvids hide caches of food for later consumption. During harsh winter conditions efficient cache recovery can result in the difference between death and survival. Protection of caches from potential pilferers may therefore present an example where an understanding of conspecifics' intentions would be a useful attribute to possess. Ravens, for example, are very cautious when hiding their caches with other ravens (and wolves). This behavior has been studied in detail by Heinrich and colleagues (Heinrich & Pepper, 1998; Heinrich, 1999), and more recently by Bugnyar & Kotrschal (2002). Storers will delay caching if other ravens are in the vicinity and wait until would-be thieves are distracted or have moved away before they resume caching. Heinrich has also observed ravens making false caches in the presence of observers, and repeatedly moving them around to distract the observer. Bugnyar & Kotrschal (2003) also reported the strategy of a raven leading others away from their caches.

Bugnyar & Kotrschal (2002) have suggested that caching and raiding ravens may present an example of tactical deception through an attempt to manipulate another's attention, either to prevent opponents from gaining opportunities for stealing (see earlier next on social learning), or to gain opportunities for learning socially from the opponents. They examined two forms in which another's attention may be manipulated; withholding information and directing another's attention away from the caches (object of interest). During caching, storers tended to withdraw from conspecifics, and were at a greater distance from conspecifics during caching than during other activities, such as feeding and resting. The storers also cached close to large objects, with 80% of the caches between the storers and the observers, and outside the view of the observers. Cachers moved their caches if an observer moved towards them, and also protected their cache sites. Cache raiders also employed a number of strategies to increase the potential for learning about cache sites, and for stealing caches. In 33% of cases, the observers changed their position relative to the structures that blocked their view of the cache sites and in 32% of cases the observers changed their orientation and distance away from the cachers. If a storer was close to a cache site, the observers delayed pilfering until the cacher was away from the caches, usually within 1-min of the cacher leaving the cache site. These behaviours suggest that caching and raiding ravens appreciate the visual perspective of one another, and produce strategies to counter the behaviour of the other.

2. Social Cognition

Social Learning

The ability to learn information about objects, individuals or locations, or the precise methods or actions required to achieve a particular goal from another individual is called *social learning* and it can have many forms. Space does not permit a thorough description of the different types of social learning, but the significant categories include stimulus and local enhancement, contagion, social facilitation, observational conditioning, copying, goal emulation and imitation (see reviews in Whiten and Ham, 1992; Tomasello and Call, 1997, and papers in Heyes and Galef, 1996).

For food-caching birds, one of the problems of living in social groups concerns the pilfering of food (kleptoparasitism; Brockmann and Barnard, 1979). Hiding food caches in the presence of others is risky because an observer may subsequently steal those caches when the storer is out of sight. For storers, there are many potential counter-strategies available to reduce the potential for pilfering (Bugnyar & Kotrschal, 2002; Emery & Clayton, 2001; Emery et al, 2003; Dally et al, 2003; Vander Wall & Jenkins, 2003). For pilferers, the ability to locate caches made by others quickly and efficiently may be the important difference between successful pilfering and potential aggression from the storer. Therefore, pilfering birds may require a sophisticated observational spatial memory for learning about the precise location of another individual's caches.

This behaviour has been studied in closely-related species of New World corvids (jays and nutcrackers). Bednekoff and Balda (1996a, b) tested the ability of pinyon jays (*Gymnorhinus cyanocephalus*), Clark's nutcrackers (*Nucifraga columbiana*), and Mexican jays (*Aphelocoma ultramarina*) to remember where another bird had cached, by examining their cache retrieval efficiency. The birds were allowed to observe another bird caching, and were then given the opportunity to recover those caches either 1 day or 2 days later. Bednekoff and Balda (1996a) found that highly-social pinyon jays could remember the location of caches made by another bird, in specific locations at 1 and 2 day retention intervals and in general locations at a 7 day retention interval.

At the 1 day retention interval, Clark's nutcrackers (a relatively asocial species, but one that relies heavily on cached food for survival over the winter) performed more accurately than chance, as both storers and observers, and there was no difference between the two groups (i.e. observers could locate other's caches as well as the birds that made the caches). At the 2 day interval, Clark's nutcrackers accurately recovered their own caches, but not those they had observed. At the 1 day retention interval, Mexican jays (a very social species that lives in large flocks) behaved the same as the nutcrackers, and were more accurate than expected by chance when recovering caches they had made and those made by another bird. As with the pinyon jays, there was no difference between recovering their own caches and another's caches at the 2 day retention interval (Bednekoff and Balda, 1996b). Balda and colleagues (1997) have suggested that as pinyon jays and Mexican jays are social species, and display sophisticated social learning capabilities; but Clark's nutcrackers are an asocial species and display constrained social learning, there may be an adaptive specialization within social corvids to learn information from others. This argument stems from their work on the adaptive specialization of spatial memory in these species (Balda et al, 1997), comparing social versus non-social species on a social learning task and a non-social learning task (Templeton et al, 2000).

The western scrub-jay is a territorial species, which only forms pairs during the breeding season, and thus might be described as asocial. If the adaptive specialization for social learning hypothesis is correct, then we would predict that closely-related asocial jays, such as the western scrub-jay would fail to locate another's caches during similar tests for observational spatial memory. Griffiths, Duarte and Clayton (unpublished observations; see also Clayton et al, 2001), examined three groups of western scrub-jays; Storers, Observers and Controls (a group that could hear another bird caching in an adjacent cage, but could not see it). The birds were given a 3-hr retention interval to enhance the possible retrieval accuracy, and to mimic natural behaviour; caches are very unlikely to remain after 1-7 days. This retention is considerably shorter than in the Bednekoff and Balda (1996a, b) experiments.

Each group was compared with the other two groups. Observers made significantly fewer looks than Controls to search in a location where food had been cached by the Storer during the caching phase, but the Observers made significantly more looks than Storers to search in a location where food had been cache compared to Observers. The Storers also made significantly fewer looks to search for the food than Controls.

Imitation has only been investigated in one study of ravens (Fritz & Kotrschal, 1999). Two groups of dyads, either controls or observer-demonstrator pairs, were presented with boxes that could be opened by levering the lids. The demonstrator was trained to open the box using a different method from levering (pulling up). Control birds only levered open the box, whereas the observers opened the box both ways (levering and the demonstrated pull and open technique). This probably does not demonstrate imitation based on current thinking, as only one action was performed, the action was probably in the raven's behavioural repertoire, and the specific action used was not copied precisely every trial. This suggests that the raven observers were responding based on stimulus enhancement, and possibly goal emulation. As such, the ravens were acting in a similar fashion to many great apes.

Visual Perspective-Taking

Distinguishing another individual's visual perspective from one's own is thought to be an important step in interpreting others' intentions and thoughts about the world (see Emery, in press, for review). This ability would be particularly useful in attempts to manipulate another's behaviour and intentions (tactical deception). Recent experiments in chimpanzees based on their natural propensity to compete over food have produced interesting findings in relation to visual perspective-taking (Hare et al, 2000). A subordinate and a dominant chimpanzee were located next to an arena which contained two pieces of food; the subordinate chimp could see both pieces, whereas the dominant chimp could only see one of them. Could the subordinate chimpanzee base their decision about which food to approach on which piece/s of food the dominant could see, i.e. could they take the dominant's visual perspective? When they were released into the arena together, the subordinate chimp went for the food hidden from the dominant's view. To eliminate the possibility that the subordinate was not reasoning about the dominant's visual perspective, but only responding to simple behavioural cues (such as gaze direction, and direction of movement), the subordinate was released a few seconds before the dominant. As before, the subordinate retrieved the food hidden from the dominant. Hare and colleagues have suggested that these positive results were due to implementation of a competitive rather than a cooperative paradigm, a more natural behavioural state for chimpanzees.

Many corvids also compete for food. In food-caching species, such as jays, magpies, rooks and ravens, some individuals cache food for later consumption, whereas others pilfer this food when presented with the opportunity. This produces a scenario in which storers and pilferers have to develop more and more sophisticated strategies in order to either protect their caches or pilfer others. Caching ravens will delay caching if other ravens are in the vicinity, and wait until would-be pilferers are distracted or have disappeared before they resume caching (Heinrich & Pepper, 1998; Bugnyar & Kotrschal, 2002). Both ravens (Heinrich, 1999) and Northwestern crows (*Corvus corinius*; James & Verbeek, 1983) make false caches in the presence of observers, which are repeatedly moved around, and ravens preferentially store food behind obstacles so that other ravens cannot see where the caches are being made (Bugnyar & Kotrschal, 2002). Clarkson (1984, Clarkson et al, 1986) showed that magpies adjust the density of their caches by spacing them further apart and placing them further away from the central food source if the risk of pilfering is high (see also crows; James & Verbeek, 1983). Finally, some corvids return alone to caches they had hidden in the presence of conspecifics, and readily re-cache them in new places (Balda & Kamil, 1992; Bugnyar & Kotrschal, 2001; DeGange et al, 1989; Emery & Clayton, 2001; Goodwin, 1956; Heinrich, 1999, Robinette Ha et al, 2003).

Dally et al (2003) examined which strategies western scrub-jays would utilise to protect their caches during caching. In the first experiment, the jays were provided with two caching trays; one located close to an observer, the other located as far as possible from the observer. The jays cached preferentially in the tray furthest from the observer, but only when observed; they did not discriminate between the trays when allowed to cache in private. Interestingly, the jays only re-cached food from the near tray, suggesting that they treated the food items in that tray as the most likely to be pilfered. In the second experiment, the jays were provided with two trays and their location was controlled for distance from the observer; one tray was located in the open, the other located behind an opaque screen (i.e. hidden from the observer's view). In test trials, the jays preferentially cached behind the opaque screen. To determine whether the jays feared the open (and so failed to cache there), control trials were ran in which powdered (uncacheable food) was provided. The jays did not spend any longer eating behind the barrier than in the open. Finally, although the jays re-cached too few food items to be analysed statistically, there was tentative evidence that the items they did re-cache were only those cached in the open tray. Further studies are in progress to determine whether jays can appreciate more sophisticated aspects of another's visual perspective, such as line of sight, rather than presence or absence in these studies.

Knowledge Attribution

In an earlier section, I described the ability of many corvids, including western scrub-jays, to recall of the exact location of another's caches seen being made during an earlier occasion (Clayton et al, 2001). Western scrub-jays routinely compete for valuable food, such as high-protein, high-fat food scraps left by humans (Nicky Clayton, unpublished observations). The birds would cache the food, but many would return later when other birds were distant from their cache sites and re-hide the caches in new locations. This behaviour appeared to be important to the protection of caches from conspecific raiders that may have seen the caches being made (and which we know to be successful pilferers through observational spatial memory). This natural behaviour suggested to us that the jays may perceive the difference between jays that possessed *knowledge* of the cache sites, and those *ignorant* to the locations of the caches (i.e. were not present at the time of caching).

With this in mind, we examined whether this re-caching behaviour would be observed in a laboratory colony of hand-raised western scrub-jays (Emery & Clayton, 2001). We initially gave a group of 7 birds the opportunity to cache worms either in private with another bird's view obscured or when another bird was present, and they could observe the location of the caches being made. After a 3-hr retention interval, the storing birds were allowed to recover their caches in private, independent of what they did during caching. During caching, the birds were provided with an ice-cube tray that was filled with sand so that the birds could make caches in it. Each tray was made trial unique by attaching novel configurations of Lego bricks to the caching tray. A bowl containing wax worms was also placed in the storer's cage. We recorded the number of caches the storer made and ate, counting the number of worms remaining in the bowl at the end of the 15-min trial. After the 3-hr retention interval, the birds were presented with the original tray containing their caches and an additional unique tray in which they could re-cache worms. We recorded the number of worms that were recovered, the number of looks made to find cache sites (as a measure of recovery accuracy) and the number re-cached; either in old cache sites (those used to make the previous caches) or new cache sites (in the new tray or elsewhere in the storer's cage). We found that the storers recovered proportionally more caches when previously observed during caching than when they had previously cached in private. The storers also re-cached significantly more worms when observed during the previous caching episode than when they had cached in private (Fig. 4a), and almost all these re-caches were made in new sites unknown to the observer (Fig. 4b).

One interpretation of these results is that the storers attributed *knowledge* of the location of the caches to the observer because they had seen them being made, and so the storer re-cached them in new sites that the observer did not have knowledge about. Conversely, the storers attributed *ignorance* to the bird whose view was obstructed by an occluder throughout caching, and so there was no need to protect their caches by re-caching them. A less cognitive expla-

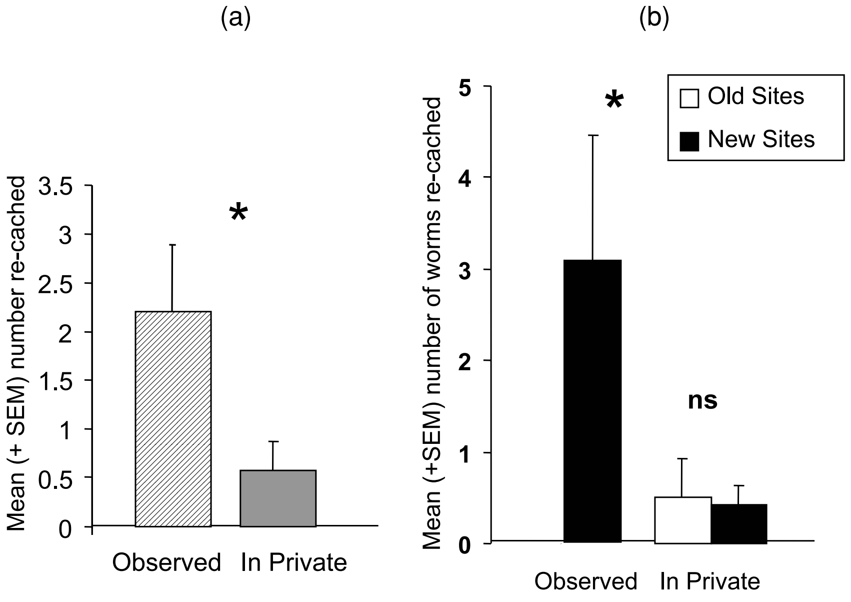

Figure 4. (a) Mean (+SEM) number of caches that were re-cached either when previously observed caching or when they had previously cached in private (b) Mean (+SEM) number of caches that were re-cached in new or old sites, either when previously observed caching or when they had previously cached in private. * $p < 0.05$. Redrawn from Emery & Clayton (2001).

nation may be that re-caching automatically occurs if observed during caching, perhaps as a stress response. This however seems unlikely due to the time delay between caching and recovery, and the absence of any discriminable stimulus during recovery (as both conditions are the same). We therefore performed an experiment to determine whether these jays could keep track of the social context of previous caching episodes that occurred in close temporal proximity.

The same storers were presented with a series of two interleaved trials, such that they were first observed caching in one unique tray, and then 10-min later in a second unique tray they cached in private. The order of the trials was counterbalanced. After a 3-hr retention interval, the two trays were returned to the storers, with an additional new tray for potential re-caching. Again, we found that the storers recovered proportionally more worms from the tray in which they had been observed caching, and they also re-cached more worms, specifically from the observed tray (Fig. 5a) and predominantly in new sites (Fig. 5b). This result shows that the birds remembered the specific social context during caching and did not automatically re-cache items if observed recently.

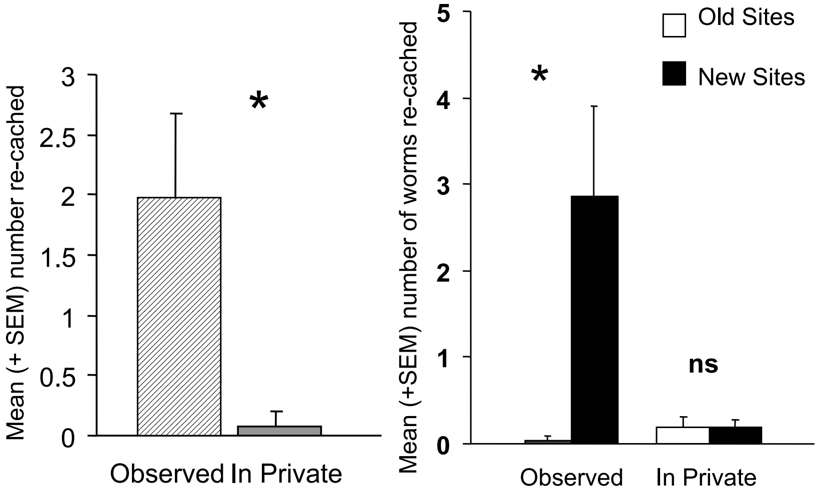

Figure 5. (a), Mean (+SEM) number of caches that were re-cached either when previously observed caching in a trial-unique tray or in a second trial-unique tray that was not observed during caching. (b) Mean (+SEM) number of caches that were re-cached in new or old sites when either observed caching in a trial-unique tray, or in a second trial-unique tray that was not observed during caching. * $p < 0.05$. Redrawn from Emery & Clayton (2001).

Experience Projection

The jays described in the previous social context of caching experiments had had prior experience of watching another bird cache and were then given the opportunity to steal those caches (Clayton et al, 2001). This Observer + Pilferer (O + P) group were almost as accurate at recovering caches they had observed being made as the birds that had made them. The storer birds in the observational learning experiment acted as observers in the experiments previously described (Observer; O group). An additional group in the observational learning study were given the opportunity to listen to another bird cache and then steal those caches, without ever observing the caches being made (Pilferer; P group). The O + P group were the birds in the previous two social context experiments. When the three groups were tested, either in private or when observed, the O + P group again demonstrated re-caching, with significantly more in new sites compared to old sites (Fig. 6a). Surprisingly, the P group also displayed significant levels of re-caching, especially in new sites (Figure 6b). In contrast, the O group, with no pilfering experience, did not demonstrate any re-caching, and the little re-caching they performed was equally distributed in new and old sites (Fig. 6c). This result suggests that the small amount of pilfering experience that the birds in the P and O + P groups had received was sufficient and necessary to trigger re-caching, whereas only observational experience failed to have this effect.

The O + P and P group birds appear to have transferred their pilfering experience to the current situation, and put themselves in the perspective of the observers, which may have the opportunity to pilfer the storers' caches in the future. Birds in the O group that had received no experience of pilfering another bird's caches did not do this. This result raises the exciting possibility that birds with pilfering experience can project their own experience of being a thief onto the observing bird, and so counter what they would predict a thief would do in relation to their hidden food. These experiments therefore suggest that western scrub-jays possess a sophisticated socio-cognitive system, but are they a demonstration of 'theory of mind'? Heyes (1993) sug-

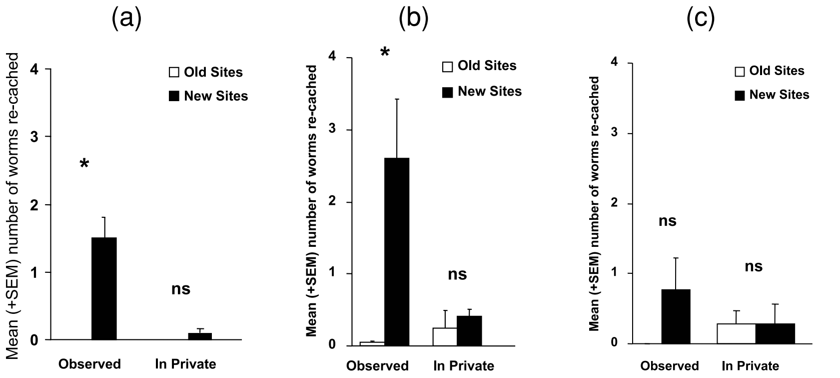

Figure 6. Mean (+SEM) number of caches that were re-cached in new or old sites when either observed during caching or when cached in private, by (a) Observer + Pilferer (O + P) group birds, (b) Pilferer only (P) group birds and (c) Observer only (O) group birds. *p < 0.05. Redrawn from Emery & Clayton (2001).

gested that the most convincing evidence for 'theory of mind' in animals will be converging data from different paradigms examined in the same species. We think that we are a significant way towards providing such convergent evidence for 'theory of mind' in western scrub-jays. First, jays attempt to reduce the amount of visual information available to potential thieves by caching as far away from them as possible or caching out of sight (*visual perspective-taking?*). Second, jays observed by a conspecific during caching, re-cache food in new locations, but do not do this when the conspecific's view is occluded (*knowledge attribution?*). Third, only those jays with experience of being a pilferer re-cache food after being observed; jays without this experience do not re-cache (*experience projection?*). Additional evidence for 'theory of mind' in scrub-jays is the proposal that 'mental time travel' (episodic memory and future planning) is essential for mental state attribution (Suddendorf & Corballis, 1997). As we will see in the section on Complex Memory (see also Clayton, this volume), western scrub-jays have demonstrated episodic-like memory (and some tentative new evidence for future planning).

Self-Recognition

Mirror self-recognition (MSR) has been tested in corvids (jungle crows; Corvus macrorhynchos), where the crows were exposed to mirrors in different orientations (horizontal and vertical). The crows aggressively attacked their reflection in the mirror as if a novel, same sex conspecific, therefore not demonstrating any aspect of self-awareness (Kusayama et al, 2000). As I discussed earlier, our recent experiments on social reasoning may provide convincing evidence of mental attribution in western scrub-jays. These results suggest that if Galllup (1982) was correct in proposing a relationship between self-recognition and 'theory of mind' (experience projection), then I would predict that western scrub-jays would also demonstrate mirror self-recognition. We therefore decided to test the responses of jays to mirrors. Unfortunately, the Gallup mark test for self-recognition is not ethologically relevant for birds. Birds cannot touch or preen their own faces, and there are few sites on their bodies which they cannot see. In a preliminary experiment (Emery & Clayton, in press), we examined whether the presence of a mirror during caching would alter the jays' re-caching behaviour later at recovery, compared to when caching in private or when observed by another bird. We predicted that if scrub-jays had a concept of self, they would interpret the image in the mirror at the time of caching as themselves and so forgo re-caching at the time of recovery (as the potential for pilfering would have been removed). If the jays interpreted the mirror image as a conspecific, they would re-cache the earlier hidden food, especially in new locations, as demonstrated in the previous study by Emery and Clayton (2001).

Scrub-jays have also been observed to cache non-food items, such as stones, so we provided the jays with a bowl containing both hazelnuts (a preferred food) and ceramic baking beans (a standardized equivalent to a stone). This was added to the design to determine whether the jays would attempt to 'deceive' the observer (or mirror reflection) by caching more baking beads than hazelnuts, and to determine whether the non-food items have similar motivational value to the food items. Heinrich & Smolker (1998) described caching of inedible items by ravens as a form of play, although adults cached such items out of visual contact of conspecifics and were found to defend the caches. This may suggest that the inedible items hold a significant motivatio for the ravens. Clayton and colleagues (1994) found that when provided with stones, Eurasian jays cached them only when there was no food available or all had been eaten or cached. They also tended to cache those stones that resembled the food items, suggesting that they were tuned to the properties of the stones that were similar to the properties of the food (such as colour, size and shape).

We predicted that the stones should retain the same motivational value independent of the social context, and therefore they should either not be re-cached, or re-cached at the same rate across conditions (Observed, In Private and Mirror). The stones were re-cached at the same rate in each of the three conditions. If the hazelnuts had a significant motivational value attached to them (as would be predicted for a preferred food, compared to an inedible stone), and the reflection in the mirror was treated as a conspecific rather than a reflection of the caching scrub-jay, then the jay should have re-cached hazelnuts at the same rate as the Observed condition. If the caching scrub-jay represented the image in the mirror as a reflection of themselves (self-concept) then they should have re-cached hazelnuts at the same rate as the In Private condition. We found that the jays re-cached hazelnuts at the same rate in the Mirror condition as the Observed condition, suggesting that they represented the reflected image in the mirror as a conspecific rather than themselves (similar to other birds and monkeys).

Most intriguingly, we have replicated this experiment using waxworms as the cacheable food, and found that contrary to the previous study, the jays did not re-cache in the Mirror condition (Dally, Clayton & Emery, in prep). This result suggests that after a short-time period (approx. 14 hr), the jays learn that their reflection is not a conspecific. The jays may therefore have either habituated to the mirror or the image in the mirror (i.e. not as a threat) or they may have come to realise in the same way as chimpanzees that the reflection is themselves. We are currently investigating these issues using jays completely naïve of mirrors.

3. Physical Cognition

Complex Memory

At the beginning of this chapter, I stated that corvids were famous for their incredible spatial memory. Recent research has suggested that western scrub-jays are in possession of a more sophisticated form of memory that has only been demonstrated in humans; *episodic memory* (Clayton, this volume; Clayton et al, 2001, 2003). In a series of elegant studies which display the power of using an animal's natural history to guide research questions; Clayton & Dickinson demonstrated that jays remembered what they cached, where they cached it and when they cached it (relatively), and that such information was integrated into a 'what-where-when' memory of a trial-unique caching event (Clayton & Dickinson, 1998). They termed this *episodic-like memory*, because only humans re-experience episodes and place themselves within their memory of the episode, something called autonoetic consciousness (Tulving, 2002). I will not begin to cover these experiments here (please read Clayton's chapter in this volume for a thorough description), however, I would like to make a couple of points in relation to the theme of this chapter. To date, there is no empirical evidence that great apes have episodic or episodic-like memory. Some investigators have suggested that monkeys solving object-place or DNMS memory tasks are displaying episodic-like memory (Gaffan, 1994), however, such tasks can be solved using relative familiarity (Griffiths et al, 1999). Menzel (1999) found that language-trained bonobos could find specific objects when asked, and Schwartz & Evans (2001) stated that a language-trained gorilla could remember who had provided a particular food in a particular place. In both cases, it is not clear whether the apes have integrated the where-what or –who information, and in neither case is the remembrance of –when information tested. Both studies also used language-trained or enculturated apes, which always appear to display more sophisticated cognitive skills than normal apes (Call & Tomasello, 1996).

These findings beg the question, why western scrub-jays, but not apes? Perhaps, episodic-like memory is specifically related to caching, and jays are inflexible in their use of these memories. This is unlikely, as Clayton and colleagues have a) demonstrated the flexibility of these memories within the caching domain, and b) Emery & Clayton (2001) have demonstrated the use of event memories in the social domain, and more importantly use of these memories to guide future behaviour. If episodic memory was specific to caching, it would probably not have evolved in humans! Clayton et al (2001, 2003) have suggested that the social domain may provide a useful starting place to look for similar abilities. Possible examples of episodic-like memory in non-caching animals may include male voles remembering the location of different females and their time of oestrous or chimpanzees remembering who aided them in a fight and in what context. Another possible function is locating food which is only available at specific times; such as squirrel monkeys that can locate a particular tree at exactly the time when the fruit becomes temporarily ripe, or elephants that locate a specific watering hole at times when all others have dried up.

Tool Use

The propensity to manufacture, transport and use tools was previously thought to be the exclusive realm of *Homo sp*. However, in the 1960's, Jane Goodall reported that chimpanzees living at Gombe in Africa, also used tools. Their tools were tree stems that were stripped of their leaves and poked into termite mounds. The termites would grab hold of the stem, the chimpanzee would pull the stem out and eat the termites (van Lawick-Goodall, 1968). The last 30 years has seen examples of tool use in primates (either in the wild or the laboratory) increase to amazing levels (Tomasello and Call, 1997), with different populations of chimpanzees using different tools for different uses, such as using anvil and hammer to crack nuts (Boesch and Boesch, 1983), or chewing leaves into a sponge for collecting liquids (Goodall, 1986).

Some birds have also been described as creating and using tools. Some examples of animal tool-use however, do not fulfil the strict criteria of tool-use demonstrated for non-human primates. Tool-use has been described as "the use of physical objects other than the animal's own body or appendages as a means to extend the physical influence realized by the animal" (Jones and Kamil, 1973; p. 1076). A number of birds manufacture and use tools in similar ways to primates. In the laboratory, Northern blue jays (*Cyanocitta cristata*) were found manipulating the shape of newspaper strips provisioned at the bottom of their cage, and using them to pull in inaccessible food pellets (Jones & Kamil, 1973). The jays did not use the paper tool when pellets were not present, and tended to use the tools more when the length of their food deprivation was greatest. The jays also were able to use a feather, thistle, straw grass, paper clip and plastic bag tie in similar ways when presented with these objects. Finally, the jays also wet the strips of paper, placed the strips in their empty food bowl and used them to collect food dust. Reid (1982) reported that a young rook used a plug to trap water in their aviary (plugging a man-made hole) for use in drinking and bathing on hot days. This has been presented as an example of tool use, but may also provide an example of insight. As the author of study did not look specifically at insight, and the plug and holes were present in the aviary for almost one year before the young rook put the two together, we do not know how much experience it had with the plug and the hole, whether the bird was just lucky the day the author noticed the occurrence or whether the rook actually demonstrated insightful behaviour.

Perhaps the most spectacular use and manufacture of tools is by New Caledonian crows (*Corvus moneduloides*). Hunt (1996) described how he observed 4 crows manufacture two types of tools and 68 crows carry or use tools in three forests in New Caledonia. The tools were used for catching prey (insects) either in trees or under detritus leaves. Hunt collected all the examples of tools that were made by the crows (although some carried useful tools on foraging expeditions and secured them when resting). The tools could be categorized into two types; hooked-twig and stepped-cut tools. The hooked-twig tools were made from living secondary twigs that were stripped of their leaves and bark, and had a hook at their wider end. The stepped-cut tools, by contrast were fashioned from *Pandanus* leaves by tapering the ends into points. Different techniques were employed in using the tools depending on the location of the prey. If the prey was located under detritus, the tool was used with rapid back and forth movements, whereas if the prey was located at the base of holes and leaves, slow deliberate movements were used. Hunt and colleagues (Hunt, 2000; Hunt et al, 2001) have recently shown that tool manufacture in New Caledonian crows is lateralized at the individual and population-level, i.e. most tool users tend to use the left-hand edge of the leaf to create the tool.

New Caledonian crows have also recently been studied in the laboratory and they appear able to choose the correct tool (a twig of certain length) from a 'tool box' (collection of differently lengthened twigs) that is appropriate for a specific task, such as reaching food placed in the middle of a transparent tube (Chappell & Kacelnik, 2002). Most intriguingly, a New Caledonian crow has demonstrated the ability to modify an unnatural material, bending a straight piece of metal wire to form a hook at one end that was subsequently used to pull up a cup containing food (Weir et al, 2002). This has not been seen in any other animal to date, including the great apes (Povinelli, 2000).

4. How Could Corvid Cognition Be Like Ape Cognition?

Corvids are perhaps the most successful family of birds, and are found in almost every ecological niche. There are 120 species of corvid that are distributed over every non-polar continent (i.e. not including the Antarctic), from Greenland and Northern Canada and Alaska, through Europe, North and Central America and Asia, to South America, Africa, New Guinea and Australia (Madge & Burn, 1994). This contrasts with the parrots which have a more conservative geographical distribution, located primarily in temperate jungle and forested areas, such as Central and South America, Southern Asia, New Guinea, Australia and New Zealand. This may be due to human influence (trapping the colourful birds for export and cutting down forests) and the rather specialized diet of parrots (fruit).

Birds and mammals share a relatively recent evolution, with modern birds and mammals both appearing around 65 mya. It has been suggested that a single ancient avian species (Archeoptyrx) survived a mass extinction event which destroyed the dinosaurs, and that all modern bird species evolved from this one survivor (Wyles et al, 1983). Within the birds, the passeriforms (perching songbirds) display the most recent evolution, appearing around 37.5 mya (the first appearance in the fossil record). Interestingly, anthropoid primates appeared around 40 mya; with the common ancestor to the modern great apes appearing in the fossil record around 16 mya (with the chimpanzees diverging from humans at 6mya; Byrne, 1995).

Although the timing of the phylogenetic tree for the corvidae is controversial, there are suggestions that the oldest corvid fossils in Europe date between 20-25 mya (Goodwin, 1986). However, the origin of the corvids has been traced to Central Asia in the Western Malaysian region (Hope, 1995). The Eurasian and North American jays appear to have become specialized in the eating of nuts and acorns, living in forested environments similar to the primitive corvids, and are therefore probably more closely related to these early species. By comparison, the magpies and crow-like birds have tended to move away from the forests into more open environments, therefore becoming less dependent on seeds for food (crows and magpies tend to be omnivorous), and so less constrained by their habitat, becoming more mobile (spreading across most regions of the world). This suggests that the magpies and crows are the most recently evolved of the corvids, and this in turn may account for their remarkable cognitive abilities compared to other birds. In general, mammals and birds demonstrate comparable rates of anatomical evolution (Wyles et al, 1983), therefore I suggest that corvids and apes may also demonstrate comparable rates of cognitive evolution.

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