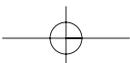
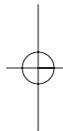
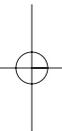
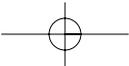
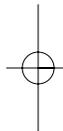
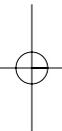
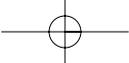


PART ONE

# Complex Cognition





## CHAPTER ONE

# Comparing the Complex Cognition of Birds and Primates

*Nathan J. Emery and  
Nicola S. Clayton*

## INTRODUCTION

At first glance, birds and non-human primates (hereafter primates) seem very different. Birds have beaks, feathers, produce offspring that gestate in shells, and can fly. Primates are covered in hair, have forward facing eyes and grasping hands, and while some are arboreal, none of them can fly. Although there are vast morphological differences between the two groups, there is growing evidence of strong similarities in their mental abilities, particularly in the realm of advanced cognitive processing. This suggestion is initially surprising considering the vast difference between the size and structure of avian and primate brains. Even more surprising is the fact that a number of recent experiments have failed to demonstrate some complex cognitive abilities in primates (including chimpanzees, gorillas, and orangutans) that have been convincingly

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demonstrated in some species of birds, such as the corvids (jays, crows, ravens, and magpies) and parrots.

In this chapter, we will review evidence that some species of birds (focussing primarily on the corvids and parrots), with their much smaller brains and relative absence of cortical structures, have been shown to possess abilities that have either not been tested in primates or that primates have not displayed. This is unlikely to be due to a direct deficit in the mental cognition of the great apes per se (certainly primates' evolutionary relatedness to humans would dispute this idea), but to a lack of ethologically based tasks for testing primate cognition. Of course, some primate studies have begun to incorporate a high degree of ethological validity (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 shown a number of feats that the less naturalistic paradigms have not. Nonetheless, we throw down the gauntlet to primate researchers to design experiments with the same ecological validity as in experiments on corvids and parrots. Although avian and primate brains differ significantly in size and structure, similar principles of organisation are evident. We suggest that birds and primates reflect a case of divergent evolution in relation to neuroanatomy, but convergent evolution in relation to mental processes.

### **WHY PRIMATES MIGHT BE SUPERIOR TO NON-PRIMATES?**

As the sub-title of this book is "Are Primates Superior to Non-Primates?" we begin this chapter by presenting seven claims as to why this question may warrant asking in the first place (but we admit that there are likely to be more). All the reasons are based on a largely anthropocentric view, namely that primates have been suggested to form a special group of animals because they demonstrate cognitive abilities that are similar to our own. The seven claims for the special status of primates are:

1. Primates have a neocortex larger than predicted for their body size.
2. Primates have an expanded prefrontal cortex.
3. Primates demonstrate social learning and imitation.
4. Primates understand others' mental states.
5. Primates display insight, innovation, and they construct and use tools.

6. Primates utilize symbolic and referential communication.
7. Primates demonstrate elements of “mental time travel” (i.e., episodic memory and future planning).

The next section will discuss these claims in detail, and for each case provide counter evidence that some avian species demonstrate some, or all, of the above traits. In some domains, namely social cognition and mental time travel, the evidence presented for birds is surprisingly more convincing than that shown for non-human primates. At the end of the chapter, we will evaluate why we think this intuitive discrepancy may have occurred, through a discussion of the perils of primatocentrism, the still prevailing influence of the concept of “scala naturae” in comparative psychology, and the use and abuse of the ethological approach to animal cognition. We close the chapter with a discussion of why corvids and parrots may present a case for convergent mental evolution when compared to primates, but also provide evidence for a complex psychological trait that has so far only been demonstrated in chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and bottle-nosed dolphins (*Tursiops truncatus*), but not in birds.

## COMPARING BIRDS AND PRIMATES

### Primates have a Neocortex Larger than Predicted for their Body Size

The great apes, including humans, have brains larger than would be predicted for their body size. Jerison (1971) called this the encephalization quotient ( $K$ ). 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 that of 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 (Deacon, 1990)). Specifically, a larger body may reflect possession of a larger gut that would require no additional computational power (Byrne, 1995). Therefore, a better indication of the influence of the body on brain size may be 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.

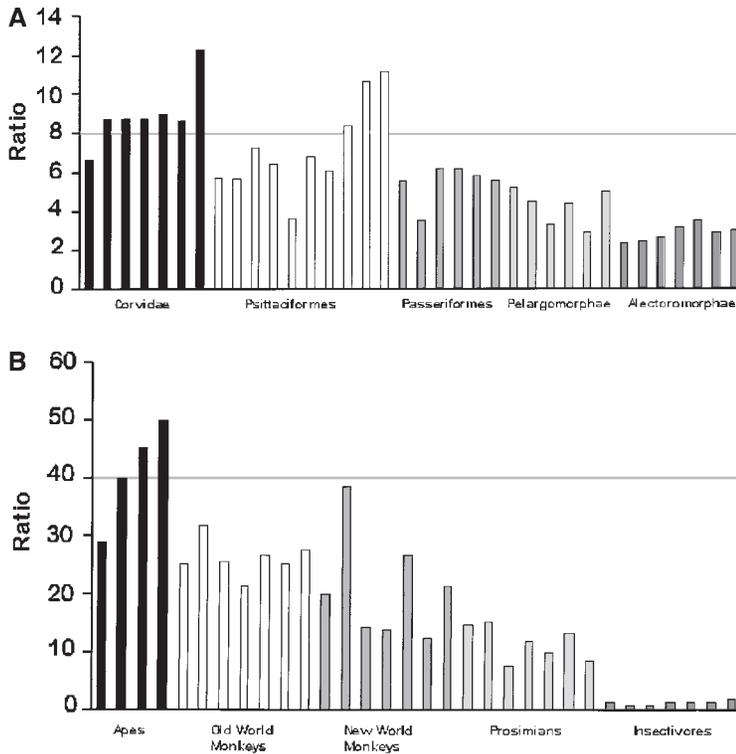
Overall brain size has also been criticized as a poor measure of cognitive capacity (Byrne, 1996; Deacon, 1990). Many brain areas that control primary sensory and motor functions are not associated with “intelligence” or cognition. Other subcortical structures, such as the amygdala, hypothalamus, and hippocampus function in the control of species-specific behaviors, such as aggression, sex, and parenting (Panksepp, 1998) and behaviors dependent on spatial memory, such as homing, brood parasitism, migration, and food-caching (Clayton, 1998).

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 a number of primate species is limited to the neocortex as a whole (Stephan et al., 1981). Birds do not have a neocortex, but certain areas of the forebrain have been suggested to represent functionally equivalent (analogous) structures to the mammalian neocortex (see next section), ones that may correlate with measures of higher cognition, such as feeding innovation (Lefebvre et al., 1997; Nicolakakis and Lefebvre, 2000; Timmermans et al., 2000) and tool use (Lefebvre et al., 2002).

A comparative analysis was performed to investigate whether the neocortex of primates represents a special case for dramatic expansion, or whether a similar pattern is seen in the forebrain of some bird species. The only comprehensive set of avian neuroanatomical data available (Portmann, 1946, 1947) presents forebrain and brainstem weights for 140 avian species (including 42 Passeriforme species, 29 Coraciomorphae species, 28 Pelargomorphae species, and 41 Alectoromorphae species). Portmann's data was 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 was therefore calculated for each species that was independent of phylogenetic anomalies. For the primates (19 Prosimian species and 26 Simian species, excluding *Homo sapiens*) and insectivores (18 species; basal mammals), a neocortex:brainstem ratio was calculated using volumetric data from Stephan et al. (1981).

Interestingly, when the forebrain:brainstem ratio of corvids (Corvidae) and parrots (Psittaciformes) is compared to other avian species (Figure 1A),

the pattern of difference closely resembles the difference of neocortex: brainstem ratio between the great apes and other primates and insectivores (Figure 1B).



**Figure 1.** (A.) Forebrain:brainstem ratios in some representative species of different groups of birds; Corvidae (corvids), Psittaciformes (parrots), Passeriformes (perching songbirds, not including corvids), Pelargomorphae (inc. birds of prey), Alectoromorphae (chickens, pigeons and doves). Original data from Portmann (1947), in which forebrain was represented as Hemisphere index, and brainstem as Brainstem index. The indices were transformed to raw data by multiplying values with a basal number (an individual value calculated from the predicted value of the brainstem of another species from the same taxonomic group of comparable body size, but less developed). (B.) Neocortex size: brainstem size ratios in representative species of different groups of primates (Apes, not including humans, Old World monkeys, New World monkeys and prosimians) and insectivores. Original data from Stephan et al. (1981) and Zilles and Rehkamper (1988).

### Primates have an Expanded Prefrontal Cortex

Although birds do not have a six-layered neocortex, Karten (1969, 1991) has suggested that the nuclear arrangement in the avian dorsal ventricular ridge (DVR) processes stimuli in similar ways to the mammalian neocortex. All mammals have a neocortex; however, an expanded prefrontal cortex has been suggested to be special to the primates and the seat of their advanced cognitive abilities. The avian equivalent of the primate prefrontal cortex may be either the hyperstriatum ventrale (HV) or the neostriatum caudolaterale (NC). Evidence for this has been derived from lesion studies on comparable tasks to those used to test mammalian prefrontal cortex function, such as delayed alternation, reversal learning, and go/no go tasks (Güntürkün, 1997; Hartmann and Güntürkün, 1998). Güntürkün and colleagues lesioned only the NC, however, and the tasks used were those traditionally used to examine dorso-lateral prefrontal cortex function in mammals, so-called executive functions (Stuss and Alexander, 2000). Although the comparable studies have yet to be performed, the avian HV may represent a functional equivalent to other prefrontal cortical areas, such as the orbitofrontal cortex. Lesions to these avian brain areas cause deficits in filial imprinting or selective attachment to the mother (Horn, 1985), and lesions of the orbitofrontal cortex in primates cause dramatic disturbances in social attachment and affiliative behavior (Raleigh and Steklis, 1981).

Additional evidence for the functional equivalence of the avian neostriatum and mammalian prefrontal cortex comes from studies of the distribution of dopamine in the avian telencephalon (Durstewitz et al., 1999), which is also widely distributed in the mammalian prefrontal cortex (Goldman-Rakic et al., 1992).

If these areas do constitute equivalent structures to the primate prefrontal cortex, and we hypothesize that corvids and parrots have cognitive abilities compatible to primates, then we may expect that these areas are larger in the corvids and parrots compared to other birds (a more precise localization to areas of the forebrain in those species demonstrated in the previous section). We therefore compared the volumes of four regions of the forebrain (the hyperstriatum accessorium [HA], hyperstriatum dorsale [HD], HV, and neostriatum) of six available avian species (*Coturnix coturnix*, *Perdix perdix*, *Phasianus colchicus*, *Passer domesticus*, *Garrulus glandarius*, and *Corvus corone* (Rehkamper et al., 1991)) and calculated ratios of these brain regions to brainstem (as previously), and as a percentage of telencephalon. Percentage of

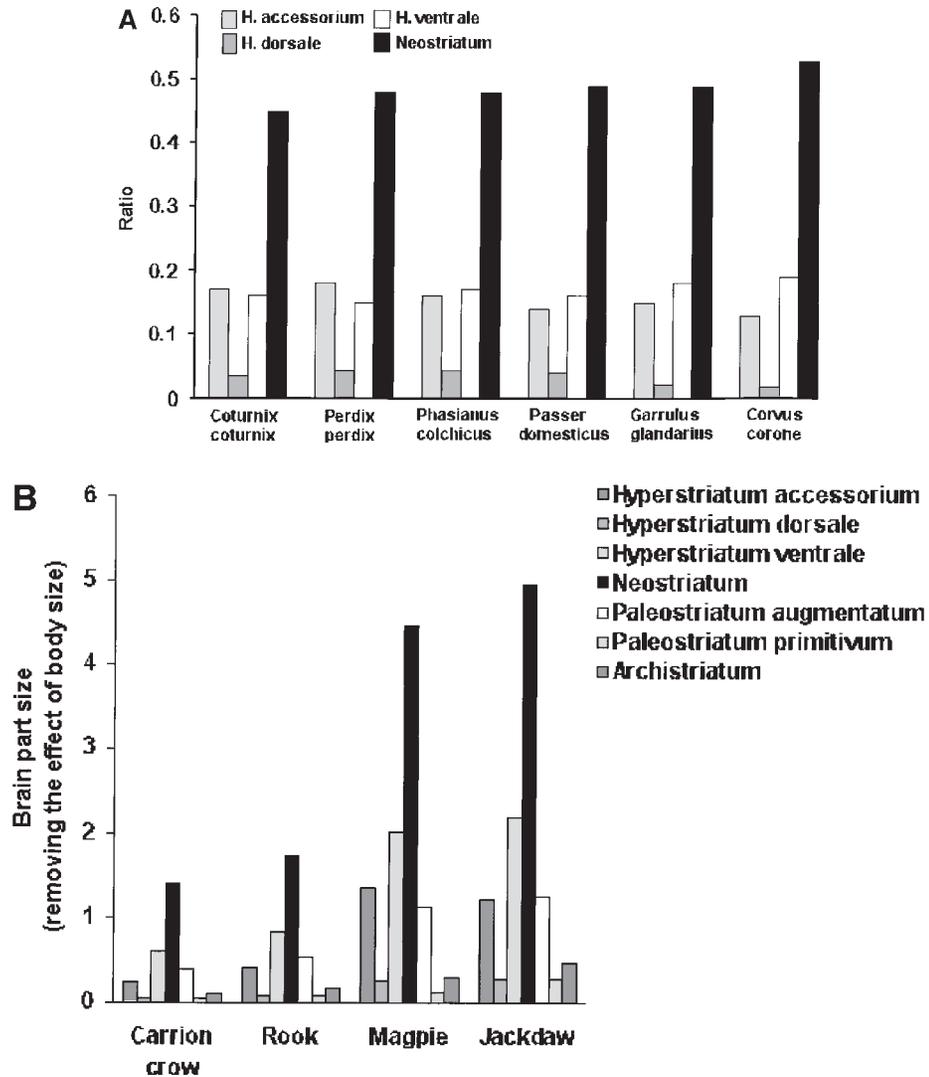
telencephalon did not differ between these species for all the examined brain structures, thereby suggesting that overall body size was an irrelevant factor. Brain area:brainstem ratio, however, revealed that the neostriatum is larger than predicted in the carrion crow (compared to the other birds; Figure 2A).

An additional data set comparing different forebrain regions (HA, HD, HV, neostriatum, paleostriatum augmentatum, paleostriatum primitivum, and archistriatum) in four corvids (Carrion crow, *Corvus corone*; magpie, *Pica pica*; rook, *Corvus frugilegus*; and jackdaw, *Corvus monedula*) confirmed that the neostriatum displays the greatest expansion within the corvid forebrain (Voronov et al., 1994; see Figure 2B), however, a somewhat surprising result is the greater neostriatal expansion in the magpie and jackdaw brain (relative to body size as brainstem size within the same birds was unavailable for these species). These patterns mirror that for the prefrontal cortex of the great apes, which are approximately the same relative size in chimpanzees, orangutans, gorillas (*Gorilla gorilla*), and humans, but larger than in gibbons (*Hylobytes lar*) and macaques (*Macaca* sp.; Semendeferi et al., 2002).

### Primates Demonstrate Social Learning and Imitation

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 us to describe the different forms of social learning in much detail, but the significant categories include stimulus and local enhancement, contagion, social facilitation, observational conditioning, copying, goal emulation, and imitation (see reviews in Tomasello and Call, 1997; Whiten and Ham, 1992; 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 (see next section). 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.



**Figure 2.** (A.) Ratios of subdivisions of the avian forebrain (Hyperstriatum accessorium, H. dorsale, H. ventrale, and Neostriatum) to the brainstem in representative species of Galliformes; *Coturnix coturnix*, *Perdix perdix*, and *Phasianus colchicus* and Passeriformes; *Passer domesticus*, *Garrulus glandarius* and *Corvus corone*. Data from Rehkamper et al. (1991). (B.) Ratios of subdivisions of the avian forebrain (H. accessorium, H. dorsale, H. ventrale, neostriatum, Paleostriatum augmentatum, P. primitivum and Archistriatum) in representative species of Corvidae; *Corvus corone* (carrion crow) *Corvus frugilegus* (rook), *Pica pica* (magpie) and *Corvus monedula* (jackdaw) to body size (brainstem values were unavailable). Original neural data from Voronov et al. (1994), and body sizes from Madge and Burn (1999).

This behavior has been studied in closely-related species of New World corvids (jays and nutcrackers). Bednekoff and Balda (1996a, 1996b) 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 storsers 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 et al. (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 (see following arguments), 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 (*Aphelocoma californica*) 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 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., 2001b),

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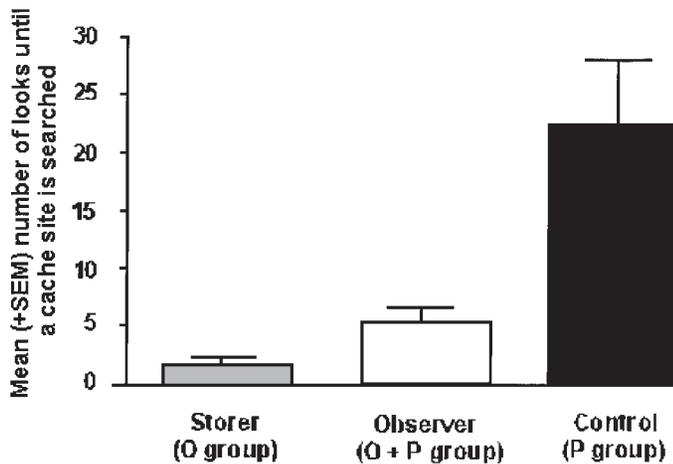
examined three groups of western scrub-jays; Storers, Observers, and Controls (a group that could hear another bird caching in an adjacent cage, but not see it). (The act of caching can be heard as a series of bill taps when the bird buries the food in the sand. This can be easily heard by other individuals in the vicinity, including the experimenter.) The birds were given a 3-hr retention interval to enhance the possible retrieval accuracy, and to mimic natural behavior; caches are very unlikely to remain after 1–7 days. This retention is considerably shorter than in the Bednekoff and Balda (1996a, 1996b) experiments.

Each group was compared with the other two groups. Observers made significantly fewer looks than Controls before searching 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 cached compared to Observers. The Storers also made significantly fewer looks to search for the food than Controls (Figure 3).

Imitation is said to represent a form of social learning that may require complex representations, not only of another's perspective, but also their intentions, and how they relate to the individual observing the actions (see reviews in Heyes and Galef, 1996; Whiten and Ham, 1992). True imitation has been defined as "the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency" (Thorpe, 1963, p. 135) and as such the copied actions/vocalizations should not already be within the animal's natural repertoire (Clayton, 1978).

In birds, two forms of imitative learning have been investigated, vocal mimicry and motor imitation. Male songbirds not only copy the song of their fathers (Catchpole and Slater, 1995), but some species, such as mynah birds (*Gracula religiosa*) and parrots (Psittaciformes) can imitate the vocalizations of other birds, human speech, and general noises (such as doors closing, and walking; Baylis, 1982). As there is little evidence for vocal imitation in non-human primates, the case of motor imitation may be more appropriate for comparison between birds and primates. To date, only one study on an African gray parrot (*Psittacus erythacus*) has examined the ability to imitate novel motor patterns (Moore, 1992), with each action associated with a verbal label.

The two-action method of motor imitation has been proposed as the most appropriate method for examining imitative behavior in animals (Heyes, 1996). The technique was initially used to test whether budgerigar observers learned to remove a red cardboard square from a white pot demonstrated by a conspecific, either using the beak or the foot (Dawson and Foss, 1965). Similar experiments



**Figure 3.** Mean (+SEM) number of looks made until a cache site is searched in three groups of western scrub-jays performing an observational spatial memory test. The Storer group (O group) made the caches, the Observer (O + P group) watched the Storer make the caches, and were then allowed to pilfer those caches, and the Control group (P group) were located in an adjacent cage, and so could hear the Storer caching, but could not see them being made. Unpublished data by Griffiths, Duarte and Clayton.

where two demonstrated actions can achieve a goal have been performed in rats (*Rattus norvegicus*; Heyes and Dawson, 1990), starlings (*Sturnus vulgaris*; Campbell et al., 1999), Japanese quail (*Coturnix japonica*; Atkins and Zentall, 1996), and marmosets (*Callithrix jacchus*; Bugynar and Huber, 1997). An example of the two-action method in corvids was provided in ravens (*Corvus corax*); two groups of dyads, either controls or observer-demonstrator pairs, were presented with boxes that could be opened by levering the lids (Fritz and Kotrschal, 1999). 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).

Perhaps, the most convincing demonstration of true imitation in non-human primates using a form of the two-action method has been the use of an “artificial fruit,” a clear Perspex box that contained food, and that could be opened using two-actions (poke a bolt or turn a pin), and with the actions performed

in a particular sequence (turn then poke). A non-functional action (twist) was also included in demonstrations to determine whether the observer would copy an action that did not lead to the goal. The artificial fruit has provided evidence for imitation in a number of non-human primates (chimpanzees, Whiten, 1998; Whiten et al., 1996; gorillas, Stoinski et al., 2001; capuchin monkeys *Cebus apella*, Custance et al., 1999).

Birds have also been demonstrated to process complex covered foods (such as shells and tough skins; Gibson, 1986). Huber et al. (2001) examined the ability of keas (*Nestor notabilis*), a New Zealand parrot, to imitate the actions of a demonstrator to gain food in an "artificial fruit". Entry to the fruit required the performance of three successive manipulations of three locking devices (a screw, split pin, and a bolt). Unlike the primate studies, conspecific demonstrators were trained to perform the appropriate actions used to gain entry to the fruit. One group of observers saw the demonstrators opening the fruit, whereas an additional control group was presented with the fruit without any experience of observing a demonstrator. The observers spent a longer time exploring the fruit, and the latency to first contact of the box was shorter in the observers. The observers also appeared to understand the goal of the task as they displayed greater perseverance in manipulating the locking devices on the fruit. Unfortunately, no bird succeeded in opening the fruit, but they displayed differences in success in opening the individual locking devices. All the observers ( $n=5$ ) succeeded in opening one device, and 2 out of 5 observers opened all devices. The observers also did not differ from the controls in matching the particular demonstrated actions with the actions they performed themselves. This suggests that the keas were drawn to the fruit by localized stimulus enhancement, but they also appeared to learn about the goal and some of the actions required to gain access to the goal.

### Primates Understand Others' Mental States

The term "theory of mind" (ToM) first appeared in a paper by Premack and Woodruff (1978) called *Do chimpanzees have a theory of mind?* In this paper, they described a study examining whether a language-trained chimpanzee, Sarah, could appreciate the correct solution to a problem presented to a human demonstrator. Sarah was presented with a video sequence of either an actor locked in a cage, shivering next to an unlighted heater, unable to

clean a dirty floor, and unable to listen to music on an unplugged stereo. After each sequence, she was then presented with a number of alternative answers (as photographs), such as a key, a lighted paper wick, a connected hose, and a plugged in cord and she had to match the correct image with the appropriate video. A significant performance was interpreted by Premack and Woodruff (1978) as evidence for an understanding of the actor's intentions ("he wanted to get out of the cage," "he intended to listen to music", etc.). Although this interpretation has been criticized as demonstrating an understanding of the relationship between previously associated objects (i.e., lock and key) that the chimpanzee would have encountered during her life in captivity (Savage-Rumbaugh et al., 1978), it cannot explain all the abilities displayed by this particular chimpanzee (Premack and Premack, 1983). For the last 26 years, the question has remained open and has been tested in many species of primates (for a recent review see Tomasello and Call, 1997), but there has yet been a persuasive demonstration of ToM in a non-human primate (Heyes, 1998). The precursors to ToM, such as gaze following have also begun to be tested in non-primate mammals, such as dolphins (Tschudin et al., 2001), goats (*Capra hircus*; Kaminski, 2002), dogs (*Canis familiaris*; Hare and Tomasello, 1999; Call, this volume), and horses (*Equus caballus*; McKinley and Sambrook, 2000). Birds have not been tested for gaze following as although birds are visually based animals, their visual system is very different from mammals, with a larger peripheral field of vision. It would therefore be extremely difficult, if not impossible to measure where a bird may be looking (however, see Dawkins, 2002). Hampton (1994), however, examined the propensity for sparrows (*Passer domesticus*) to intensify fear behavior when a human experimenter stared at them with two eyes, compared to one eye or turned backwards. This suggests at least a rudimentary appreciation of eye configuration representing forward attention (Emery, 2000).

ToM has also been investigated in pigs (*Sus scrofa*; Held et al., 2001) and dolphins (Tschudin, 2001), but conclusive answers to whether non-human mammals have a ToM remain wanting. This situation may be due to a prominent primatocentric view of complex cognition (discussed further), and the fact that the initial species chosen by Premack and Woodruff was a language-trained, enculturated chimpanzee.

Although birds display many of the forms of social organization seen in primates, ornithologists have tended to neglect research on complex social

cognition in birds (Marler, 1997). There are a few studies, however, that do suggest that corvids and parrots, at least, have some of the hallmarks of ToM. Pepperberg and McLaughlin (1996), for example, discussed the important role of a precursor to ToM; shared attention, in the acquisition of language in African gray parrots, but they have yet to test whether parrots can understand another's mental states.

Tactical deception, or the intentional manipulation of another's beliefs leading to deception, has been proposed as another important indication of ToM (Whiten and Byrne, 1988). Very little experimental work has been performed on this cognitive capacity, with the predominant source being data compiled from a large number of anecdotes produced by primatologists (Whiten and 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 and Call, 1997).

Ristau (1991) has argued that the broken-wing display in piping plovers (*Charadrius melodus*), and Wilson's plovers (*Charadrius Wilsonia*) on sand dunes in the eastern United States may provide some evidence of tactical deception in birds. The plovers utilize a so-called broken-wing display (BWD), where a plover feigns injury through a suite of behaviors that are concordant with injury, such as fanning of the tail, an increase in awkwardness of walking, arching of both wings, fluttering and dragging of the wings, and loud raucous squawks. It is argued that this collection of behaviors appears to cause a pretence that the bird is injured, and thus a potential predator follows the plover (as injured birds are easy prey) away from the plover's nest. Once the predator has been drawn hundreds of meters away from the nest, the plover flies away uninjured. Ristau argued that the plovers were intentionally deceiving predators (in this case humans) because in 98 percent of cases, the plovers moved in a direction away from the nest, never close to the nest, and in 98 percent of cases the plovers produced the BWD in front of the predator. In all cases, the plovers moved to an appropriate position before displaying, therefore suggesting that the display is not a reflex. Finally, the plovers appear to have monitored the predator's behavior by looking over their shoulder back towards them, and the plovers also modified their displays in response to the changing behavior of the predators. In 55 percent of cases, when the predator did not follow the plover, they stopped their display and re-approached the predator. In 29 percent of cases, the plovers increased the intensity of their display if the predators did not follow the plover.

The plovers' behavior has been interpreted using a number of alternative non-intentional explanations. Some have argued that the plovers perform a reflexive or a fixed action pattern response, but this seems unlikely given the plasticity of the plovers response that changes depending on the actions of the predator. What is not known is the role of learning in the development of such displays, in the absence of any information about the previous reinforcement history of these birds. And there is no evidence that plovers transfer this ability to other situations, such as social interactions with conspecifics, where tactical deception is more traditionally employed and more likely to be dependent on mental attribution. Ristau's behavioral studies were limited in scope, restricted to a single geographical population of plovers, and based only on a few trials (but this is likely to have been controlled for habituation effects).

Such field studies provide us with important insights into the behavior of animals in their natural environment, but tightly controlled experiments in the laboratory on a wide variety of species (not just the traditional subjects of comparative psychology experiments; rats, pigeons, and rhesus monkeys) are essential, especially when examining the question of complex cognitive abilities, and the presence of mental states in other individuals.

Recent laboratory studies of mental attribution have been conducted on some species of corvids. As discussed earlier, 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 therefore presents an example where understanding the intentional behavior of conspecifics might be a useful attribute to possess.

Ravens, for example, are very cautious when hiding their caches when in a flock. This behavior has been studied in detail by Heinrich and colleagues (Heinrich, 1999; Heinrich and Pepper, 1998), and more recently by Bugnyar and Kotrschal (2002). It has been shown that storsers 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.

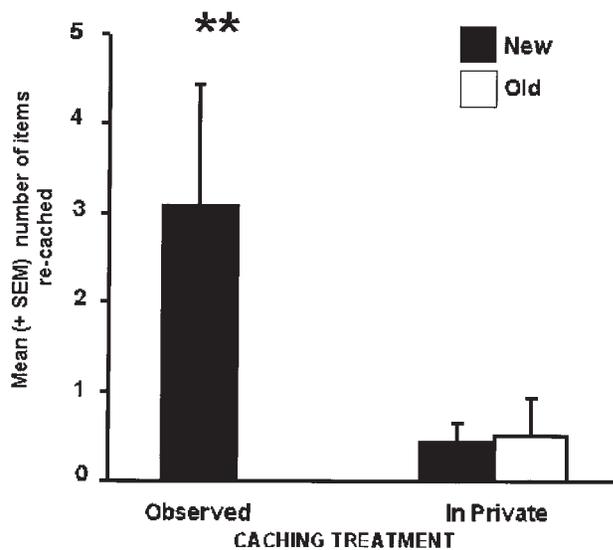
Bugnyar and Kotrschal (2002) have suggested that caching and raiding ravens may present an example of tactical deception through an attempt to manipulate another's attention, either to prevent opponents from gaining opportunities for stealing (see earlier section on social learning), or to gain

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 percent 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 percent of cases, the observers changed their position relative to the structures that blocked their view of the cache sites and in 32 percent 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 behaviors suggest that caching and raiding ravens appreciate the visual perspective of one another, and produce strategies to counter the behavior of the other.

As with ravens and other corvids, western scrub-jays pilfer each other's food when presented with the opportunity, and pilferers have excellent recall of the location of another's caches seen being made during an earlier occasion (Griffiths, Duarte, and Clayton, unpublished observations). One of us (NSC) routinely observed western scrub-jays on the campus of the University of California at Davis, USA, compete over scraps of food left by humans. 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.

With this in mind, we examined whether this re-caching behavior would be observed in a laboratory colony of hand-raised western scrub-jays (Emery and Clayton, 2001). We initially gave a group of seven 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<sup>®</sup> 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 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, and almost all these re-caches were made in new sites unknown to the observer (Figure 4).

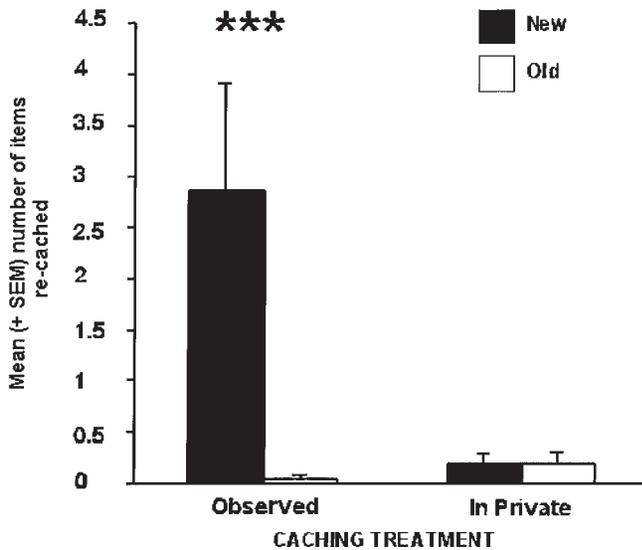


**Figure 4.** Mean (+SEM) proportion of caches that were re-cached in new or old sites, either when previously observed caching or when they had previously cached in private 3 hr earlier by O + P group birds in Davis, USA.  $**p < 0.01$ . Re-caching data presented in Emery and Clayton (2001) was mean (+SEM) number of re-caches. Same statistical results when proportions were analyzed.

One interpretation of these results is that the storers predict the observer's intentions (i.e., to pilfer caches when given the opportunity), and use counter strategies to prevent this, by re-caching the worms in new sites. But being observed recently during caching could lead to an automatic tendency to re-cache when presented with the opportunity to do so at a later time, irrespective of whether the bird remembers anything specific about the caching event such as who was watching and where it had cached. An alternative explanation is that the bird remembers whether or not it had been watched during caching in a specific tray. We discriminated between these two possibilities by testing whether these jays could keep track of the social context of previous caching episodes that occurred in close temporal proximity.

We, therefore, tested this by presenting the same storers 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 in new sites, specifically from the observed tray (Figure 5). This result shows that the birds remembered the specific social context during caching and did not automatically re-cache items if observed recently.

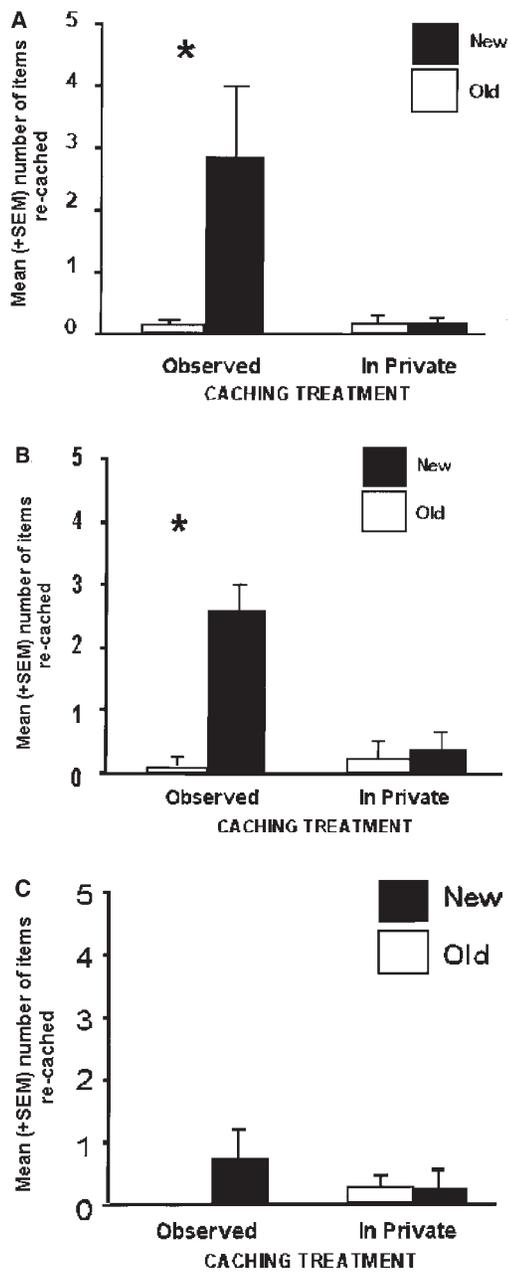
The jays described in the two previous experiments had had prior experience of watching another bird cache and were then given the opportunity to steal those caches (see earlier section on social learning and experiment by Griffiths et al., 1999). This Observer + Pilferer (O + P) group were almost as 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 (Figure 6A). Surprisingly, the P group also displayed significant levels of re-caching, especially in new sites (Figure 6B). The O group, by contrast, with no pilfering experience, did not demonstrate any re-caching, and the little



**Figure 5.** Mean (+ SEM) proportion 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, by O + P group birds in Cambridge, UK. \*\*\* $p < 0.001$ . Re-caching data presented in Emery and Clayton (2001) was mean (+ SEM) number of re-caches. Same statistical results when proportions were analyzed.

re-caching they did was equally distributed in new and old sites (Figure 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. These experiments suggest the presence of a sophisticated level of social cognition in western scrub-jays, and one that depends on prior experience as a pilferer, but is it ToM? The storage and pilfering of food presents a case in which individuals have to play two different and competing roles; storer and pilferer, roles which require different behavioral strategies. So, in corvids, elements of ToM may be a byproduct of the



**Figure 6.** (A.) Mean (+SEM) proportion of caches that were re-cached in new or old sites when either observed during caching or when cached in private, by (A) O + P group birds. (B) P group birds and (C) O group birds in Cambridge, UK. \*  $p < 0.05$ . Re-caching data presented in Emery and Clayton (2001) was mean (+SEM) number of re-caches. Same statistical results when proportions were analyzed.

arms race of strategies and counter-strategies in relation to the hiding and stealing of food (such as experience projection and perspective taking). Presumably other species in which individuals play competing roles in forms of behavior, be it storer and pilferer, or dominant and subordinate, may also possess rudimentary forms of ToM.

### **Primates Display Insight, Innovation, and they Construct and Use Tools**

*Insight and Innovation:* Insight has been defined as “the sudden production of a new adaptive response not arrived at by trial behavior or as the solution of a problem by the sudden adaptive reorganization of experience” (Thorpe, 1963, p. 110). The classic studies on animal insight were performed during World War I on chimpanzees by Wolfgang Köhler on the island of Tenerife (described in detail in Köhler, 1925). These studies have been described and discussed many times previously, but briefly, chimpanzees were presented with many different problems (usually associated with the procurement of inaccessible foods) and a number of potential objects to solve those problems. A famous example was a banana hanging out of reach from a string and a collection of boxes located underneath. The chimpanzees were described as attempting to reach the bananas first by standing on one box, then attempting to balance one box on top of another, and finally the chimpanzee placed one box on top of the other climbed up and hit the banana with a stick, thereby knocking the banana from its string and allowing it to fall to the ground to be retrieved. What remains to be determined is how long the chimpanzees took to produce this “insight,” and whether they had previous experience with the boxes. In essence, the question is whether they could have learned through a series of instrumental responses, and thus what this “insight” actually represents. Indeed, it has been suggested that the chimpanzees could not have demonstrated insight in its classical terms because the solution to the problem would have been achieved by previous experience with sticks and boxes (Birch, 1945) and was not solved immediately after the problem was presented (i.e., arose as a consequence of many trial-and-error responses; Povinelli, 2000).

Is there any evidence of insight in birds, and if so, can supposed cases of “insight” be explained more simply in terms of associative learning or is there any evidence of something more complex? Although this problem has hardly been studied in many non-primates, there is some evidence that corvids

(ravens and rooks) display some form of insight, at least similar to that displayed by primates.

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 the study did not look specifically at insight, and the plug and holes were present in the aviary for almost 1 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 behavior.

A more controlled series of experiments in ravens may present a clearer indication of insight in corvids. Heinrich (1996, 2000) provided hand-raised ravens with a novel opportunity to gain food, by attaching pieces of meat to string suspended from a branch. This constrained the ravens in their method of food acquisition, as they would be unable to hover under the food like hummingbirds. The ravens would have to use their grasping feet (present in all corvids and parrots) to pull the string up, and trap each piece of pulled-up string with their feet. This would have to occur at least five times before the bird could grab the meat in its bill. At first, birds attempted to grab at the food from underneath, or pecked at the string on the branch. Three birds, at their first attempt, pulled up the string and grabbed the meat (before being shooed off). The ravens did not attempt to fly off with the food when shooed off (i.e., had some concept that the meat was attached to the string). When presented with two strings; one attached to the meat and a second to a similar sized rock, the ravens tended to pull on the string attached to the meat (or immediately moved onto the correct string if they attempted to pull up the string with the rock attached). If the strings were crossed, most of the birds chose randomly, but eventually one bird pulled more strings attached to food than rocks. When the birds were presented with a novel string (dark green shoelaces rather than twine string), the birds almost exclusively pulled on the laces attached to food. This suggests that the birds have not just formed an association between a particular string and food, but have generalized to all string-like substrates with food. Finally, the ravens were presented with two strings, one attached to a small piece of meat, the other to a large sheep's head (that they would be unable to pull up). In all cases, the birds avoided pulling

up the sheep's head (not due to fear of the head), and always pulled up the smaller piece of meat.

This series of experiments suggest that this group of hand-raised ravens do demonstrate some form of insight, given that the solution was largely achieved at the first attempt. Random chance may also be discounted as an explanation, because the probability of producing the five or six actions leading to a series of 30+ complex steps would be too high for actions performed on the first trial. These arguments cannot be said to be the case for Köhler's studies with chimpanzees described earlier (Köhler, 1925).

**Manufacture and Use of Tools** The propensity to manufacture, transport, and use tools was previously thought to be the exclusive realm of *Homo* sp. However, in the 1960s, 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 have 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). These variations in tool-use have been proposed as a potential cultural phenomenon (Whiten et al., 1999).

Some birds have also been described as creating and using tools (see chapter by Kaplan, this volume). Some examples of animal tool-use however, do not fulfill 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). Vultures (*Neophron percnopterus*), for example, crack open eggs by dropping them onto rocks (van Lawick-Goodall and Lawick, 1966). This is not a demonstration of tool-use as the rock is not an extension of the vulture's body. However, vultures that throw stones at ostrich eggs are demonstrating tool-use (Thouless et al., 1987). Similarly, thrushes that open snail shells by smashing them onto stones (Gibson, 1986), or crows in Japan and California that open hard shelled walnuts by dropping them from great heights onto hard-surfaced roads (Cristol and Switzer, 1999; Nikei, 1995) are not demonstrating tool-use.

These may be innate responses, and they may not require the mental manipulations required to transform an object with one distinct function into different functions.

A number of birds do 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 and 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. Similar behavior was observed by Clayton and Joliffe (1996) in another food-storing species, the marsh tit (*Parus palustris*).

Tool-use and manufacture has also been demonstrated in wild birds. A species of Galapagos finch; the woodpecker finch (*Camarhynchus pallidus*) was reported to use a stick to probe for insects in the holes of trees (Millikan and Bowman, 1967). The finches would break off a twig, leaf stem, or cactus spine and then use it to dig into an inaccessible hole. The birds also transport the best tools with them when foraging and change the length of the tools when they are an inappropriate length for the next hole. Tebbich et al. (2001), using aviary housed finches, examined whether this tool-using was learned socially or through individual trial-and-error learning. Some captive adult finches learned to gain access to a beetle larva hidden in a hole in an artificial tree trunk using a twig. However, the non-tool users (when exposed to many weeks in the presence of tool-users) did not learn to use this technique. Hand-raised finches exposed to tool-users, however, did not learn to use tools any better than young exposed to non-tool-users, thereby suggesting that tool use in finches is independent of social learning, and may represent an example of learning during a critical period. Tebbich (2000) also found that the best finch tool-users were found in dry habitats (where prey is located under dry bark that is difficult to access), and virtually none in humid habitats (where prey is located under wet moss).

Perhaps the most spectacular use and manufacture of tools in an avian species is by the 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 (2000) has recently shown that tool manufacture in New Caledonian crows is lateralized at the population-level, that is 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 appear able to choose the correct tool (a twig of certain length) from a “tool box” (collection of different lengthen twigs) that is appropriate for a specific task, such as reaching food placed in the middle of a transparent tube (Chappell and 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, Chappell, and Kacelnik, 2002). This has not been seen in any other animal to date, including the great apes (Povinelli, 2000).

### **Primate Utilize Symbolic and Referential Communication**

Perhaps the most famous demonstration of symbolic and referential communication in the wild are the alarm calls of vervet monkeys (*Cercopithecus aethiops*). Vervet monkeys use at least three different alarm calls to discriminate between different predator types: leopards, eagles, and snakes (Struhsaker, 1967). It has also been demonstrated that the signals are not just emotional reactions to the appearance of a predator. Through the use of alarm call playbacks, it was demonstrated that the vervets responded to each different alarm with different avoidance behaviors appropriate for the predator the call was elicited by (Cheney and Seyfarth, 1990; Seyfarth, Cheney, and Marler, 1980). A leopard call caused the monkeys to run into the trees, a snake call caused a mobbing response towards the ground and an eagle call caused the monkeys to run into the bushes. This may suggest that the information contained

within the different alarm calls represents an image of the associated predator type (symbolic representation). A second line of evidence suggesting that the calls were not reactive emotional exclamations was the fact that there were dramatic audience effects on calling rate (i.e., effects of social context). Alarm calls were not given if an individual experienced a predator when alone (Cheney and Seyfarth, 1990), and calling rate was also dependent on whether other monkeys in the vicinity were kin or non-kin (Cheney and Seyfarth, 1985).

Interestingly, a similar pattern of response has been demonstrated for domestic chickens (*Gallus gallus*). Using artificially constructed predators (such as video images of cardboard silhouettes of birds of prey), Evans et al. (1993) found that chickens also responded to the sight of the artificial predators with different alarm calls and responded to the playbacks of the different alarm calls in different appropriate ways, crouching after hearing an alarm call representing an aerial predator. Similar to vervets, Marler and colleagues also found significant audience effects in chickens (Gyger et al., 1986; Karakashian et al., 1988).

Tomasello and Call (1997) have suggested that when discussing the work on vervet monkey alarm calls “one must be careful in interpreting the cognitive underpinnings of these phenomena ... because several nonprimate species also give alarm calls differentially depending on the presence of others and differentiate kin from other conspecifics” (p. 252). We find this position difficult to reconcile based on the available evidence. Why should the presence of a complex cognitive ability in chickens be less plausible and less valid than the same ability in primates?

Although we do not have the space here to discuss this in great detail, a second form of symbolic communication found in some primates is the acquisition of human language to animals, particularly in enculturated apes. Earlier studies concentrated on the use of American Sign Language (ASL) that was acquired from observing human trainers sign, but never speak. Washoe, a chimpanzee, for example, learned over 100 signs and could combine signs into new combinations, such as “water bird” to represent swan (Gardner and Gardner, 1969). Terrace et al. (1979) however, using the same method of teaching ASL found that Nim, another chimpanzee, learned 125 signs and produced 4 sign combinations, but had no understanding of syntactical structure, as signs were often repeated and most used personal pronouns, such as “me.” Other studies in chimpanzees have examined directly the

understanding of symbols as representations of objects, such as Sarah (described earlier) who learned to associate plastic tokens of various colors and shapes with the objects they represented (Premack, 1971) and Lana who learned that geometric designs on a keyboard represented different words (“Yerkish,” Rumbaugh, 1977).

Most impressively, a bonobo named Kanzi, learned to use Yerkish after observing his foster mother being taught to use the lexigrams, and eventually learned to respond to human speech (equivalent to that of a 2-year-old human child; Savage-Rumbaugh and Lewin, 1994).

It is not our place in this chapter to criticize or champion these studies. Whether you agree or disagree that the previously described studies have demonstrated human language abilities in apes, for the purpose of this chapter the important point is that similar abilities have been reported in great detail for an African gray parrot, named Alex (Pepperberg, 1990). Pepperberg was successful in teaching human language to Alex and other gray parrots because parrots are excellent vocal mimics (Baylis, 1982). Also, the parrots were provided with live, interactive trainers who supplied referential and contextual use of each label associated with each object it represented, and the reward objects were inherently interesting (i.e., not food).

Furthermore, Pepperberg used the model/rival technique (Todt, 1975), in which the parrots are trained in the presence of two humans; a model trainer who shows an object to the second human (model and rival). The trainer asks the model/rival questions about the object (such as “What’s here?”), and gives praise and the object as a reward. The trainer also displays disapproval if the answer is incorrect. Therefore, the parrot can learn which is the correct label for each object. Alex, to date, has demonstrated object identification by requesting specific objects, categorizing objects based on their color and shape, forming abstract concepts, such as same/different or absent, and appears to have a concept of number of objects (reviewed in Pepperberg, 1999). All these abilities have largely been demonstrated only in non-human primates (reviewed in Shettleworth, 1998; Tomasello and Call, 1997).

### **Primates Demonstrate Elements of Mental Time Travel**

One of the remaining bastions of human uniqueness may be the ability to travel backwards and forwards mentally in time; so-called “mental time travel”

(Suddendorf and Corballis, 1997). The mental time travel hypothesis posits that, unlike humans, animals cannot travel backwards in time to re-experience and recollect specific past episodes (episodic memory) or travel forwards in time in order to anticipate future states of affairs (future planning). The idea that animals do not share with us a sense of the past and of the future is something that has been suggested several times within comparative psychology, but the idea that mental time travel might be exclusive to humans was initially proposed by Köhler. Although he believed his chimpanzees were capable of many complex cognitive feats such as insight (see earlier section), he suggested that there was one important limitation “The time in which the chimpanzee lives is limited in past and future” (Köhler 1927/1917, p. 272). The same idea was later expressed by Bischof (1978) and Bischof-Köhler (1985).

Mental time travel has two components: retrospective and prospective.

1. The retrospective component: “Episodic memory receives and stores information about temporally dated phases or events, and temporal-spatial relations among those events” (Tulving, 1972).
2. The prospective component: “... animals other than humans cannot anticipate future need or drive states, and are therefore bound to a present that is defined by their current motivational state. We shall refer to this as the Bischof-Köhler hypothesis ...” (Suddendorf and Corballis, 1997).

***The Retrospective Component—Episodic Memory.*** Both humans and animals are capable of learning from past experience and using that information at a later date. But there is one form of memory that is thought to differentiate us from other animals, and that is the ability to episodically recall and re-experience unique past events. Cognitive psychologists such as Tulving make the distinction between semantic factual knowledge and episodic recall (Tulving, 1972, 1983). Thus, knowing that Paris is the capital of France, or the date and time we were born, are examples of semantic memory. But remembering what we did when we went to Paris, or what we did on our wedding day, are examples of episodic memory. Aside from the distinction between knowing (semantic memory) and remembering (episodic memory), the two types of memory differ in whether or not they involve chronesthesia (Tulving, 2002). Whereas semantic memories transcend space and time, episodic memories are concerned with specific events in one’s personal past that involve information about when as well as what-and-where. Furthermore, language-based reports of episodic recall suggest that the retrieved experiences are not only explicitly

located in the past but are also accompanied by the conscious experience of one's recollections, so-called auto-noetic consciousness (e.g., Wheeler, 2000). But this definition makes it impossible to demonstrate episodic memory in animals because there are no agreed nonlinguistic behavioral markers of conscious experience. The dilemma can be resolved to some degree by using Tulving's original definition that episodic memory "receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events" (Tulving, 1972). Episodic memory provides information about the what and when of events (i.e., temporally-dated experiences) and where they happened (i.e., temporal-spatial relations). An animal's ability to fulfill the behavioral criteria regardless of auto-noetic consciousness is termed episodic-like memory (Griffiths et al., 1999).

*Do Animals have Episodic-like Memory?* Most studies of animal memory have not distinguished between episodic recall of events from semantic knowledge for facts, but it was generally assumed that in animals events are remembered with no specific past-time reference. Typically, the tasks require the animal to retrieve information about only a single feature of the episode as opposed to testing its ability to form an integrated memory of temporal-spatial relations. It is also common for the animal to be given multiple training experiences thereby removing the trial-uniqueness of the task (see Griffiths et al., 1999). Furthermore, in many of the tasks that have been used, the animal does not need to recall the what, where, and when of an event. Instead, the task may be solved by discriminating on the basis of relative familiarity, a process that is dissociable both psychologically and neurobiologically from episodic memory recall. For example, a face can appear highly familiar without any recall of where and when one has previously met its owner.

In many studies that appear to demonstrate episodic-like recall in animals, the results observed can be explained more in terms of simple familiarity (Griffiths et al., 1999). Consider the case of monkeys that have been trained to choose between two complex objects on the basis of whether they are same as (delayed matching-to-sample—DMS) or different from (delayed non-matching-to-sample or oddity—DNMS) an object they were shown some time previously at the start of the trial. The monkey may have recalled episodically the events at the start of the trial. A simpler explanation, however, is that the monkey learned to choose- or avoid- the most familiar object. By only requiring the monkeys to recognize a stimulus, but not recollect where and when it was previously seen, these matching tasks are most readily solved by familiarity

rather than episodic recall. Indeed, the fact that monkeys learned more rapidly when novel objects are used supports this account. The point is that experiments such as this do not provide convincing evidence for episodic recall because they can be explained in simpler terms.

*Episodic-like Memory in Scrub-Jays.* An alternative strategy is to consider cases in nature in which an animal might need to retrieve and integrate simultaneously information about what happened, where, and when during a specific previous experience. When considering the evolutionary history of episodic-like memory in animals, it might seem intuitively logical to focus on the abilities of non-human primates. The study of non-human primate coalition or alliance formation might provide a useful starting point given that the social partners need to keep track of cognitively complex social relationships. Males are distinguished from each other based on size, strength, fighting ability, etc., and the greater these attributes, the higher the individual's social status, and the greater their access to resources, such as food and mating partners (Tomasello and Call, 1997). The need to keep track of trial unique events concerning who did what to whom and where might, therefore, provide a candidate for episodic memory, though it is less clear whether a when component is critical. It is also difficult to think of a good experimental paradigm for testing episodic memory in such complex social interactions.

The food-caching paradigm, however, provides an opportunity to combine ethological validity with rigorous laboratory control because food-caching animals readily hide food caches in the laboratory and rely on memory to recover their caches at a later date. Experiments in the laboratory and field show that birds can remember accurately the location of their caches based upon a single caching experience, but there is also good reason to believe that at least some species form richer representations of caching events than others. Some species cache different types of food and can remember the contents of their caches as well as the location; and some species also cache perishable foods. It therefore may be adaptive for these species to encode and recall information about when a particular food item was cached, as well as what was cached and where. As discussed earlier, experiments on food-caching memory in scrub-jays do provide evidence of episodic-like memory. On the basis of a single caching episode, scrub-jays remember when and where they cached a variety of foods that differ in the rate at which they degrade, in a way that is inexplicable by relative familiarity (Clayton and Dickinson, 1998, 1999a; Clayton et al., 2001a).

Griffiths et al. (1999) have argued that previous demonstrations of trial-unique memory in animals could have been mediated by relative familiarity rather than the temporal encoding of the episode and do not require an integrated memory of the features of the episode. Recently, however, Menzel (1999) demonstrated that a chimpanzee can remember both the what and where of food sources, and experiments by Schwarz and Evans (2001) suggest that a gorilla can also remember who, but it remains to be seen whether this memory has an integrated what-where-when or who-where-when structure. (“Who” information is not likely to be processed differently from other kinds of what information.)

*The Prospective Component—Future Planning.* As with episodic memory, the ability to anticipate future states of affairs (future planning) has been thought to be unique to humans, in part because of the reliance on language for assessing such abilities. Is there any evidence that animals show any signs of forethought?

In order to address this question it is important to distinguish mental time travel into the future from simple prospective behavior. Any species-specific behavior that appears to involve the anticipation of future states of affairs may not actually involve any planning (learning), but may simply result from natural selection, in much the same way as some fixed action patterns such as nest provisioning by hunting wasps (Fabre, 1916). And in some cases a behavior that is orientated towards the future is inherited. Consider the case of migratory behavior in black capped warblers attempting to migrate. Although migration might appear to have some of the features of prospective behavior, because the birds migrate in order to acquire a new, more profitable territory for a given time of year, the “decision” of whether to migrate, and in which direction, does not involve future planning (Berthold et al., 1992).

So in order to test whether animals are capable of mental time travel into the future one needs to rule out simple explanations of prospective behavior that need not involve learning, and as Suddendorf and Corballis (1997) state, “many behaviors involve anticipation of future events in some way, but need not involve the actual simulation or imagining of future events.” Thus experiments using delayed reinforcement, where the animal is trained to discriminate between two choices, and different groups of animals receive varying delays between the choice response and the rewarded or non-rewarded outcome, do not provide evidence of future planning. The fact that a reinforcer can be delayed by a few seconds or even minutes and yet still be viewed as relevant to the preceding behavior, is not evidence for future planning because

it need not involve anything more complex than simply associating the reward and the response. With short time intervals into the future, the learning can be promoted by the contiguity between the reinforcement and the memory of the correct response. Furthermore, implicit in the Bischof-Köhler hypothesis that mental time travel is unique to humans is the idea that non-human animals may be unable to dissociate a previous or future mental state from their current one, and therefore unable to take actions to ensure that a future need will be satisfied. Thus a sated animal may be unable to understand that it will be hungry again later and thus “a full-bellied lion is no threat to nearby zebras, but a full-bellied human may be” (Suddendorf and Corballis, 1997).

A number of anthropologists and primatologists have suggested that some great apes might share with humans the ability to plan for the future. Unfortunately most of these claims rest on anecdotal evidence. Byrne (1995), for example, recounts the following anecdote as an example of future planning in chimpanzees: A group of Mahale chimpanzees surrounded a cave in which a leopard mother and infant had hidden. After several attempts, an old male lunged into the cave and stole the cub. Afterwards it pummeled the cub, bit it, and eventually killed it. But none of the chimpanzees attempted to eat the cub so this behavior cannot be explained in terms of simple foraging. Byrne suggests that this is evidence of future planning and that the

Humans might well carry out this action, with the ultimate ends of reducing the population of dangerous carnivores and deterring the mother from continuing to inhabit their particular range. It is not easy to account for the chimpanzees' actions without attributing similar goals to them, which implies long-term anticipatory planning (Byrne, 1995, pp. 157–158).

But a number of other explanations are possible, none of which assume anything about the possible thought processes underlying the behavior. Perhaps the chimpanzee was showing re-directed aggression following a fight with other more dominant males, for example.

The chimpanzee's response could have been controlled by currently observable stimuli. A better candidate for future planning is the ability of some animals, notably chimpanzees and New Caledonian crows, to manufacture and use tools (discussed earlier). Chimpanzees, for example, have been described carrying stones over long distances to be used as tools for cracking nuts found in an area where no stones were available. Although this example might be taken to suggest that (some) animals can anticipate a future event, their ability

to do so may be limited. Critics have argued that the preparation of a tool to crack nuts may be largely bound up in the act of consuming the food item only a short time into the future. Importantly, these signs of anticipatory thought concern items that are relevant to the individual's current motivational state: in this example, the hungry chimpanzee's anticipatory use of tools is bound by the context of the animal's current hunger state. The same argument applies to the acquisition of mental maps for future use in foraging. Suppose an animal were capable of taking the shortest route to an invisible goal, and across previously untraversed terrain, as a result of having previously formed a mental map of the environment. This need not involve future planning for there is no reason to believe that it requires an explicit reference to a future-need state. For future planning, then, the critical component is evidence that the animals can anticipate future needs and desires, "independent" of their current needs.

Inevitably with field observations, the problem is that one has no idea whether a particular action is learned or not. And in the absence of any information about the animals' previous reinforcement history, and other important control procedures, it is not possible to assess whether or not these instances of chimpanzee behavior involve future planning. No field study can establish whether or not animals are capable of anticipatory thought. To do so one needs carefully controlled experiments to establish that the behavior in question is learned, in the absence of any previous reinforcement, and that it genuinely involves the anticipation of a future need state not merely the current one.

*Is there any Evidence of Future Planning in Animals?* Laboratory studies have seldom addressed the issue of whether animals can travel mentally in time. There are some studies that claim to have tested future planning with emotive titles such as "Medial prefrontal lesions in the rat and spatial navigation: Evidence for impaired planning" (Granon and Poucet, 1995) and "Anticipation of incentive gain" (Flaherty and Checke, 1982). But none of these studies test the animal's ability to anticipate a future-need state, and most of these studies involve short retention intervals that only appeal to the animal's immediate future.

As with episodic memory, an alternative approach is to consider natural behaviors that might be likely to require the ability to travel forwards in time as well as backwards. And food-caching might also be a good candidate for testing the Bischof-Köhler hypothesis. At first sight, food caching would seem to contradict this claim—functionally at least, it is a behavior that is oriented towards future needs because food-caching animals hide food for future

consumption, and over long retention intervals. A Clark's nutcracker for example, may cache food in October and recover it up to 9 months later. Of course food-caching would not be an example of future planning if the individuals instinctively cached all food items irrespective of the consequences of their actions, or if they were insensitive to the difference between their current-need state at caching and their future one at recovery. But a couple of recent experiments on the caching behavior of scrub-jays suggest that this might be a productive paradigm for testing mental time travel in animals.

*Food Caching by Scrub-Jays: A Candidate for Future Planning in Animals?* If caching is controlled by prospective cognition, we should expect the birds to anticipate the conditions at future recovery opportunities on the basis of past recoveries and to use these anticipated conditions to control present caching. Preliminary experiments by Clayton, Dally, Gilbert, and Dickinson (in prep.) have tested whether jays are sensitive to the state of the food caches at recovery. Jays were given the opportunity to cache two foods, worms and peanuts, simultaneously in the morning and then recover their caches later that afternoon. All birds received fresh food items to cache, but the groups differed in whether the worms were still fresh at recovery or whether they had degraded by the time of recovery. If jays can anticipate the recovery conditions at the time of caching then birds that are only able to recover degraded worms should reduce the amount of worms cached. The results were consistent with this hypothesis in that birds whose worm caches were degraded at recovery substantially reduced the number of worms cached and increased the number of peanuts cached. Note that the birds in all groups continued to eat worms which rules out any explanation in terms of a conditioned taste aversion. And interestingly, all birds continued to cache worms in their home cage, suggesting that a reduction in worm caching was restricted to those sites in which the worms appeared to degrade. The important next step is to test whether jays are sensitive to a future motivational state as opposed to the current one. Can animals learn that they should cache now even when they are not hungry in order to fulfill a future-need state? And is there any evidence of future planning in other behaviors, in primates or in birds?

### THE PERILS OF PRIMATOCENTRISM AND "SCALA NATURAE"

Why have primates achieved this special status when the evidence suggests that species of birds have cognitive abilities that are equal to or more sophisticated

than have been demonstrated for primates? We believe that this harks back to the beginnings of primatology as a discipline. Early studies of primates in zoos or the laboratory were performed to determine whether the cognitive abilities of primates could be compared to the cognitive abilities of humans (stemming from the evolutionary arguments of Darwin and others). This approach has continued unabated since, culminating in the work of David Premack and Duane Rumbaugh that was concerned with whether chimpanzees have the capacities for human language, relational learning, and ToM. The tradition of comparing primates with humans on tests of cognition continues to this day.

Early field researchers studying primates in their natural habitat may have had a similar aim, with almost all being anthropologists investigating the behavior patterns of monkeys and apes as an indicator of how our extinct ancestors may have behaved (see papers in DeVore, 1965 and papers in a more recent volume edited by de Waal, 2001, that continues this tradition in other disciplines in addition to anthropology). Of particular note were Jane Goodall, Dian Fossey, and Birute Galdikas, who were hired and directed by Louis Leakey to study the natural behavior of three great apes (chimpanzees, gorillas, and orangutans) and use the data to form models of early human behavior. Although all field workers are not anthropologists, and ethologists tend to study their selected animal as a means to its own end, the tendency to study primates as models of human behavior still pervades the animal behavioral sciences.

The social or Machiavellian Intelligence hypothesis revolution, for example, started in the 1960s (Jolly, 1966) and 1970s (Humphrey, 1976), and gaining pace in the late 1980s (Byrne and Whiten, 1988) continued this line of research, using anecdotes recorded in the field to establish testable hypotheses relating primate social behavior to the evolution of social behavior in humans. (We would like to note that these researchers have never claimed that anecdotes can wholly replace experiments and the collection of “proper” data.)

Although our aim is not to criticize these fields of endeavor, we would like to make the comment that this way of thinking about the cognitive abilities of primates may have had detrimental effects on constructive thoughts about non-primate animal cognition. The argument follows thus. Primates are our closest relatives (discussed previously) and therefore are likely to have similar cognitive abilities to humans. Anything that does not resemble human cognition must be viewed as less “intelligent.” As primate cognition is structurally similar to human cognition (Tomasello and Call, 1997), primates must be cognitively more advanced than non-primate species. Although space does not permit us to discuss the abuses of the concept of degrees of animal intelligence

(i.e., the incorrect assumption that one animal is more intelligent than another based on experimental tests; Macintosh, 1988) and the concept that this idea was based upon, that is, the flawed idea that animals can be ranked on a continuous scale (the *scala naturae*; Hodos and Campbell, 1969), we would like to suggest that the assumption that primates are a special case arises as a direct consequence of the propagation of these two concepts.

### USES AND ABUSES OF THE ECOLOGICAL/ETHOLOGICAL APPROACH TO COGNITION

One concept that the majority of primate researchers have so far failed to incorporate into their research programs is the ecological/ethological approach (EEA) to cognition (Balda et al., 1997; Kamil, 1988; Shettleworth, 1998). This approach utilizes conspecifics (or images/vocalizations of conspecifics) as stimuli, and also utilizes an appreciation of the natural behavior and ecology of the test species in the design of experiments. The EEA is used primarily to reduce any potential confounds from using synthetic objects or heterospecifics (such as humans) as stimuli.

Many cognitive experiments in non-human animals are drawn from studies in humans, particularly those in developmental psychology, such as the preferential looking time and expectancy violation paradigms. This has been especially true for non-human primates (Hauser, 2000). This methodology, however, may not be compatible for use with other non-human species, which do not have the same visual system as primates. For example, bird vision is as well developed as primate vision, but their field of vision is  $>180^\circ$  (much larger than primates), and their eyes are located at the sides of their head, rather than forward facing (although this is not always the case, such as in owls). This presents a problem for measuring where the birds are looking. The ethological approach may be particularly appropriate for species that are of a greater evolutionary distance from humans, such as birds.

And clearly, an understanding of the species' natural history allows the experimenter to design an ethologically relevant task by predicting what sort of motor responses may occur, what kind of stimuli the experimental subjects are more sensitive to, and what kind of cognitive constraints characterize their learning abilities (see Gerlai and Clayton, 1999). That said, adopting an ethological approach poses some problems of its own. The ethological view is that species differ because they have adapted to different environments that have

different sets of problems to solve. But in order to test this hypothesis we need to make certain assumptions about what the different demands imposed by the different environments in which the animals live might be. Which ecological variables are important, and to what extent are they good predictors of how species might differ in cognitive abilities, if at all?

### **Species Differences in Ecology and Cognition**

Western scrub-jays provide an example of the first case in point. In the comparative studies of spatial and social cognition in four species of North American corvids by Balda and Kamil's laboratories; Clark's nutcrackers and Pinyon jays are thought to have the greatest reliance on stored food, Mexican jays are intermediate and western scrub-jays are the least reliant on stored food. And, whereas the Pinyon jays and Mexican jays are social, western scrub-jays and Clark's nutcrackers are territorial. According to the adaptive specialization hypothesis then, one would predict that the nutcrackers and Pinyon jays should perform more accurately on spatial tests of memory because they are more dependent on accurately relocating their caches than Mexican jays and western scrub-jays. And for social tasks, then one would predict that the two social species, Pinyon jays and Mexican jays, would perform more accurately than territorial Clark's nutcrackers and western scrub-jays.

Is there any evidence for this? Western scrub-jays do perform least accurately of the four species at a number of the tasks requiring spatial memory, including an adapted radial arm maze and delayed non-matching to sample tasks (Balda and Kamil, 1989; Balda et al., 1997; Kamil et al., 1994; but see Gould-Beierle, 2000, for a counter-example). As we described earlier, these results seem surprising when contrasted with their seemingly sophisticated ability to remember the "what, where, and when" of caching events (see earlier section on mental time travel; Clayton and Dickinson, 1998, 1999; Clayton et al., 2001b). The mechanism for cache recovery in these scrub-jays, however, does not appear to be based on a sophisticated appreciation of spatial location, rather the binding of "what," "where," and "when" a unique event occurred (see earlier section, and Clayton et al., 2001b). Also, the relative size of the hippocampal formation in western scrub-jays is larger than would be predicted from body size or size of the telencephalon (Basil et al., 1996).

Western scrub-jays do not appear to have a complex social system, when compared with Pinyon jays, for example. Individual western scrub-jays come

together in pairs largely only during the breeding season and during territory disputes. The adults mate during the breeding season, form short-term selective bonds, and the father contributes to the raising of his offspring. Group size is therefore small compared to related corvid species and is even different from the closely related Florida scrub-jay, that demonstrates cooperative breeding (helpers at the nest), and possess a sentinel system (Woolfenden and Fitzpatrick, 1984). Balda et al. (1997), therefore, predicted from the standpoint of adaptive specialization in the social domain, as in the spatial domain, that the social cognition of *Aphelcoma californica* should be relatively unsophisticated compared to the more sociable Mexican and Pinyon jays. However, as we described earlier, western scrub-jays form complex representations of individual social events, remember the context in which they occurred and use the information to influence their future behavior (Emery and Clayton, 2001). It remains to be seen whether social cognition is an adaptive specialization. But clearly, any hypothesis about the adaptive specialization of social cognition based on group size or traditional measures of social complexity may not be the most productive avenue for constructing testable predictions based on selective adaptation.

### **Ethologically Relevant Stimuli are Difficult to Control**

One productive use of the ethological approach to cognition may be the use of naturalistic stimuli in experiments. A problem with this is how these stimuli are accumulated and presented. Conspecifics as demonstrators, for example in social learning and social cognition experiments provide a higher ethological relevance than use of human demonstrators. Those studies in primates, for example, that have either used videos of conspecifics (Emery et al., 1997) or live conspecifics (Hare et al., 2000, 2001; Tomasello et al., 1998) have produced less ambiguous data than those that relied on humans as stimuli (Povinelli and Eddy, 1996; Povinelli et al., 1990). Conspecifics have been used in studies of bird song learning for many years (Catchpole and Slater, 1995, for review), as have playbacks of primate vocalizations in free-ranging primates (e.g., Cheney and Seyfarth, 1990).

There are some problems with using conspecifics as stimuli, specifically that they are very difficult to control when a particular behavior will occur. This can be overcome through the use of video, although video playback has its own problems, such as a lack of realism, no potential for social interaction, and the question of whether some species perceive video stimuli as representatives of

conspecific (as some monitors have a high flicker-fusion rate that disrupts perception; D'Eath, 1998).

### **How Far can the Natural Behavior of an Animal be Translated to the Laboratory?**

Some experimental psychologists who utilize primates (primarily the great apes) as subjects have taken an extreme position with negligible external validity in their cognitive experiments, such as using enculturated chimpanzees and household objects (see Povinelli, 2000; and Povinelli and Eddy, 1996 for examples). This situation, however, is not exclusive to primate studies, as it has also been adopted in long-term studies using African gray parrots (Moore, 1992; Pepperberg, 1990). There may also be the question that hand-raised birds represent an unnatural case of avian cognition, but the birds are not raised as humans. Although an EEA should clearly increase the external validity of experimental designs in cognitive studies (for a primate example, see Hare, 2001), studies in the laboratory do not equate to the behavior of an animal in its natural environment. We therefore have to appreciate this fact when we interpret the data accumulated from cognitive experiments performed in the laboratory, and we have to maintain a balance between ecological validity and appropriate control in our experiments.

### **THE GREAT DIVIDE: AWARENESS OF "SELF"**

So what may separate the corvids and parrots from primates in mental ability? As yet, the only evidence that an animal may have an awareness of the "self" versus awareness of other individuals has been demonstrated in chimpanzees (and possibly orangutans and dolphins; Reiss and Marino, 2001; Suarez and Gallup, 1981). Although the mark test developed by Gallup (1970) to demonstrate mirror guided self-recognition (MSR) has been criticized on many counts (Heyes, 1998), these have been convincingly countered (Gallup et al., 1995). The use of mirrors still provides the only convincing demonstration of self-directed behavior in relation to specific body locations, which has been suggested to be an indication of a self-concept (Gallup, 1970, 1982; also see papers in Parker et al., 1994).

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). MSR has also been tested in African gray parrots, but although they were shown to use a mirror to locate hidden objects, however they did not demonstrate any self-exploratory behavior (Pepperberg et al., 1995).

An earlier study (Gallup and Capper, 1970) compared the orientation behavior of parakeets (*Melopsittacus undulates*) to either a mirror, a conspecific, food, or a blank piece of cardboard. The parakeets spent a significantly greater amount of time sitting on the perch in front of the mirror compared to the other conditions, however the birds were found to display and vocalize toward their reflection, thereby demonstrating a failure to understand that the reflection represented themselves. A study that claimed to train pigeons to demonstrate self-awareness through associative learning (Epstein et al., 1981) had little to do with self-awareness per se, and has yet failed to be replicated (Thompson and Contie, 1994).

Gallup (1982) has suggested that an awareness of self is an important prerequisite for understanding others' mental states. Understanding one's own actions and mental states may provide the basis for attributing those same states to others. In fact, Gallup (1994) stated that "in addition to being able to recognize themselves in mirrors, organisms that can conceive of themselves ought to be able to use their own experience and knowledge to infer comparable experiences and knowledge in other organisms" (Gallup, 1994, p. 48).

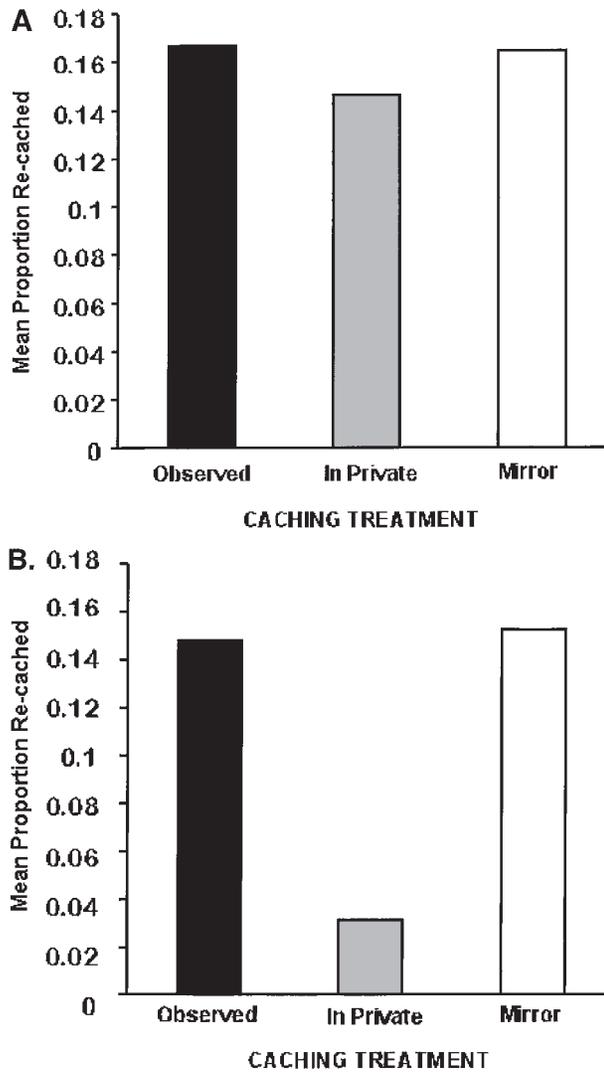
As discussed above, our recent experiments on social reasoning in scrub-jays (Emery and Clayton, 2001) may provide convincing evidence of mental attribution. But these results suggest that if Gallup's hypothesis is correct, western scrub-jays should also demonstrate mirror self-recognition. We decided that an aesthetic mark test for mirror-guided self-examination (similar to previous studies) was not ethologically relevant to the jays. So in a preliminary experiment by Emery, Gilbert, and Clayton we examined whether the presence of a mirror during caching would alter the jays' re-caching behavior 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 caching as themselves and 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 and 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 motivation value to 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 color, 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 (Figure 7A). 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 regarded the image in the mirror as 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 regarded the reflected image in the mirror as a conspecific rather than themselves (similar to other birds and monkeys; Figure 7B).

These results and the earlier results from jungle crows, parakeets, and African gray parrots tend to suggest that self-awareness may be out of the capacity of the avian brain. This does not mean that Gallup’s hypothesis is incorrect, as we have not demonstrated human ToM in the scrub-jays only some of the hallmarks of ToM. We need to examine the scrub-jays’ reactions



**Figure 7.** Mean proportion of (A) stones and (B) hazelnuts that were re-cached when the scrub-jays were either observed during caching, when they had cached in private or when they had cached in front of a large mirror. Unpublished data by Emery, Gilbert, and Clayton.

to the presence of the mirror more closely. The jays received very little experience with mirrors, in comparison to the studies with non-human primates, and this may have been insufficient. But a human-like ToM may still require the concept of self-recognition.

### **IS THERE A CASE FOR CONVERGENT COGNITIVE EVOLUTION AND DIVERGENT NEUROLOGICAL EVOLUTION?**

In this chapter, we have described how some of the supposed “uniqueness” of primates in the structure of their brains and their advanced cognitive abilities are also present in a number of bird species, primarily the corvids and parrots. Initial thoughts on the distinct evolutionary histories of birds and mammals led us to presume that these neural and cognitive similarities do not exist between corvids, parrots, and primates. A number of significant factors draw us to the conclusion that although the common ancestor of mammals and birds lived over 280 million years ago, the recent evolution of these three taxonomic groups would facilitate the enhancement of cognition not demonstrated in other species (with the exception of Cetaceans). We have shown that some species of birds have forebrains larger than would be predicted from their body size, and that the neostriatum of the forebrain displays the greatest expansion, possibly representing an equivalent structure to the primate prefrontal cortex. We have also demonstrated that some of the bastions of primate intelligence; tool use, insight, symbolic communication, social learning, mental attribution, and mental time travel are also present in similar degrees to the primates, and in some cases surpass the available evidence for the primates. We suggest that this may largely stem from a lack of research in avian cognition, a primatocentric view of animal cognition inherited from field anthropology, and a paucity of studies in primate cognition that utilize EEA.

The brains of birds and mammals are very different, and the neural substrates of cognition are located within such diverse brain structures, however the behavioral outcome of cognitive processing is very similar and likely based on similar principles. Surely then, one can argue a case for divergent neurological evolution yet convergent mental evolution (particularly within the realms of mental attribution and mental time travel).

We have a long way to go before birds and primates can be compared properly to a full extent on identical cognitive skills. New experimental studies in the field and in the laboratory need to be initiated, ones based on a high degree of ecological validity. One group therefore that would benefit from collaborating with comparative psychologists interested in animal cognition would be behavioral ecologists (Yoerg, 1991), especially those working with birds (Marler, 1997).

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### REFERENCES

- Akins, C. K., and Zentall, T. R., 1996, Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method, *J. Comp. Psychol.* **110**:316–320.
- Balda, R. P., and Kamil, A. C., 1989, A comparative study of cache recovery by three corvid species, *Anim. Behav.* **38**:486–495.
- Balda, R. P., Kamil, A. C., and Bednekoff, P. A., 1997, Predicting cognitive capacity from natural history: Examples from species of corvids, in: *Current Ornithology*, Volume 13, V. Nolan and E. D. Ketterson, eds., Plenum Press, New York, pp. 33–66.
- Basil, J. A., Kamil, A. C., Balda, R. A., and Fite, K. V., 1996, Differences in hippocampal volume in food-storing corvids, *Brain Behav. Evol.* **47**:156–164.
- Baylis, J. R., 1982, Avian vocal mimicry: Its function and evolution, in: *Acoustic Communication in Birds*, D. E. Kroodsma, E. H. Miller, and H. Ouellet, eds., Academic Press, London, pp. 51–83.
- Bednekoff, P. A., and Balda, R. A., 1996a, Observational spatial memory in Clark's nutcrackers and Mexican jays, *Anim. Behav.* **52**:833–839.
- Bednekoff, P. A., and Balda, R. A., 1996b, Social caching and observational spatial memory in Pinyon jays, *Behaviour* **133**:807–826.
- Berthold, P., Heilbig, A. J., Mohr, G., and Querner, U., 1992, Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**:668–670.
- Birch, H. G., 1945, The relation of previous experience to insightful problem solving, *J. Comp. Psych.* **38**:367–383.
- Bischof, N., 1978, On the phylogeny of human morality, in: *Morality as a Biological Phenomenon*, G. Stent, ed., Berlin, Abakon, pp. 53–74.
- Bischof-Koehler, D., 1985, Zur Phylogenese menschlicher motivation [On the phylogeny of human motivation], in: *Emotion und Reflexivitaet*, L. H. Eckensberger and E. D. Lantermann, eds., Vienna, Urban & Schwarzenberg, pp. 3–47.
- Boesch, C., and Boesch, H., 1983, Optimization of nut-cracking with natural hammers by wild chimpanzees, *Behaviour* **83**:265–286.

- Brockmann, H. J., and Barnard, C. J., 1979, Kleptoparasitism in birds, *Anim. Behav.* **27**:487–514.
- Bugnyar, T., and Huber, L., 1997, Push or pull: An experimental study on imitation in marmosets, *Anim. Behav.* **54**:817–831.
- Bugnyar, T., and Kotrschal, K., 2001, Do ravens manipulate others' attention in order to prevent or achieve social learning opportunities? *Adv. Ethol.* **36**:106.
- Bugnyar, T., and Kotrschal, K., 2002, Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it "tactical" deception? *Anim. Behav.* **64**:185–195.
- Byrne, R. W., 1995, *The Thinking Ape: Evolutionary Origins of Intelligence*, Oxford University Press, Oxford.
- Byrne, R. W., 1996, Relating brain size to intelligence in primates, in: *Modelling the Early Human Mind*, P. A. Mellars and K. R. Gibson, eds., MacDonald Institute for Archaeological Research, Cambridge, pp. 49–56.
- Byrne, R. W., and Whiten, A., eds., 1998, *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*, Clarendon Press, Oxford.
- Campbell, F. M., Heyes, C. M., and Goldsmith, A. R., 1999, Stimulus learning and response learning by observation in the European starling, in a two-object/two action test, *Anim. Behav.* **58**:151–158.
- Catchpole, C. K., and Slater, P. J. B., 1995, *Bird Song: Themes and Variations*, Cambridge University Press, Cambridge.
- Chappell, J., and Kacelnik, A., 2002, Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*), *Animal Cognition* **5**:71–.
- Cheney, D. L., and Seyfarth, R. M., 1985, Vervet monkey alarm calls: Manipulation through shared information? *Behaviour* **93**:150–166.
- Cheney, D. L., and Seyfarth, R. M., 1990, *How Monkeys See the World: Inside the Mind of Another Species*, University of Chicago Press, Chicago.
- Clayton, D. A., 1978, Socially facilitated behavior, *Q. Rev. Biol.* **53**:373–391.
- Clayton, N. S., 1998, Memory and the hippocampus in food-storing birds: A comparative approach, *Neuropharmacol.* **37**:441–452.
- Clayton, N. S., and Dickinson, A., 1998, Episodic-like memory during cache recovery by scrub jays, *Nature* **395**:272–278.
- Clayton, N. S., and Dickinson, A., 1999a, 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., and Dickinson, A., 1999b, Memory for the contents of caches by Scrub jays, *J. Exp. Psychol.: Anim. Behav. Proc.* **25**:82–91.
- Clayton, N. S., and Jolliffe, A., 1996, Marsh tits (*Parus palustris*) use tools to store food., *Ibis* **138**:554.

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- Clayton, N. S., Griffiths, D. P., and Bennett, A. T. D., 1994, Storage of stones by jays *Garrulus glandarius*, *Ibis* **136**:331–334.
- Clayton, N. S., Yu, K., and Dickinson, A., 2001a, Scrub jays (*Aphelocoma coerulescens*) can form an integrated memory for multiple features of caching episodes, *J. Exp. Psychol.: Anim. Behav. Proc.* **27**:17–29.
- Clayton, N. S., Griffiths, D. P., Emery, N. J., and Dickinson, A., 2001b, Elements of episodic-like memory in animals, *Phil. Trans. Roy. Soc. Lond.: B.* **356**:1483–1491.
- Cristol, D., and Switzer, P. V., 1999, Avian prey-dropping behavior. II. American crows and walnuts, *Behav. Ecol.* **10**:220–226.
- Custance, D., Whiten, A., and Freedman, T., 1999, Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*), *J. Comp. Psychol.* **113**:13–23.
- Dawkins, M. S., 2002, What are birds looking at? Head movements and eye use in chickens, *Anim. Behav.* **63**:991–998.
- Dawson, B. V., and Foss, B. M., 1965, Observational learning in budgerigars, *Anim. Behav.* **13**:470–474.
- Deacon, T., 1990, Rethinking mammalian brain evolution, *Am. Zool.* **30**:629–705.
- D'Eath, R. B., 1998, Can video images imitate real stimuli in animal behaviour experiments? *Biol. Rev.* **73**:267–292.
- De Vore, I., ed., 1965, *Primate Behavior: Field Studies of Monkeys and Apes*, Holt Reinhart Winston, New York.
- de Waal, F. B. M., ed., 2001, *Tree of Origin: What Primate Behavior can tell us about Human Social Evolution*, Harvard University Press, Cambridge.
- Durstewitz, D., Kroner, S., and Gunturkun, O., 1999, Dopamine innervation of the avian telencephalon, *Prog. Neurobiol.* **59**:161–195.
- Emery, N. J., 2000, The eye have it: The neuroethology, evolution and function of social gaze, *Neurosci. Biobehav. Rev.* **24**:581–604.
- Emery, N. J., and Clayton, N. S., 2001, Effects of experience and social context on prospective caching strategies by scrub jays, *Nature* **414**:443–446.
- Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., and Baker, C. I., 1997, Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*), *J. Comp. Psychol.* **111**:286–293.
- Epstein, R., Lanza, R. P., and Skinner, B. F., 1981, “Self-awareness” in the pigeon, *Science* **212**:695–696.
- Evans, C. S., Evans, L., and Marler, P., 1993, On the meaning of alarm calls: Functional reference in an avian vocal system, *Anim. Behav.* **46**:23–38.
- Fabre, J. H., 1916, *The Hunting Wasps*. Hodder and Stoughton.
- Flaherty, C. F., and Checke, S., 1982, Anticipation of incentive gain, *Anim. Learn. Behav.* **10**:177–182.
- Fritz, J., and Kotrschal, K., 1999, Social learning in common ravens, *Corvus corax*, *Anim. Behav.* **57**:785–793.

- Gallup, G. G., Jr., 1970, Chimpanzees: Self-recognition, *Science* **167**:341–343.
- Gallup, G. G., Jr., 1982, Self-awareness and the emergence of mind in primates, *Am. J. Primatol.* **2**:237–248.
- Gallup, G. G., Jr., 1994, Self-recognition: Research strategies and experimental design, in: *Self-Awareness in Animals and Humans: Developmental Perspectives*, S. T. Parker, R. W. Mitchell, and M. L. Boccia, eds., Cambridge University Press, Cambridge, pp. 35–50.
- Gallup, G. G., Jr., and Capper, S. A., 1970, Preference for mirror-image stimulation in finches (*Passer domesticus domesticus*) and parakeets (*Melopsittacus undulates*), *Anim. Behav.* **18**:621–624.
- Gallup, G. G., Jr., Povinelli, D. J., Suarez, S. D., Anderson, J. R., Lethmate, J., and Menzel, E. W., Jr., 1995, Further reflections on self-recognition in primates, *Anim. Behav.* **50**:1525–1532.
- Gardner, R. A., and Gardner, B. T., 1969, Teaching sign language to a chimpanzee, *Science* **165**:664–672.
- Gerlai, R., and Clayton, N. S., 1999, Analyzing hippocampal function in transgenic mice: An ethological perspective, *TINS* **22**:47–51.
- Gibson, K. R., 1986, Cognition, brain size, and the extraction of embedded food resources, in: *Primate Ontogeny, Cognition and Social Behavior*, J. G. Else and P. C. Lee, eds., Cambridge University Press, Cambridge, pp. 93–105.
- Goldman-Rakic, P. S., Lidow, M. S., Smiley, J. F., and Williams, M. S., 1992, The anatomy of dopamine in monkey and human prefrontal cortex, *J. Neural Trans. Suppl.* **36**:163–177.
- Goodall, J., 1986, *The Chimpanzees of Gombe. Patterns of Behavior*. Harvard University Press, Cambridge.
- Gould-Beierle, K., 2000, A comparison of four corvid species in a working and reference memory task using a radial arm maze, *J. Comp. Psychol.* **114**:347–356.
- Granon, S., and Poucet, B., 1995, Medial prefrontal lesions in the rat and spatial navigation: Evidence for impaired planning, *Behav. Neurosci.* **109**:474–484.
- Griffiths, D., Dickinson, A., and Clayton, N. S., 1999, Episodic and declarative memory: What can animals remember about their past? *Trends Cog. Sci.* **3**:74–80.
- Güntürkün, O., 1997, Cognitive impairments after lesions of the neostriatum caudolaterale and its thalamic afferent in pigeons: Functional similarities to the mammalian prefrontal system? *J. Hirnforsch* **38**:133–143.
- Gyger, M., Karakashian, S., and Marler, P., 1986, Avian alarm calling: Is there an audience effect? *Anim. Behav.* **34**:1570–1572.
- Hampton, R. R., 1994, Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behaviour* **130**:41–51.
- Hare, B., 2001, Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim. Cog.* **4**:269–280.

- Hare, B., and Tomasello, M., 1999, Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food, *J. Comp. Psychol.* **113**:173–177.
- Hare, B., Call, J., and Tomasello, M., 2001, Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**:139–151.
- Hare, B., Call, J., Agnetta, B., and Tomasello, M., 2000, Chimpanzees know what conspecifics do and do not see, *Anim. Behav.* **59**:771–785.
- Hartmann, B., and Güntürkün, O., 1998, Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons: Possible behavioral equivalencies to the mammalian prefrontal system, *Behav. Brain Res.* **96**:125–133.
- Hauser, M. D., 2000, *Wild Minds: What Animals Really Think*. Henry Holt and Company, New York.
- Heinrich, B., 1996, An experimental investigation of insight in common ravens, *Corvus corax*, *Auk* **112**:994–1003.
- Heinrich, B., 1999, *The Mind of the Raven: Investigations and Adventures with Wolf-Birds*.
- Heinrich, B., 2000, Testing insight in ravens, in: *The Evolution of Cognition*, C. M. Heyes and L. Huber, eds., MIT Press, Cambridge, pp. 289–309.
- Heinrich, B., and Pepper, J. W., 1998, Influence of competitors on caching behavior in the common raven, *Anim. Behav.* **56**:1083–1090.
- Heinrich, B., and Smolker, R., 1998, Play in common ravens (*Corvus corax*), in: *Animal Play: Evolutionary, Comparative and Ecological Perspectives*, M. Bekoff and J. A. Byers, eds., Cambridge University Press, Cambridge, pp. 27–44.
- Held, S., Mendl, M., Devereux, C., and Byrne, R. W., 2001, Behaviour of domestic pigs in a visual perspective taking task, *Behaviour* **138**:1337–1354.
- Heyes, C. M., 1996, Genuine imitation? in: *Social Learning in Animals: The Roots of Culture*, C. M. Heyes, and B. G. Jr. Galef, (eds.) Academic Press, San Diego, pp. 371–404.
- Heyes, C. M., 1998, Theory of mind in nonhuman primates, *Behav. Brain Sci.* **21**:101–148.
- Heyes, C. M., and Dawson, G. R., 1990, A demonstration of observational learning using a bi-directional control, *Q. J. Exp. Psychol.* **42B**:59–71.
- Heyes, C. M., and Galef, B. G. Jr., eds., 1996, *Social Learning in Animals: The Roots of Culture*, Academic Press, Inc., San Diego.
- Hodos, W., and Campbell, C. B. G., 1969, Scala naturae: Why there is no theory in comparative psychology, *Psych. Rev.* **76**:337–350.
- Horn, G., 1985, *Memory, Imprinting and the Brain: An Inquiry into Mechanisms*. Oxford University Press, Oxford.
- Huber, L., Rechberger, S., and Taborsky, M., 2001, Social learning affects object exploration and manipulation in keas, *Nestor notabilis*, *Anim. Behav.* **62**:945–954.

- Humphrey, N. K., 1976, The social function of intellect, in: *Growing Points in Ethology*, P. P. G. Bateson and R. A. Hinde, eds., Cambridge University Press, Cambridge, 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, Human-like, population-level specialization in the manufacture of pandanus tools by the New Caledonian crows (*Corvus moneduloides*), *Proc. Roy. Soc. Lond. B.* **267**:403–413.
- Jerison, H. J., 1971, *Evolution of Brain and Intelligence*, Academic Press, Inc., New York.
- Jolly, A., 1966, Lemur social behavior and primate intelligence, *Science* **153**:501–507.
- Jones, T. B., and Kamil, A. C., 1973, Tool-making and tool-using in the northern blue jay, *Science* **180**:1076–1078.
- Kamil, A. C., 1988, A synthetic approach to the study of animal intelligence, in: *Nebraska Symposium on Motivation*, Volume 35, D. W. Leger, ed., University of Nebraska Press, Lincoln, pp. 257–308.
- Kamil, A. C., Balda, R. P., and Olson, D. J., 1994, Performance of four seed-caching corvid species in the radial-arm maze analog, *J. Comp. Psychol.* **108**:385–393.
- Kaminski, J., 2002, Do animals know what others can and cannot see. Paper presented at the 2nd International Symposium on Comparative Cognitive Science, Inuyama, Japan.
- Karakashian, S. J., Gyger, M., and Marler, P., 1988, Audience effects on alarm calling in chickens (*Gallus gallus*), *J. Comp. Psychol.* **102**:129–135.
- Karten, H. J., 1969, The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon, in: *Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System*, J. N. Petras and C. Noback, eds., New York Academy of Sciences, New York, pp. 164–179.
- Karten, H. J., 1991, Homology and the evolutionary origins of the “neocortex”. *Brain, Behav. Evol.* **38**:264–272.
- Köhler, W., 1927, *The Mentality of Apes*. Routledge & Kegan Paul (original work published in 1917, English translation by E. Winter, 1927).
- Kusayama, T., Bischoff, H.-J., and Watanabe, S., 2000, Responses to mirror-image stimulation in jungle crows (*Corvus macrorhynchos*), *Anim. Cog.* **3**:61–64.
- Lefebvre, L., Nicolakakis, N., and Boire, D., 2002, Tools and brains in birds. *Behaviour* **139**:939–973.
- Lefebvre, L., Whittle, P., Lascaris, E., and Finkelstein, A., 1997b, Feeding innovations and forebrain size in birds, *Anim. Behav.* **53**:549–560.
- Macintosh, N. J., 1988, Approaches to the study of animal intelligence, *Br. J. Psychol.* **79**:509–525.
- Madge, S., and Burn, H., 1999, *Crows and Jays: A Guide to the Crows, Jays and Magpies of the World*, Houghton Mifflin Co., Boston.

- Marler, P., 1997, Social cognition: Are primates smarter than birds? in: *Current Ornithology*, Volume 13, V. Nolan and E. D. Ketterson, eds., Plenum Press, New York, pp. 1–32.
- McKinley, J., and Sambrook, T. D., 2000, Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*), *Anim. Cog.* **3**:13–22.
- Menzel, C. R., 1999, Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays, *J. Comp. Psychol.* **113**:1–9.
- Millikan, G. C., and Bowman, R. I., 1967, Observations on Galapagos tool-using finches in captivity, *Living Bird* **6**:23–41.
- Moore, B. R., 1992, Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning, *Behaviour* **122**:231–263.
- Nicolakakis, N., and Lefebvre, L., 2000, Forebrain size and innovation rate in European birds: Feeding, nesting and confounding variables, *Behaviour* **137**:1415–1429.
- Nikei, Y., 1995, Variations of behavior of carrion crows (*Corvus corone*) using automobiles as nutcrackers, *Jap. J. Ornithol.* **44**:21–35.
- Panksepp, J., 1998, *Affective Neuroscience*, Oxford University Press, New York.
- Parker, S. T., Mitchell, R. W., and Boccia, M. L., eds., 1994, *Self-Awareness in Animals and Humans*, Cambridge University Press, Cambridge.
- Passingham, R. E., 1982, *The Human Primate*, WH Freeman, Oxford.
- Pepperberg, I. M., 1990, Some cognitive capacities of an African Grey Parrot (*Psittacus erithacus*), *Adv. Study Behav.*, **19**:357–409.
- Pepperberg, I. M., 1999, *The Alex Studies: Communication and Cognitive Capacities of an African Grey Parrot*. Harvard University Press, Cambridge.
- Pepperberg, I. M., and McLaughlin, M. A., Effects of avian-human joint attention in allospecific vocal learning by grey parrots (*Psittacus erithacus*), *J. Comp. Psych.* **110**:286–297.
- Pepperberg, I. M., Garcia, S. E., Jackson, E. C., and Marconi, S., 1995, Mirror use by African grey parrots (*Psittacus erithacus*), *J. Comp. Psychol.* **109**:182–195.
- Portmann, A., 1946, Etude sur la cérébralisation chez les oiseaux I, *Alauda* **14**:2–20.
- Portmann, A., 1947, Etude sur la cérébralisation chez les oiseaux II. Les indices intra-cérébraux, *Alauda* **15**:1–15.
- Povinelli, D. J., 2000, *Folk Physics for Apes*, Oxford University Press, New York.
- Povinelli, D. J., and Eddy, T. J., 1996, What young chimpanzees know about seeing, *Mono. Soc. Res. Child Dev.* **61**(3) (Serial No. 247).
- Povinelli, D. J., Nelson, K. E., and Boysen, S. T., 1990, Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*), *J. Comp. Psychol.* **104**:203–210.
- Premack, D., 1971, Language in chimpanzee? *Science* **172**:808–822.
- Premack, D., and Premack, A. J., 1983, *The Mind of an Ape*, W. W. Norton & Co., New York.

- Premack, D., and Woodruff, G., 1978, Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **1**:515–526.
- Raleigh, M. J., and Steklis, H. D., 1981, Effects of orbitofrontal and temporal neocortical lesions on the affiliative behavior of vervet monkeys (*Cercopithecus aethiops sabaecus*), *Exp. Neurol.* **73**:378–389.
- Rehkamper, G., Frahm, H. D., and Zilles, K., 1991, Quantitative development of brain and brain structures in birds (*Galliformes* and *Passeriformes*) compared to that in mammals (Insectivores and Primates), *Brain, Behav. Evol.* **37**:125–143.
- Reid, J. B., 1982, Tool-use by a rook (*Corvus frugilegus*) and its causation, *Anim. Behav.* **30**:1212–1216.
- Reiss, D., and Marino, L., 2001, Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence, *Proc. Nat. Acad. Sci.* **98**:5937–5942.
- Ristau, C. A., 1991, Aspects of the cognitive ethology of an injury feigning plover, in: *Cognitive Ethology: The Minds of Other Animals*, C. A. Ristau, ed., Erlbaum, Hillsdale, pp. 91–126.
- Rumbaugh, D. M., ed., 1977, *Language Learning by a Chimpanzee*, Academic Press, New York.
- Savage-Rumbaugh, E. S., and Lewin, R., 1994, *Kanzi, the Ape at the Brink of the Human Mind*. John Wiley & Sons, New York.
- Savage-Rumbaugh, E. S., Rumbaugh, D. M., and Boysen, S. T., 1978, Sarah's problems of comprehension. Commentary to Premack and Woodruff (1978), *Behav. Brain Sci.* **4**:555–557.
- Schwartz, B. L., and Evans, S., 2001, Episodic memory in primates, *Am. J. Primatol.* **55**:71–85.
- Semendeferi, K., Lu, A., Schenker, N., and Damasio, H., 2002, Humans and great apes share a large frontal cortex, *Nature Neurosci.* **5**:272–276.
- Seyfarth, R. M., Cheney, D. L., and Marler, P., 1980, Vervet monkey alarm calls: Semantic communication in a free-ranging primate, *Science* **210**:801–803.
- Shettleworth, S. J., 1998, *Cognition, Evolution, and Behavior*. Oxford University Press, New York.
- Stephan, H. D., Frahm, H., and Baron, G., 1981, New and revised data on volumes of brain structures in insectivores and primates, *Folia primatol.* **35**:1–29.
- Stoinski, T. S., Wrate, J. L., Ure, N., and Whiten, A., 2001, Imitative learning by captive Western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task, *J. Comp. Psychol.* **115**:272–281.
- Struhsaker, T. T., 1967, Auditory communication among vervet monkeys (*Cercopithecus aethiops*), in: *Social Communication among Primates*, S. A. Altmann, ed., University of Chicago Press, Chicago.

- Stuss, D. T., and Alexander, M. P., 2000, Executive functions and the frontal lobes: A conceptual view, *Psychol. Res.* **63**:289–298.
- Suarez, S. D., and Gallup, G. G., Jr., 1981, Self-recognition in chimpanzees and orangutans but not gorillas, *J. Comp. Psychol.* **343**:35–56.
- Suddendorf, T., and Corballis, M. C., 1997, Mental time travel and the evolution of the human mind, *Genetic Soc. Gen. Psychol. Monographs* **123**:133–167.
- Tebbich, S., 2000, *Tool Use in the Woodpecker Finch Cactospiza Pallida: Ontogeny and Ecological Relevance*. Unpublished Doctoral thesis, University of Vienna, Austria.
- Tebbich, S., Taborsky, M., Fessl, B., and Blomqvist, D., 2001, Do woodpecker finches acquire tool-use by social learning? *Proc. Roy. Soc. Lond.: B.* **268**:2189–2193.
- Templeton, J. J., Kamil, A. C., and Balda, R. P., 1999, Sociality and social learning in two species of corvids: the Pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*), *J. Comp. Psych.* **113**:450–455.
- Terrace, H. S., Pettito, L. A., Sanders, R. J., and Bever, T. G., 1979, Can an ape create a sentence? *Science* **206**:891–902.
- Thompson, R. K. R., and Contic, C. L., 1994, Further reflections on mirror usage by pigeons: Lessons from Winnie-the-Pooh and Pinocchio too, in: *Self-Awareness in Animals and Humans: Developmental Perspectives*, S. T. Parker, R. W. Mitchell, and M. L. Boccia, eds., Cambridge University Press, Cambridge, pp. 392–409.
- Thorpe, W. H., 1963, *Learning and Instinct in Animals*, Second edition, Methuen, London.
- Thouless, C. R., Fanshawe, J. H., and Bertram, C. R., 1987, Egyptian vultures *Neophron percnopterus* and Ostrich *Struthio camelus* eggs: The origins of stone-throwing behaviour, *Ibis* **131**:9–15.
- Timmermans, S., Lefebvre, L., Boire, D., and Basu, P., 2000, Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds, *Brain, Behav. Evol.* **56**:196–203.
- Todt, D., 1975, Social learning of vocal patterns and modes of their application in grey parrots (*Psittacus erithacus*), *Z. Tierpsychol.* **39**:178–188.
- Tomasello, M., and Call, J., 1997, *Primate Cognition*, Oxford University Press, New York.
- Tomasello, M., Call, J., and Hare, B., 1998, Five primate species follow the visual gaze of conspecifics, *Anim. Behav.* **55**:1063–1069.
- Tschudin, A., 1999, Relative neocortex size and its correlates in dolphins: comparisons with humans and implications for mental evolution. Unpublished Doctoral thesis, University of Natal, Pietermaritzburg, South Africa.
- Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., and van der Elst, C., 2001, Comprehension of signs by dolphins (*Tursiops truncatus*), *J. Comp. Psych.* **115**:100–115.

- Tulving, E., 1972, Episodic and semantic memory, in: *Organisation of Memory*, E. Tulving and W. Donaldson, eds., New York, Academic Press, pp. 381–403.
- Tulving, E., 1983, *Elements of Episodic Memory*. Clarendon Press, Oxford.
- Tulving, E., 2002, Chronesthesia: Conscious awareness of subjective time, in: *The Age of the Frontal Lobes*, D. T. Stuss and R. C. Knight, eds.
- van Lawick-Goodall, J., 1968, The behaviour of free-living chimpanzees in the Gombe Stream reserve, *Anim. Behav. Mono.* **1**:161–311.
- van Lawick-Goodall, J., and van Lawick, H., 1966, Use of tools by the Egyptian vulture, *Neophron percnopterus*, *Nature* **212**:1468–1469.
- Voronov, L. N., Bogoslovskaya, L. G., and Markova, E. G., 1994, A comparative study of the morphology of forebrain in corvidae in view of their trophic specialization, *Zoo. Z.* **73**:82–96.
- Weir, A. A. S., Chappell, J., and Kacelnik, A., 2002, Shaping of hooks in New Caledonian crows, *Science* **297**:981.
- Wheeler, M. A., 2000, Episodic memory and autoethic awareness, in: *The Oxford Handbook of Memory*, E. Tulving and F. I. M. Craik, eds., Oxford, Oxford University Press, pp.597–625.
- Whiten, A., 1998, Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*), *J. Comp. Psychol.* **112**:270–281.
- Whiten, A., and Byrne, R. W., 1988, Tactical deception in primates, *Behav. Brain Sci.* **11**:233–244.
- Whiten, A., Custance, D. M., Gomez, J. C., Texidor, P., and Bard, K. A., 1996, Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*), *J. Comp. Psychol.* **110**:3–14.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., and Boesch, C., 1999, Cultures in chimpanzees, *Nature* **399**:682–685.
- Whiten, A., and Ham, R., 1992, On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research, in: *Advances in the Study of Behavior*, Volume 21, P. J. B. Slater, J. S. Rosenblatt, C. Beer, and M. Milinski, eds., Academic Press, Inc., New York, pp. 239–283.
- Woolfenden, G. E., and Fitzpatrick, J. W., 1984, *The Florida Scrub Jay: Demography of a Cooperative-breeding Bird*, Princeton University Press, Princeton.
- Yoerg, S. I., 1991, Ecological frames of mind: The role of cognition in behavioral ecology, *Q. Rev. Biol.* **66**:287–301.
- Zilles, K., and Rehkamper, G., 1988, The brain, with special reference to the telencephalon, in: *Orang-utan Biology*, J. H. Schwartz, ed., Oxford University Press, New York, pp. 157–176.

