14 The 3E's Approach to Social Information Use in Birds: Ecology, Ethology, and Evolutionary History

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14.1. Introduction

The field of social learning has attracted considerable attention over the last few years. Researchers from various fields, including psychologists, zoologists, and ecologists, have been working on both the theoretical framework and the practical methods for studying social information use in animals, from mammals and birds to reptiles and fish. A significant obstacle for learning about how the mechanisms and functions of social learning may interact arises from the lack of communication between these fields, resulting in nonunified definitions, noncomparable results due to different methodologies, and different ways of interpreting results.

Kamil (1998) underlined the importance of integrating the different approaches to the study of animal behavior that developed from two scientific revolutions: the cognitive revolution that stemmed from comparative psychology, and the behavioral ecology revolution that originated in biology. As discussed by Dukas (1998e, 405) in the first edition of this book, the philosophy underlying cognitive ecology is that "cognition must be studied with regard to an animal's ecology and evolutionary history, and that knowledge of cognitive mechanisms can help us explain behavioral, ecological, and evolutionary phenomena."

In this chapter, we shall evaluate the success of this integrative approach, focusing specifically on social information use by birds. We shall argue that investigating the psychological mechanisms underlying social learning processes in the light of an animal's *Umwelt*, that is, in terms of the "3E's"—ecology, ethology, and evolutionary history (as shown in fig. 14.1, but see also section 14.1.2)—is critical for gaining a more complete, unified picture of social information, not only for interpreting existing results, but also in designing new experiments with high ecological validity as well as rigorous experimental control.

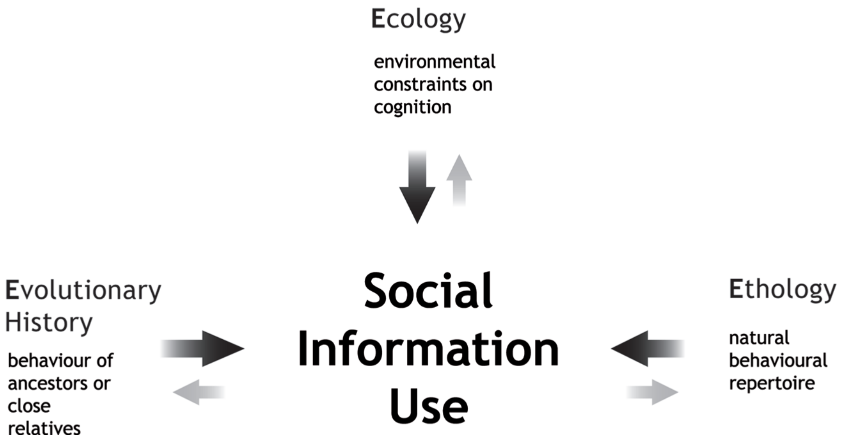

FIGURE 14.1. Diagram of the 3E's that influence social information use: ecology, ethology, and evolutionary history. Black arrows represent the influence of the 3E's on social information use; gray arrows indicate the possible influence of social information use on the ecology, ethology, and evolutionary history of a species.

Studying the psychological mechanisms of social learning in the light of the 3E's and drawing conclusions from such studies may help us to *define* the underlying mechanisms, whereas in reverse it is more difficult, and consequently, explaining an animal's ecology by examining its cognition is more complicated and more speculative. In this chapter, we shall largely concentrate on the former approach, but a good example of how a specific type of social learning can influence a species' ecology is the caching (i.e., food hoarding) behavior of corvids. The sophisticated arms race between cachers and pilferers (i.e., thieves) would not be possible without the basic cognitive ingredient of observational spatial memory, in which pilferers can accurately locate the caches others have made, even when the cacher has left the scene (see section 14.2.1).

As highlighted by Kendal and colleagues (chapter 13, in this volume), the successful use of social information is a matter of gaining benefits (i.e., fitness) and avoiding costs. Being part of a social group or a pair-bond appears to be a prerequisite for exploiting the knowledge of others, since only being in the company of others opens up opportunities to "scrounge" information from knowledgeable conspecifics (Giraldeau et al. 2002; Laland 2004). Different types of social information and a varying number of opportunities to access that information are available, depending on the social and mating system (Lefebvre and Giraldeau 1996). For example, for territorial birds there may be fewer opportunities for picking up social information than for gregarious birds, and for pair-bonded birds there may be different types of information than for lekking birds.

Social learning, defined as "changes in the behavior of one individual that result, in part, from paying attention to another" (Box 1984, 213), involves various factors, ranging from "low-fidelity copying mechanisms" (Whiten et al. 2004), which include mechanisms of social influence, such as social facilitation (i.e., the mere presence of another animal affects the motivation or arousal of the observer) and contagious behavior (i.e., species-typical behavior is released by the sight of others engaged in that activity), to "high-fidelity" social learning, such as imitation and emulation. Animals can learn from others using a variety of different mechanisms, such as local enhancement (i.e., facilitation of learning that results from drawing the observer's attention to a location or object with which the other individual is interacting), stimulus enhancement (i.e., attention is drawn to a certain stimulus), and observational conditioning (learning about the positive or negative reinforcement of an object or event). In Great Britain, a small population of blue tits (*Parus caeruleus*), great tits (*P. major*), and coal tits (*P. ater*) learned how to open milk bottles to get to the cream off the top of the milk. Different bottle-opening techniques were observed, indicating a social learning mechanism other than imitation (i.e., copying the exact action of another), most likely stimulus enhancement (J. Fisher and Hinde 1949; Hinde and Fisher 1951; Sherry and Galef 1984).

Imitation and emulation (i.e., copying the goal or result of an action sequence or learning about the operating characteristics of objects) are often considered more complex forms of social learning than those already discussed, although some authors argue against that view (Heyes 1999; for reviews and definitions see Thorpe 1956; Zajonc 1965; Mineka et al. 1984; Galef 1988; Zentall and Galef 1988; Whiten and Ham 1992; Heyes 1994; Heyes and Galef 1996; Tomasello 1996; Custance et al. 1999; Whiten et al. 2004; Zentall 2004). Well-known examples of imitation include vocal imitation, used to increase the repertoire size (Pepperberg 2007), and the imitation of human's greeting gestures (B. Moore 1992) in African Grey parrots (*Psittacus erithacus*).

In addition to commonly described forms of social learning, the use of other types of social information may play a role in decision making (Bonnie and Earley 2007). Mechanisms for copying another's choice of mate and eavesdropping (the use of information in signals by individuals other than the primary target; Peake 2005), for example, learning the whereabouts of potential predators, are also important information resources. In eavesdropping, some authors distinguish between interceptive and social eavesdropping (Peake 2005). Interceptive eavesdropping is common when the eavesdropper is a different species from the signaler, for example, prey detecting predator cues or individuals from one species picking up information from individuals of another. For example, in a playback experiment it was found that black-casqued hornbills (*Ceratogyma atrata*) responded to alarm calls given by Diana and Campbell's monkeys (*Cercopithecus diana* and *C. campbelli*) and could distinguish between calls that for these monkeys referred to crowned eagles and leopards (Rainey et al. 2004; see Manser, chapter 12 in this volume). Within species, animals of the same sex may pick up information that was intended for the opposite sex (Mennill et al. 2002; Peake 2005). Social eavesdropping takes place within a species when individuals intercept signals that were sent between conspecifics; for example, female great tits (*Parus major*) gain information about potential mates by listening to song interactions between neighboring males (Otter et al. 1999), and domestic fowl (*Gallus gallus domesticus;* Hogue et al. 1996) and pinyon jays (*Gymnorhinus cyanocephalus*) infer their own dominance rank after watching encounters between conspecifics (Bond et al. 2003; see also later in this chapter).

However, there are also good reasons not to use social information. First, although "less expensive" than information acquired via individual trial-and-error learning, information gained through social learning may come at a cost. Observing others performing an action involves forgoing other behaviors that could have been pursued in the meantime, such as watching out for predators, looking for food, or finding a potential mate (McGregor and Dabelsteen 1996). Second, there is the possibility of learning incorrect or inefficient behaviors. Therefore, an animal should employ social learning only if it contributes to its survival or reproductive success (see Kendal et al., chapter 13 in this volume).

Another reason for suggesting that social learning might be costly is that social species often have large brains relative to their body size (Dunbar 1992), although this does not hold for all social species, and there are a number of positive correlations between brain size and various indices of sociality, such as grooming (Kudo and Dunbar 2001), forming coalitions (Shultz and Dunbar 2007), and deceiving others (Byrne and Corp 2004). Indeed, according to the social function of intellect hypothesis (Humphrey 1976; see also Jolly 1966), it is the ability to survive the political dynamics of a complex social world that has been the primary driving force shaping primate intelligence. Keeping track of others' interactions and relationships in addition to their own in large social groups may be beneficial in future interactions when it comes to deceiving others, knowing whom to ask for support in a fight, or climbing up the dominance hierarchy. This imposes an additional burden, since a large amount of social information has to be processed every day, and may have led to the development of social intelligence in animals living in large groups (Humphrey 1976).

In primates, relative neocortex volume (neocortex volume/brain volume remainder) increases with increasing group size, indicating an effect of social complexity on the brain (Dunbar 1992). But other indications of social complexity—such as size of grooming networks (Kudo and Dunbar 2001), whether the species forms coalitions (Dunbar and Shultz 2007b), and the rate of tactical deception (Byrne and Corp 2004)—are all positively correlated with relative neocortex volume in many social primates.

Striking similarities between apes and corvids suggest that these social skills may not be unique to primates: for example, to stabilize their bonds in a group, birds engage in allopreening bouts, similar to grooming in apes (Emery et al. 2007). Furthermore, there is evidence for postconflict affiliation (Seed et al. 2007) and deception in corvids (Bugnyar and Kotrschal 2004). The different types of mating systems, such as monogamy or promiscuity, seem to also have an impact on brains in birds (Dunbar and Shultz 2007a). Birds that form lifelong pair-bonds or are cooperative breeders were found to have the largest relative brain size (Emery et al. 2007). Similar to primate alliances, members of lifelong pairs in birds spend a lot of time and energy on maintaining their relationship. The benefits of pair-bonding include, but are not limited to, food sharing, allopreening, support during fights, and reducing stress levels by initiating affiliative postconflict behaviors such as bill twining, the avian equivalent of chimpanzee kissing (Emery et al. 2007; Seed et al. 2007; von Bayern et al. 2007). These skills require high levels of coordination and may have led to a certain form of intelligence, so-called relationship intelligence (Emery et al. 2007).

14.1.1. A COMPARATIVE APPROACH

It has been suggested that social learning may be an adaptive specialization to group living in birds (Klopfer 1959) and that scramble competition in opportunistic species (i.e., simultaneous competition over food in a group) may have pushed the development of learning skills in a "mental arms race" (Lefebvre and Palameta 1988, 155). This was tested using two species of columbid (the pigeons and doves). The investigation compared social information use in the gregarious, group-foraging feral pigeon *Columba livia* and in the territorial tropical dove *Zenaida aurita* (Lefebvre et al. 1996). The animals had to find food and were provided with information about the location of the food by a demonstrator (social condition) or by the apparatus that contained the food itself (nonsocial condition). The pigeons learned much faster than the doves in both conditions. Thus, the species differences appeared to be due to some general difference in learning abilities rather than a specialization for social learning (Shettleworth 1998). Social species seem to be generally better at learning tasks, but this is probably the result of being simply more attentive or better at detecting information.

In a similar study using corvids, social pinyon jays (*Gymnorhinus cyanocephalus*) and territorial Clark's nutcrackers (*Nucifraga columbiana*) were provided with two tasks—a motor task (lifting a lid off a shallow well containing food) and a color discrimination task (lifting a lid of a particular color off a well containing food)—that could be learned individually or socially (J. Templeton et al. 1999). The pinyon jays learned faster in the social condition than in the nonsocial condition, whereas there was no difference in learning rate for the social and nonsocial conditions in Clark's nutcrackers. These results run contrary to Lefebvre and Palameta's (1988) study, because the pinyon jays were significantly worse at the individual condition than the pigeons, which displayed a more general learning ability. Although the authors suggest that their results support the idea of an adaptive specialization for social learning, we believe these studies highlight the importance of taking other aspects of an animal's natural history into consideration when designing cognitive ecological tasks and interpreting the findings from them. Emery and Clayton (Emery et al. 2004; Emery and Clayton 2008) have recently suggested the importance of the 3E's approach for studying comparative cognition, extending Kamil's (1988) synthetic approach to animal intelligence to integrate information about the evolutionary history and ethology of an animal as well as its ecology.

14.1.2. THE 3E'S APPROACH AND WHY IT IS IMPORTANT

At the outset it is important to make a distinction between the ecological factors that affect an animal's behavior, namely its diet, the habitat in which it lives, and its social system and mating system, and the ethology, by which we mean the natural history of a species-specific behavior, which also contributes to "skillful" social information use. For example, knowing who associates with whom may play a major role for social birds, such as colonial, cooperatively breeding (ecology) pinyon jays (Marzluff and Balda 1992). As intense social cachers (ethology), they need to know whom to protect caches from and who is safe as an observer, which they can infer from watching interactions between conspecifics coupled with an understanding of their social relationships. Transitive inference in social scenarios is defined as the ability to infer the relative dominance status of an individual based on observed interactions, and it should be an essential skill in this type of complex social environment. In a laboratory experiment designed to test this ability, three groups of pinyon jays with a linear hierarchy were formed: group 1 with birds A to F, group 2 with birds 1 to 6, and group 3 with birds P to S. Group 1 was dominant to group 2, and group 2 was dominant to group 3. An observer, bird 3, was allowed to compete with bird B. Bird 3 had never met bird B before, but he had watched encounters between bird A and B and between 2 and B. Also, bird 2 was part of 3's group and therefore bird 3 would have information that bird 2 was dominant to him from their previous interactions. In the observed encounters, bird 3 could watch bird B being submissive to bird A but dominant to bird 2. Bird 3 was then allowed to interact with bird B, and during their encounter, bird 3 demonstrated a greater number of submissive displays to bird B, suggesting that bird 3 had formed a representation of the relative dominance of those birds from its previous observations. All of the tested birds showed similar appropriate behaviors across different combinations of birds (Paz-y-Miño et al. 2004). It would be most informative to know whether these birds could also extrapolate this information about dominance relationships in order to determine from whom they should protect their caches and when.

In tests of this transitive inference ability using arbitrary stimuli, pinyon jays outperformed the less social western scrub jays; however, the scrub jays did learn (Bond et al. 2003). In an initial experiment, learning to discriminate between successive color pairs that were implicitly ordered was tested. Social pinyon jays were faster at learning the dyadic relationships and made fewer errors. Whereas both species learned the first pair without problems, pinyon jays adapted more rapidly to reversals and thus made fewer errors in subsequent reversal trials, in which the previously rewarded pair was incorrect. When more pairs were included in the tests, pinyon jays learned and improved faster than the less social scrub jays. In a second experiment, the birds were tested for transitive inference by intermixing familiar pairs with novel, nonadjacent pairs. Both species showed high accuracy and, thus, transitive inference. However, differences were found in the responses to the position of the stimulus color pair in the implicit rank order. Pinyon jays responded more slowly to low-ranking pairs, although no effect was found with the highest-ranking pair, whereas western scrub jays displayed a first-item accuracy with almost no effects on latency. The authors concluded that the two species may have used different methods for representing the rank order, with pinyon jays using relational representations in which novel pairs can be inserted into a preexisting structure, and western scrub jays building a series of associative representations (Bond et al. 2003).

It therefore appears that differences in socioecology between these species may have driven them to develop different social information use skills.

Pinyon jays are colonial birds, living in large groups, that breed in aggregated pairs of 50 and show cooperative breeding. By contrast, western scrub jays are semiterritorial birds that breed in single pairs (Clayton and Emery 2007). Inferring the dominance status of conspecifics therefore seems to be much more important for the pinyon jays, since using social information to gain knowledge about one's own and others' relationships seems to be an (adaptive) advantage for species living in large, social groups.

Finally, considering the putative evolutionary history of the species under consideration is also important. Although a specific aspect of an animal's ethology or ecology may not be present in the extant species, it may have been present in the common ancestor of the group in question. For example, there is no evidence that jackdaws cache in the wild, but there are anecdotes that jackdaws do display proto-caching, by which we mean they are sometimes seen to place food in nooks and crannies without ever hiding it or leaving it for any length of time. A reconstruction of the evolution of caching in corvids has suggested that the common ancestor of corvids was a caching species (de Kort and Clayton 2006). Therefore, taking these points into consideration may aid in interpreting the results of cognitive ecological studies and help in the design of experiments comparing closely related species that appear to differ in ecology and ethology, that is, in the challenges they face in their given environment and their natural behavioral repertoire.

In justifying the 3E's approach we have described a few studies on a small number of different species. In the following sections, we will discuss further why the 3E's approach, combining ecology, ethology, and evolutionary history, is important, but will focus on social information use in birds (fig. 14.1). By using detailed case studies of a small number of species, we hope to show how the 3E's determine when the solution to a problem is learned socially and what mechanism may be employed.

14.2. Case studies

14.2.1. CORVIDAE

14.2.1.1. *Western scrub jays and ravens*

Many birds, including western scrub jays and ravens, cache temporary surpluses of food for future consumption, which they recover days, if not months, later. Krebs (1990) argued that, for efficient cache recovery, there has likely been considerable selection pressure for them to have highly accurate and long-lasting memories of where they hid the food, and he argued that, as a consequence, food-caching birds had an adaptive specialization in behavior, in terms of this enhanced spatial memory, and an adaptive specialization in the brain, in terms of an enlarged hippocampus relative to the rest of the brain. The most striking example of an adaptive specialization in caching, memory, and the hippocampus comes from two populations of black-capped chickadees that live in very different environmental conditions, one in the harsh climatic conditions in Alaska and one in the milder conditions in Colorado, thereby highlighting the importance of ecology (Pravosudov and Clayton 2002). The Alaskan chickadees cache considerably more food than the Colorado ones, even when housed in identical conditions in the laboratory. Furthermore, the Alaskan birds were much more efficient at cache recovery, and their performance of spatial but not nonspatial memory tasks was much more accurate. They also had much larger hippocampal volumes than the Colorado ones, both in terms of absolute size and in relation to the rest of the brain. Taken together, these findings support the hypothesis that population differences within a species reflect adaptations to ecological conditions.

The abilities needed for recovering food have been investigated in a study combining spatial memory and social learning and have been called observational spatial memory (Balda et al. 1997). Three corvids that differ in levels of sociality and the number of caches made were required to remember where a conspecific had hidden food (Bednekoff and Balda 1996a, 1996b). Clark's nutcrackers, territorial birds that are thought to be able to remember up to 30,000 food caches (Balda et al. 1997), were less accurate in finding another's caches and could not remember for as long as social pinyon jays and Mexican jays (*Aphelocoma ultramarina*), two species that cache much less food than Clark's nutcrackers. However, less social western scrub jays (*Aphelocoma californica*), which also cache much less food than Clark's nutcrackers, remembered the location of the caches almost as accurately as the cachers themselves (Clayton et al. 2001). Ravens (*Corvus corax*) were more successful in raiding another's caches if the caches were made more than 3 meters away from them, suggesting that they were accurate in recovering caches when the cacher was not present to defend them (Bugnyar and Kotrschal 2002).

Although spatial memory is essential for the birds' accurate cache recovery, the birds also need to keep track of not only what they have cached but also what has been recovered, for cache sites may have been emptied, either by themselves or by pilferers. To protect against cache theft, cachers have to employ strategies to either distract others from their caches or to defend them when conspecifics approach them (Dally et al. 2006a). This may be an issue only for corvids, because there is little evidence that other caching species, such as parids (e.g., black-capped chickadees), can remember where another

FIGURE 14.2. A raven caching food in the snow. Photograph by I. G. Federspiel.

individual has cached (Hitchcock and Sherry 1995; but see Pravosudov 2008 for contrary evidence on mountain chickadees).

Most of the studies on social information use in caching experiments have been performed on two species of corvid: common ravens and western scrub jays. These two species have similar ecologies; both live in monogamous, territorial (common ravens) or semiterritorial (western scrub jays) pairs or in flocks that include pairs (Clayton and Emery 2007). Although these species are not particularly social in the traditional sense, social information plays an important role for both species in their caching and pilfering. One striking fact is that each individual can play the role of both cacher and pilferer simultaneously, caching their own food while at the same time watching others cache food and them attempting to pilfer those caches (fig. 14.2).

This "cognitive arms race" between cachers and pilferers seems to have driven the food-caching corvids to excel when it comes to social skills (Bugnyar and Kotrschal 2002) such as keeping track of who was watching when and where. Applying the necessary tactics to the acquired knowledge would seem to be beneficial in such a highly competitive environment.

Western scrub jays, a species also known for its skills in mental time travel (i.e., recollecting what they cached where and how long ago and planning for the future in terms of what to cache for tomorrow's breakfast; Clayton and Dickinson 1998; Clayton et al. 2003; Correia et al. 2007; Raby et al. 2007), are also able to use various cache protection strategies in a flexible manner, choosing the technique most suitable to the context in which the caches were made (fig. 14.3).

When given the opportunity to cache in full view of an observer or behind a barrier, cachers chose to hide more food items behind the barrier

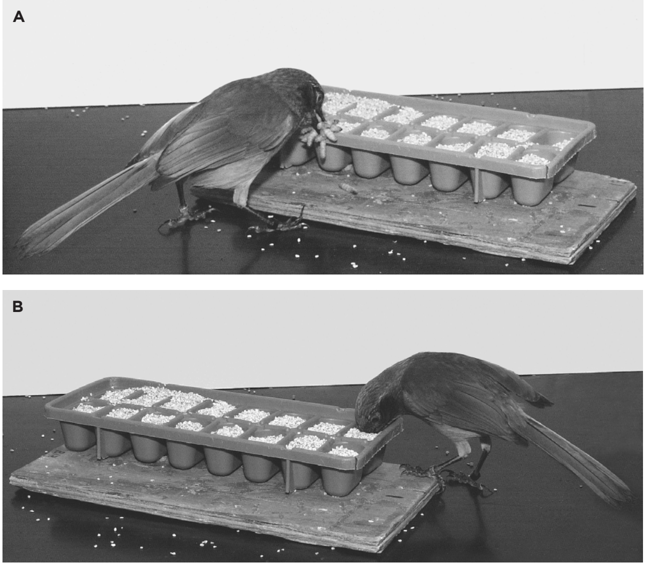

FIGURE 14.3. A western scrub jay (a) carrying worms toward a caching tray and (b) caching a worm. Photograph by I. Cannell.

(fig. 14.4a; Dally et al. 2005). When given the opportunity to either cache close to or further away from an observing bird, they chose to cache at a distance but showed no preference when they were visually isolated from the potential observer (fig. 14.4b; Dally et al. 2005). When caching in view of the observer, they moved the food item around multiple times during the caching process. In recovery sessions, during which the food-hiding birds were allowed to approach the caches without being observed, they tended to retrieve the caches made either close to or in view of the observing conspecifics and recached them in new sites. When provided with the opportunity to choose between "shady" and "well-lit" sites for caching when observed, the jays showed a clear preference for the shady sites, whereas they cached equally at both sites when no observer was present (fig. 14.4c; Dally et al. 2004). When recovering, they tended to recache those food items hidden in the well-lit sites once the observer had left the scene.

The scrub jays therefore appear to use different strategies in different caching contexts. Caching out of view clearly limits the information that can be gained by an observer. In addition to the strategies mentioned, the jays were often observed redistributing the substrate after caching, making it almost impossible to tell where they had hidden their food (Dally et al. 2005). Increasing the number of caches made in view of the observer may have been used as a strategy to offset the risk of cache loss. Confronted by a single trial with a

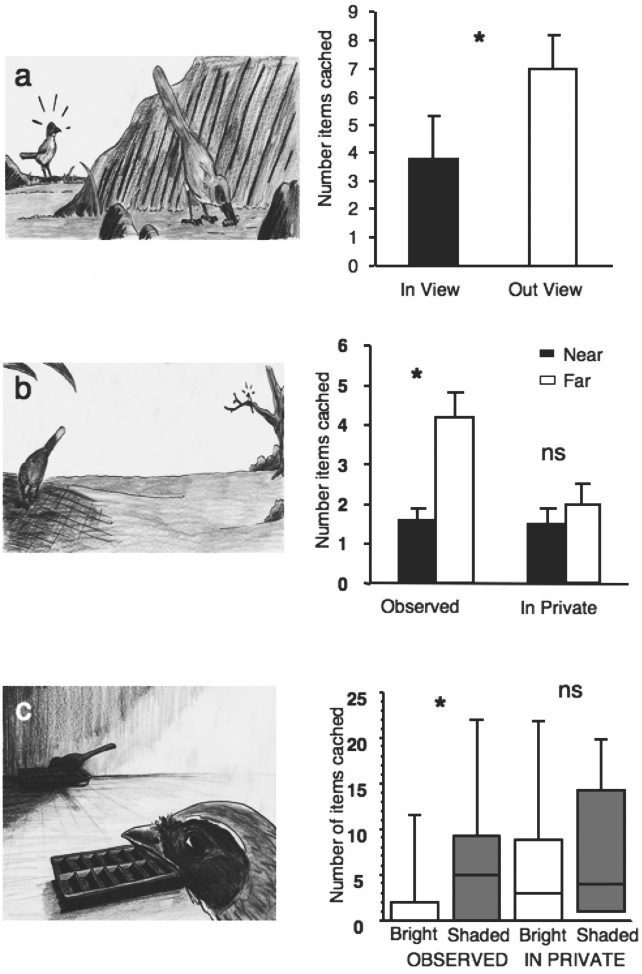

FIGURE 14.4. Cache protection strategies of western scrub jays. a. Drawing of scrub jay caching behind a rock, out of view of a competitor. Number of food items cached either behind a barrier or in the open. $^{*}P < 0.05$. Adapted from Dally et al. 2005. b. Drawing of scrub jay caching as far as possible from another scrub jay. Number of food items cached in private or when observed by another scrub jay. In each condition the cacher could store food in two trays: one close to the observer, the other farther away. $^{*}P < 0.05$. Adapted from Dally et al. 2005. c. Drawing of a scrub jay caching in front of another scrub jay in a shady part of their environment rather than in a well-lit part. Number of food items cached in private or when observed by another scrub jay. In each condition, the cacher could store in two trays: one in a darkened part of the cage, the other in a brightly lit part of the cage. $^{*}P < 0.05$. Adapted from Dally et al. 2004. All illustrations by Scott Stevens.

pilfering conspecific or a human experimenter taking away the caching trays after food had just been hidden, jays switched from checking the caches to predominately eating them and caching in "out-of-tray" sites that the human experimenter or conspecific could not get to (Emery at al. 2004). Cachers also use combinations of at least two strategies; for example, when forced to cache in view of the observer, scrub jays chose to cache at a distance and increase the number of caches, which they later recached if they had not been stolen. Especially the caches that were at high risk (i.e., those cached in the sight of and/or close to the observer) were later recached (Dally et al. 2005). Scrub jays also remembered who was watching them when they made caches and which caches were witnessed by whom (Dally et al. 2006b). They were given the opportunity to recache food in private or in front of one of two observers, one of which had been present during caching. When in the presence of an observer, they moved more caches from the tray in which they had been watched making caches by that same observer. When recaching in private, jays cached in out-of-tray locations, whereas when recaching in front of an observer, the jays seemed to use a confusion tactic, moving the caches twice as often as during private recaching (Dally et al. 2006b).

Experience as a pilferer also appears to play an important role. Birds were allowed to cache either in private or while a conspecific was watching. Individuals given the chance to pilfer others' caches prior to the experiment recached only those caches that they had made in front of an observer. Jays without pilfering experience did not, suggesting some sort of experience projection (Emery and Clayton 2001, 2008). Social information use plays a role not only in the caching context but also during foraging at a new food resource. In a field study, Florida scrub jays (*Aphelocoma coerulescens*) learned to forage at a novel patch where conspecifics had already foraged successfully. Juveniles that watched others digging for peanuts and were able to scrounge learned more about the technique than control individuals. Watching the demonstrations increased the probability that the birds would approach the novel patch, and occasionally, demonstrators modified their behavior "in a way that suggested teaching" (Midford et al. 2000, 1205).

Ravens have also demonstrated impressive performances in social information use, including caching and pilfering tasks. Recently, ravens have been found to learn about their competitors in caching bouts during play caching of objects (Bugnyar et al. 2007). In the wild, ravens were observed to hide themselves when caching food (Heinrich and Pepper 1998) and to protect their caches by retrieving the food or aggressively approaching others who came close to their caches (Heinrich 1999). Controlled experiments revealed that they appeared to differentiate between birds that were present during a

FIGURE 14.5. Ravens during a caching experiment; the observer (left) watches the storer (right) through a window. Photograph by T. Bugnyar.

caching event and those that were not (fig. 14.5; Bugnyar and Heinrich 2005, 2006).

When released back into the caching area, storers retrieved more caches when they were accompanied by a knowledgeable conspecific (present during caching) than they did when they were with ignorant birds (absent at caching) (fig. 14.6a). However, they retrieved the caches only when the conspecific was moving toward them, suggesting that the ravens were acting in response to the behavior of the competitors (fig. 14.6b). To rule out the possibility of the ravens acting on the basis of whom they had seen during a caching event, a second experiment was performed, this time with a human experimenter making the caches. A subject was able to observe the experimenter and could then enter the site, with either a co-observer or a nonobserver or in private. The subjects delayed retrieving the caches when given access to the site with a dominant nonobserver but did not differentiate between dominant and subdominant co-observers, going straight to the cache with either observer. This led to the subjects being first at the cache in all but one of the cases with the nonobservers, even though they delayed approaching the cache with the dominant nonobserver. In cases in which the subject was dominant, it always reached

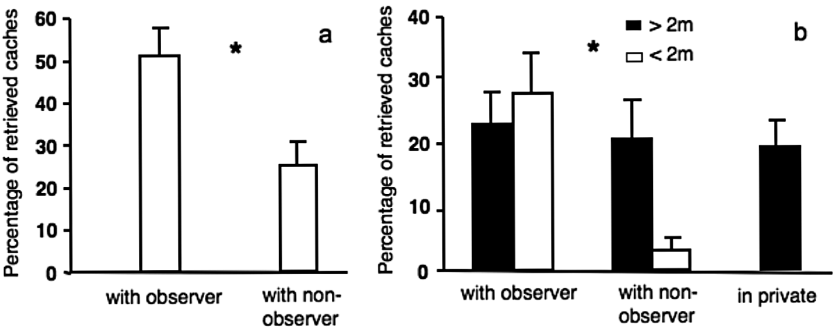

FIGURE 14.6. Mean percentage of caches retrieved by storers (a) with previous observers and nonobservers and (b) when competitors approached the caches (white bars) or did not come near them (black bars). $^*P < 0.05$. Adapted from Bugnyar and Heinrich 2005.

the cache before the co-observer, but with a dominant co-observer, the subjects almost always failed (Bugnyar and Heinrich 2005). Approaching the cache as fast as possible when in the presence of a co-observer therefore seemed to be the only method of getting the food that these ravens employed.

Ravens adjust their behavior in line with the social relationship and knowledge state of their opponent. As storers, they selectively retrieved caches that others were able to watch being made, and as pilferers they hurried to the cache with a co-observer but delayed approaching with a dominant nonobserver (fig. 14.6). Similar to western scrub jays, ravens not only appear to understand that objects such as rocks and tree stumps can degrade visual information but also demonstrate some understanding of another's perspective. Further evidence for this comes from an experiment in which a subordinate began to lead a dominant conspecific away from a food resource that only the subordinate knew about. Subsequently, the dominant bird learned not to stop following the knowledgeable subordinate bird and started searching for the food itself (Bugnyar and Kotrschal 2004).

Ravens feed opportunistically on animal and plant material and are also carrion scavengers, feeding on road kill. Information about new food resources may be shared at so-called information centers (Heinrich 1999) through food calls (Bugnyar et al. 2001) or via visual social information. Individuals accessing new food resources are thus an interesting stimulus for others. In an experiment with a small group of ravens, birds observing others opening a food box tended to open the box using the same technique (Fritz and Kotrschal 1999). A demonstrator was trained to open the box by pulling a flap to open the lid. Nonobserver birds (i.e., the birds in the control group, which did not watch demonstrations of how to open the box by pulling the flap) exclusively opened the box by pecking at a crevice in the middle and then levering the lid open. The observer birds (i.e., the birds that could watch demonstrations) were faster at approaching the box and also at opening it than the nonobservers. They also initially used both possible opening techniques: pecking and pulling. It therefore seems likely that the observing birds were influenced in their choice of technique by the demonstrating birds. Whereas two of the three observers went on to almost exclusively open the box by pecking, the third retained the pulling technique. Due to the two different initial positions a bird had to assume in order to perform one of the two actions, the authors concluded that both imitation and stimulus enhancement could have accounted for the observers' performance (Fritz and Kotrschal 1999).

Social information use seems to be somewhat enhanced between siblings. When they were able to watch a conspecific manipulate an object, ravens manipulated the same object (out of a choice of five) if the conspecific was their sibling (Schwab et al. 2008). This may have been due to socially biased learning (Fragaszy and Visalberghi 2004), with individuals tending to learn from siblings rather than nonsiblings.

Social learning was also found to have an effect on the spread of vocalizations by ravens (Enggist-Dueblin and Pfister 2002). Similar to other songbird species, ravens learn calls from other individuals in their group, and specific dialects spread within subpopulations via social learning (Gwinner 1964). Enggist-Dueblin and Pfister (2002) recorded the vocalizations of free-ranging ravens interacting with a captive pair and analyzed the different types of vocalizations, their distribution, and their differences and similarities. Interestingly, there seemed to be no difference in repertoire size between males and females, which contrasts with the majority of songbirds (Catchpole and Slater 1995). The calls were mainly transmitted within sex and, in a few cases, to the partner, leading to a sex-specific call repertoire. The authors were able to divide the study site into three different parts on the basis of the geographical distribution of the different call types, suggesting a cultural process.

In summary, although territorial, ravens need to be able to use social information to deal with a highly competitive environment. An additional selection pressure is their diet and heterospecific competitors, such as wolves (*Canis lupus*), at carcasses. It was observed that ravens adjust their behavior to the presence of wolves, which occasionally kill ravens when defending food, but do not adjust their behavior to boars (*Sus scrofa*), which do not pose a threat to ravens. When at the carcass with wolves, ravens specialized in scrounging rather than approaching the food resource themselves (Bugnyar and Kotrschal 2002). Finding a new food resource, dealing with competition over food, and also establishing a vocal repertoire and communicating with others require social information use in a raven's life.

For caching species in general, the ability to use social information seems to be vital in order to pilfer another's caches, remember who was watching during a caching event, and protect one's own caches. Furthermore, the evolutionary history of the species must also be taken into account. De Kort and Clayton (2006) concluded that the common ancestor of all corvids was a moderate cacher and that the emergence of specialized cachers evolved independently at least twice. It seems obvious that moderate and specialized species possess the skill of using social information for employing cache protection strategies, and since the ancestors of the western scrub jay were either moderate or specialized cachers and the ancestors of the raven were moderate cachers (de Kort and Clayton 2006), one can legitimately assume that the ancestors of both of these species were able to use social information.

Together these findings indicate that scrub jays and ravens use flexible caching and recovery strategies when hiding and protecting their caches from thieves and also in their role as thieves of others' caches. Their feeding ecology and social system and the evolution of caching behavior have shaped their skills in social information use with respect to storing and stealing.

14.2.1.2. *Jackdaws*

In another corvid species, the jackdaw (*Corvus monedula*), social information may play a role during foraging. Jackdaws are gregarious birds that are especially attentive to their partners' behavior (fig. 14.7; Röell 1978; von Bayern and Emery, in press). However, they are less attentive to conspecifics than ravens (Scheid et al. 2007). Jackdaws feed mainly on invertebrates, including opportunistically catching insects on the wing, but they also forage in flocks on the ground for seeds, etc., with single birds joining these flocks when searching for a food resource (Wechsler 1988a).

Although jackdaws are a noncaching corvid species, they can remember the location of food on the basis of spatial and object-specific information, whereas food-caching Eurasian jays (*Garrulus glandarius*) respond preferentially to spatial cues (Clayton and Krebs 1994b). In a field study on the social influences on foraging, a jackdaw colony was presented with food hidden in nine containers (Röell 1978). The alpha male had been trained to find the food, and which individuals approached and explored the containers was also recorded. The jackdaws hardly ever approached the containers in the absence of others. However, when the alpha male was present and gaining food, other jackdaws immediately joined him, exploring the containers and so learned

FIGURE 14.7. A jackdaw foraging (left) and a conspecific (right) paying close attention (a), then approaching and exploring at the same location (b). Photographs by I. G. Federspiel.

how to open them. Most of the birds learned by supplanting a bird exploring the food source, indicating local enhancement followed by individual learning as the underlying learning mechanism. Similar results were found in a study using two different food dispensers (Wechsler 1988b). The birds had to either press a lever or pull a plastic disk to gain food. The behavior spread through the group within two months, and 22/28 birds learned to press the lever, 23/28 to pull the plastic disk; however, the birds did not preferentially choose to copy the method of their social partner. These results could not rule out individual trial-and-error learning, and it appears that there was some general enhancement effect, because the birds' attention was drawn to the dispensers, but in the beginning of the study they did not seem to know exactly how to operate the mechanisms. A similar result was found in a recent experiment in which jackdaws that had the opportunity to watch a conspecific opening a food box and feeding from it approached the box faster, stayed close to the box for longer, and showed a higher persistency in exploring the box than birds who were tested without demonstrations (Federspiel and Emery, in preparation).

In conclusion, social information seems to play a less vital role in jackdaws than ravens and western scrub jays. Although jackdaws are a more social corvid species, their ecology does not require them to use social information to the same extent as scrub jays and ravens. They feed on abundant types of food; jackdaws may therefore not need to learn much about food via social information. However, the fact that they learn where to find food from their conspecifics in an experimental context shows that they have the capacity to do so. Since their diet does not include hard-to-access or -process foods (no evidence for extractive foraging), they need to learn only the location of the food but not how to process it. Therefore, the relatively simple mechanism of local enhancement seems to be adequate for their requirements.

14.2.2. PSITTACIDAE

14.2.2.1. *Keas*

In contrast to jackdaws, some birds that feed on hard-to-access foods may need more complex social learning mechanisms, such as imitation or emulation, to learn how to access the palatable part of the fruit, nut, meat, etc. One example of the influence of ecology on social information use is the kea (*Nestor notabilis*), New Zealand's mountain parrot. Little is known about the mating system of this species, but certain occasions, such as feeding, appear to bring them together in large gatherings. As juveniles, keas form large flocks and travel around exploring their environment together (Diamond and Bond 1999). A complex dominance network, a relatively long developmental period of the young, and various forms of social and object play may have contributed to their social intelligence (Diamond and Bond 1999; Keller 1975). Furthermore, the lack of predators and the patchy distribution of food in the winter are thought to have led to their extreme neophilia (Diamond and Bond 1999). A group of captive keas demonstrated flexible use of different social techniques to gain food in cooperative tasks (Federspiel 2006; Werdenich 2006), and dominant birds were even found to manipulate lower-ranking birds to coerce them into producing a food reward (Tebbich et al. 1996). In social learning tasks, ambiguous results have been found. In some field studies (tube lifting: Gajdon et al. 2004; rubbish bin opening: Gajdon et al. 2006) and laboratory studies (social learning apparatuses: Pesendorfer 2007), there is little or no evidence of social learning, but in others, indicators of imitation and emulation have been reported. In a task with an artificial fruit and three locking devices (a bolt, a pin, and a screw), birds that observed a conspecific performing the opening sequence displayed shorter latencies to approach the apparatus, a greater persistence in manipulating the devices, and a higher success rate at opening the apparatus than those that did not observe a demonstrator (fig. 14.8; Huber et al. 2001).

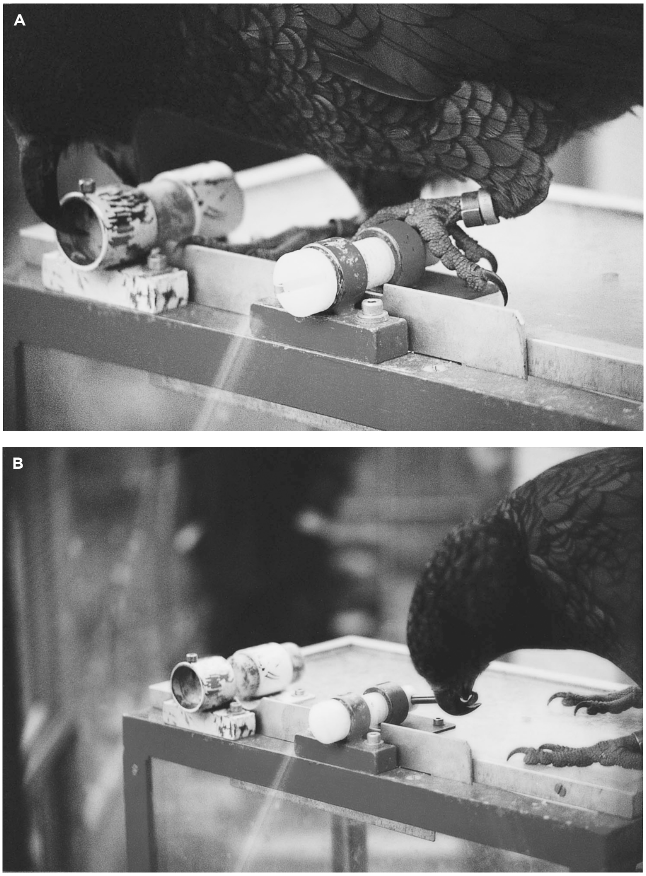

FIGURE 14.8. A kea performing two of the three required actions: (a) poking out the bolt and (b) pulling out the pin. Photographs by L. Huber.

A second experiment with just one opening mechanism revealed keas' use of imitation; a crank had to be rotated repeatedly to get to the food reward, and two of the six observers copied the model's actions rather than just the outcome (L. Huber, personal communication). Although generalization across the whole species cannot be drawn from just two individuals, there does seem to be an indication of the capacity to imitate. Why the keas did not use imitation in the more complex task with the three locking devices remains unclear. There may be an urge to employ individual learning once they have learned about the affordances of an object, that is, what can be done with/to the object.

Ecology must be a strong factor in the keas' use of social information. With no predators around and the urge to always search for food, especially in winter, when the surroundings are covered in snow (B. Campbell 1976), keas have become a flexible, opportunistic, and very curious species (Diamond and Bond 1991). They live in the Southern Alps of New Zealand between elevations of 700 and 2000 meters and in winter fly down to the coast to find food. They feed on at least 89 plant species (including nectar and fruit) and 9 animal species, turning over stones to get to bugs and larvae (Breejaart 1988). Foraging on hard-to-access foods is thought to result in the development of larger brains in primates (K. Gibson 1986), and so the same argument could be made for large-brained birds, such as keas, that feed on similar food types. In general, habitat opportunists show lower levels of neophobia (Greenberg 1990), and island populations show more exploratory behavior (Mettke-Hofmann et al. 2002). This may have led to keas' well-developed manipulation skills and their persistence on instrumental tasks (Kubat 1992), influencing their approach to solving technical problems and the development of an advanced form of technical intelligence. During object play, they train their manipulatory skills and gather information about the affordances of an object (Inglis 1983). They are also well known for their playfulness and destructiveness around human settlements (Forshaw 1977), exploring and tearing apart everything they can get to.

As mentioned earlier, the social component may have also contributed to the keas' skills in social information use. They experience an extended post-fledging period of dependency on the parents and join juvenile flocks in their second summer. Under these conditions there are plenty of opportunities to utilize social information (Lint 1958; Jackson 1963; Porter 1947). Furthermore, there is an intricate dominance hierarchy in kea groups (Diamond and Bond 1999), which resembles a network rather than a linear hierarchy such as found in chickens. Keeping track of relationships in the group may have further driven their skills for picking up social information, similar to pinyon jays.

Evolution also suggests the presence of social information use in the ancestors of the kea. The order Psittaciformes includes roughly 350 species that are commonly grouped into two families, namely cockatoos (Cacatuidae) and true parrots (Psittacidae), although different systematics exist. One tribe of the subfamily of the typical parrots (Psittacinae) is the Nestorini, consisting of three species: the Norfolk kaka (*Nestor productus*), which became extinct in the first half of the nineteenth century, the kaka (*Nestor meridionalis*), and the kea (Pies-Schulz-Hofen 2004). The ancestor of the three species was a "Proto-kaka," which is thought to have lived 15 million years ago, when New Zealand was still a single, large island. During the Pleistocene, New Zealand was dissected into two smaller islands, the climatic conditions changed, and the differences between the northern and southern environments became extreme. The population living under harsh conditions in the south became keas; the population in the north became kakas, which specialized on fruits and insects of the rain forest (Diamond and Bond 1999). During the Holocene, there was an increase in the growth of forests, and the kaka returned to the South Island of New Zealand, pushing the keas out of their foraging niche and thus forcing them into the alpine habitat. Although little is known about the behavior of the ancestors of the kea, their habitat and the extreme changes in temperature and environment they experienced suggest that the use of social information would have been advantageous for them. The kaka's varied diet suggests something similar to the kea. Similarities in the complexity and diversity of social play in keas and kakas (Diamond and Bond 2004) also indicate pronounced social skills in the kaka, a close relative of the kea. The relatively solitary lifestyle and the less complex play of the kakapo (*Strigops habroptilus;* Diamond et al. 2006), another close relative of the kea belonging to the Psittacinae and the tribe Strigopini, indicate that the kea's social information use is a relatively novel phenomenon in evolutionary terms in this group of birds (kea, kaka, and kakapo). However, this is necessarily speculative as it is constrained by information on the number of species.

14.2.3. ANATIDAE

14.2.3.1. *Geese*

Another gregarious species, greylag geese (*Anser anser*), live in large flocks of families and form lifelong pairs in their third or fourth year. Their diet mainly consists of roots, fruits, flowers, leaves, and stems (Cramp 1977). Certain behaviors related to feeding, such as adopting a novel food into the diet, are transmitted via social information use within groups (fig. 14.9).

One year after some individuals were first observed to bite through the stems of butterbur leaves (*Petasites hybridus*), almost all the individuals of a

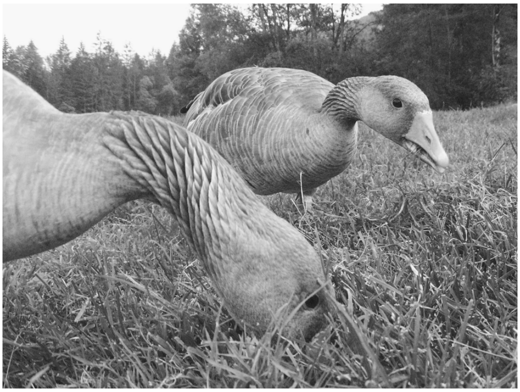

FIGURE 14.9. A goose foraging in the grass (front) and another watching (back). Photograph by I. Nedelcu.

semi-tame flock of geese displayed that behavior (Fritz et al. 2000). The behavior spread particularly quickly between birds that spent most of their time together, such as related animals, suggesting social influence on the learning process (Coussi-Korbel and Fragaszy 1995). It was even observed that ganders left stems to goslings if the goslings approached them while the gander was biting on the stems. To gain an insight into the processes involved, Fritz and colleagues (2000) conducted an experiment with a food box that could be opened by sliding a lid open. A human demonstrator showed seven geese how to open the box, and all seven observers learned the action, whereas only one of the seven control animals that had not received a demonstration managed to solve the task. The observers showed no imitation but explored more often the location at which the demonstrator had touched the box, which facilitated individual trial-and-error learning. Thus, observing an experienced conspecific chewing through the stems of butterbur leaves may have accounted for the spread of the behavior through the group (Fritz et al. 2000; Fritz and Kotrschal 2002).

The social lifestyle of the geese provides them with numerous opportunities to use social information. They are gregarious, except when nesting, live in flocks made up of families, and come together during molting and migration. Individuals in a group support one another actively (participation of a social ally) and passively (mere presence of an ally reduces stress) during agonistic encounters (Scheiber et al. 2005; Weiss and Kotrschal 2004). Lifelong monogamy is the rule, with males and females associating all year round (Cramp 1977). Nevertheless, their diet suggests no particular need to learn from others. They feed on abundant food resources, such as plants on the ground or on the surface of water, flowers, and fruits. It seems that geese will pick up social information if they are able to but do not rely on it. Similar to jackdaws, local enhancement may therefore be sufficient for their requirements.

Although numerous fossil species have been suggested as ancestral to this genus (Brodkorb 1964; Short 1970; Livezey 1986), little is known about the social life of the ancestors of geese, and living close relatives share a similar ecology. Species of the genus *Anser* are largely herbivorous wetland species (Cramp 1977). Given the similar diet and environment, it is unlikely that the relatives and the common ancestor of the genus *Anser* employed more complex forms of social information use.

14.2.4. TETRAONIDAE

14.2.4.1. *Black grouse*

A different form of social information use is employed by some families of the order Galliformes, such as certain game birds of the family Phasianidae (for

Japanese quail, *Coturnix japonica,* see Galef and White 2000; D. White 2004) and grouse (family Tetraonidae). One example is the European black grouse (*Tetrao tetrix*). Black grouse tend to be gregarious throughout the year with stable lekking groups in the spring and less stable groups in the autumn and winter (Cramp 1977). At leks (i.e., mating areas), males gather within sight of each other to court and compete at the outset of the breeding season. They perform mating displays and thus attract females they subsequently mate with (Tomkins et al. 2004).

At the leks, it was found that, after being chosen by one female, a male is generally more likely to be chosen by other females. Further experiments with model females revealed that, rather than just seeing a male close to other females, watching a male actually copulating with a female made him more attractive to other females (Höglund et al. 1995). Young, inexperienced animals may benefit from copying others' choices. Copying the choice of others seems to be a process additional to the normal mate choice process of females (Höglund et al. 1995); since some females may not have the opportunity to copy others, mate choice copying may not always be employed. Although a well-known phenomenon, it seems that the ultimate reasons for mate choice copying are not yet clear. Theories range from avoiding the costs of independently sampling mates, managing information and filtering out the unimportant information, to simply reducing the errors made during mate choice and learning from knowledgeable conspecifics about the quality of potential mates (D. White 2004). Although the costs and benefits of mate choice copying are not clear, using the social information of a conspecific about a male's fitness seems to have an advantage over individual learning. Furthermore, local adaptations of the population in terms of heritably transmitted mate preferences could lead to a change in reproductive patterns and genetic changes (Freeberg 1998, 2004).

The diet of European black grouse consists predominantly of abundant plants, such as berries and grasses (Cramp 1977), suggesting no particular requirement for social information use when it comes to accessing or processing food. Their usage of social information may therefore be restricted to the context of mate choice, but more experimental work needs to be performed to draw firm conclusions.

In terms of the influence of evolutionary history on the existence and the type of social information use, the close relatives of the black grouse may provide an insight. The birds of the genus *Tetrao,* such as the Caucasian black grouse (*Tetrao mlokosiewiczi*), the capercaillie (*Tetrao urogallus*), and the black-billed capercaillie (*Tetrao parvirostris*), all form leks to display and choose mates (Madge and McGowan 2002). Even earlier in the genealogy, within the family Tetraonide, the males are polygamous in all but one species, the willow grouse (*Lagopus lagopus*). This suggests similar social information use in the common ancestor.

14.3. Conclusions

In this chapter we have argued that knowledge of the ecology (environmental pressures), ethology (natural behavior), and evolutionary history of a species is essential for understanding how the mechanisms responsible for social information use have been shaped. However, to understand these mechanisms and to define in what ways, if any, they differ between species we must adopt an integrative approach, combining the 3E's with knowledge of experimental psychology, in order to obtain rigorous experimental validity. Only then can we hope to understand why two behaviors that, when taken at face value, appear identical are in fact examples of convergent evolution resulting from similar ecological, but not evolutionary, histories. Similarly, it is only by taking this integrated approach that we can hope to show that two "different" behaviors share an evolutionary antecedent and components of the same underlying mechanisms. Instead of only analyzing the psychological processes involved in social learning mechanisms, taking these other components into consideration provides us with a more complete picture. There are still obvious gaps in our knowledge that restrict our use of this approach when it comes to investigating the evolutionary history of social information use. For these cases, the 3E's approach may nevertheless be a useful tool for making predictions about how to direct future research. More comparative work is clearly needed to determine the influence of ecology and evolutionary history on social information use, and experiments using different tasks should shed light on whether the capacity to use social information is domain specific.

For example, rooks and jackdaws both pair for life, yet rooks engage in extrapair copulations (Røskaft 1983) and jackdaws do not (Henderson et al. 2000). We might predict that rooks will copy another's choice of sexual partner during acts of promiscuity (because this is within the capacity of the species), whereas we might also predict that it is futile to test mate choice copying in jackdaws because they do not appear to possess the capacity for infidelity. Jackdaws' social information use may be restricted to certain domains (e.g., behavioral coordination within the pair-bond, learning about the location of good food patches), excluding others (e.g., choice of partners during extrapair relations, extractive foraging techniques). We can therefore use knowledge of how the 3E's have influenced a particular species' life history not only to drive the development of appropriate research questions and methodology but also to provide post hoc explanations of successes and failures in psychological experiments. This makes the 3E's approach a very powerful research tool for cognitive ecology—but one that is only as good as the information provided by ecologists, ethologists, evolutionary biologists, and comparative psychologists.

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