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17 Spatial and Social Cognition in Corvids: An Evolutionary Approach

Russell P. Balda and Alan C. Kamil

Research Questions

The central research questions that have guided our studies since 1981 combine issues and techniques from both comparative psychology and avian ecology. Most of our questions originate from the cognitive implications of extensive field studies on the natural history, ecology, and behavior of seed-caching corvids. Because our questions have evolved as our studies progressed, we have chosen to give a historical perspective outlining the progression of our ideas and questions (see Shettleworth, chapter 16 in this volume for a description of a similar program with seed-caching tits and chickadees).

Research Paradigm

Our research program began by examining the amazing spatial memory system of the Clark's nutcracker (*Nucifraga columbiana*). A single nutcracker buries up to 33,000 food items in thousands of different subterranean sites and retrieves them months later with a high degree of accuracy. These birds are highly adapted for this behavior because they possess a strong, sharp bill for opening cones, extracting seeds, and burying them in the substrate; a sublingual pouch (Bock et al. 1973) for carrying large numbers of seeds (up to 90 pinyon pine, *Pinus edulis*, seeds); and strong wings for carrying seeds great distances (up to 22 km). Birds have been observed digging up seeds in the field with seemingly uncanny accuracy (Vander Wall and Balda 1977, 1981; Vander Wall and Hutchins 1983). Although this behavior occurs regularly in the field, field conditions do not allow the design of studies to address the questions of how nutcrackers are able to locate their stored food.

Studies of the cognitive mechanisms involved in cache recovery required the development of a

research plan using controlled laboratory experiments and captive birds. Fortunately, nutcrackers are quite willing to cache and recover seeds in laboratory settings and do so with a high degree of accuracy, both in a sandy floor indoors (Balda 1980; Balda and Turek 1984) or out of doors (Vander Wall 1982), as well as in a room with a raised floor containing sand-filled cups as potential cache sites (Kamil and Balda 1985). The ability to study caching and cache recovery under controlled laboratory conditions allowed us to test hypotheses on how the nutcrackers find their caches.

For example, because we were able to control when and where the birds cached, we were able to rule out odor, marking the site, list learning, and site preferences (Kamil and Balda 1985). We also learned that these birds remember some cache sites better than others and recover food from the better-remembered sites first, and with greater accuracy (Kamil and Balda 1990a). Birds sometimes revisit cache sites after they have recovered the seeds. On these revisits they treat the cache site differently than when they previously emptied it (Kamil et al. 1993). These birds also showed a long retention interval for cache memory, recovering caches with high levels of accuracy up to 9 months after creating them (Balda and Kamil 1992).

The results of several studies showed that nutcrackers were using visual landmarks for accurate cache recovery (Vander Wall 1982; Balda and Turek 1984). Data obtained by using a clock-shift technique, popular in studies of migratory birds and homing pigeons, suggest that seed-caching corvids may use the sun as a compass under some circumstances (Wiltshko et al. 2000). Thus we successfully brought a behavior prominent in the field into the laboratory, where we could examine it in great detail. From these studies we concluded that nutcrackers were using

a spatial memory system to recover their caches and that this system was of long duration and robust (Kamil and Balda 1990b).

Comparative Studies

On the slopes of the San Francisco Peaks in Northern Arizona, five species of corvids cache and recover seeds. These species differ in their degree of dependence on their seed caches to survive winter, as well as in their adaptations for this behavior. The Clark's nutcracker is the most highly specialized of these species and lives at the highest elevations, where winters are harsh and alternative foods are very scarce. At mid-elevations, moderately specialized Steller's jays (*Cyanocitta stelleri*) and pinyon jays (*Gymnorhinus cyanocephalus*) coexist and also cache pine seeds when they are available. Both species have a relatively sharp bill for extracting seeds and an expandible esophagus for carrying pine seeds. A pinyon jay may cache up to 26,000 pine seeds when cone crops are abundant (Balda 1987). At lower elevations, the less specialized western scrub jays (*Aphelocoma californica*) and Mexican jays (*A. ultramarina*) cache and recover seeds much less intensely than the birds at higher elevations. Scrub and Mexican jays possess no morphological adaptations for the harvest, transport, caching, and recovery of seeds, and the lower elevations where they live have mild winters and a year-round supply of arthropods, seeds, and berries.

These differences in natural history raise a compelling question about evolution and cognition. Are these differences in morphological adaptations for food caching, and the concomitant dependence on cached food, associated with differences in the spatial cognitive abilities of these species? Are species that have the highest level of dependence on cached food also better at finding their caches? In a comparative test with three of these species, we found that although all three performed above chance, nutcrackers and pinyon jays recovered their caches more accurately than western scrub jays (Balda and Kamil 1989).

Specificity of Spatial Memory

This difference in the accuracy of cache recovery raises an interesting issue that is important in understanding the evolution of cognitive abilities: Is this spatial memory restricted to remembering where food has been stored or is it more general? Natural selection selects for outcomes, not mechanisms. Thus it could be that the nutcrackers' ability is highly specific. On the other hand, selection could have operated to sharpen already existing spatial cognitive abilities, in which case nutcrackers should perform quite well on a variety of spatial tasks. Therefore, we embarked on a series of comparative studies using different procedures to test spatial memory. These included two- and three-dimensional open-room analogues of the radial maze (Kamil et al. 1994; Balda et al. 1997) and operant nonmatching-to-sample tests. These studies all involved spatial memory, but not the recovery of food previously cached. The results of these studies were consistent with our hypothesis. The species most dependent on seed caches for winter survival performed at higher levels. If dependence on stored food has selected for improved spatial cognitive abilities, it has done so in a way that is not completely domain specific.

However, there is some specificity. Olson et al. (1995) tested three species in an operant nonmatching-to-sample test. In one experiment, the birds were required to remember a spatial location; in another, a color. As in many other experiments, the most seed-dependent species performed best in the spatial test, showing much longer retention intervals. However, this difference disappeared completely during the color test. This suggests a modularity for spatial cognition.

Social Cognition

More recently, we have become interested in extending our natural history-based analysis of cognition to another domain. Primatologists (e.g., Humphrey 1976) have developed a hy-

pothesis about the evolution of intelligence based on the cognitive demands of sociality. Animals that live in large, stable social groups must be able to assess the consequences of their behaviors, classify other animals as members of various groups and coalitions, and recognize and remember traits of many other individuals. Success within the group will be improved if an individual possesses a rich internal representation of the group that will allow it to adjust to the fluid nature of the group. These cognitive demands will necessarily increase as group size increases and can be expected to be greatest for those animals living in larger, well-structured groups. Although the social complexity hypothesis has been considered primarily for primates, its logic is general and its implications can be tested with any appropriately chosen taxon (Balda et al. 1996).

The species we have worked with vary considerably in sociality. Pinyon jays are possibly the most social bird in North America, living in permanent groups of up to 400 individuals. Many of these individuals never leave their natal flock. Mexican jays are also highly social, living in relatively stable groups of 12–18 individuals, where helping at the nest is especially prominent. The Clark's nutcracker and western scrub jay, in contrast, live in family units or pairs year round. Young of the year disperse before the next breeding season. These differences in social living led us to hypothesize that pinyon jays and Mexican jays should be able to solve more complex cognitive tests than the less social nutcracker and western scrub jay. If this hypothesis is correct, the ordering or gradient of the four species will be different from that along the dependency gradient; that is, nutcrackers and scrub jays should perform poorly whereas pinyon jays and Mexican jays should demonstrate superior cognitive skills.

The selection of appropriate tasks for testing this hypothesis presented a challenge. We began with some comparative studies of observational learning. In one series of experiments, nutcrackers, pinyon jays, and Mexican jays watched a conspecific make caches in a room

with many open holes for caching in the floor. The observer bird could view all areas of the floor. Later the observer was allowed to attempt to recover the caches it had observed being made. While pinyon jays and Mexican jays recovered caches with an accuracy above chance levels, nutcrackers did not perform above chance (Bednekoff and Balda 1996a,b).

In another experiment, pinyon jays learning a novel task were facilitated by being able to observe a conspecific performing the same task, but nutcrackers were not so facilitated (Templeton et al. 1999). In a third experiment (Bond et al. MS), pinyon jays performed better than western scrub jays in an operant test of transitive inference. Further studies of the ability to identify conspecifics and to form equivalence sets are planned for the near future.

Methodologies

We have combined two methodologies. First, we have used a classical biological comparative method, comparing closely related species that differ in their adaptations. This necessarily involves using natural history as a clue for asking relevant questions about relevant species. Principles of Darwinian evolution are central for understanding the dynamics of biological systems. The results of our studies led us to an important conclusion concerning the evolution of cognition. The accuracy of locating seed caches is an adaptive trait and as such is shaped by the actions of natural selection.

Cognitive abilities are a part of the adaptive arsenal that consists of a collective suite of characters that allows for swift and efficient harvest, transport, and caching and then accurate recovery of the cache at a later time. As such, cognitive traits can be viewed as playing a role in the biological success of an organism, much as morphological and physiological traits do. Species differences reflect, in part, differences in selective pressures among the species that are due to differences in their ecologies. Thus, cognitive pro-

cesses have evolved and must be viewed as biological processes, not only because they have their roots in neurophysiology, but also because they are biologically significant as adaptations that contribute to the biological success of the organisms so endowed.

Second, we have dealt with the learning–performance distinction that bedevils comparative studies of cognition by using multiple behavioral test procedures. That is, if one species performs differently from another in any specific test, this could be due to differences in how well the test situation is suited to each species rather than to differences in ability. However, when substantially different tasks (such as cache recovery and operant tests) produce similar patterns across species, the likelihood that the behavioral differences are due to real species differences in ability grows. These varied tests provide converging operations, an approach first outlined by Kamil (1988).

Internal States

Our experiments are designed to inform us about the knowledge that our birds possess about their physical and social environments. We do not generally think of this knowledge in terms of internal psychological states because the meaning of this term is unclear. We take the term *internal psychological states* to be equivalent, at least for some people, to internal subjective states (e.g., awareness or consciousness), and we have never found it useful to speculate about the subjective states of our birds.

Future Work

Cache Location

Although it is well established that Clark's nutcrackers (and other seed-caching birds) remember their cache sites, we know relatively little about exactly what they remember. To put it

another way, how does a nutcracker know when it is at a cache site? We know that they use the position of landmarks to locate caches (e.g., Balda and Turek 1984). Kamil et al. (1999) compared the body orientations used during caching with those used during recovery. We found that nutcrackers perform just as accurately when they use different orientations as when they use the same orientation. This suggests that they remember each site separately. Recently, Kamil and Cheng (2001) suggested that when the distances between the landmarks and the goal are relatively great, as they often are in nature, the birds remember the directional relationship between the goal and each of several landmarks. We are beginning a series of experiments to test this hypothesis.

Selection for Spatial Cognition

The results of comparative studies such as those reviewed here that indicate that spatial cognition is correlated with dependence on cached food are consistent with the hypothesis that in food-storing, scatter-hoarding species, natural selection has favored spatial abilities. We are currently attempting a more direct test of the hypothesized link between cognitive abilities and biological fitness in natural populations by obtaining measures of spatial abilities and measuring reproductive success in a wild population of pinyon jays.

Social Cognition

Our initial results of the social cognition hypothesis (outlined earlier) are quite exciting. We hope that we and other investigators will be able to expand this work in two ways. First, many more taxa need to be studied, so that we have many independent comparisons, each testing the hypothesis (Felsenstein 1985; Kamil 1988). Second, more tests of social cognition need to be developed and used in this effort.

From Limits to Opportunities

Yesterday's limits are often today's opportunities, and we are reluctant to set limits on the study of animal cognition. However, the study of the adaptive nature of animal cognition and its evolution is much more difficult and challenging than the study of morphological and physiological traits for a number of reasons. Animals are not necessarily programmed to maximize the performance of cognitive behaviors with the same degree of certainty that they often exhibit in morphological and physiological experiments. Cognitive behaviors are often more subtle, are governed by very complex and involved neural circuitry that is not obvious, and are not often performed with maximum intensity. As Humphrey (1976) once pointed out, we would learn little from watching Albert Einstein through a pair of binoculars!

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