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. As 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 chapter by Shettleworth, this volume, for description of similar program with seed-caching tits and chickadees).

I. 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 retrieve them months later with a high degree of accuracy. These birds are highly adapted for this behavior as 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 with seemingly uncanny accuracy in the field (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 were able to re-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 with 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 zero in on just 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, or site preferences (Kamil and Balda 1985). We also learned that these birds remember some cache sites better than others and recover 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 nine 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). Using a clock-shift technique popular in studies of migratory birds and homing pigeons data suggest nutcrackers may use the sun compass under some circumstances (Wiltschko 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 this system was of long-duration and robust (Kamil and Balda 1990b).

II. 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 and lives at the highest elevations where winters are harsh and