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The Ecology and Evolution of Spatial Memory in Corvids of the Southwestern USA: The Perplexing Pinyon Jay

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The ecological stage

It is a cold, crisp morning in mid-September at about 1800 m in the pinyon-juniper woodland in north-central Arizona, on the lower slopes of the San Francisco Peaks. Most Pinyon Pine (*Pinus edulis*) trees bear some green cones and a few bear hundreds, if not thousands. The “locals” refer to this situation as a “bumper crop”, and the Native Americans will be busy harvesting the pine seeds for food and profit. The cones have spineless scales still tightly closed over large, wingless, highly nutritious seeds. Pitch glistens off the cones as the early morning sunlight strikes. Soft “kaws” and “ka-ka-kas” can be heard in the distance. Suddenly the Pinyon Pine trees explode with hundreds of medium-sized light blue birds hopping and flying about, attacking pine cones, some by pecking at the green cones attached to the branch, some by attempting to break cones free of their twigs. Loud “kaws,” “kraws” and all variations on the crow call are heard continuously. A flock of 150 Pinyon Jays (*Gymnorhinus cyanocephalus*) has just descended on the area to begin their day-long

seed harvesting. The birds seem very peaceful and seldom engage in agonistic behaviors while intently harvesting seeds. Within minutes it sounds like the drumming of a hundred woodpeckers as birds hammer at the closed cone scales while standing or hanging on the cones. Birds that have successfully removed cones carry them to forked branches where they wedge the cone securely into the fork. Birds now hack the cone scales to smithereens in their attempt to get at the prized Pinyon Pine seeds. A small pile of empty cones gradually accumulates under these forks. Are these forks tools in the same sense that man uses an anvil? Ripening seeds are extracted with a stout, sharp bill that is curiously feather-free at its base. Through all this frenzy, birds are careful not to smear sticky pitch on to their bills. The feather-free area of the bill certainly aids in this attempt. As harvesting continues, torn cone scales fall like rain drops from the pine trees. Every bird in the flock, males and females, young and old, seem intent on harvesting its share of seeds (Marzluff and Balda, 1992).

This commotion has attracted the attention of other birds. A few rather large gray, black and white birds join in the exploitation of seeds from cones. These birds have massive, sharp-pointed bills with which they can tear open a green pine cone in a matter of minutes. After some time the throats of these birds begin to bulge with seeds, and the birds leave the flock of Pinyon Jays and fly high up onto the nearby San Francisco Peaks with long, strong wings that may carry them up to 22 km from the harvest area. Loud sharp drawn-out "kaas" often signal their departure. Most often these birds are seen singly or in small groups of 2-5. The Clark's Nutcrackers (*Nucifraga columbiana*) have departed with their share of the bounty.

Another bird attracted to the hustle and bustle of cone opening is a slender, quiet, light-blue bird with a short, rather weak bill, the Western Scrub Jay (*Aphelocoma californica*). This bird's demeanor is just the opposite of the nutcracker and Pinyon Jay, which are both bold and noisy. The Scrub Jay sits inconspicuously hidden in thick vegetation, waiting and watching. When an individual of one of the other species has broken or removed all the cone scales from the cone it has been working on diligently, our silent stalker screams loudly and flies directly at the unsuspecting forager. Invariably, the foraging bird is frightened, drops the cone and flies off. The Scrub Jay retrieves the partly opened cone and proceeds to pry out the partly exposed seeds. This is the only way this species, with its relatively weak bill, can share in the bounty until the cone scales mature and open naturally (Vander Wall and Balda, 1981). After placing 3-5 seeds in its mouth and bill, the Scrub Jay flies a short distance behind some vegetation, to sit quietly on a branch before descending to bury its seeds secretly in subterranean caches.

In areas where Pinyon-Juniper woodland and Ponderosa (*Pinus ponderosa*) Pine forest interdigitate to form an ecotone, Steller's Jays (*Cyanocitta stelleri*) also participate in this seed harvest. This jay has a partially distensible esophagus in

which it can carry up to 18 seeds. It is not a strong flier, does not have a particularly strong bill, and only carries seeds 2-3 km into the Ponderosa Pine forest (Vander Wall and Balda, 1981).

As the pine seed harvest progresses this morning, casual observation reveals that the throat region of the Pinyon Jay is beginning to swell as well. Soon, a few birds with throats bulging, and then many, appear at the tips of high trees where they perch silently. Shortly thereafter, a rhythmic series of "kaws" spreads as a loud din throughout the flock and the remaining birds leave the ground and fly up to perches in the low trees. The flock then departs in unison for one of their traditional caching areas that this flock uses every year. Birds usually fly just above tree level on their way to the caching area where the harvested seeds will be stored in subterranean caches. These traditional areas, which may number 8-10 for a flock, will often be some kilometers from the harvest area (Marzluff and Balda, 1992). After the flock departs, the area becomes deadly silent.

We have just witnessed a flock of Pinyon Jays and three flocking associates (Balda *et al.*, 1972) harvesting Pinyon Pine seeds from green cones. This autumnal foraging frenzy by nutcrackers and Pinyon Jays in the southwestern USA will continue from sunrise to sunset every day as long as fresh cones are available and the ground is free of snow. In some areas the species composition will differ but the process is the same. For example, 130 km south of the location described above, no Pinyon Jays exist, but Mexican Jays (*Aphelocoma ultramarina*) harvest pine seeds there. In areas to the north, Black-billed Magpies (*Pica pica*) are involved in the seed harvest (Balda, personal observation).

The exploitation of pine seeds by species of the family Corvidae is a common occurrence in the western USA. These pine seeds are all nutritious, but the seed of the Pinyon Pine is especially so, containing up to 18% protein and 60% fat (Bodkin and Shires, 1948; Blair *et al.*, 1995). This is powerful fuel to sustain these birds through the long, cold, unproductive winter. The behavior of nutcrackers and Pinyon Jays is immediately altered at the sight of these cones or seeds as they abruptly stop all other behaviors and begin harvesting. These birds spend vast amounts of time and energy harvesting, transporting, and caching these seeds. This dramatic change in behavior is a clue that these pine seeds are of special biological significance, at least to some of these corvids. Even when these seeds are placed in conspicuous traps, some Pinyon Jays will allow themselves to be captured 3-4 times in a single day in their attempt to collect these seeds (Marzluff and Balda, 1992). Once, when a trap was set in the snow and pine seeds placed inside the trap, directly on the snow, Clark's Nutcrackers tunneled under the trap in an apparent attempt to get the pine seed without entering the trap (Balda, personal observation). Eurasian Nutcrackers (*Nucifraga caryocatactes*) that had dispersed thousands of kilometers into Germany owing to lack of pine seeds in Siberia immediately began harvesting, eating and caching seeds when presented to them (Conrads and Balda, 1979). We

know of no other object or substance that is so addictive to birds as these pine seeds are to these corvids.

The pine tree also has an interesting role in this ecological play. In one out of every five to six years, the Pinyon Pines make it easy for the jays and nutcrackers to harvest their seeds. In these years, every Pinyon Pine tree for kilometers may produce hundreds or even thousands of cones, and the birds do not have to travel far to locate seeds (Ligon, 1978). Seeds are extracted with ease as the pine cones have no sharp spines on their relatively short cone scales to deter extraction. Cones are easily located as they face outward and upward on the tips of branches, and their seeds are held tightly in the cone scale after opening. These traits make it relatively easy for the birds to collect large numbers of seeds (Vander Wall and Balda, 1977). In these years, it is as if the trees are bearing their crop of pine seeds in a manner that facilitates harvesting by jays and nutcrackers (Smith and Balda, 1979; Balda, 1980a). In sharp contrast to these years of bountiful production, there are periodic lean years. In one out of every 5-6 years, trees over a large region may be absolutely barren of cones. In the majority of years, however, pine cones are produced in modest to heavy amounts in small geographic areas or "hot spots," interspersed with areas of no cone production. Nutcrackers have been observed making long exploratory flights in late summer that appear to be for the purpose of locating these pockets of cones (Vander Wall and Balda, 1977). In autumns when the pine cone crop fails on the home range of a Pinyon Jay flock, the flock sometimes departs its home range in search of these "hot spots" (Marzluff and Balda, 1992). Thus, during most years, these strong fliers were able to take advantage of cone crops outside of their normal range of occupation. Relatively strong powers of flight may have been a preadaptation for seed-caching behaviors to become fully developed (Vander Wall and Balda, 1981). The Mexican and Scrub Jays are certainly much weaker fliers than nutcrackers and Pinyon Jays, and therefore can not take full advantage of scattered crops of pine cones that occur in most years. These species must "sit and wait" for a crop of pine seeds to occur where they exist.

The actors

The corvids of the southwest possess many adaptations for the harvest, transport, caching and recovery of pine seeds. However, there is a large degree of between-species variation in the distribution of these traits. These corvids have a well-accepted phylogeny (Hope, 1989), live within close proximity to one another and have relatively well-known natural histories. They therefore present an excellent opportunity to apply the comparative method (Kamil, 1988) to the study of these species differences (Balda *et al.*, 1997). The comparative method for the study of adaptation and evolution of behavioral traits begins with a care-

ful study of the natural histories of the study species which should reveal how a particular trait (or suite of traits) is utilized, and provide some information about the selective pressure and potential fitness which differentially influence the trait in the different species. Species differences (and similarities) in the use of the trait can be attributed to the ecology and/or phylogeny of the species. Two processes are particularly powerful in these types of investigations, convergence and divergence. Convergence leads to similarities among distantly related species owing to the influence of similar ecological constraints. Divergence leads to differences among closely related species that correlate with the influence of different ecological constraints. The strongest support for the evolution of a trait or set of traits is found when one can find patterns of convergence between distantly related groups and divergence between similar groups for a single suite of traits. Here, we examine the natural history of the various southwestern corvids with particular attention paid to the traits involved in seed harvest, caching and cache recovery.

Clark's Nutcracker

This 144-150 g species is a member of the genus *Nucifraga*, which includes only one other species, the Eurasian Nutcracker (*N. caryocatactes*). Clark's Nutcracker is believed to be the more ancient of the two (Goodwin, 1986). Named for Captain Clark of the Lewis and Clark expedition, these birds range from central British Columbia to central Arizona. They live and breed at high elevations within coniferous forest and up to the treeline, where in winter they experience low temperatures, high winds, deep snow and many cloudy days. Primary and secondary productivity is nil in winter and birds depend on their cached food for winter survival and reproduction, using this food for between 80 and 100% of their winter diet (Giuntoli and Mewaldt, 1978). Nutcrackers continue to draw on their caches into the next summer, 9-11 months after they have been made (Vander Wall and Hutchins, 1983). Birds may undertake long-distance irruptions when the pine cone crop fails (Davis and Williams, 1957, 1964; Vander Wall *et al.*, 1981).

Clark's Nutcrackers are well equipped for the harvest, transport, caching, and recovery of hidden pine seeds, which play a major role in the annual cycle of these birds (Figure 1). Nutcrackers have a relatively long, stout, sharp bill which is a very efficient tool for opening green pine cones, extracting seeds and burying seeds in the substrate. Both species of *Nucifraga* possess a sublingual pouch, a unique structure that opens under the tongue, and that can hold up to 90 medium-sized Pinyon Pine seeds (Bock *et al.*, 1973). The sublingual pouch is often full during transport of seeds from harvest area to caching area. These strong-flying birds range widely in search of seeds and have been observed carrying pouches full of seeds up to 22 km. In a year when pine cones are superabundant, a single nutcracker will cache between 22,000 and 33,000 individual

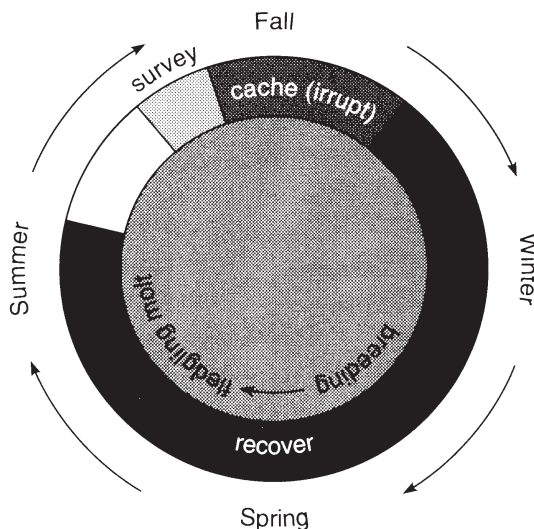


Figure 1. Yearly activity pattern of pine seed use by nutcrackers. The outer circle describes the different behaviors associated with different periods of the year.

seeds in about 6,000-8,000 subterranean caches. Nutcrackers can distinguish between edible and inedible seeds by “bill clicking” and “bill weighing” (Ligon and Martin, 1974) and also by color (Balda, personal observation). Edible seeds have a dark brown seed coat, whereas inedible seeds have a light brown to yellow seed coat.

Birds cache seeds on their breeding territories and also on “communal” caching areas where winds are strong and snow melts rapidly. These are communal areas in the sense that many birds may intermix caches and the birds do not act aggressively towards each other. Caches, however, are not shared communally with other individuals. In these areas, nutcrackers act very secretly, often perching in a tree for several minutes, peering down intently before swooping to the ground. After a few hops, the bird stops, drives its long bill into the ground with a strong plunge, as if to test the substrate and then proceeds to place up to 14 seeds in a cache, forcing them in with strong, direct thrusts of the head and bill. The seeds in the sublingual pouch are retrieved into the mouth with strong downward strokes of the head. After caching, the bird usually smooths over the soil or places an object such as a leaf, twig, piece of moss, or pine cone on the site. If no object is placed over the cache, it is almost impossible for a human observer to locate the cache. Objects that are placed over the sites seldom remain there for more than a few days (Balda, personal observation). Birds seldom spend more than 30 seconds creating a single cache.

Even at the high elevations inhabited by these birds, they breed in late winter and early spring in large, well-insulated nests. They are also known to feed pine seed to their nestlings (Mewaldt, 1956), a trait shared with few other birds.

Pinyon Jay

Pinyon Jays live and breed from Oregon, Montana, and South Dakota to Baja California, central Arizona, and New Mexico. These 100-125 g birds inhabit the Pinyon-Juniper woodland and lower reaches of the Ponderosa (*Pinus ponderosa*) Pine forest, where winter conditions can be harsh. This bird is probably the most social bird in North America, living and breeding in permanent flocks of 50-500 individuals on large home ranges. These birds nest colonially, and often use the same traditional areas for nesting year after year and other traditional areas for caching seeds. Seed caching by the Pinyon Jay is a social event, as birds harvest, transport and cache seeds as a collective unit. Upon arriving at a caching area, birds quickly descend to the ground. Flock members usually walk (not hop) in the same direction as they rapidly stick seeds in the ground. Sometimes they move at a brisk pace as they hide seeds singly in caches, either in a straight line or in small circles. Birds spend less than 15 seconds at each cache site and "a dozen caches could be made in a minute or less" (Stotz and Balda, 1995). Sometimes birds are shoulder to shoulder during these caching bouts. Pinyon Jays rely heavily on pine seeds in winter when they constitute between 70% and 90% of the diet (Ligon, 1978). Pinyon Jays draw upon their caches for 6-7 months after they are created. These jays are known to perform long-distance irruptions when pine cone crops fail (Westcott, 1964; Bock and Lepthien, 1976).

Pinyon Jays possess a relatively long, sharply pointed bill that is featherless at its base. The loss of nasal bristle may be an adaptation to dig more deeply into pine cones without getting pitch on the bill or nasal bristles. Pinyon Jays can readily open green pine cones, and can hold and carry pine seeds in an esophagus that is distensible for about two-thirds of its length. This structure can be expanded to hold up to 39 medium-sized pine seeds (Vander Wall and Balda, 1981). Birds have been observed flying up to 12 km with throats full of seeds. When cones are common, a single Pinyon Jay may cache up to 25,000 seeds in an autumn (Balda, 1987). Ligon (1978) estimated a single flock of Pinyon Jays cached 4.5 million seeds in one autumn. Birds can distinguish between edible and inedible seeds by color, as well as "bill-weighing" and "bill-clicking" (Ligon and Martin, 1974). Like the nutcracker, Pinyon Jays began nesting in late winter and early spring, especially when a large crop of seeds occurred the previous autumn. Nestling Pinyon Jays are fed a diet containing between 10 and 32% pine seeds (Ligon, 1978; Bateman and Balda, 1973).

Aphelocoma jays

Western Scrub Jays and Mexican Jays (*Aphelocoma ultramarina*) live at lower elevations and experience much milder winter conditions than either Pinyon Jays or Clark's Nutcrackers (Pitelka, 1951). They are less dependent on stored

food for winter survival and concomitantly have few special adaptations for the harvest, transport, caching and recovery of pine seeds. Western Scrub Jays (weighing about 95 g) inhabit the Pinyon-Juniper woodland from Oregon to Baja California, the Mexican plateau, and southwestern Mexico. These jays breed in pairs on territories, have short broad wings and are relatively weak fliers, when compared to nutcrackers and Pinyon Jays, although they can maneuver well in dense Pinyon-Juniper stands (Pavlick, Balda, and Bednekoff, unpublished data). These birds do not engage in irruptive behavior in years when cone crops fail. They do cache pine seeds, but are noticeably less motivated to do so than are Pinyon Jays and nutcrackers (Hall, unpublished data). Balda (1987) calculated that a single Scrub Jay, in a year with a good cone crop, may cache up to 6,000 Pinyon Pine seeds. These jays have no morphological adaptations for carrying seeds and can carry only 3-5 seeds in the mouth and bill. The bill is rather short and broad (Peterson, 1993) and not strong enough for prying open cones with green cone scales. Consequently, Western Scrub Jays must wait for the normal opening of the cones before they can harvest seeds. In years when the cone crop is poor, nutcrackers and Pinyon Jays can harvest the entire crop before the cones open naturally. In these cases Scrub Jays can harvest only the seeds they can steal using their kleptoparasitic behaviors described above. This species usually caches seeds under trees and bushes, although on occasion it will venture into small openings and treeless valleys to cache (Hall, personal observation). Little is known about the caching behavior of the highly social Mexican Jay except that it does spend considerable time and effort caching pine seeds each autumn, and recovers them through the winter and early spring (Gross, 1949; Brown, 1963; J. L. Brown, personal communication). Both *Aphelocoma* species do not breed particularly early, nor do they feed seeds to their nestlings.

A comparison of the characteristics of these four species based on their ability to harvest and cache seeds is presented in Table 1. The two species that show the greatest number of behavioral, morphological and ecological adaptations for this behavior, the Clark's Nutcracker and Pinyon Jay, also cache the largest number of seeds each autumn. They are stronger fliers and move pine seeds greater distances from harvest to cache sites. Nutcrackers and Pinyon Jays are highly dependent on cached seeds during the long, cold, harsh winter for survival and reproductive energy. When cone crops fail, they undergo major irruptions, moving hundreds of kilometers out of their normal range (Davis and Williams, 1957, 1964). In contrast, the two *Aphelocoma* jays, which live at lower elevations and in more hospitable winter climates, are less dependent on cached seeds for winter survival because other seeds and berries are available, and some insects and arachnids are active throughout the winter. These two species do not undergo long-distance irruptions when cone crops fail, as alternate foods are available. They breed in spring and do not feed seeds to their young. Thus, these four species show a clear specialization

Table 1. Comparison of Physical and Natural History Traits for Harvesting and Caching Seeds by Four Corvid Species.

Trait	Clark's Nutcracker	Pinyon Jay	Scrub Jay	Mexican Jay
Breeding habitat	High coniferous forest (2300-3200 m)	Ponderosa Pine forest/Pinyon-Juniper woodland (1700-2100 m)	Pinyon-Juniper woodland (1700-2000 m)	Pine-Oak woodland (1800-2100 m)
Winter weather conditions	Extremely harsh	Harsh	Moderate	Moderate
Dependence on caches for winter food	Yes	Yes	No	No (?)
Time of breeding	Late winter	Late winter	Spring	Spring
Seeds fed to nestlings	Yes	Yes	No	No
Body mass	150 g	125 g	100 g	140 g
Bill shape	Long, stout, sharp	Moderately long, stout, sharp	Short, broad, hooked	Short, broad, hooked
Seed-carrying structure	Sublingual pouch	Distensible esophagus	Mouth, bill	Mouth, bill
Maximum number of seeds transported	90	39	4-5	4-5 (?)
Maximum distance seeds transported	22 km	11 km	1-2 km	1-2 km (?)
Number of seeds per cache	Many	1	1	1 (?)
Maximum number of seeds cached per season	33,000	22,000	6,000	(?)
Social structure during caching and recovery	Single, pairs	Highly social	Single, pairs	Highly social
Duration of cache utilization	9-11 months	8-11 months	6 months	6 months (?)

gradient in both morphological and behavioral traits, from more highly specialized obligate species, to more generalist species that act opportunistically when cone crops are present.

The evolutionary play

How did this particular assemblage of corvids end up in north central Arizona? Where did these birds first appear? Who were their ancestors? How did the seed-caching habit come into being? What is the pine tree and seed doing in this scenario? These are all important questions that need to be explored if we are to understand fully how evolution, ecology, behavior, and psychology are interrelated in the development of a set of adaptations. To answer them we need first to consider the taxonomy and biogeography of this group in order to clarify the evolutionary relationships of these species.

Taxonomy and biogeography of the players

There is little doubt that the Clark's Nutcracker is an Old World corvid, a descendent of an ancient, unspecialized relative of the Eurasian Nutcracker (*Nucifraga caryocatactes*) and probably invaded the New World via the Bering Land Bridge during the Pleistocene (1 million years ago) and possibly brought a bird-dispersed species of pine with it (Stegmann, 1934, personal communication; Lanner, 1981; Tomback, 1983)! The coniferous forest of Alaska and the western Canadian mountains probably provided all necessary niche requirements for this species. The extension of this forest type down the west coast of Canada provided a natural corridor for the southward colonization of the nutcracker (Figure 2). Because of their ability to monopolize conifer seeds and breed early, and because they are strong and aggressive birds, they may have spread rapidly southward. The Cascades, Sierras, and Rockies provided excellent corridors for the nutcracker to use to extend its range down into the southwestern USA. In areas from California and Colorado south where Pinyon Pines grew at lower elevations, nutcrackers were quick also to take advantage of that seed source once they encountered them. The seeds of the pinyons are very similar in size and shape to those of *Pinus cembra*, the Old World Stone Pine favored by Eurasian Nutcrackers in the Old World. The above scenario is the most plausible for the invasion and distribution of Clark's Nutcracker into the Nearctic.

The taxonomy of the New World Corvidae has been dealt with by many authors (Amadon, 1944; Pitelka, 1951; Hardy, 1969; Ligon, 1974; Goodwin, 1986; Zusi, 1987; Hope, 1989). There is general agreement about the taxonomy of the New World corvids except for the status of the Pinyon Jay. The question of the origin of the Pinyon Jay has driven avian taxonomists crazy for the past cen-

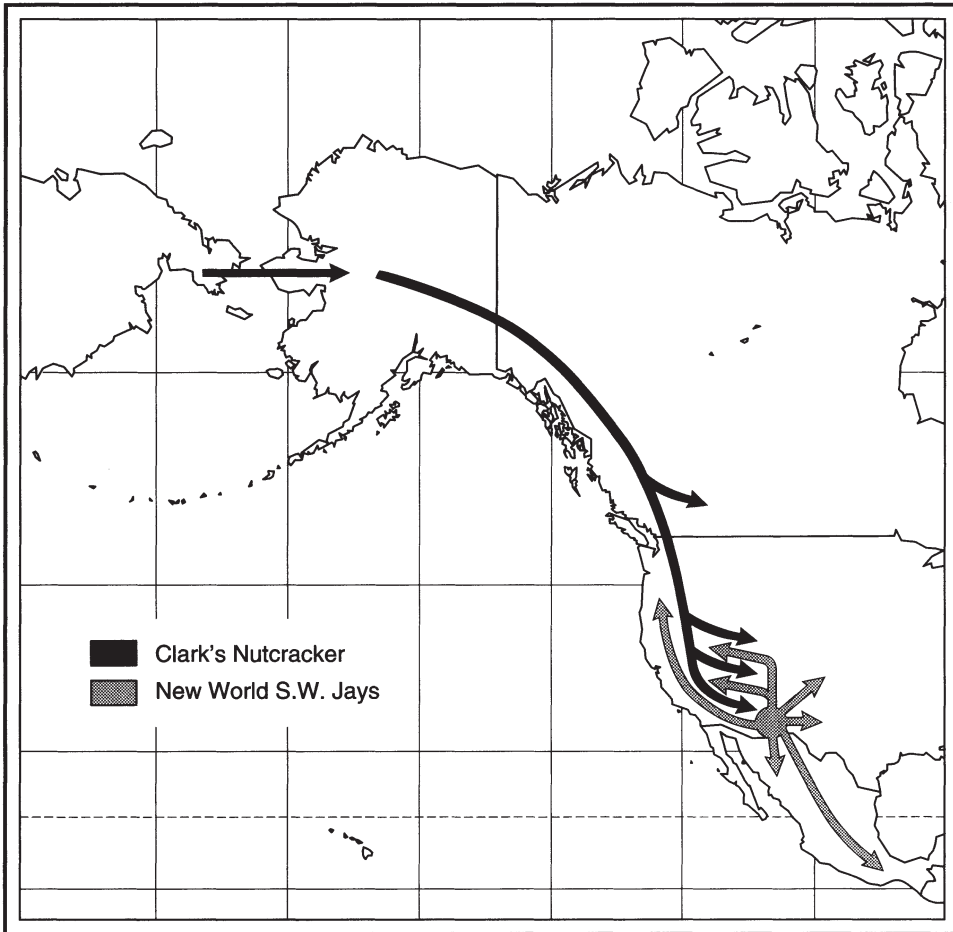


Figure 2. Colonization of North America by nutcrackers and southwestern US jays. Nutcrackers used the Bering Land Bridge and jays differentiated on the Mexican Plateau.

tury. This species has been referred to as the Blue Crow, the Pinyon Crow, and Maximillian's Crow. While some taxonomists have argued that the Pinyon Jay was of Old World origin, essentially an Old World crow or nutcracker with a mutated blue plumage, others argued that it was of American origin and closely related to the *Aphelocoma* jays. In 1969, Hardy referred to it as "a jay in color only" (but see Ligon, 1974), and as late as 1970, Mayr and Short (1970) stated that the relationship of the Pinyon Jay was "obscure." Others, such as Amadon (1944) and Goodwin (1986), considered the similarity between nutcrackers and Pinyon Jays to be a homoplasy, a case of character convergence owing to intense use of pine seeds for survival and reproduction. Zusi (1987) showed convincingly that the Pinyon Jay possesses a type of jaw articulation with a pe-

culiar morphological “buttress” that is present in almost all New World jays and absent in Old World corvids. He argued that Pinyon Jays and nutcrackers were convergent on many aspects of morphology and behavior for the harvest of pine seeds. This hypothesis received strong support from Hope (1989). She used a series of morphological characters and found that the closest relative of the Pinyon Jay was the Mexican Jay. Scrub Jays were also closely related to Pinyon Jays. Thus, it seems reasonable to conclude that the complex of species that includes the Western Scrub Jay, Mexican Jay, and Pinyon Jay arose on the Mexican Plateau in the southwestern USA and northern Mexico (Pitelka, 1951; Lanner, 1981, 1996), in an area covered with Madro-Tertiary Flora. As the climate and food sources permitted, these species then colonized new areas to the north and occupied their present distribution by the end of the Pleistocene, 11,000 years ago.

Coevolution by bird and tree

One cannot describe the evolution of food storing in southwestern New World jays without brief mention of the trees that coevolved with them. Without the Pinyon Pines, there would be no modern Pinyon Jay. This information has been reviewed most extensively by Lanner (1981, 1996). The Madro-Tertiary Flora contained a number of tree species that were drought-resistant and able to withstand a climate that was changing from subtropical warm/moist to hot/dry about 60 million years ago. The normal pines with small seeds would have had severe problems becoming established because the seeds provided only a minimal amount of energy and nutrients for the seedlings during the critical time of early growth. Moisture was scarce and the drying winds hot. A larger seed, however, would allow the plants to germinate and successfully establish themselves before depleting all nutrients and energy from the embryonic tissues. These larger-seeded pines would not only be successful at traditional germination sites but also in many more sites because the additional energy and nutrients they contained would allow the tree to penetrate into what had originally been inhospitable areas. Thus, large-seeded plants would leave more offspring than small-seeded ones, and natural selection would have favored the large-seeded individuals.

However, the price for producing these larger seeds was high. The trees had to capture additional, valuable materials, and the larger, more conspicuous seeds would be more attractive to predators. Trees now had an “adaptive choice” to make. They could produce relatively few high-quality seeds each year and gamble that seed predators would not get them, or produce a huge crop of seeds at longer, unpredictable intervals. Short-lived seed predators would die between cone crops and long-lived species would be forced to survive on other sources of energy, and thus not be able to specialize on this seed type. When the ancient pines did produce a mass of seeds in a single sea-

son, they could "swamp" the seed predators. The number of seeds produced would be very high, the number of seed predators would be relatively low and many seeds would survive to germinate. The timing of seed production had to be synchronized among all neighboring pine trees in the area, for a tree out of synchrony would be at a severe disadvantage and have all its seeds consumed by predators (Ligon, 1978).

We can only speculate that the combination of severe climatic conditions and persistent seed predators was responsible for the pattern of seed production seen in Pinyon Pines. These large seeds would not be transported with ease by wind, water, or gravity, the usual ways pine seeds are dispersed. Yet, as the Pinyon Pine ancestor(s) left the Mexican Plateau, this species spread rapidly northward through Arizona and New Mexico and into southern California by 25 million years ago, and by 11,000 years ago it had the distributional range we see today. With the advent of the great advances and retreats of the glaciers, the pinyons showed similar movements. After the last glacial retreat, pinyons still continued their active movement into hospitable regions when they became available and out of those areas when they became inhospitable. In fact, paleontologists generally agree that Pinyon Pines, because of their active movement patterns, must be (and have been) moved by a dispersal agent other than wind, water, or gravity. The paradox is complete: the seed is large and wingless, yet moves rapidly over the landscape. The most likely scenario is that the seeds did indeed move on wings, the wings of Pinyon Jays.

Our scenario continues with a proposed early response of the Pinyon Jay to the large, periodically abundant seed of the Pinyon Pine. Ancestors of this jay probably lived in the same habitat as the Pinyon Pine and simply ate pine seeds when present and found alternate foods when pine seeds were absent. All corvids are inquisitive and are known to explore nooks, crannies and crevices as part of their daily routine. When crops were large, jays may have carried seeds around in their bill (not an uncommon sight at modern-day bird feeders), occasionally stopping to deposit one or more in concealed locations. (R. P. Balda and N. Stotz have observed that very young hand-raised jays will frequently store and retrieve objects in their cages.) Maybe the birds first deposited seeds they could not eat in crevices or crotches in the trees near where they had been eating. These seeds were not totally concealed and may have been found by the original storer upon return of the bird to a familiar location when it happened to look into the spot. The use of inconspicuous locations to place seeds would help ensure that they would not be found by other birds.

The use of subterranean caches was probably favored early on, as seeds were then completely hidden from other birds and seed predators. This movement of seeds from trees to ground storage sites was an important aspect of the coevolution of bird and tree, for now seeds were placed in sites where they could germinate and survive. However, now the caching bird had to pos-

sess some technique(s) to relocate these caches, as they were totally hidden from view. Simply returning to a familiar location to open seeds would not suffice to locate buried ones. The use of subterranean caches and the development of successful recovery techniques probably were linked. In addition to being well concealed, another problem with subterranean caches is that some rodents with a good sense of smell could locate and plunder the caches. Pinyon Jays may have moved caches out of areas where rodent density was high and into areas where it was low, as reported by Mattes (1982) for Eurasian Nutcrackers in Switzerland. Thus, active dispersal within and among habitat types would have occurred. Pinyon Jays could now manage their food supply, storing seeds when supplies were abundant and using them when other foods were in short supply.

However, one important aspect of this system is still absent. How many seeds should a bird cache when seeds are abundant? The answer to that question will always be problematic because of a series of unknowns. Birds cannot predict: (1) the amount of snowfall that could bury caches, making some of them inaccessible; (2) the densities of rodents in areas where seeds were cached, which would indicate what proportion of their cached seeds would be plundered; (3) the rate of spoilage of cached seeds; and (4) the length or intensity of the long, cold winter. It is also possible that birds will forget the location of some cache sites. These unknowns should lead the bird to cache as many seeds as it possibly can to ensure that, even if all the above occur, the bird still has enough seeds to survive the winter and possibly breed. In average years and in many places this "insurance policy" would not be necessary and, by mid-summer, thousands of seeds might be left unharvested. This number would be enhanced by the number of seeds cached by birds that perished before having an opportunity to retrieve them.

Now coevolution of the bird and the tree would be complete, with both bird and tree receiving benefits from the interaction. The pines could spread rapidly on bird wings to colonize new areas or retreat from inhospitable ones. Numerous seeds would then be available to germinate in subterranean sites and establish themselves. Jays were assured of a food supply for many months after a bumper crop. The nutritious seeds also allowed the birds to uncouple the breeding season from the spring production of food, allowing them to breed very early and giving their young time to grow and mature before the onset of caching and winter weather. Hoarded food also allows birds the possibility to uncouple foraging from eating, as stored food can be eaten directly without extended searching (Sherry, 1984).

At this time, trees and birds were able to disperse rapidly, invading new habitats where terrestrial seed predators had not yet been exposed to these seeds. In their newly invaded habitats, they would have a ready supply of food with a known distribution, simply because they cached it there. As the north-

ward and upward dispersal progressed, the trees eventually came in contact with the Clark's Nutcracker invading from the north (Figure 2). Now both bird species moved the pine and benefited from the high-quality seed. In fact, today, in the San Francisco Peaks just north of Flagstaff, no other pine enjoys the wide altitudinal range of the Pinyon Pine. Because both of these caching species are strong fliers relative to Mexican and Scrub Jays, when cone crops occurred only in "hot spots," these birds would eventually locate them. In years when crops were absent, both species could undergo long-distance movements in search of alternate foods, returning months later to their home ranges and territories (Vander Wall *et al.*, 1981; Marzluff and Balda, 1992).

Of course, none of this is really plausible if this intense caching behavior is not linked with a successful recovery system. Andersson and Krebs (1978) argued that the fitness of the hoarding individual must exceed that of the non-hoarder, as recovered food must increase survival and/or reproductive output over that of a nonhoarder. If nonhoarders can steal caches made by hoarders, then this is a density-dependent game (Maynard Smith, 1974) in which the pay-offs depend on the proportion of hoarders in the population. However, any strategy on the part of hoarders that reduced the probability of a nonhoarder being able to locate caches would reduce the average payoff to nonhoarders.

Recovery of cached seeds in nature

Obviously, in order to receive any benefit from food storage, birds must be able to recover their buried seeds. Early reports in the 1940s through to the 1960s by a host of European workers observing Eurasian Nutcrackers indicate that at times these birds were highly accurate when retrieving seeds from subterranean caches (reviewed by Turcek and Kelso, 1968; Tomback, 1980; Lanner, 1996). Most of these conclusions, however, were based on indirect measures of accuracy. When recovering caches, nutcrackers usually sit silently on a branch, intently peering at the surrounding area below. Birds may then descend with a strong, silent swoop to the ground. After a few hops, the bird stops, looks about and drives its powerful bill into the substrate. Although there are no conspicuous signs that seeds are located at these probe sites, birds often do extract a seed in their bill on the first probe. Nutcrackers may then proceed to extract the remaining seeds from the cache and hold them in their sublingual pouch. Often the bird remains at the extraction site, slowly removing seeds from its pouch and eating them one at a time, either by crushing the seed hull with its powerful bill or puncturing the seed hull with its bill tip while holding the seed in its toes. The seed hulls drop to the ground, next to or in the emptied cache site. It is this extraction by the cache site that most early workers used to try to determine the recovery accuracies of nutcrackers. When nutcrackers have been searching for seeds in an area, it is quite easy to see the holes they have dug and therefore

easy to calculate the percentage of such holes with seed hulls nearby. These counts usually revealed that birds were between 60% and 86% accurate when probing for hidden seeds (reviewed in Turcek and Kelso, 1968). However, such indirect estimates must be regarded as lower limit estimates, for at least two reasons. First, nutcrackers often retrieve seeds from more than one cache before opening and consuming seeds. Thus, some probe holes from which seeds were recovered do not have empty seed hulls around. Second, rodents are known to pilfer between 14% and 80% of the seeds cached by nutcrackers (Vander Wall, 1990). A searching nutcracker may dig at a site where it had previously buried seeds and have no way to ascertain that the seeds had been pilfered by a cache robber. These sites would also lack empty seed hulls and would also be counted as errors. Thus, because the goal is to estimate the proportion of probes that are directed at locations where caches had been placed, the above estimates are conservative at best (Balda, 1980b).

There are some reports of direct observations of nutcrackers recovering caches. Five irruptive Eurasian Nutcrackers that had been fed Stone Pine seeds (*Pinus cembra*) one winter for 60+ consecutive days made thousands of caches in a local park in Bielefeld, Germany. These birds were observed directly removing seeds from their caches. They were 86% accurate when recovering their hidden seeds weeks and months later, even through 4-6 cm of snow (Figure 3) (Balda and Conrads, 1990). Vander Wall and Hutchins (1983) directly observed Clark's Nutcrackers recovering buried seeds with accuracies that ranged from 33% to 84% over a 9-month interval. However, these and other field observations lack a great deal of information as we do not know whether the bird retrieving the cache actually made the cache, or when the cache was made relative to when it was recovered, or what techniques the bird used to recover its cache, or how many seeds the bird ordinarily placed in the cache, or how many caches this bird had in this vicinity, etc.

These field observations do, however, reveal that nutcrackers are incredibly accurate when locating their caches. This high level of accuracy is truly remarkable when one recalls that nutcrackers: (1) spend about 30 seconds at the site creating a cache; (2) make thousands of caches when pine seeds are available; (3) return to harvest their caches many months after they were created; and (4) recover many caches from a substrate that has changed drastically since the caches were made, i.e. birds cache in late summer and fall before snow covers the ground but must recover caches through the snow in fall, winter and early spring (Figure 3).

Less field data on cache recovery are available for Pinyon Jays. Balda and Bateman (1971) reported accurate cache recovery by Pinyon Jays digging through snow to recover seeds. Ligon (1978) also reported a high level of accuracy for Pinyon Jays relocating seed caches. Pinyon Jays must perform under the same four constraints listed above, but also experience additional constraints owing to their social organization. Individual Pinyon Jays do not select

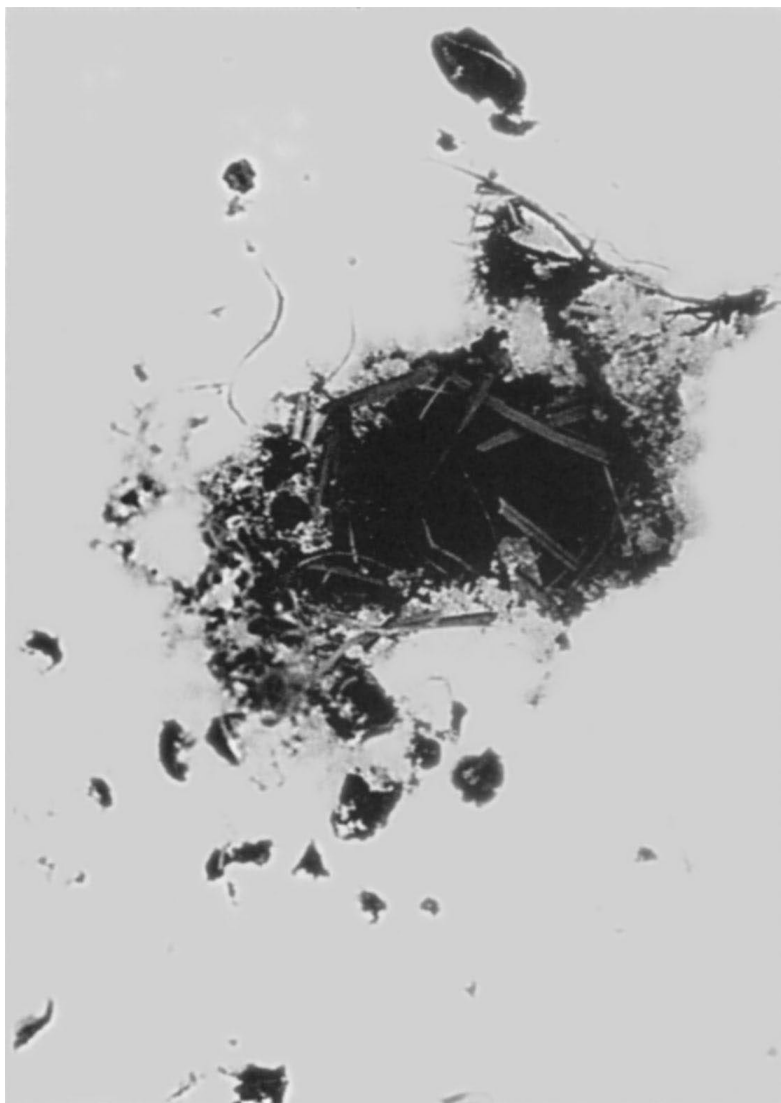


Figure 3. Photograph of hole probed in the snow by a nutcracker to recover a seed cache. Parts of the seed hull are visible around the hole indicating the bird fed on the recovered seeds at this site. (Photograph by Rolf Seebrasse.)

the general area in which they will create caches because the flock as a whole visits “traditional areas.” So a bird must use the general area to cache where it landed, relative to the position of the flock. It also appears that birds have little time to deliberate about where to place specific caches once they have landed. The flock as a whole moves in unison and all birds follow this direction. Birds also appear to be very automated when caching, often walking at a steady pace

and sticking seeds in the ground at a continuous rate. They must also be constrained by conspecific cache pilferers (Stotz and Balda, 1995; Bednekoff and Balda, 1997).

Little is known about the recovery accuracy of the two *Aphelocoma* species in the field, except that they harvest their caches, appear reasonably accurate, and may do so at least into the beginning of the breeding season (Balda, personal observations; J. R. Brown, personal communication). The hidden food stores of these two jays may provide winter sustenance during those periods when winter weather is unusually severe. Thus, these birds may be able to live on alternate foods most of the time but, during 10–12 days each winter, cached food may provide an important and necessary emergency food.

The evolution of spatial memory

The “payoff” for caching seeds must be the use of these seeds at a later time. Many alternative mechanisms for cache recovery are possible, including random probing, the use of odor, markings made at cache sites, route reversal, and site preferences. The high levels of accuracy observed in field studies argue against random probing but fail to discriminate against most of the other alternatives. A series of controlled laboratory experiments over the past 15 years (Balda, 1980b; Balda and Turek, 1981; Vander Wall, 1982; Kamil and Balda, 1985; Balda *et al.*, 1986; Kamil *et al.*, 1994) have conclusively shown that the use of spatial memory based on visual landmarks is the primary technique employed by all four corvid species that have been studied to date. This makes sense in terms of possible historical competition between hoarders and nonhoarders. The use of spatial memory would provide a method for relocating cached food available to the creator of the caches but not to a noncacher, thus tipping the game in favor of the evolution of caching.

An important historical issue, about which we can currently only speculate, is the question of the evolutionary relationship between general spatial abilities and the special problems faced by seed-caching corvids. Spatial relationships are important to many animals, probably to any animal that can move. A particularly relevant case may be that of migratory birds which are also known to have a keen sense of space. Both migratory and seed-caching birds possess the ability to return to specific locations, migratory birds on a global scale and food-caching birds on a much finer scale (Gallistel, 1990). Perhaps it is more than a coincidence that the two species that recover their caches most accurately (nutcrackers and Pinyon Jays, see below) are the species that are strong fliers, fly many kilometers in search of hot spots of pine cones, and irrupt long distances when the pine cone crop fails.

One important mechanism for migratory birds and homing pigeons is the use of a compass. Birds are known to possess a number of different compasses including sun compass, star compass, and magnetic compass that are

used during migration and homing (Emlen, 1975; Wiltschko and Wiltschko, 1988). A compass is a quite general mechanism in the sense that it can be used in many different settings. For example, a compass could be used by animals that had left their territories, as in searching for pine cone hot spots, and now needed to return. Compasses may also play an essential role in cache recovery. Wiltschko and Balda (1989) and Balda and Wiltschko (1992) have demonstrated that the sun compass is used during the relocation of cached seeds by Western Scrub Jays, even when a complex set of landmarks was present and available for their use. Clark's Nutcrackers and Pinyon Jays have recently been shown to use the sun compass when retrieving seeds (Wiltschko *et al.*, unpublished observations).

The landmark/compass system might be a necessary preadaptation to the evolution of seed caching. One can speculate that subterranean seed caching could not evolve without a means of locating hidden seeds. Picture the problem faced by the first bird in an evolutionary lineage to cache. Without a method for relocating the caches, there could be no benefit. A compass-based spatial memory system may have provided this ancestral cacher with the necessary ability. Once this process began, the spatial memory system may well have been intensely selected for, modified, and enhanced in species most dependent on hidden food for survival and reproduction (Balda and Kamil, 1989), becoming a key component of the constellation of adaptations that seed-caching animals possess.

The nature of this selection process can be inferred from an analysis of how demands of the seed-caching and recovery problem differ from more global spatial problems. In cases such as migration and homing, there are relatively few specific locations to be remembered, and these often have specific stimuli (e.g. the natal territory, a loft) associated with them. For seed-caching birds such as nutcrackers or Pinyon Jays, thousands of locations must be remembered for up to 9 or 10 months. This clearly implies a memory system of greater capacity and duration. More subtle possibilities exist. For example, there are usually no identifying stimuli located near individual cache sites. A bird who has just made 20 or 30 caches in one end of a meadow may be using one set of landmarks to define the location of each of these cache sites. The use of a compass in this setting would require that each site be identified by a unique set of bearings with respect to the landmarks. This differs markedly from how a compass is used by a migrating bird returning to a single, specific location. One interesting implication of this analysis is the suggestion that nutcrackers and Pinyon Jays may be particularly sensitive to the compass bearings of landmarks.

The evolutionary play: species differences in spatial memory in the laboratory

These birds are strong fliers, wary about being watched and quick to vocalize the approach of an intruder, thus making field studies on seed caching and re-

covery almost impossible. We have conducted a series of controlled laboratory tests with the southwestern US corvids. Four different comparative tests of seed caching and recovery have been completed. Not all four species participated in all four of the tests, but the results clearly indicate that, although spatial memory is used by all four species to locate caches, there are also important species differences that correlate with ecological differences.

Cache recovery tests of spatial memory

Three species, two conditions test (Balda and Kamil, 1989) This experiment compared the cache recovery performance of Clark's Nutcrackers, Pinyon Jays, and Western Scrub Jays under two conditions. The experiment was conducted in an experimental room (3.4×3.4 m) with a raised floor that had 180 holes measuring 5.5 cm in diameter, each separated by a center-to-center distance of 23.5 cm. Each hole could be filled with sand for caching or fitted with a wooden plug to prevent caching. The room contained many landmarks on the floor, posters on the walls, and a centrally located feeder. During the experiment the cache recovery performance of each bird was tested twice, once with many holes (90) available for cache site selection and once with only a few holes (15) available. The purpose of this design was to assess the accuracy of cache recovery after the birds were given free choice in cache placement so that a cache placement strategy could be employed compared to accuracy of cache recovery after severely limiting the availability of cache sites, so that cache placement strategies would be inhibited. After a 7-day retention interval, birds were released back into the room to recover their caches. The basic measure of accuracy was the proportion of holes probed that contained a seed.

In 40 of the 42 trials the accuracy of the birds was greater than would be expected by chance. Both nonsignificant cases involved Scrub Jays. In general, Scrub Jays performed significantly worse than either nutcrackers or Pinyon Jays, which did not differ from each other. All three species performed better under the 90-hole condition than under the 15-hole condition (Figure 4). Although the species by condition interaction was not significant, the effects of 15 vs. 90 open holes condition appeared to be greatest for Pinyon Jays, who made conspicuous clumps of caches during the 90-hole condition. When the average distance between cache sites was calculated, we found that Pinyon Jays had placed their caches significantly closer together (0.81 m) than either nutcrackers (1.22 m) or Scrub Jays (1.5 m).

These results support the hypothesis that accuracy of cache recovery is a function of some aspect of the ecology of the species being tested. The two species best adapted morphologically for this behavior (and also most dependent on these cached seeds for winter survival and subsequent reproduction) performed significantly better than Scrub Jays. However, the different pattern of space use by Pinyon Jays was unexpected and intriguing. The clumping of

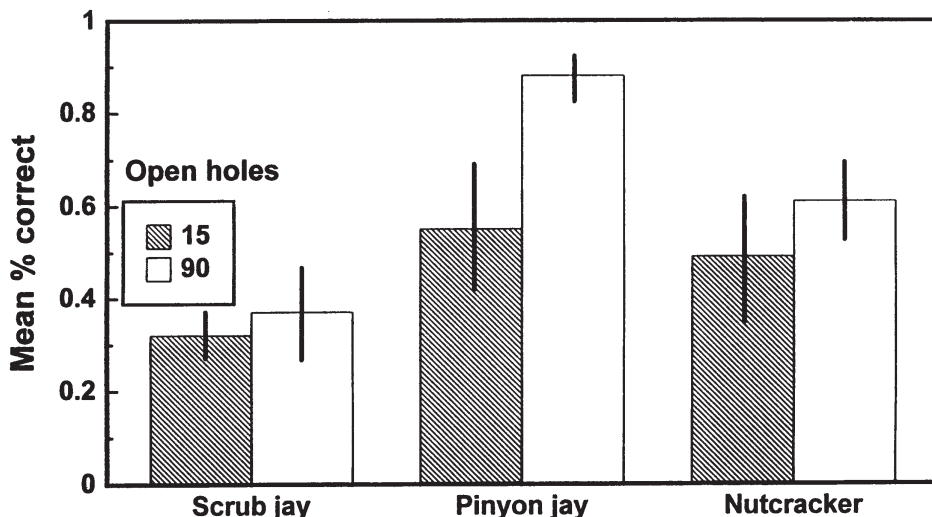


Figure 4. Performance of the three species under the 15- and 90-hole condition.

caches may allow the Pinyon Jays to use a nonmnemonic technique, such as area-restricted search, to locate their caches. Recovery of clumped caches could be highly accurate but result from limited memory ability if the jay fills all of the cups with seeds in a relatively small area and then restricts its search to this small, saturated area. Because these birds cache as a social unit, they may also be more inclined to create caches close together owing to the movement restrictions imposed by other members of the group.

Two species, open field (Romonchuk, 1995) This experiment looked more closely at the unexpected clumping of caches by Pinyon Jays. In this study, only individual nutcrackers and Pinyon Jays that were totally unfamiliar with the experimental room and paradigm were used. The experiment was conducted in a $9.1 \times 15.3 \times 2.8$ m room with a raised plywood floor that contained 330 sand-filled holes that were open during both caching and recovery sessions. A number of structures were scattered on the floor and posters lined the walls for visual orientation. Each bird was allowed in the experimental room until it made 25 caches. If a bird stopped caching, it was removed from the room and allowed another session the next day during which previously made caches were capped with wooden plugs. Recovery sessions began 7 days after caching was completed, and birds were allowed to retrieve 25% of their caches during each of four recovery sessions. Sessions were separated by 7 days. The mean inter-cache distance was measured by averaging the intercache difference between all possible unique pairs of caches. Mean nearest neighbor distance was measured by averaging the distances to a cache's nearest neighbor for all caches.

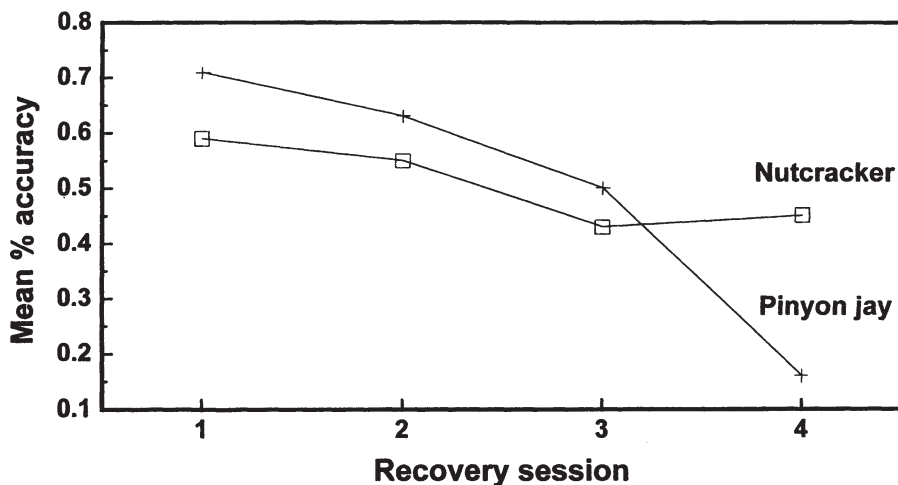


Figure 5. Performance of the nutcracker and Pinyon Jay over four recovery sessions.

As in the earlier experiment, the species did not differ in recovery accuracy (Figure 5). Mean intercache distance was significantly closer for Pinyon Jays ($\bar{x} = 2.66$ m) than for nutcrackers ($\bar{x} = 3.86$ m) (Figure 6). Nutcrackers placed significantly more seeds per cache ($\bar{x} = 2.50$) than did Pinyon Jays ($\bar{x} = 1.12$). These results corroborate the findings of Balda and Kamil (1989) for both recovery accuracy and cache distribution.

Pinyon Jay spacing pattern (Romonchuk, 1995) Can Pinyon Jays accurately find their caches when they are not allowed to cache in clumps? The findings that Pinyon Jays cache in clumps and recover their seeds very accurately do not prove that the clumping is necessary to achieve accurate recovery. Field studies cannot provide an answer because, when given free access to cache sites, Pinyon Jays will always cache in clumps (Stotz and Balda, 1995).

This experiment used two unique sets of cache sites in the large experimental room with 330 holes in the floor. The location of holes for each condition was determined by attempting evenly to distribute the holes throughout the entire room. In one condition, 72 holes were open in the floor and the bird allowed to make 15 caches. With this number of holes open, Pinyon Jays could clump their caches. In the other condition, only 36 holes were open, allowing less opportunity to clump caches. We hypothesized that birds would clump caches under the 72-hole condition, but that this would not be possible under the 36-hole condition. If birds used area-restricted search to locate their caches, they should perform with higher accuracy when recovering from the 72-hole condition than from the 36-hole condition.

Unfortunately, this manipulation of number of sites available during caching had no significant effect on intercache distance. Mean intercache distance

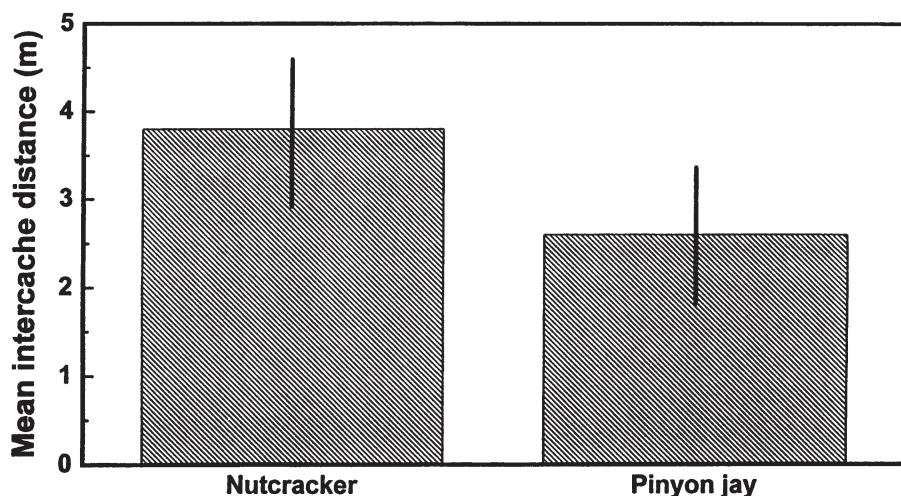


Figure 6. Mean intercache distance for 25 caches made by nutcrackers and Pinyon Jays.

was smaller for the 72-hole condition ($\bar{x} = 3.62$ m) than for the 36-hole condition ($\bar{x} = 4.01$ m). However, these intercache distances were greater than those obtained during the Kamil and Balda (1989) study and can reasonably be thought of as representing nonclumped caches.

Accuracy in this experiment was measured using the single cache recovery attempt procedure (SCRAP) developed by Kamil and Balda (1990). Using this procedure, during recovery the bird was presented with a set of clusters, each consisting of a cache site and three empty holes that had not been cached in. The number of errors to find a cache within a cluster could vary between zero (find the cache on the first probe) and three (find the cache after having probed the three noncache holes in the cluster). If birds were probing at random, then each possible outcome, zero through three, should occur with equal frequency and the mean number of errors would be 1.5. For every cluster of holes containing a cache site, a matching cluster was presented that did not contain a cache site. During recovery sessions, birds had a choice of what type of cluster to probe (one that contained a cache or a matching one that did not) and also which hole in a cluster to probe.

There was no significant difference in recovery accuracy between the 36-hole condition and the 72-hole condition. Most importantly, Pinyon Jays performed very accurately, making about 0.75 errors per cluster during both conditions. "Good" clusters were visited significantly sooner than "bad" ones. This experiment provides strong evidence that Pinyon Jays do not need to place their caches in clumps and then use area-restricted search to locate them. Birds must have precise spatial information about the exact location of their individual caches.

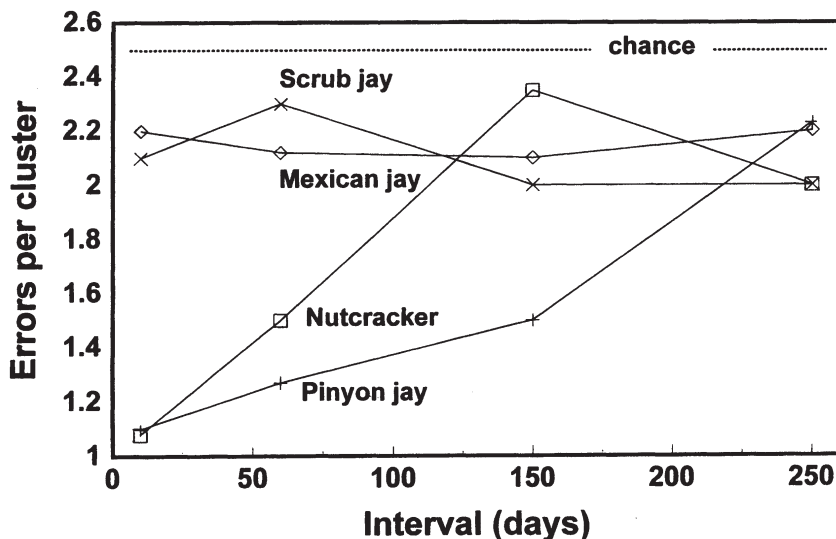


Figure 7. Mean errors per cluster for the four species of corvids at retention intervals of 50, 100, 150, and 250 days.

Comparative long-term spatial memory by four seed-caching corvids (Bednekoff *et al.*, 1997) Are there species differences in the duration of the cache site memory of Clark's Nutcrackers, Pinyon Jays, Western Scrub Jays, and Mexican Jays? As reviewed above, in nature, nutcrackers and Pinyon Jays cache greater quantities of pine seeds each fall and rely on them for a longer time period than either Mexican or Western Scrub Jays. In addition, earlier research showed that nutcrackers could remember the location of their caches for at least 285 days (Balda and Kamil, 1992).

We used the large caching room described above, and provided 62 holes as potential cache sites during caching sessions. Birds were allowed to make 24 unique caches. We then allowed birds to recover one-fourth of their caches during each of four recovery sessions conducted 10, 60, 150, and 250 days after caching sessions were completed. During recovery testing, we used the SCRAP procedure (as described in "Pinyon Jay spacing pattern," above) to assess accuracy. Each cache site was a member of a 2×3 cluster of adjacent holes, so that chance performance was 2.5 errors per recovery.

We used two types of analysis to assess cache recovery accuracy. First, we used *t*-tests to compare accuracy with that expected by chance. When we collapsed data across all retention intervals; each of the four species was more accurate than expected by chance. However, Scrub Jays and Mexican Jays performed only modestly at all retention intervals and did not become less accurate with time. Nutcrackers and Pinyon Jays were very accurate at the 10- and 60-day interval, but only modestly accurate at the 150- and 250-day interval (Figure 7). Second, to assess accuracy, we used a species by interval ANOVA of the

mean number of errors. There was a significant main effect of species. Multiple comparisons revealed that nutcrackers and Pinyon Jays did not differ significantly, and that Scrub Jays and Mexican Jays did not differ significantly but that these two pairs of species clearly differed. This result adds further evidence that seed-caching species differ in their ability to locate their hidden seed caches. Again, the species more dependent on seed caches for winter survival and reproduction had the best long-term spatial memory and species with less dependence on this food source had the poorest performance. However, the results of this study fail to clarify any possible species differences in the effects of retention interval. Because the performance of the Scrub and Mexican Jays was so mediocre at all retention intervals, we were unable to detect any effect of retention interval on the performance of these two species.

Other comparative tests of spatial memory

The results of the comparative cache recovery experiments indicate that nutcrackers and Pinyon Jays recover their caches more accurately than either Mexican or Western Scrub Jays. However, does this mean that the species differ in some kind of general spatial memory ability or are these differences limited to tests of cache recovery? It might be argued that these birds are highly specialized for the recovery of seed caches but on other tasks of spatial memory they would perform in an uninteresting or marginal fashion. In addition, differences obtained during any single experiment may be due to differences in spatial cognition or to the effects of contextual variables that may reflect a coincidental effect of some detail of the experimental paradigm (Bitterman, 1965; Macphail, 1982). For example, one species may adapt to laboratory conditions better than another or the rewards could be more suited to one species than to the others. In order to reach a conclusion about these issues, tests with different paradigms are necessary (Kamil, 1988). Therefore, we have conducted a series of spatial memory tasks utilizing procedures quite different from cache-recovery procedures.

Comparative radial maze study (Kamil *et al.*, 1994) This experiment was carried out with the four species in a small room (3.6×3.2 m) with 12 holes arranged in a circle in the floor. The floor contained numerous objects, and the walls were hung with posters. After habituation to the room, members of all four species were given 60 acquisition trials. Each of these trials consisted of two parts, a preretention stage and a postretention stage, separated by a 5-minute retention interval. During the preretention stage, each bird entered the room where four holes chosen at random each day were open and each contained a buried food reward. This stage continued until the bird found and ate the four morsels of food. The bird then left the room and the retention interval began. During the retention interval, four more holes were opened and a food reward placed in each of these newly opened holes. After the 5-minute retention in-

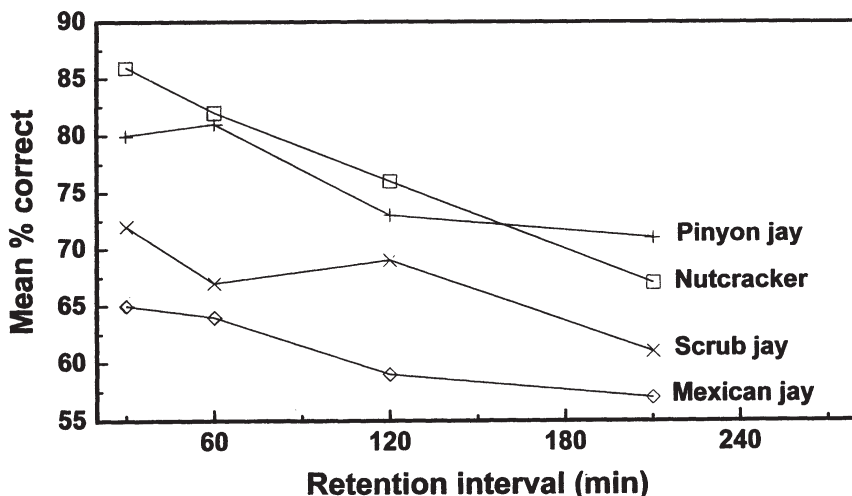


Figure 8. Performance of each species at each interval during an ascending series in the radial maze test.

interval the bird was released back into the room that now contained eight open holes, four new holes with seeds and the original four holes that were previously emptied by the bird. The postretention interval continued until the birds either recovered the four rewards or probed six unique holes. Thus, in order to respond accurately, the bird had to remember which four holes it had emptied during the preretention phase and visit the newly opened holes.

Although all four species had similar levels of performance at the start of acquisition, they rapidly diverged. Nutcrackers and Pinyon Jays learned the task more rapidly and performed at higher levels than either Western Scrub Jays or Mexican Jays. As retention intervals were increased, all four species declined in accuracy (Figure 8). The results of this experiment are consistent with earlier comparative findings and suggest that the species differences observed during cache recovery are quite robust and are not limited to cache recovery tasks. The selective pressure acting on the spatial memory abilities of these species are general enough to influence performance on a variety of spatial tasks.

Comparative operant spatial and nonspatial memory test (Olson, 1991; Olson *et al.*, 1995) In an attempt test for memory abilities using procedures as far removed from cache recovery as possible, we have conducted experimental tests of spatial memory with these species in an operant chamber where birds had to peck at lights to receive food rewards (Olson, 1991; Olson *et al.*, 1995). The initial purpose of these experiments was to determine whether these operant procedures would produce the same pattern of species differences in spatial mem-

ory as seen during cache recovery and radial maze experiments. In the first of these experiments, Olson (1991) found that nutcrackers performed much better than Western Scrub Jays in this type of task.

We then designed a pair of follow-up experiments. One purpose was to test all four species on an operant task. In addition, we wanted to determine if the species differences we had observed were limited to spatial tasks or would also be found in nonspatial tasks. This experiment was conducted in an operant chamber with a computer monitor at one end and a pecking key and feeder at the other. Each trial began with the illumination of a spot in the center of the monitor. This spot could be red or green; the color illuminated was chosen at random on each trial. A single peck at this sample caused the screen to clear and a yellow light behind the key on the rear panel to be illuminated. One peck at the rear key extinguished that light and two choice stimuli were presented on either side of the monitor, one red and one green. Two pecks directed at either stimulus caused the trial to end. A trial was correct, and followed by delivery of a reinforcer, only if the bird pecked the new color. This procedure required the bird to remember the color it had pecked in the first part of the trial and to avoid that color in the second part. After the birds had learned the task, a titration procedure was employed to assess the duration of nonspatial memory for the sample color. A retention interval was added between the end of the sample presentation and the choice test. If the birds made a correct response, the retention interval increased by 0.1 seconds during the next trial. If the bird made an incorrect response, then the retention interval was decreased by 0.2 seconds. This titration procedure results in a very gradual increase in the retention interval as long as performance is above 67% correct.

The results of this experiment were clear. In stark contrast to the findings of our comparative spatial experiments, the performance of the birds in this nonspatial experiment did not correlate with dependence on stored food and none of the species differences was statistically significant.

Although speed of acquisition and retention interval did not correlate well with dependence on stored food, it seems to correlate with their social organization. Pinyon Jays and Mexican Jays that live in permanent social groups performed better than the more solitary Clark's Nutcracker and Western Scrub Jay (Figure 9). The possible significance of this finding has been discussed elsewhere (Balda *et al.*, 1997).

As soon as this experiment was complete, birds were switched to an almost identical task which required memory for a spatial location rather than a color. Everything remained the same except that in the first stage of each trial, one of two locations, chosen at random for each trial, was illuminated. Then, during the choice phase, two identically colored spots were illuminated, one in the same location as the sample, the other in the novel position. Correct responses were responses to the new location. Titration now produced very different re-

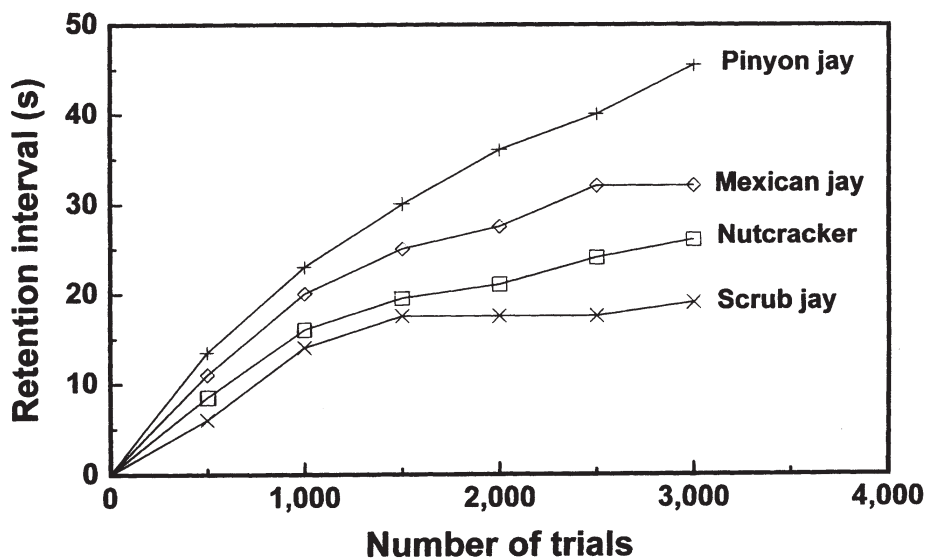


Figure 9. Performance of each species during color memory nonmatching-to-sample titration.

sults. Clark's Nutcrackers performed much better than the other three species, duplicating the finding of Olson (1991) with nutcrackers and Scrub Jays (Figure 10). This is consistent with the results of our cache recovery and radial maze tests. This is the first result from a spatial test in which nutcrackers were clearly superior to Pinyon Jays and the performance of the Pinyon Jays could not be separated from the *Aphelocoma* jays.

The failure to find species differences on the nonspatial test is particularly important. First, it rules out several alternative hypotheses for the species differences we have observed in spatial tasks, such as general intelligence or general adaptability to laboratory test environments. If such general factors were important, then we should have obtained the same species differences in this nonspatial test of memory that we did in spatial tests. Second, they indicate that natural selection can have specific effects on one type of memory while other types are unaffected. This finding substantially increases our confidence that the species differences in dependence on cached food are crucial for the differences in performance on spatial memory tasks.

The evolutionary play: the neural substrate responsible for spatial memory

The pioneering work of Krushinskaya (1966) showed that lesioning the hyperstriatum and hippocampus of Eurasian Nutcrackers impaired their ability to

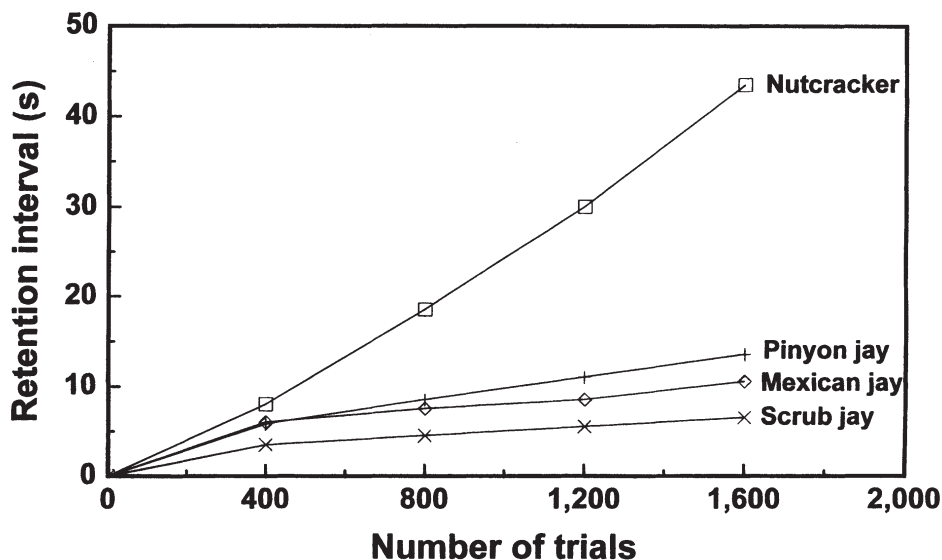


Figure 10. Performance of four species of corvids during spatial memory nonmatching-to-sample titration.

recovery caches accurately. More recently, when Sherry and Vaccarino (1989) lesioned the hippocampus of black-capped chickadees, they could not locate previously made caches, although they continued to make caches and foraged normally. Orientation and recognition of home loft were disrupted when the hippocampus was lesioned in homing pigeons (Bingman *et al.*, this volume). Food-storing birds have a hippocampal complex of greater volume than non-storing birds, relative to either body size or forebrain volume (Krebs, *et al.*, 1989; Sherry *et al.*, 1989).

We have found differences in the relative size of the hippocampal formation among the nutcracker, Pinyon Jay, Scrub Jay, and Mexican Jay (Basil *et al.*, 1996). When the ratio of hippocampal volume to telencephalon volume was calculated for each of these four species and compared on the regression line of this ratio for a wide variety of New and Old World corvids (Krebs *et al.*, 1989; Sherry *et al.*, 1989), nutcrackers had the largest relative hippocampal volume. The three species of southwestern US jays, including the Pinyon Jay, all had small relative hippocampal volumes. Thus, the Pinyon Jay with its excellent spatial memory abilities, especially for cache recovery and radial maze performance, does not follow the pattern whereby a large hippocampus is correlated with excellent spatial memory abilities (Shettleworth and Hampton, this volume).

The evolutionary play: the final act

Vander Wall and Balda (1977, 1981) have described the suite of morphological and ecological adaptations that these birds possess for efficient harvest, transport, and caching of the seeds. In general, they concluded that Clark's Nutcrackers and Pinyon Jays are more specialized than either *Aphelocoma* species. The results of our comparative studies of spatial memory lead to the same conclusion, and this buttresses the argument that spatial memory is an adaptation for cache recovery in these animals. In this section, we attempt to integrate this new information with the biogeography, natural history and taxonomy of these species.

When we first began our comparative program of research, we thought of our strategy as the study of divergence among a series of four closely related species. After all, nutcrackers, Scrub Jays, Pinyon Jays, and Mexican Jays are all in the same family. Now, however, we think this was too simple. The evidence we have reviewed above is more consistent with the idea that the differences among Scrub Jays, Mexican Jays, and Pinyon Jays represent divergence while the similarities between nutcrackers and Pinyon Jays represent convergence. According to this view, the origins of specialized spatial memory and seed-caching behavior are different in the New World jays than in the Old World corvids as this trait has originated more than once in the family Corvidae.

The evidence for the multiple origin of cache site memory is indirect. It seems unlikely that the ancestral *Aphelocoma* jay(s) were very dependent on cached food because of the subtropical habitat in which they lived. This suggests that the spatial abilities of the Pinyon Jay are a relatively recent development. All New World jays examined to date have smaller hippocampuses than many of their Old World relatives that store seeds and retrieve them. This also suggests that New World jays had a noncaching species as an ancestor. Finally, as reviewed above, the biogeography of pine trees with large seeds that do not have wings is consistent with this picture. There appear to have been two distinct historical patterns of distribution. In one, pines have moved north to south, as if transported by invading Clark's Nutcrackers; in the other, the movement has been south to north, as if transported by dispersing Pinyon Jays. The distribution of nutcrackers and Pinyon Jays is consistent with this historical biogeography. While nutcrackers and Pinyon Jays overlap in terms of north-south distribution, nutcrackers range much further to the north than do Pinyon Jays, and Pinyon Jays range farther south.

The details of one of the major adaptations for seed harvesting also fits with the idea that nutcrackers and Pinyon Jays are convergent. The functional similarity of the expandable esophagus of the Pinyon Jay and the sublingual pouch of the nutcrackers is often commented upon (Goodwin, 1986; Marzluff and Balda, 1992). However, analysis of the anatomy of these two adaptations shows

that they are completely different in terms of structure (Bock *et al.*, 1973; Marzluff and Balda, 1992). The sublingual pouch is the result of relatively minor modifications of the location and structure of two throat muscles. In contrast, the expandable esophagus is the result of changes in the cell structure of the wall of the esophagus which increases expansibility. These are clearly independently evolved adaptations.

This idea of convergence also helps understand a puzzling aspect of our data on spatial memory and relative hippocampal size. How does the Pinyon Jay recover caches as accurately as the nutcracker, yet have a smaller hippocampal complex? Natural selection works on outcomes and only indirectly on mechanisms (Shettleworth, 1984). In other words, any mechanism that improved the ability to recover caches could be favored by natural selection. The difference in hippocampal volume between nutcrackers and Pinyon Jays suggests that different neural mechanisms may have been involved, but we could only speculate about the location and function of these, as yet unknown, areas. Comparative neuroanatomical studies of the hippocampal complex of nutcrackers and Pinyon Jays may prove very informative.

The results of our comparative operant study also lend support to the idea of different mechanisms in nutcrackers and Pinyon Jays. Pinyon Jays are the equal of nutcrackers in cache recovery accuracy and performance in the radial maze. However, they did not perform nearly as well as nutcrackers in the operant spatial titration task. This may be another indication of different cognitive mechanisms underlying accurate cache recovery in these two species.

At first glance, the Pinyon Jay is truly perplexing. Its subtropical origins suggest that caching is a relatively recent development in its lineage, but it is extremely adept at caching and recovering pine seeds. The taxonomic status of the Pinyon Jay has driven systematists crazy over the years. Its similarities to nutcrackers have suggested one phylogenetic status, as an Old World corvid; other similarities have suggested another classification with the New World jays. We have argued that these perplexities are now largely resolved: that the Pinyon Jay is most reasonably classified with the New World jays, and its adaptations to a caching lifestyle convergent with Old World corvids such as Clark's Nutcrackers. Resolving these perplexities has required consideration of evolutionary history, natural history and even contemporary and historical biogeography. Furthermore, this resolution suggests novel hypotheses about the nature and evolution of the cognitive abilities of animals.

Afterword

Daniel Lehrman was fond of stating that the ultimate reason we study animals in the laboratory is to increase our appreciation of their beauty and so-

phistication outside of the laboratory, in the field. We know, from personal experience, that the knowledge we have gained through our laboratory research about these wondrous birds has forever changed our perceptions of them. The “kaws” and “kraws” will never sound the same; the commotion around the pine trees at harvest time will never seem the same; the sight of a nutcracker or Pinyon Jay arriving at its nest laden with pine seeds will never look the same. Awareness of the cognitive abilities of these animals forever changes our perception of them and their place in nature, and ours.

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