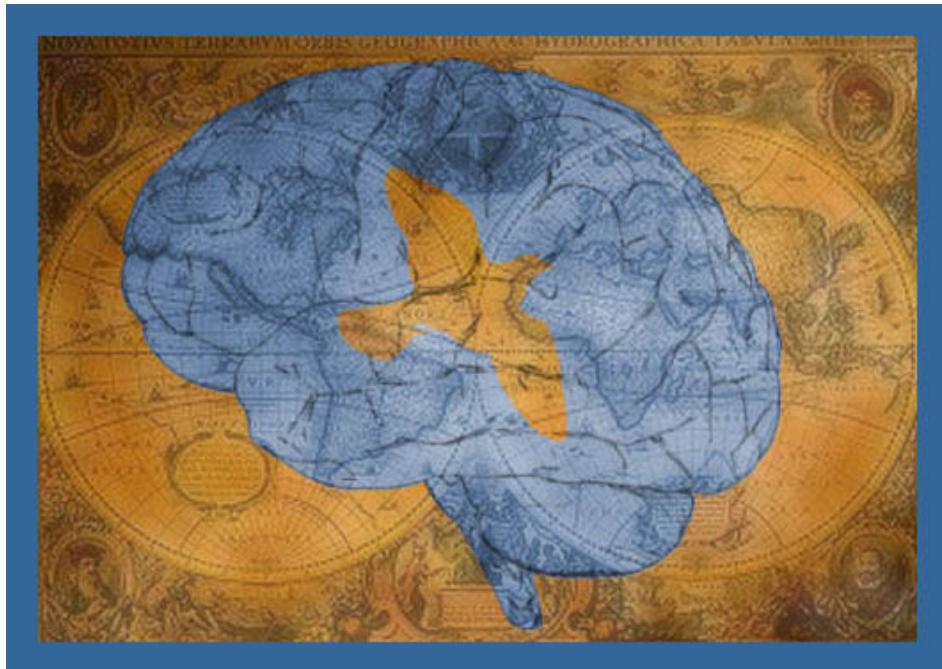


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Animal Spatial Cognition: Comparative, Neural & Computational Approaches

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Linking Life Zones, Life History Traits, Ecology, and Spatial Cognition in Four Allopatric Southwestern Seed Caching Corvids

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Abstract

This report will review the similarities and differences of four species of pine seed caching members of the avian family Corvidae that live on the slopes and base of the San Francisco Peaks in north-central Arizona. The four species include the Clark's nutcracker (*Nucifraga columbiana*), pinyon jay (*Gymnorhinus cyanocephalus*), western scrub-jay (*Aphelocoma californica*), and Mexican jay (*A. ultramarina*). These corvids demonstrate a specialization gradient for the harvesting, transporting, caching and recovering of buried pine seeds. This gradient is reflected in their dependence on cached pine seeds for winter and early spring survival and reproduction. Species most dependent on these cached seeds have the greatest number of adaptations for utilizing these seeds which is especially evident in their spatial memory abilities to locate their caches. The two most dependent species, nutcrackers and pinyon jays have spatial memory abilities more accurate than in the species less dependent on cached seeds, western scrub-jays and Mexican jays. Using converging operations to test these memory abilities, comparative tests were conducted in an open field cache/recovery experiment, an analogue radial maze test and operant tests of spatial and non-spatial memory. Also discussed are the techniques used by nutcrackers to recognize and relocate caching sites. These birds have the ability to learn and generalize geometric rules about the placement of landmarks. This geometry, especially using multiple landmarks, aids this species greatly. The use of the sun compass by pinyon jays, scrub jays and nutcrackers reveal that in experimental conditions where birds are clock-shifted they respond to this shift, thus digging for caches in locations predicted by the shift. It appears that pinyon jays are converging on a distant relative the nutcracker in many characteristics, thus diverging from their close relatives the western scrub-jay and Mexican jay. Each species has a suite of adaptive traits that reflects its natural history and life history.

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I. Introduction

Temperate and alpine regions experience large climatic shifts between summer and winter. To survive, animals must deal with these seasonal changes. Tactics used to address with these changing conditions include migration, hibernation, laying over-wintering eggs, or living off the land (finding food and shelter under changing conditions). Animals that live off the land are referred to as permanent residents. Often these animals have to change the amount and types of foods they eat to accommodate the energetic and nutritional demands imposed by the physiological needs of the different seasons of the year. For example, most permanent resident birds eat insects and arachnids during the summer when these food types are abundant, and seeds, berries, and over-wintering eggs and larvae, during the winter when these food items may be abundant. Some birds, however, do something quite different. They prepare for the upcoming winter by provisioning food in the late summer and autumn and then recover and consume it during the harsh winter season, days, weeks, or even months after the items were initially stored. In this chapter we will define the ecological conditions under which these behaviors occur and the suite of adaptive behaviors used by the birds in their quest for survival and reproduction.



Figure 1. C. H. Merriam (white shirt)

Food-storing adaptations have been observed in many avian taxa, including woodpeckers, nuthatches, chickadees and tits (see Vander Wall, 1990 for review of this topic). In this chapter, we will concentrate on a group of seed caching birds of the family Corvidae, the Clark's nutcracker (*Nucifraga columbiana*), pinyon jay (*Gymnorhinus cyanocephalus*), Western scrub jay (*Aphelocoma californica*) and Mexican jay (*Aphelocoma ultramarina*). These birds co-exist in a relatively small area of north-central Arizona, the San Francisco Peaks. These peaks are geographically compact and isolated from other mountainous areas, thus providing an unusual natural laboratory to study food-storing, particularly for describing similarities and differences among the four species. In the first part of this chapter, we describe the habitats occupied and utilized by the seed caching corvids. In succeeding sections, we use this background information to illustrate the how and why these conditions, acting as selective forces, have affected the behavioral patterns of these birds.

The San Francisco Peaks were made famous in the 1880's when they were studied by C. Hart Merriam, an early ecologist and the first Director of the present U.S. Fish and Wildlife Service (Figure 1). He described the distribution of plants and animals along an elevational gradient on the sides of the Peaks and compared this distribution to the latitudinal distribution of plants and animals from temperature to artic regions of the eastern U.S. He published a famous monograph on this topic in 1889 (Figure 2). Bands of like plants and animals that had the same elevational

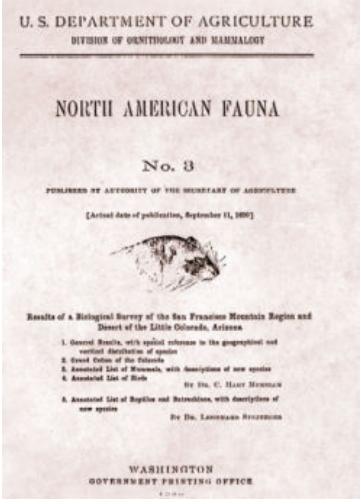


Figure 2. Cover of North American Fauna No. 3.

distribution were referred to as *life zones* (Figure 3B). Because the mountain is rather simple, both geologically and geographically, the zones were relatively easy to identify and describe. It was possible to visit all the life zones on the Peaks in half a day. This made it easy to record the similarities and differences in the behaviors of the birds of interest. A brief description of the life zones on the San Francisco Peaks, beginning with the highest elevations and moving downward, will set the stage for understanding the ecological reasons that these seed caching birds behave as they do.



Figure 3A. San Francisco Peaks.

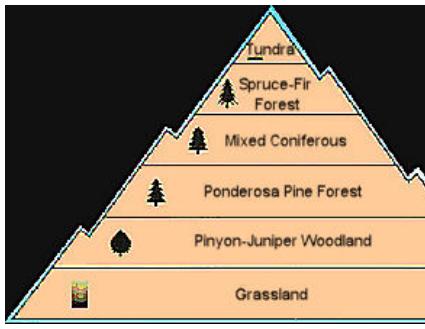


Figure 3B. Life Zone Distribution on San Francisco Peaks

II. The San Francisco Peaks

1. Alpine Tundra. (Figure 4)

This zone exists on the very top of the Peaks, 3,865 m (12,670 ft). Vegetation at this elevation is sparse. This area is above tree line and supports only two small species of shrubs. At tree line there are small gnarled patches of Engelmann spruce (*Picea engelmannii*) and bristlecone pine (*Pinus aristata*). In winter, the tundra zone is subjected to strong winds, low temperatures and heavy snow that may be present in protected pockets well into summer. Summer rains can be torrential. The growing season is short as freezing temperatures can occur in May and August. The single seed caching corvid that regularly visits this zone is the Clark's nutcracker and it does so in late summer and early fall before the snow flies. Here it can be found with its offspring of the year, foraging, digging in the soil, catching insects, and caching seeds of bristle cone pine, limber pine (*Pinus flexilis*), and southwestern white pine (*Pinus strobiformis*) that are carried upward by the adults as the seeds mature at lower elevations in late summer and early fall. All or most of this activity by nutcrackers ceases once the zone is covered with snow. Thus, these cached seeds are not recovered until the area is free of snow the next spring and summer, some 8-10 months later.



Figure 4. Alpine Tundra.

2. Spruce-fir Forest. (Figure 5)



Figure 5. Spruce-Fir Forest.

This zone of dense coniferous trees consisting of Engelmann spruce, alpine fir (*Abies lasiocarpa*), limber pine, and bristle cone pine exists directly below the tundra at elevations from about 2,745 m (9,000 ft.) to 3,660 m (12,000 ft.). Forests can be dense with a continuous layer of canopy cover so thick that few under story plants can thrive in this extreme shade. A thick layer of litter and duff covers the ground in most areas. Grassy alpine meadows are interspersed with tree covered areas. This zone is characterized by high winds, heavy snow fall in winter and rain fall in summer, cold winter temperatures and cool summer temperatures. Clark's nutcrackers and Steller's jays (*Cyanocitta stelleri*) are common inhabitants of this zone. Both nest here, extract seeds from the cones of both species of pine, and readily cache seeds here. (Although Steller's jays are industrious cachers we have studied them little because they do not do well in captivity.) Occasionally in late summer and early fall flocks of pinyon jays can be seen and heard traveling through the area. Presumably, these birds are searching for pine seeds.

3. Mixed Coniferous Forest. (Figure 6)

This zone exists at elevations between 2,287 m (7,500 ft) and 2,745 m (9,000 ft). The principal trees are firs, primarily Douglas fir (*Pseudotsuga menziesii*) with occasional white firs (*Abies concolor*) and ponderosa pines (*Pinus ponderosa*) found on warmer exposures. Here, two closely related species of pine intergrade, the southwestern white pine (*Pinus strobiformis*) and the limber pine (*Pinus flexilis*), and form large stands on the side of the Peaks. A deciduous tree, Gambel oak (*Quercus gambeli*) is present in low numbers. The canopy is complete so the forest floor is well shaded and contains a thick mat of litter and duff. Alpine meadows and stands of quaking aspen (*Populus tremuloides*) are interspersed among the conifer stands. Winters are cold and windy, with heavy snows at times and modest amounts of summer rains. Climatic conditions in this zone are more moderate than in the above spruce-fir zone, but still rather harsh in winter. Clark's nutcrackers and Steller's jays are the principal seed caching corvids inhabiting this zone with occasional visitations by flocks of pinyon jays.



Figure 6. Mixed Coniferous Forest.

4. Ponderosa Pine Forest. (Figure 7)



Figure 7. Ponderosa Pine Forest.

This zone is present from 2,105 m (6,900 ft) to 2,287 m (7,500 ft). This forest is a monoculture, as the dominant and predominant tree is ponderosa pine. In some areas Gambel oak may be present at modest densities. Ponderosa pine forest form open stands of large trees, in contrast to the above forests where the canopy is complete. Pine nettles and cones from past years accumulate on the forest floor and can form a thick mat of 5-10 cm. In some areas pine trees are dense and small forming dog-hair thickets. Winters are modest with snowfall amount below those experienced in the above zones with summer rains also occurring in moderation. The growing season extends from late April to early September. In recent years wild fires have commonly consumed large tracts of this forest. This is the lowest elevational extension of the coniferous forest on the peaks. Steller's Jays occur at maximum densities here and readily cache the seeds of ponderosa pines. These jays also descend to the upper reaches of the next lower zone to harvest and carry pine seeds up into this forest. Flocks of pinyon jays roam through portions of this forest, harvesting and caching ponderosa pine seeds and, like the Steller's jay descending into the woodland to harvest and carry seeds up into this zone. Pinyon jays commonly nest in this forest. At the lower edges of this zone and on drier sites Western scrub-jays and Mexican jays occur. They also harvest and cache ponderosa pine and pinyon pine seeds here.

5. Pinyon-Juniper Woodland. (Figure 8)

This extensive zone occupies the base of the mountain and lies between 1,680 m (5,500 ft) and 2,135 m (7,000 ft). This zone occupies the largest amount of area of all the zones because there is more land mass at the lower elevation where these trees live. The predominant trees are Colorado pinyon (*Pinus edulis*) and a host of junipers (*Juniperus osteosperma*, *J. monophylla*, *J. scopulorum*, *J. deppeana*). The upper elevations are dominated by pinyon pine and the lower regions may consist solely of junipers. Because moisture is limiting, trees are spread out with large openings between them. The under story supports some shrubs, succulents and cacti. The climate is mild in winter and hot in summer. Modest rains occur in summer and winter moisture is in the form of both rain and snow. Winter snows melt relatively quickly. Insects and arachnids and some small mammals are active throughout the year. Populations of western scrub jays and Mexican jays reached their highest levels here. These jays harvest and cache pinyon pine seeds when available. Also resident, are flocks of pinyon jays that use the pinyon pines in great numbers. Steller's jays and Clark's nutcrackers descend the mountain and collect large amounts of pine seeds that they then carry up into their normal habitats. The pinyon pine is the most heavily sought after pine on the San Francisco Peaks.



Figure 8. Pinyon-Juniper Woodland.

Some important ecological patterns emerge along the Life Zone gradient. At the top of the mountain it is cold in winter, with heavy snow, but cool in summer with heavy rains, and frequent clouds that obscure the sun, especially in winter and mid-summer. Plant and animal productivity is restricted by a short growing season in late spring and summer. In the higher coniferous forests, tree density is high and canopies are closed, with a thick layer of decomposing plant parts on the ground. At lower elevations, it is cool but mild in winter, with little snow, but hot in summer, with sparse rains. Clouds are much less frequent than at higher elevations. Plant and animal productivity is spread out over a 9-10 month period and most animals remain active year round due to the mild and hospitable climatic conditions. The pine forest and woodland have an open canopy with sunlight reaching ground level throughout. Almost no plant decomposition is occurring on the woodland floor and bare ground is often exposed.

Consequently, each Life Zone has a unique set of ecological properties and constraints that act as selective forces shaping the adaptive traits of the creatures inhabiting it. Because of the compactness of the mountain and the compressed nature of these adaptive zones it was relatively easy to observe the similarities and differences among the seed caching corvids. There is a general trend of increasing numbers of seed caching corvid species with decreasing elevation throughout the forest and woodland zones. For example, only the nutcracker visits the alpine tundra, but all five species (nutcracker, Steller's jay, pinyon jay, western scrub jay, and Mexican jay) visit the pinyon-juniper woodland. In the high coniferous forests the nutcracker and Steller's jay are resident whereas in the low woodland three species of jays (pinyon jay, Western scrub jay and Mexican jay) are resident. Only the scrub jay apparently uses the grassland which occurs below the woodland.

2.1 The Trees

On the slopes of the San Francisco peaks, four species of pines produce seeds that are harvested, transported, cached and later recovered by the seed caching corvids. In order of descending importance to the birds these are: pinyon pine, limber/southwestern pine, ponderosa pine, and bristlecone pine. A brief description of the characteristics of each that make them attractive to the seed caching birds follows in order of descending elevational distribution.

1. Bristlecone pine.

This species is the rarest of the pines and exists at the highest elevations, usually at or near tree line in the spruce-fir forest. The seeds are tiny, ranging in size of between 10-13 mm (Schopmeyer, 1974) and contain a 10-13 mm wing. The seeds are grey to brown to black. The cone, as the trees name indicates, is armed with narrow, sharp, pointed needle-like spines to protect the seeds from predators. The cone is oriented downward on the branch. Bristlecone pine produces some cones most every year, and seeds readily fall when they open. This pine relies mainly on wind to disperse its seeds, and little is known about the harvest transport, caching and recovery of this species by seed caching corvids, primarily Clark's nutcrackers and Steller's jays. This pine is probably not a significant source of food for either of these species.

2. Limber and southwestern white pine complex.

This species complex reaches its high densities in the mixed coniferous forest with a few individuals extending upward in the spruce-fir forest and down into the upper edge of the ponderosa pine forest. (On the San Francisco Peaks these two species interbreed thus we refer to them here as ? a species complex?) The wingless seeds are relatively small (10-15 mm in length) and brown in color. The cone contains either weak spines or no spines at all. Cones are oriented downward. This pine is prized by nutcrackers and Steller's jays which work with great industry to harvest the seeds, which are cached within this forest type and in nearby open meadows (Benkman et al., 1984). Both Steller's jays and nutcrackers extract the seeds from open cones. Pinyon jays occasionally visit these trees in late autumn, harvest seeds and carry them down hill into the ponderosa pine

forest and pinyon-juniper woodland where they are cached.

3. Ponderosa pine.

This species exists in almost pure stands below the mixed coniferous forest. The tree produces some cones in almost every year and huge crops in some years. The small seeds (3-4 mm in length) are attached to a wing that may be five times as long as the seed (16 mm in length). The seed coat is brown with occasional dark mottling. Cones contain many sharp, decurved spines for protective armament. Cones are oriented downward on the end of branches and seeds are readily released from ripe cones. All four jays (Steller's, pinyon, scrub and Mexican) and Clark's nutcracker harvest, transport, cache, and recover the seeds from this tree, even though this species relies mainly on wind for the dispersal of its seeds. Wings are broken off the seeds before they are transported. Nutcrackers clip them off with their bills while the jays use a branch or other stationary object to smash the wing with a strong swipe of the bill.

4. Colorado pinyon pine. (Figure 9)



Figure 9. Pinyon pine tree.

This species lives below the ponderosa pine forest. Trees are spaced more openly than any of the above. This species is the only masting species of the conifers harvested by the birds. Usually a few cones are produced on many trees every year but in extreme years no cones are produced, or just the opposite, with most trees producing thousands of cones per tree. When trees produce such a large crop of seeds this is known as a "mast" crop. These extremes occur about once every seven years (Table 1).

Table 1. Qualitative Measures of Pine Cone Density & Cache Intensity

1. No Cones (2 of 7 years)	No cones = No seeds = NO CACHING
2. Low Cone Crop (2 of 7 years)	Few cones = Few seeds = NO CACHING
3. Modest Cone Crop (2 of 7 years)	Modest cones = Modest seeds = CACHING
4. Heavy Cone Crop (1 of 7 years)	Many cones = Many seeds = INTENSE CACHING



Figure 10. Yellow seeds (right); dark brown seeds (left).

It has been suggested that masturing insures that the seed caching birds and other seed predators are unable to harvest and consume all available seeds and thus the predators are "swamped". They cannot build up populations of sufficient numbers to totally decimate the seed crop (Vander Wall, 1990; Vander Wall & Balda, 1977). This species places its cones near the end of branches, where they are positioned to point outward or upward. Cones open asynchronously on each tree and in different regions. Seeds are relatively large (10-15 mm) and wingless and held in deep grooves on the cone scale. The cone scales are relatively short and contain flanges that act to hold the seeds in the cones so they are not easily dislodged. The flange disintegrates after the first frost in autumn and then the seeds fall out of the cone. Seed coat color differs drastically between seeds that are full of female gametophyte material (dark, chocolate brown) and those that are empty (light yellow) (Figure 10).

All five seed caching corvids are attracted to the cones of pinyon pine to extract seeds. The Clark's nutcracker and pinyon jay are able to open tightly closed green cones, whereas the three other jays must wait for the cones to open naturally. The scrub-jay may not recognize that the yellow hulled seeds are empty (Vander Wall & Balda, 1981). This species of tree enjoys the widest elevational range of any pine on the San Francisco Peaks. Trees grow from 1,680 m (5,500 ft) to over 3,600 m (11,000 ft). These higher stands were most likely "planted" by nutcrackers, as we have seen them transport seeds to these areas (Vander Wall & Balda, 1977).

2.2 The Birds

When pine cones are present, the seed caching corvids expend considerable time and energy harvesting, transporting, and caching pine seeds each autumn. Each species shows different types of morphological, ecological and behavioral specializations for this task. Here we describe these specializations for each species.

1. Clark's nutcracker. (Figure 11)

This species lives and nests at the highest elevations on the San Francisco Peaks, of all the seed caching corvids. They nest in spruce-fir, mixed conifer and ponderosa pine zones. Nutcrackers have a number of morphological adaptations that are used for the harvest, transport, caching, and eating of pine seeds. A conspicuous example is the long, heavy, sharp bill. This bill is used for hacking open green, closed cones, many of which are covered with pitch. Nutcrackers can open the green cones of most of the pines mentioned above. The bill is also used to thrust seeds into the substrate with strong japes of the head and neck. As their name implies, nutcrackers can open thick-hulled pine seeds by crushing them in their bills (Johnson et al., 1987).

During transport, seeds are held in a unique sublingual pouch that is located in the floor of the mouth in front of the tongue (Bock et al., 1973, Figure 12). When full of seeds the sublingual pouch is greatly distended but it is not conspicuous when empty. This structure can be filled with up to 95 pinyon pine seeds and weigh up to 13% of the total weight of the bird.



Figure 11. Clark's nutcracker in snow.

Nutcrackers have long, pointed wings for strong flight. They often fill their sublingual pouches with pinyon pine seed and fly up to 22 km to a caching area (Vander Wall & Balda 1977, 1981). They also can carry seeds 1,900 m up the side of the Peaks.

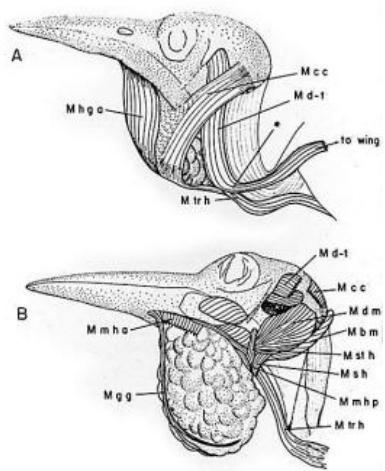


Figure 12. Sublingual pouch. Muscle names in Bock et al., 1973.

Nutcrackers can distinguish between pinyon pine seeds that contain female gametophyte material (nut meat) and those that are empty by observing the color of the hull or shell. The other species of pines do not label their seeds. Nutcrackers also use Bill clicking, the rapid opening and closing of the mandibles, to help determine if the seed is full (Ligon & Martin, 1974) and also help determine the thickness of the seed coat (Johnson et al., 1987). In an autumn when the pinyon pines have masted, thousands of discarded cones occur on the ground containing a large numbers of seeds with yellow hulls.

The daily sequence of events during the autumn caching season proceeds as follows. Birds open seeds and consume pine seeds at first light. Then seed collecting begins and pouches are filled. Birds continue to harvest seeds for the entire day traveling 5-7 times from harvest area to caching area and back.

Seeds are cached in the substrate at depths of 2-3 cm. (Figure 13) These caches are totally concealed from view as birds often place soil, litter, pine needles, pine cones and even small stones on top of the hidden seeds. These objects seldom remain in place for long due to wind, water, and gravity. Most likely these objects are placed on top of the cache to conceal the soil disturbance made by creating caches, not to conspicuously mark the location of the cache.

Caches are created in a wide variety of sites, including meadows, tundra, open woodlands, closed canopy forest, rocky outcrops, thick needle layers, cinders, and bare soil. Many of these sites experience low amounts of snowfall

or early snow melt thus allowing birds' ready access to their caches. Often nutcrackers cache seeds at sites used by numerous other nutcrackers for caching. However, even though the site may be communal the caches are not, as birds can only locate the caches they have created (Vander Wall, 1982; Vander Wall & Balda, 1977).

Nutcrackers often proceed to cache in two stages. First, when seeds are plentiful birds will extract them and cache them near the harvest tree. Second, after the cones have been depleted these caches are recovered and the seeds transported some distance and then recached (Tomback, 1998) The former may be a technique to get as many seeds as possible out of the conspicuous cones and into hidden sites, the locations of which are known only to the cache. Later seeds may be moved to more protected sites or sites with fewer seed predators present.

In a year with a heavy cone crop a single nutcracker can cache between 22,000 and 33,000 seeds in over 7,000 individual cache sites (Vander Wall & Balda, 1977). Birds may place between one and 14 seeds per cache. Birds continue caching until the crop is depleted or snow covers the caching areas (Vander Wall & Balda, 1977). Possibly, birds curtail caching after snow remains on the ground because to cache in these conditions would reveal cache location by their foot prints left in the snow.

Seed caches may be harvested immediately after the harvest is finished. Often, birds eat the recovered seeds directly at the site of recovery, thus providing a measure of recovery accuracy. Most workers report that nutcrackers recover seeds from about 80% of their probe holes (Tomback, 1980; Turek & Kelso, 1968). This estimate must be low as some seeds recovered from caches are carried off before consumption, and some sites must be pilfered by cache robbers. This high estimate is a truly a tribute to the spatial memory ability of the Clark's nutcracker when one considers: 1) nutcrackers spend less than 30 sec. making a cache (Kamil et al., 1999); 2) they make thousands of caches each autumn; 3) they returned to accurately recover their caches many months after creating them; 4) they recover through a substrate that has been greatly altered between the time of caching and recovery. This means that caches created under one set of substrate characteristics are recovered under a very different set of substrate characteristics. For example, caches made in the fall before snow is present are recovered through snow (Figure 14). Caches made when green vegetation is present are recovered after this vegetation has died and disintegrated. This suggests that these local cues or landmarks are not used by the birds as the sole source of information about the location of their caches.

Nutcrackers are heavily dependent on their cached seeds for survival in winter and as food for their offspring. Giuntoli and Mewaldt (1978) found that between 80 and 100% of the winter diet of nutcrackers was made up of conifer seeds, most likely recovered from caches. Other foods are consumed, when present, as the nutcracker becomes a feeding generalist during warmer weather. Clark's nutcrackers are among the earliest nesting species of North American birds initiating nesting at high elevations in the San Francisco Peaks in February or early March (Tomback, 1998). Early breeding may occur because of having stored enough food to provide the energy and nutrients for this early reproductive effort. To withstand the cold temperatures, nutcrackers build large, sturdy, well insulated nests. Both males and females have brood patches and can thus share in the duties of incubating eggs and brooding nestlings. This also allows each member of the pair to go off, individually, to locate its own pine seed caches. The diet of nestling nutcrackers is almost exclusively conifer seeds (Bendire, 1889; Johnson, 1900; Mewaldt, 1956). This is a highly unusual food for nestling birds and requires a major adaptive change in the digestive physiological of the birds to produce specific digestive enzymes to digest these seeds. After fledging, young birds follow their parents to caching areas where they are also fed pine seeds. This event normally occurs 9-11 months after the seeds have been stored (Vander Wall & Hutchins, 1983).

In late spring and early summer adult nutcrackers are often seen far from their normal haunts. These birds fly slowly just above the tips of trees. We suspect these birds are assessing the location and size of the cone crop that will be harvested in the coming months (RPB, pers. obs.). In years when cone crops fail nutcrackers leave their high mountain haunts and fly long distances in search of alternate foods. These irruptions take birds hundreds of km from their normal range (Vander Wall et al., 1981; Westcott, 1964). Thus, nutcrackers are highly specialized in morphology, physiology, and behavior for the extraction, transport, caching and recovery of conifer seeds and these specializations form a suite of adaptations that extend into all aspects of the bird's life history.



Figure 13. Exposed pine seed cache.



Figure 14. Cache site where nutcracker has recovered cache through snow.

2. Pinyon Jay. (Figure 15)



Figure 15. Adult male (above), adult female (middle), and juvenile (lower)Pinyon pine with cones.

This species, as its name implies, is closely linked to the pinyon pine which lives that the base of the San Francisco Peaks. In the San Francisco Peaks, however, these jays interact with most species of pines across all Life Zones. They nest in the pinyon-juniper woodland and ponderosa pine zones, where seeds are readily cached. In fall, they also roam far above these zones in search of seeds.

Pinyon jays possess a number of adaptations for harvesting, transporting, caching and recovering seeds. They have a relatively long, sharp bill that is featherless at its base. Consequently, the bird's nostrils are exposed and can be a source of heat loss under cold conditions. However, the loss of these feathers means that the featherless length of the bill is effectively lengthened, an adaptation especially useful for extracting seeds from pitch laden pine cones. The trade-off must be in favor of the longer, feather-free bill compared to the amount of heat potentially lost. The sharp bill is used to hack open closed pine cones and also the hulls of pine seeds, thrust seeds into the soil, and probe into the soil to recover hidden seeds. A special articulation of the jaw allows birds to absorb the bill's impact during strong pounding (Zusi, 1987).

Seeds are held during transport in an expandable esophagus which when full, can hold about 40 seeds. This amounts to about 12% of its body weight (Vander Wall & Balda, 1981). Pinyon jays can distinguish between empty and full pinyon pine seeds using the color of the seed coat. Pinyon pine seeds are also "Bill Weighed" and "Bill Clicked" as done by nutcrackers (see above) (Ligon & Martin, 1974). Cones can be opened on the tree branch or broken off and carried and wedged tightly into a forked branch. When wedged in a fork, the bird can grip the surrounding branches tightly with both feet and forcibly hammer the cone open. Shredded cones commonly accumulate under such sites.

Cone opening, seed harvesting, pouching, transporting, and caching seeds is a flocking event. These behaviors are performed by all members of the flock in synchrony. These flocks have permanently mated pairs, stable membership, contain extended family units, and remain on

permanently delineated home ranges. Pine seeds are transported to traditional caching areas that are used year-after-year. Flocks have between 8 - 10 of these traditional caching areas on their home ranges. These "traditional" areas are often located where the substrate is loosely packed, contains patches of exposed soil, rocks, and cinders, and has a shallow litter layer. These characteristics indicate a well drained soil (Balda, 1987, 2002). Flocks move in synchronous fashion from harvest to caching area and can make between 5-9 round trips per day from harvesting to caching areas depending on density of the cones, and distance from the caching areas. Flocks may fly up to 11 km, on long strong wings, between harvest and caching areas

Pinyon jays seem to favor specific microhabitats as cache sites. They appear to prefer to cache near objects, including the base of cliffs, large boulders and especially tree trunks, often on the south side. These southern exposures are first to melt free of snow or accumulate less snow following a winter storm (Balda & Bateman, 1971, 1972). Jays however, have been observed digging through a layer of snow 5 cm deep to recover caches. Pinyon jays use sites other than the substrate for caching. Stotz and Balda (1995) found that 86% of 114 above ground cache sites were crevices in tree bark. Other sites include in rock piles, grass tufts, and pine nettle clusters high in trees..

Caches are created as the flock walks slowly and silently over the substrate. Birds continuously thrust their bill into the soil and litter as they deposit one or more seeds per site (Stotz & Balda, 1995). A single bird can make a dozen caches in less than a minute. Generally, flock members move in a particular direction during caching but individual birds may move in any direction. Pinyon jays normally place a single seed in a cache but on occasion they may place up to seven seeds per cache. At times, however, birds will thrust their bills into the substrate but not deposit a seed. This is often referred to as false caching (Balda, 2002) and may be a technique used to confuse potential intra- and inter-specific cache pilferers. In a year when cone crops are dense, a single bird can cache up to 26,000 seeds in up to 20,000 individual sites (Marzluff & Balda, 1992). Ligon (1978) estimated that a flock of 250 birds in New Mexico could collectively cache 4.5 million seeds in a single autumn when cone crops are heavy.

Although caches are made synchronously by the flock, field observations (Balda & Bateman, 1969, 1971) suggest that birds accurately recover their own caches. This is especially interesting for pinyon jays because they: 1) cache within the structure of the flock which means birds move in unison over the terrain when creating caches, so individuals have little control over the general area where they can cache; 2) have little time for individual decisions about where to make specific caches because the flock is always on the move; 3) make caches in rapid succession resembling the needle of a sewing machine; 4) must be concerned with pilfering.

Young-of-the-year pinyon jays and adult Steller's jays often watch intently as flock members are caching and then attempt to locate their caches when they move on. Most attempts appear to fail, but sometimes the bird that has created the cache will respond by either chasing the potential pilferer away or digging up the cache and moving it to a new location (RPB pers. obs.). Mated pairs of pinyon jays appear to coordinate their movements during caching so that they can observe the creation of each other's caches (Chen, 2000; Shulzitski, 1999). These findings come solely from laboratory studies. It is difficult to follow individual birds in a flock because of the sheer numbers and continual movement, thus these observations have not been confirmed for pairs in the wild.

Pinyon jays nest in late winter and early spring when cone crops are large. Nests are large and well insulated, and often constructed on the south side of the tree (Balda & Bateman, 1972). The female is the sole incubator of the eggs as only she possesses a brood patch. Males must feed their females during the incubation and early brooding phase of nesting because of low temperatures. Adult jays rely heavily on pine seeds in winter when they may constitute between 70 and 90 percent of the diet (Ligon, 1978). At this time, seeds are no longer present in cones so these seeds must come from caches created by the birds. Males must procure and deliver these seeds to the nesting female. Young pinyon jays are also fed pine seeds as a portion of their diet. Bateman and Balda (1972) found that pine seeds comprised 11% of the nestling's diet while Ligon (1978) found pine seeds made up 32% of the diet. As mentioned for nutcrackers, the ability of nestlings to digest plant material is a rare adaptation in song birds, requiring major changes in the digestive enzymes possessed by the birds. Juvenile birds first began caching when 3 weeks post-fledging. For the first 9 weeks of caching young birds cached primarily non-food items such as rotten pinyon and ponderosa pine seeds, flakes of tree bark, rabbit scat, dead insects, and a roofing nail. After 12 weeks of age jay began caching edible pine seeds (Stotz & Balda, 1995)

In years when pinyon pine cone crops are low, pinyon jays cache seeds of the other pines, many of which have large wings. Birds are efficient at removing the wing by holding the seed in their mouth with the wing protruding directly outward and then knocking the wing off on a branch or other object. This behavior differs from that of the nutcracker which appears to simply bite off the wing (RPB, pers. obs.) No detailed studies are

available of the use of these pines by pinyon jays. However, Balda and Bateman (1971) report that pinyon jays are highly industrious in the harvest and caching of ponderosa pine seeds. When there is a general failure of the pines to produce cones pinyon jays may irrupt from their normal range and emigrate hundreds of km in search of food (Westcott, 1964). These irruptions may consist of huge numbers of birds or small bands of birds that scour the country side for food (RPB pers. obs.).

3. Steller's Jays. (Figure 16)



Figure 16 Steller's Jay.

This species is a permanent resident of the coniferous forest zones on the San Francisco Peaks. It readily caches ponderosa and pinyon pine seeds in autumns when cone crops are available. Steller's jays also cache acorns of local oaks. This jay does not have a strong, sharply pointed bill for opening green cones and thus must wait for cones to open before it can extract seeds. It does have an expandable esophagus, for about one-third of its length that can hold up to 20 seeds during transport. Birds can carry seeds about 5 km (Vander Wall & Balda, 1981) from pinyon pine trees in the woodland and cache them in the ponderosa pine forest. This jay appears to cache in small family units or pairs. Steller's jays appear highly motivated to harvest and cache seeds. A single bird may make 5-7 trips with seeds per day between woodland and ponderosa pine forest. Thus, at this intensity one bird can cache about 7,800 seeds per autumn.

When pinyon pine seeds are placed on a feeder Steller's jays are quick to collect these seeds in their expandable esophagus (RPB pers. obs.). Few studies have been done on their relationship to pine seeds and acorns (Abbot, 1929; Christensen & Whitham, 1991; Vander Wall & Balda, 1981). At a feeding station where inedible (hollow) seeds were dyed dark brown to make them look edible, these jays carried them off. Steller's jays have never been seen to test the quality of seeds by bill-clicking or bill weighing so it is possible they cannot discriminate seeds as well as the above two species (Vander Wall & Balda, 1981). Steller's jays may be efficient cache robbers on nutcrackers and pinyon jays, (Burnell & Tombach, 1985). When a flock of pinyon jays comes through areas inhabited by Steller's jays they sit silently in trees observing where pinyon jays are creating caches.

Little is known about the caching and recovery behavior of Steller's jays even though they share habitats with humans and readily come to feeders and picnic tables to collect and carry off seeds (Brown, 1994). In a year of heavy cone production Steller's jays were observed to cache 46% of the time in soil, 22% of the time in bark crevices, 18% of the time in rock and stump crevices, and in ponderosa pine needle clusters 15%. Most often one seed is placed per cache. (Vander Wall & Balda, 1981). Around dwellings birds will cache under litter in gardens, in lawns, in tree crevices, in storm gutters, under roofing shingles, in depressions and cracks in wood siding and decks, and in cracks in sidewalks (RPB pers. obs.).

Steller's jays probably use their cached food solely for winter survival as there are no reports of them feeding cached seeds or acorns to nestlings. Possible all cached food is consumed before nesting is initiated. No observations have been reported on the accuracy of recovery of stored food in the wild. Observations near homes would suggest the jay is quite accurate when recovering cached food (RPB pers. obs.). Steller's jays nest in late April and early May. Thus, they show no tendency for unusually early nesting and do not build bulky, well insulated nests.

This bird has not been studied under closely controlled laboratory conditions because it is extremely difficult to hold in cages and aviaries (RPB pers. obs.). Consequently little is known about its spatial memory abilities. However, the amount of food stored, the presence of an expandable esophagus, and the amount of time birds spend caching would suggest that the bird is readily able to find the seeds it caches. This species does not nest in late winter, does not build a large nest and does not feed its young pine seeds. Also, it does not usually undergo huge irruptions when cone crops fail. Thus, many of the Steller's jay's life history traits are not affected by the presence or absence of pine seeds.

4. Mexican Jays (Figure 17) and Western Scrub Jays. (Figure 18)



Figure 17. Photograph of Mexican Jay by Ralph Shant.



Figure 18. Photograph of Western Scrub Jay by D. Von Gausig.

These two species (Figures 17, 18), closely related congeners, are permanent resident species in the pinyon-juniper woodland on and at the base of the San Francisco Peaks. Both species harvest and cache pinyon pine seeds from open cones. The western scrub-jay is the most common species in the woodland habitat and may maintain permanent, year round territories occupied by a single pair of birds. The Mexican jay is highly social with 5-25 birds occupying permanent territories (Brown, 1994). Neither species posses any specialized structures for the collecting, transporting, caching or recovery of pine seeds. Scrub jay bills, for example are relatively short ($x = 19.6$ mm, $n = 20$), rather blunt, and therefore relatively poorly adapted for opening green cones (Balda, 1987). Scrub jays that cache pinyon pine seeds have slightly more pointed, but rather thin bills, used for extracting seeds from open pine cones, holding the seeds during transport and thrusting seeds into the substrate (Peterson, 1993).

Neither species is able to open green cones and must wait for cones to ripen. Scrub jays have been observed silently watching nutcrackers and pinyon jays opening green cones then flying rapidly at them while vocalizing loudly. The startled birds drop the partly opened cones and fly up into the trees. Scrub jays proceed to retrieve the cone and extract the exposed seeds (Vander Wall & Balda, 1981). These jays have no specialized structure for carry seeds from tree to cache site except in mouth and bill. Consequently they can only carry 3-5 seeds per trip. These jays do not have strong long wings, but relatively short rounded ones. They usually carry pinyon pine seeds no more than 500 m to 1 km. Scrub jays do possess the buttress complex which makes the lower mandible effective for pounding open hard shelled seeds (Zusi, 1987).

Both species may be able to distinguish good (dark brown hulled) seeds from empty (yellow hulled) seeds but they are not known to bill click or bill weigh seeds. Both species usually cache one seed per cache and make repeated caches within one m of each other. Cache sites are primarily along edges of trees and stumps and under dense foliage. Of 62 observed caches made by scrub jays, 29 were under pinyon pine trees, 8 were under junipers, 8 were near a bush, 3 were near logs, and 14 were out in open meadows (Hall & Balda, unpublished MS). The majority of caches placed under trees were south of the trunk. These observations indicate that scrub jays have a set of preferred caching sites that are frequently used.

Scrub jays and Mexican jays nest in late April and early May, showing no tendency to nest earlier when cone crops are heavy. Neither species builds a large well insulated nest, nor is known to feed pine seeds to its nestlings. These two species are the most general feeders in the group and although they store pine seeds in autumn they are not as motivated as the nutcracker, pinyon and Steller's jay. Scrub jays store about 6,000 seeds in an autumn when the cone crop is large. They do not spend every waking moment harvesting, transporting and caching pine seeds. If they did so they could easily double the number of seeds cached (Balda, 1987). This is so because they transport seeds relatively short distances compared to the other species, and have many more snow-free days to cache. These two jays do not undergo major eruptive movements when cone crops fail. This may be an indication that these species are not as heavily dependent on cached food as the nutcracker and pinyon jay.

2.3 Summary of Natural History and Ecology of Caching Behavior

The corvids of the San Francisco Peak region show an ecological, morphological and behavioral gradient in their adaptations for the harvest, transport, and storage of pine seeds. Ecologically, species living in the harshest environments where winter productivity is nil are most dependent on cached seeds during winter, whereas species living where winter is milder are less dependent on cached seeds. Morphological features that show this pattern include bill size and shape (Figure 19), the structures used to carry seeds, and variation in wing length and shape for long flights. Behaviorally, the number of seeds that can be transported is highly correlated with the distance they are carried (Figure 20), and the presence of a specialized structure for doing so. The Clark's nutcracker and pinyon jay, the two species living at the highest elevations, cache huge numbers of seeds compared to the two jays that inhabit the lower, warmer woodlands. Of the five species discussed above only nestling nutcrackers and pinyon jays are equipped to digest pinyon pine seeds. The scrub jay and Mexican jay do not show the same levels of intensity to harvest seeds as is shown by the nutcracker and pinyon jay.

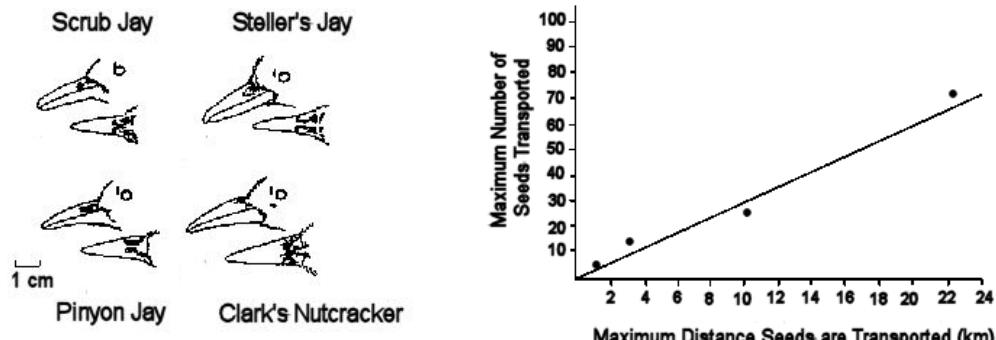


Figure 19. Bill sizes and shapes of four seed caching corvids.

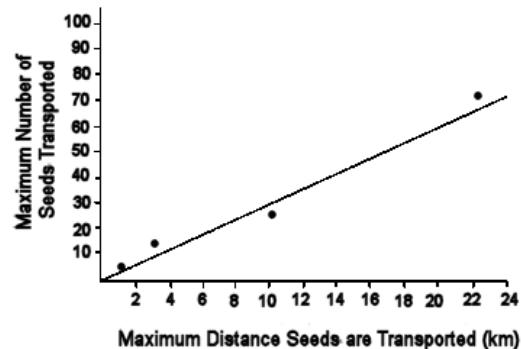


Figure 20. The relationship of distance seeds are transported and average number of seeds carried. Nutcracker is far right, Western Scrub jay far left, Steller's jay, second from left with pinyon jay in the middle.

There can be no doubt that these birds have an adaptive suite of characteristics for the harvest, transport, and caching of seeds. The components of this adaptive suite vary depending on the selective forces present in the Life Zones each species inhabits, and the life history strategy employed by each species. The four species show a clear specialization gradient from more highly specialized species, to more generalist species.

III. Hypothesis and Questions

The phenomenon we described above makes it clear that there is a complex interaction of natural history and ecology on the one hand, and behavior and physiology on the other. While these phenomena strongly suggest that the ability to find stored food is critical for the survival of these species, they do little to explain how the different species manage to perform the extraordinary task of relocating hidden seeds from thousands of sites months after they were created. However, the pattern in behavioral and physiological traits strongly suggests a similar pattern may exist in certain cognitive traits. This led us (Balda & Kamil 1989; Kamil & Balda, 1990) to propose the following hypothesis: Species that are most dependent on cached seeds for survival in winter and early spring when no other foods are available will have better spatial memory abilities than those species that are less dependent on stored food for

winter survival.

More specifically, we predicted that Clark's nutcrackers and pinyon jays have spatial memory abilities that are superior to those of scrub jays and Mexican jays (Figure 21). Findings to support this hypothesis will strongly support the suggestion that spatial memory ability is another trait in the adaptive arsenal employed by species to enhance their fitness.

Although field observations suggest an accurate spatial memory in seed cachers, these observations are incomplete because simply observing the act of recovering a cache is inconclusive. The observer does not know the identity of the recovering bird, what bird made the cache, how long the cache was present, if the seeds were visually apparent to the bird, if the soil was disturbed in such a manner to suggest that a cache of seeds was present at this location, etc. Also, most birds are highly secretive when creating caches and avoid making caches when being observed. Pinyon jays are an exception, but they cache at such a rapid rate it is almost impossible to keep track of their cache sites. They also create false caches which makes finding their caches very difficult. Consequently, in order to study the accuracy of spatial memory for finding cached seeds, it was necessary to develop laboratory techniques that could control or hold constant many potentially intervening variables. Below we will describe our methods in detail.

When using controlled laboratory experiments to explore species differences in mental capabilities there are many potential problems. Species may respond differently to the experimental apparatus, or to the stimuli used to elicit a response. Also, some species may simply be able to adjust to captivity or to the experimental manipulations better than others. In addition, some species may simply be better test takers than others. In our attempt to overcome these potential problems we employed three different experimental paradigms, in a process referred to as converging operations (Kamil, 1988). If the pattern of results across species remains consistent over these three different tests, we can then be more confident of the reality of these species differences than we could on the basis of a single task.

IV. Cache Recovery Tests of Spatial Memory

4.1 Introduction and General Methodology

In order to directly test for accuracy of spatial memory when recovering caches we conducted a series of experiments in large free-flying, experimental rooms. These rooms contained raised floors with holes at regularly spaced distances (Figure 22, 23). Each hole was 5.5 cm in diameter and could be filled with a sand-filled cup for caching or a wooden plug to prevent caching. These rooms contained many landmarks, posters on the wall, observations windows, a porthole through which the bird entered and exit the room, a door, and a centrally located feeder. Because the experimental rooms were designed to enhance the internal validity (Kamil, 1988) of our experiments there was a question if the birds would cache in the sand-filled cups (Figure 24).



Figure 22. Photograph of large experimental room. Note objects on the floor and wall.

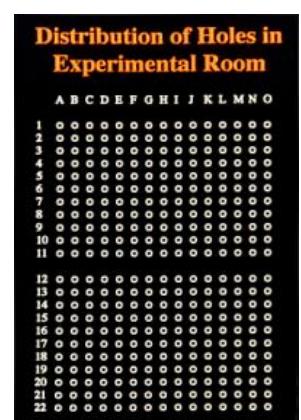


Figure 23. Distribution of holes in experimental room.



Figure 24. Clark's nutcracker caching in a sand filled cup.

During experiments birds were allowed to enter the experimental room directly from their cages through a porthole in the wall. Before entering the room the cages were darkened and the experimental room was illuminated. Birds thus flew into the lighted room. After a session was completed the lights in the room were extinguished and the cage illuminated. The birds then left the experimental room and flew directly through the porthole into their cages. Thus, birds were not handled before, during or after an experiment. For caching sessions a predetermined number of holes were opened and were filled with sand in a predetermined pattern. A feeder was placed in

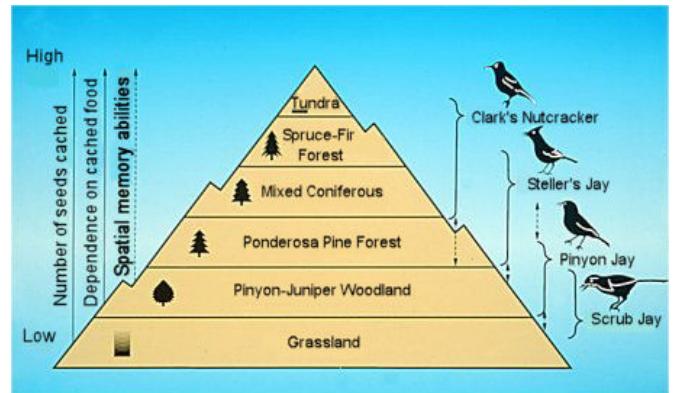


Figure 21. Distribution of four species on San Francisco Peaks. The hypothesis is listed on the left side.

the center of the room and contained a predetermined number of pinyon pine seeds. For recovery sessions all signs of digging in the sand-filled holes was swept up from the floor, one seed was placed into cups where caches had been made, and the feeder was empty. There were no signs of digging or presence of seeds in the cups that the birds could have used as cues to locate caches.

4.2. Cache Recovery by Clark's Nutcrackers, Pinyon Jays and Scrub Jays (Balda & Kamil, 1989)

This test of spatial memory was conducted in a 3.4 x 3.4 m experimental room with 180 holes in the raised floor. The accuracy of recovery was tested under two conditions. In one condition 90 holes were available for caching and in the other condition only 15 holes were opened for caching. The rationale for this two stage design was to assess the accuracy of the three species after they the birds were given free choice of cache placement so that a placement strategy could have been employed (90 hole condition). This accuracy can then be compared to that achieved after severely limiting the number of available cache sites (15 hole condition). Under this condition a cache site placement strategy would be severely inhibited. Seven days after making caches birds were allowed back into the experimental room to recover their caches. Accuracy was assessed as the proportion of holes probed that contained a seed.

In most of the recovery trials birds preformed better than chance (40 out of 42) and all three species performed better in the 90 hole condition than they did in the 15 hole condition. Nutcrackers and pinyon jays were significantly more accurate than scrub jays in both conditions (Figure 25). There was no significant difference between nutcrackers and pinyon jays in recovery accuracy. Pinyon jays appeared to be most affected by the 15 vs. 90 hole condition. During the 90 hole condition they placed their caches in conspicuous clumps. The average distance between caches was 0.81 m for pinyon jays, 1.22 m for nutcrackers and 1.5 m for scrub jays.

These results support our hypothesis that recovery accuracy is a function of the ecology and natural history of the species being investigated. Nutcrackers and pinyon jays which have morphological, and physiological adaptations for this behavior and are also most dependent on their cached seeds for winter survival and reproduction, performed significantly better than scrub jays. However, pinyon jays could have used a nonmnemonic technique such as area restricted search to find their caches. If caches are placed in all available cups in a cluster then birds need to only search in this small restricted area. The clumping of caches may be a result of the social nature of pinyon jays as they cache as a social unit (Figure 26, 27, 28).

Because of this, they may be prone to place caches close together as their movements may be restricted by the presence of other group members. In nature pinyon jays appear to place caches close to one another (RPB pers. obs.). In a follow up experiment (Romonchuk, 1995) allowed nutcrackers and pinyon jays to create 25 caches in 330 sand filled cups in the floor of a large experimental room (9.1 x 15.3 x 2.8m) The mean intercache distance was measured by averaging the intercache distances between all possible unique pairs of caches. Mean intercache distance was significantly closer for pinyon jays (mean = 2.66 m) than for nutcracker ($x = 3.86$). These results corroborate the findings of the first experiment.

4.3. Spacing Patterns of Pinyon Jays (Romonchuk, 1995)

This experiment set out to test if pinyon jay cache recovery accuracy was dependent on placing caches close together so an area restricted search pattern can be used rather than employing spatial memory. This was a follow up to A1.

The experiment was conducted in the large room in which the floor contained 330 holes. This experiment used two unique sets of holes chosen from the 330 holes available. In one condition, 72 evenly spaced holes were opened and in the other 36 evenly spaced holes were opened. Birds were allowed to make 15 caches. In the former condition the jays could clump caches but the in the latter condition clumping should have been prevented. If birds use area restricted search to locate caches than accuracy should be higher during recovery in the 72-hole condition than in the 36 hole condition. Mean intercache distances were not significantly different between the two conditions but was smaller for the 72-hole condition (mean = 3.62) than for the 36-hole condition (mean = 4.01). However, both of these distances are much greater than the distances found by Balda and Kamil (1989) and described above for all three species.

Accuracy was measured using a single cache recovery attempt procedure (SCRAP) developed by Kamil and Balda (1990). During recovery sessions caches were presented to the bird as a series of clusters. Each cluster consisted of four holes arranged in a square. The cache was one of the holes in this square. The other three holes had not been cached in. The number of probes that were used to find a cache within a cluster could vary from zero (found cache on first probe) to three (found cache on fourth probe after probing the three none-caching holes. If a bird was probing at random the mean number of errors would be 1.5. For each cluster

Mean Accuracy of First Four Recoveries

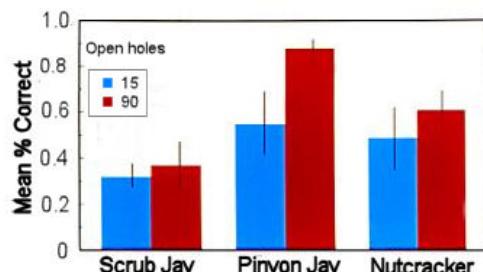
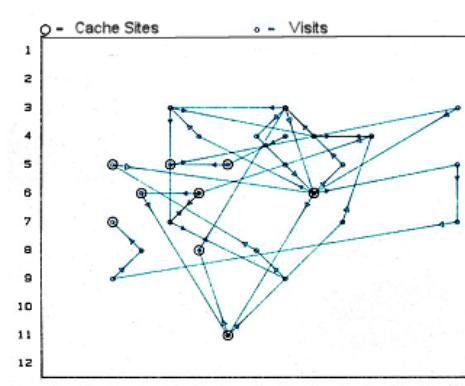
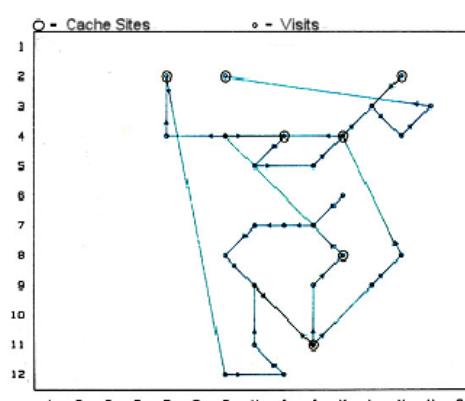
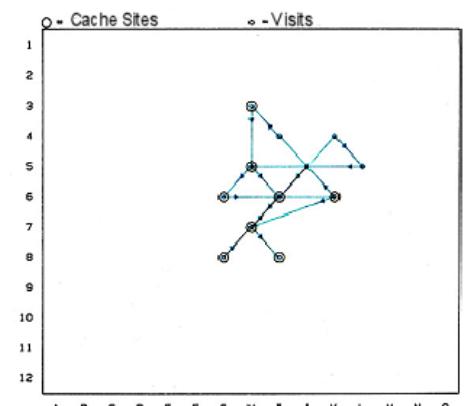


Figure 25. Mean accuracy for three species of seed caching birds in the 15 and 90 hole conditions of the experiment.



containing a cache site another cluster was opened but did not contain a cache site. Thus, during recovery birds had a choice of which cluster to visit (those with a cache site imbedded and those without cache sites) and which hole to probe within a cluster (hole with seeds or hole without seed).

Pinyon jays performed impressively under both conditions making about 0.75 errors per cluster. There was no significant difference in accuracy between the two conditions. Birds also visited good clusters significantly sooner than they visited bad clusters. This experiment provides strong evidence that it is not necessary for pinyon jays to place their caches in clumps and then use area restricted search to find them. Pinyon jays have precise spatial memories for the location of their caches.

4.4 Comparing Long-term Spatial Memory (Bednekoff et al., 1997)

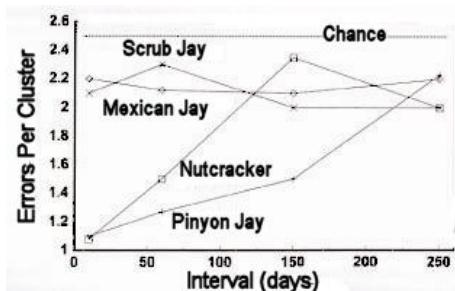


Figure 29. Mean errors per cluster for the four species of corvids at retention intervals of 50, 100, 150, 200 and 250 days.

did not differ significantly from each other, but the two groups differed significantly. Thus, these results support the hypothesis that species most dependent on their caches to survive the winter and for reproduction have more accurate spatial memory than species less dependent on their caches.

Above we have shown that nutcrackers and pinyon jays have better spatial memory than scrub jays. These findings however, are for relatively short durations. In fact, much shorter than those expected in nature (based on the natural history observations presented earlier). In this experiment we asked if the duration of memory for cache sites varied among the four species. Earlier research (Balda & Kamil, 1992) indicated that Clark's nutcrackers accurately remembered the location of cache sites for up to 285 days. Here we tested nutcrackers, pinyon jays, Mexican jays and scrub jays for recovery accuracy at 10, 60, 150, and 250 days after caching. The SCRAP procedure (described above) with cache sites imbedded in a cluster of 6 open holes in a 2 x 3 rectangle was used. Chance performance would thus be 2.5 errors per recovery. Nutcrackers and pinyon jays were highly accurate at the 10 and 60 day interval but only modestly accurate at intervals of 150 and 250 days. The scrub jays and Mexican jays performed at above chance levels at all intervals but were generally less accurate than the former species. (Figure 29). A species by interval ANOVA of the mean number of errors, showed that nutcrackers and pinyon jays did not differ significantly from each other, and the scrub and Mexican jay

V. Other Tests of Spatial Memory in Seed Caching Corvids

Although the comparative tests of spatial memory reveal that the species more dependent on their caches for survival and reproduction than less dependent species, these differences might be due to the effects of contextual variable that could result in this consistent pattern of species differences. As mentioned above, one or more species might be better suited for this type of research paradigm than other species. Also, is this spatial memory gradient limited to cache recovery or can this ability be generalized to other tests of spatial memory? To address these potential problems, we conducted a series of spatial memory experiments using procedures other than direct tests of cache recovery (Kamil, 1988).

5.1 An Analogue of the Radial Maze (Kamil et al., 1994)

This experiment was carried out in a small room (3.6 x 3.2m) where birds could fly free as they searched for seeds. The raised floor contained 12 holes arranged in a circle (Figure 30). Numerous objects were present on the floor and posters were hung on the walls. Birds entered and exited the room through a porthole in the wall. Members of each species were habituated to the room and learned to dig for seeds in holes that were filled with sand. After habituation birds were given 60 acquisition trials. Each trial consisted of three parts, a pre-retention stage, a retention interval, and a post retention stage. During the pre-retention stage the room contained four randomly selected open holes. Each hole contained a carefully buried seed. The bird entered the room and proceeded to harvest and eat the seeds. This stage continued until the bird found and ate the four food rewards. The bird then departed the room and the retention interval started. During the retention interval the room was swept clean of all signs of digging, and four additional holes were opened and a seed buried in each. After the five minute retention interval the bird was allowed back into the room. The room now contained eight open holes, the four original holes that the bird had previously emptied and the four newly opened holes. Only the newly opened holes contained seeds. During the post-retention stage the bird remained in the room until it located the four food rewards or it made six probes. For each bird to perform accurately it had to remember the four holes it had visited during the pre-retention stage, avoid them, and visit the newly opened holes. A different set of randomly selected holes were used daily. Trials were run six days per week. During the 60 acquisition trials, all four species initially had similar levels of performance, but they rapidly diverged (Figure 31). Nutcrackers and pinyon jays learned the task faster and performed more accurately than the western and Mexican jay.

These results compliment our earlier findings about dependence and spatial memory. They also show that spatial memory is general and not simply a specialization for finding hidden food caches made by an individual. What other tasks these species with highly accurate and robust spatial memory can perform is unknown at the present time.

Figures 26, 27, 28. Diagram of the distribution of cache sites used by a pinyon jay, a nutcracker, and a western scrub jay in the 90 hole condition.



Figure 30. Photograph of radial arm experimental room.

However, the possibilities are numerous and potentially exciting.

5.2 Operant Spatial Memory and Non-spatial Memory Test (Olson, 1991; Olson et al., 1995)

Test of spatial memory in an operant chamber strips away most all environmental influences from the organisms taking the test, and allows exerting control of the subject and the stimuli. Thus, this task allows us to enhance and maximize the intrinsic validity of the experiment (Kamil, 1988). For example, birds are rewarded when they peck at the correct spot when illuminated. This is a huge difference from pecking at a spot in the ground where a cache has been previously created.

Olson (1991) found that nutcrackers out performed western scrub jays in this type of task. The present experiment was designed to extend those findings and also to determine if the species differences we had observed in other tasks were also present in nonspatial tasks. In the nonspatial task, birds were asked if they could remember a color in order to receive a food reward. The experiment was conducted in an operant chamber with a computer monitor at one end and a pecking key and feeder at the other.

Trials were initiated when an illuminated spot appeared in the middle of the monitor. The spot was either red or green, chosen randomly for each trial. When the bird pecked this spot, the screen became clear. Now, a yellow light was illuminated behind the key. The bird now was required to go to the rear of the chamber and pecked the yellow light causing it to extinguish. At this time two lights were illuminated on the monitor, one red and one green. Now, when two pecks were delivered to either color, the trial was ended. A trial was considered correct, and a food reward given, if the bird choice the new color. The bird was required to remember what color it had seen and pecked during the initial part of the trial and then avoid that color and peck the alternate color during the final stage of the trial. This type of test is known as a non-matching to sample test.

After the birds learned to perform this test we wanted to determine how long the birds could remember the color presented during the first portion of the trial. To do this we introduced a titration procedure. A retention interval was added between the first peck at the illuminated color on the monitor and the final choice test. This retention interval increased when the bird made a correct choice and decreased when the bird made an incorrect response. A correct response caused the retention interval to increase by 0.1 seconds and an incorrect response caused the retention interval to decline by 0.2 seconds.

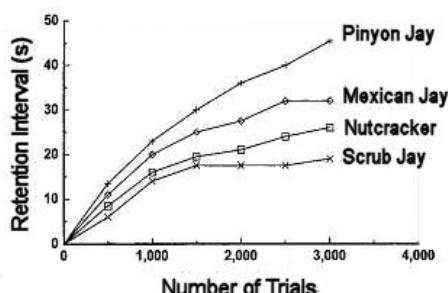


Figure 32. Performance of each species during color memory nonmatching-to-sample titration.

a new location. Again employing the non-matching to sample paradigm, the novel location was the correct one. This time very different results emerged. Clark's nutcrackers were far superior to the three species of jays, thus duplicating the findings of Olson for nutcrackers and scrub jays. These findings are consistent with the results from radial maze and cache recovery tests. It is, however, the first test to demonstrate a difference between nutcrackers and pinyon jays as the latter species' performance could not be separated from that of the scrub and Mexican jay.

The results of these tests are particularly important as they allow us to rule out some alternative explanations for the species differences we found in spatial memory tests. We can eliminate explanations such as general intelligence or general adaptability or compatibility to laboratory experimental procedures. If any of the above factors were involved, then we should have found the same rank order of species differences in the non-matching to sample color test as we found in spatial tests. We did not.

5.3 Comparative Observational Spatial Memory (Bednekoff et al., 1996a, 1996b)

In the wild, pinyon jays and Mexican jays live in integrated flocks and may cache together as a unit each fall when pine cones ripen. In contrast, Clark's nutcrackers cache either as single individuals, pairs, or small family groups. We asked if the three seed caching species had the ability to locate caches made by conspecifics. We hypothesized that species differences may occur that reflect their social life style. If so then pinyon jays and Mexican jays should be able to locate caches made by flock members but nutcrackers should not.

To test this hypothesis we used a small caching room (3.7×3.4 m) with 237 holes in a raised floor. Twenty holes contained a sand-filled cups were available for caching. A bowl with 70 pinyon pine seeds was placed on the floor. One caged bird was placed on a 1 m high platform in the center of the room. A second bird was allowed into the room to cache in the 20 holes. After caches were created both birds were removed from the room for 24 hrs. During this time all signs of digging were swept up and one seed was placed into each cache site. Cachers and observers were now allowed to individually recover caches in the room. Pinyon jay and Mexican jay observers were just as accurate as their respective catchers (Figures 33, 34, 35). Nutcracker observers, however, were not accurate at locating caches made by the catchers, even though the catchers themselves were the most accurate of the three species when locating caches they had made (Figure 38). These results support our hypothesis that social species may have the ability to locate caches made by conspecifics and therefore must take special precautions when creating caches to avoid being detected.

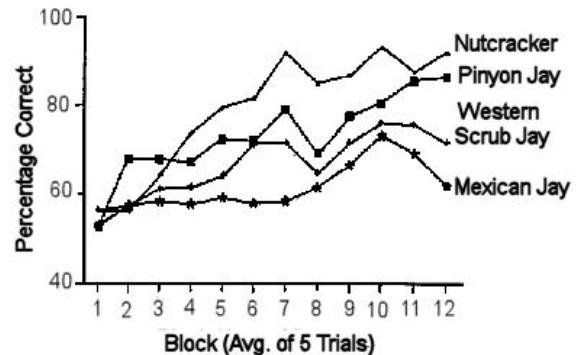


Figure 31. Comparative Radial Maze. Performance of the four species of seed caching corvids during acquisition of the radial maze experiment.

The results of this experiment were unambiguous and did NOT correlate with our earlier findings. Species most dependent on cached food did not perform more accurately than species less dependent on hidden food. None of the species differences were statistically significant (Figure 32). However, the speed of acquisition and retention interval did appear to be correlated with social organization. The best performance was by pinyon jays and Mexican jays. Both species live in permanent social groups. The worst performance was by nutcrackers and scrub jays that have a more solitary life style. Sociality may require certain types of cognitive abilities not found in non-social species (Balda et al., 1996).

Immediately after the above experiment was finished we placed these same birds into another, almost identical test. This time, however, they were tested for spatial memory rather than for color memory. All details of the experiment remained the same, however, when the monitor was first illuminated one of two locations, chosen at random, lit up. Then during the choice phase of the test two identical spots were illuminated. One of the spots was at the exact location on the monitor where the initial spot had appeared. The second spot occurred at

demonstrates that neither traveling to a specific cache site nor creating a particular cache are necessary for locating that cache. These findings also show that pinyon jays and Mexican jays are not simply matching the view from the cache site during caching because they never cached at these sites. Also, birds did not follow a particular route to the cache site. If so, they would have landed on the platform where their cage was originally located and then preceded to the cache site. These results suggest that the evolution of caching behavior may have been different for social and nonsocial species and suggests a number of studies with other caching species, i.e. the relatively nonsocial western scrub jays and the closely related but social Florida scrub jays.

VI. How Seed Caching Corvids Recognize the Locations of Their Caches

Clearly, the ability of Clark's nutcrackers (and other seed-caching birds) to relocate their cache sites is remarkable, and based on spatial memory. But this raises a very interesting question: When a nutcracker is searching for stored pine seeds, exactly how does it recognize that a particular location is a cache site? That is, exactly what is it about that location that the nutcracker has encoded and remembered? This question is particularly compelling given the precision with which they return to a specific location that has no marker or beacon, sometimes even digging through snow to find seeds (Crocq, 1978). Nutcracker caches are often located in the middle of open meadows with few local features (Tombback, 1977, 1980; Vander Wall & Balda, 1981). There are landmarks (henceforth abbreviated "LMs"), but many of them are distant from the cache sites, and there is usually no surface feature identifying the cache site within the surrounding terrain. Yet the nutcracker lands on the spot and digs up seeds that it buried months ago. Its bill is a relatively small shovel, requiring it to dig within a few centimeters of the buried seeds, which are themselves quite small. Indeed, Bednekoff and Balda (1997) demonstrated that nutcrackers are extremely accurate when they use response topography of vertical head movements, with little side-to-side motion, for digging.

Although these characteristics of cache recovery imply that nutcrackers navigate with exceptional accuracy, little is known about how the task is accomplished, except that it is based on the location of LM. Balda (1980), Vander Wall (1982), and Balda and Turek (1984) showed that if LM are either removed or shifted between caching and recovery, accuracy of seed recovery deteriorates markedly, to chance levels in some cases. This suggests that the geometry of the relationships among LM and cache positions might affect search behavior.

Kamil, Balda, and Good (1999) analyzed videotapes of caching and recovery to try to understand how movements during caching were related to those during cache recovery. Among caching behaviors quantified were time spent and number of probes at individual sites and the compass direction used to approach and leave the site. There was no evidence that any of these measures correlated with recovery accuracy. Especially important in its implications for LM use, birds recovered caches very quickly and accurately when approaching or probing the cache site from a completely different direction than that used during caching. Consistency of direction of approach was completely unrelated to recovery accuracy. Because the birds' view of the LM in the room varies with the direction of movement, this suggests that, as implied by Basil (1993), multiple relationships between goal locations and LM arrays were being used.

We then began a series of studies using what has been called the transformational design (Cheng & Spetch, 1998), a powerful technique for investigating LM use. Animals are first trained to find a hidden goal (such as a buried piece of food) located at a fixed place relative to an array of LM. During training, the LM array is presented in different locations (but with constant relationships among the LM within the array) to ensure that the LM array is the only feature that accurately predicts goal location. Once the animal has learned to find the goal, occasional trials are conducted with the goal absent and the LM array transformed in some way. Response to the transformation is used to infer how the LM array is being used.

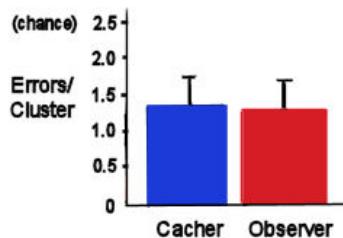
Gould-Beierle and Kamil (1996) examined how nutcrackers integrated information when a landmark was located near an edge. Like the pigeons and black-capped chickadees studied by Cheng and Sherry (1992), nutcrackers responded more to shifts in LM position that were parallel to the edge than to shifts perpendicular to the edge. In two subsequent studies (Gould-Beierle & Kamil, 1998, 1999), we found that global cues had more control over search when local cues were further from the goal. This extends previous work suggesting that cues close to a goal location can exercise more control over search than LM further away (e.g., Cheng et al., 1987; Morris, 1981; Spetch, 1995).

The transformational approach has been applied to the question of how many LM are remembered. A location of an object in space can usually be defined in multiple ways. For example, consider a cache site located in a meadow within 6 m of three big rocks. The cache location could be defined in terms of its distance and direction from any one of the rocks, or in terms of its directional relationship to any two of the rocks, or its distance from one rock and direction from another, etc. Thus, it is logically possible to use only a single LM to define and remember a goal location. And the phenomenon known as overshadowing suggests that this may be the case, at least under certain circumstances.

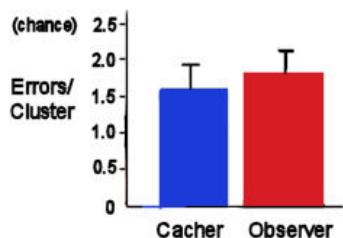
In a typical overshadowing experiment, animals are trained to find a goal whose position is defined by a set of LM whose distance from the goal varies, and are tested during occasional probe trials with only a single LM present. The accuracy of search during the probe trials. Several studies with pigeons have found that search is most accurate when the LM present during the probe trial is that LM that was located closest to the goal during training (Cheng, 1988; Spetch, 1995). However, these experiments employed landmarks that were very close to the goal location and the results may not generalize to the use of more distant landmarks. Furthermore, the results of several studies with nutcrackers indicate that these birds remember the spatial relationships amongst multiple LM and a goal location.

For example, Vander Wall (1982) had nutcrackers cache seeds in a large outdoor aviary. Then, during recovery sessions, LM in one part of the aviary were shifted 20 cm east, with seeds remaining in their original locations. In the area in which LM were shifted, the birds' search was also shifted east by 20 cm. But on the edge of that area, where some LM had been shifted and others had not, search was intermediate between the

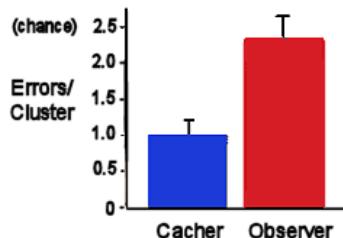
Pinyon Jays: Two Day Interval



Mexican Jays: Two Day Interval



Clark's Nutcrackers: Two Day Interval



Figures 33, 34, 35. Accuracy of caching and observing pinyon jays, Mexican jays, and Clark's nutcrackers when recovering caches. Observer is recovering caches made by the cacher.

shifted and nonshifted locations. The birds must have been averaging information from different LMs.

In another instance, Basil (1993) used nutcrackers with a technique similar to Bennett (1993) with European jays. Birds were trained to find a goal location defined by a LM array that was presented in many different locations and orientations within the test room. LMs in the array varied in size and distance from the goal. Probe trials with some LMs removed showed that large, close LMs were more important than smaller ones further away from the goal, as in Bennett (1993). However, Basil conducted a more extensive set of probe tests than Bennett (1993), obtaining clear evidence that the nutcrackers learned multiple rules for locating the goal. Basil had 9 LMs in her array, and tested for ability to find the goal with various sets of 3 LMs each. Although the birds performed better with some arrays than others, they could find the goal regardless of which set of three LMs was present. Clearly, they had learned more than one small set of the available goal-LM relationships. (This result was different from that of Bennett, who found that only the two tall LMs nearest the goal controlled search. This may be a species difference but is more likely due to Bennett's placing these LMs only 30 cm from the goal, producing an overshadowing' effect (Spatch, 1995). Basil used distances of 40-60cm.)

A recent study by Goodyear and Kamil (2004) examined overshadowing and the effects of goal-LM distance in nutcrackers. Three groups of Clark's nutcrackers were trained to find a goal location defined by a landmark array. Each group was trained with an array of four LMs, with the goal located in the midst of the array. The different groups were trained with arrays that varied in the goal-LM distances (Figure 36).

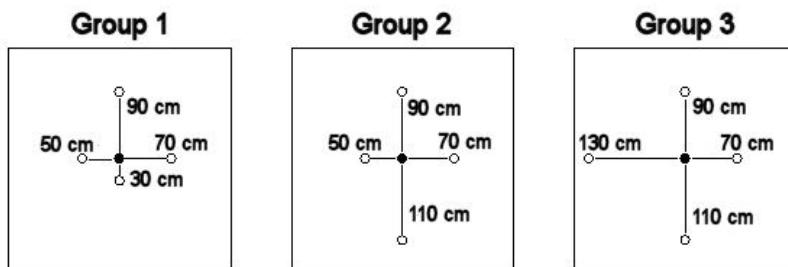


Figure 36. Diagram of landmark array for the three experimental groups of Goodyear and Kamil (2004). Gray circles represent landmarks while black circles represent the goal location. Goal-landmark distances are labeled for each landmark. Lines are not drawn to scale.

These goal-LM distances were chosen so that the effects of both relative and absolute goal-landmark distance could be assessed. All three groups readily learned the task and were subsequently tested in probe tests with only single landmarks from the array available. Search error in tests with landmarks the same distance away from the goal was compared across groups where only the relative position of the landmarks varied. When the LM array was located relatively close to the goal, overshadowing occurred, and only that LM closest to the goal resulted in accurate search. As the goal-LM distance of the array increased, however, this effect diminished. Thus the results of this study indicate that multiple LMs are more likely to be simultaneously encoded when goal-LM distances are relatively great.

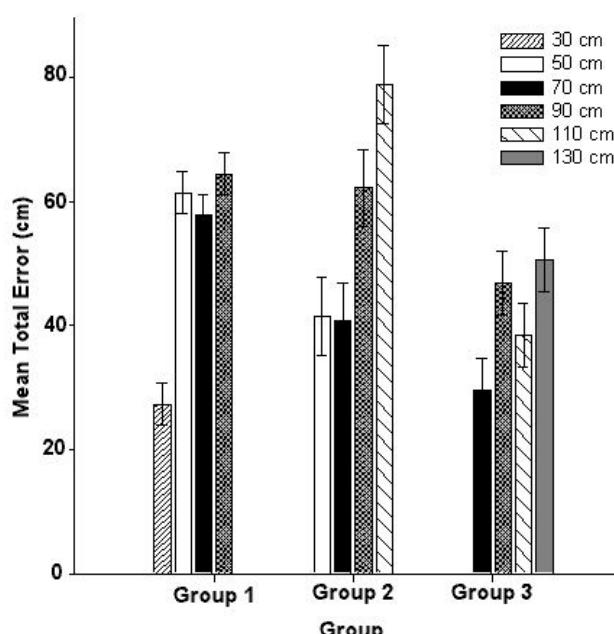


Figure 37. Mean total error in single landmark tests for each group. Error bars represent standard error.

that line reflects error in the judgment of direction from goal to LM. Furthermore, as the axes are perpendicular, the estimates are independent. We have repeatedly found that the functions relating search error to goal-LM distance are very different for distance and direction estimation (Kamil & Jones, 1997, 2000). The problem of locating a point on a line has two components: locating the LM-LM line and finding the correct position along it. These are problems in direction and distance estimation, respectively. When the search error of birds trained to find a point on the LM-LM line was partitioned into the two appropriate axes, we have always found that error in each axis increases as goal-LM distance increases, but with much steeper slope in the distance than the direction axis (Figure 38). This suggests that when the LMs that control search are far from the goal, information about the direction from goal to LM will produce more accurate search than information about the distance from the goal to the LM.

The next step in the development of our thinking about the use of LMs during cache recovery was provided by a study by Kamil and Jones (1997) that suggest that directional evidence is emphasized when the goal-LM distance is relatively great. Nutcrackers were trained to dig for a seed hidden halfway between two LMs. Five interLM training distances were used. The birds readily learned the task, generalizing to new distances interpolated between training distances. Detailed analysis of the distribution of search behavior showed the birds were very accurate with both the interLM distances with which they were trained and the new interLM distances (Figure 37).

The nutcrackers appeared to have learned a general principle, although the exact nature of that principle remained to be specified. These results have been extended in several additional studies. Kamil and Jones (2000) showed that the birds could learn and generalize geometric rules other than halfway, while Jones and Kamil (2001) found that the birds could learn the geometry of arrays that were rotated during training. However, the most important result regarding the general use of LMs was an unanticipated feature of the data from the halfway learning experiment. Error in judging distance from a LM increased more rapidly than error in judging direction as goal-LM distance increased.

Because the birds had been trained to find a goal that was located on the line connecting the two LMs, it was possible to measure distance error and direction error separately. Simply put, error in the axis of the line from goal to LM reflects error in the estimation of the distance to the LM while error in the axis perpendicular to

This conclusion raises the question of how search accuracy can be achieved in the face of error in the compass used for the estimation of direction. The task of locating a buried seed calls for a high degree of accuracy. A compass with an error of measurement of 1% will induce an error of "6.3 cm in search location when the goal is 1 m from the LM (and an additional "6.3 cm for each additional meter of goal-LM distance). Kamil and Cheng (2001) suggested that the use of multiple LMs provides a powerful way to reduce the effects of error in directional estimation and achieve precise search. If the direction from the goal to each of a number of different LMs is the primary information in the representation of the goal location, these multiple bearings can be used to overcome inaccuracies caused by compass errors.

Suppose a goal location has been encoded in terms of n bearings, one to each of n different LMs. What happens to search accuracy as n increases, given error in the compass used to determine bearings? The information provided by increases in n can decrease search error.

Consider n = 2. In most cases (it depends on the angular separation of LMs) there will be two intersecting bearings. However, if there is compass error, the point of intersection will not be at the goal and there will be no information available about size or direction of the error. Now consider n = 3. In many cases, the three bearings will describe a triangle, whose size will contain information about magnitude of the compass error.

Kamil and Cheng (2001) investigated this issue with a Monte Carlo simulation in which the compass measurement of bearing to each LM was given a random error of "2%. Search accuracy decreased significantly as n, the number of LMs encoded, increased. In fact, search error was reduced by 35% by increasing the number of LMs being used from two to four. There can be little doubt that increasing the number of LMs represented in directionally based encoding can dramatically increase search accuracy.

Based on these empirical results and their simulation, Kamil and Cheng (2001) proposed the multiple-bearings hypothesis: goal locations that are relatively far from LMs will be remembered in terms of the directional bearings from the goal to each of several LMs. This hypothesis makes many specific predictions. Search accuracy should increase as the number of available LMs increases, which was confirmed by Kamil, Cheng, and Goodyear (2001), and should be sensitive to the detailed geometrical relationships among the available LMs and the goal. As of this writing, several studies are underway testing predictions of the model in Clark's nutcrackers.

Evidence from several experiments suggests that when caching in the field, nutcrackers, pinyon jays and scrub jays do use a compass based on the sun as one of their sources of directional information. It is well known that migratory birds use a number of different compasses, including the sun compass, to find their way during migration (Wiltschko & Wiltschko, 1998), and this ability may also be present in non-migratory seed caching birds.

Wiltschko and Balda (1989), Balda and Wiltschko (1991), and Wiltschko, Balda, Jahnel, and Wiltschko (1999) studied the role of the sun compass in Clark's nutcrackers, pinyon jays and scrub jays in a series of cache recovery experiments. An octagonal outdoor aviary with a diameter of 4.90 m served as the experimental chamber. The floor of the aviary was divided into eight pie-shaped segments, each containing six holes that could be filled with a sand-filled cup for caching or a wooden plug that prevented caching. This aviary was placed within a courtyard surrounded by four high buildings of different heights and shapes, each having a unique set of window and door patterns.

Birds were habituated to this aviary and then allowed to create between one and four caches in 12 holes contained in two adjacent segments of the floor. These two segments are referred to as the caching sectors and were varied among birds and tests. After caching, birds were removed from the aviary and placed in their home cage in a light-tight holding room. For all recovery sessions all 48 holes were opened and one seed was placed into each cup the birds had cached in. The experiments were performed in the following manner:

1. Control 1: Each bird was allowed to recover the seeds it had cached 4-7 days earlier. The location of all probes in this control served as a reference for comparison with the manipulated sessions.
2. Six hour slow clock shift. After caching each bird was returned to its home cage and its internal clock was reset 6 hrs. slow. Now the artificial photoperiod began and ended six hours after normal sunrise and sunset. Birds were confined for at least five days under these conditions. That is, if the sun normally rose at six a.m., then the lights in the room would go on at 12 o'clock noon. If sunset was a 6 p.m., then the lights in the room would go off at midnight. On the first sunny day after the birds had experienced the shifted condition for five days, the birds were allowed to recover their caches. All 48 holes were now open and filled with sand. A single seed was placed in the holes where the bird had originally cached. In addition, a single seed was also placed in the cups 90 degrees clockwise from the original set. If the birds were using their sun compass, then these 90 degrees clockwise locations would be the probed by the searching bird.
3. Re-shift to normal photoperiod. While birds were still in the clock-shifted condition they were again allowed to cache in the octagonal aviary. After caching, however, the internal clock of the birds was shifted back to normal, which is a six-hour fast clock shift. Now the light would go on and off at the time coinciding with the normal outdoor light/dark cycle. Recoveries were conducted as in #2 above with both original and shifted holes containing a seed.
4. Control 2. Same as in Control 1.

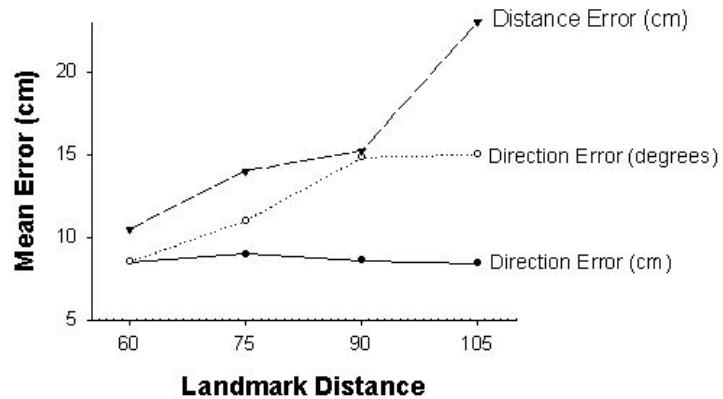


Figure 38. As the distance between the landmarks increased from 60 to 105 cm, distance and direction error both increased, but the rate of increase was greater for distance error. However, when the direction error was calculated in degrees, it did not change as interlandmark distance increased.

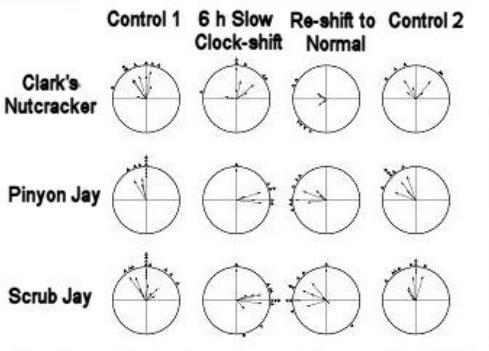


Figure 39. Distribution of Probing. Arrows representing the center of probing for individual birds, with the mean heading of each bird indicated by a triangle at the edge of the circle.

Figure 39 gives the vectors indicating the center of probing activity when recovering caches for individual birds of the three species. In Control 1, the majority of the vectors are pointed toward the segment originally cached in. After the six hour clock shift, the majority of the pinyon jays and scrub jays show the clockwise deflection indicating that the sun compass is being employed to relocate their caches. The Clark's nutcracker, however, continued to mainly search in the original sectors. Under the reshift condition all three species show expected counterclockwise deflection. The rather short vectors for the nutcracker, however, indicate a large amount of scatter. In Control 2, the pinyon jay and scrub jay showed a tendency to probe left of the caching sector.

These experiments show that resetting the internal clock influences the location where birds probe for previously hidden seeds. This strongly suggests that compass information is also involved, in some manner, in the spatial memory system of these birds. These findings are especially of interest because the courtyard where the aviary was located was rich with a diverse set of landmarks.

Species difference in response to the resetting of the internal clock were evident. Nutcrackers showed a response in only the reshift condition, and that was weak. Pinyon jays and scrub jays, on the other hand showed significant responses to both shift and reshift manipulations. Thus, it appears that the sun compass is a more important component of spatial memory in these jays and is less important for nutcrackers. We can suggest some possible reasons for this difference.

Nutcrackers live at high elevations where the trees of the coniferous forests often form complete canopies, impeding any sunlight from reaching the forest floor. In spring, autumn and winter these high elevation habitats have many cloudy, overcast, rainy days. Also, maybe the sun compass is not effective when nutcrackers must dig through deep snow to recover their caches. The pinyon and scrub jay live at lower elevations where the canopy of the ponderosa pine forest and pinyon-juniper woodlands are open as there are fewer trees present. Sunny days are more prevalent at these lower elevations, and less snow is present in winter, especially in the woodlands.

Therefore the general habitat structure and prevailing weather conditions in the environments of the two jay species may be more conducive for sun compass use. For the Clark's nutcracker the sun compass may represent a factor not always present, or easy to use, so they rely on other cues to locate their caches.

VII. The Evolution of Seed Caching

We began this chapter with a description of the environment within which these four species live, the San Francisco Peaks in north central Arizona. How did this particular set of species end up on this mountain?

The origins and dispersal patterns of these species is well understood. The Clark's nutcracker is undoubtedly of Old World origin, a close relative of the Eurasian nutcracker (*Nucifraga caryocatactes*). It probably invaded the new World by crossing the Bering Land Bridge about one million years ago during the Pleistocene. It may even have carried a pouch full of seeds across the strait (pers. communication, Lanner, 1981; Stegmann, 1934; Tombak 1983)! The mountains of Alaska, Canada, and western North American were covered with alpine coniferous forest. This habitat supplied the early invaders with the requisites needed for survival and reproduction. The corridor stretched from Berangia to central Arizona, allowing the nutcracker ease of passage from north to south (Figure 40). Nutcrackers have strong, long wings for rapid, long distance flights so latitudinal movements and flights up and down mountains were probably swift and efficient.

The origin of the jays in this study probably occurred on the Mexican Plateau located in the southwestern USA and northern Mexico (Pitelka, 1951) The three species are closely related (de los Monteros & Cracraft, 1997) These birds then dispersed from their ancestral home and were possibly in their present locations by the end of Pleistocene, about 11,000 years ago. The difference in origin between the jays and the nutcracker brings a whole series of issues to bear on the evolution of the seed caching traits (Table 2).

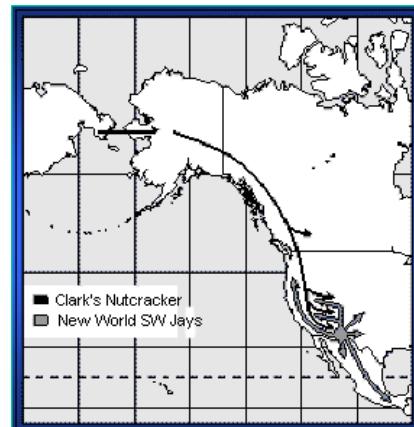


Figure 40. Colonization of North America by nutcrackers and southwestern U.S. jays. Nutcrackers used the Bering Land Bridge and jays differentiated on the Mexican Plateau.

Table 2. Convergence & Divergence Among Some Seed Caching Corvids

Character	Pinyon jay and Nutcracker	Western scrub-jay and Mexican jay
<u>Seed Harvest and Transport</u>		
1. Sturdy, sharp, bill	Yes	No
2. Long, strong wings	Yes	No
3. Structure for holding seeds	Yes	No
4. Open green cones	Yes	No
5. Cache huge numbers of seeds	Yes	No
6. Rely on cached food	Yes	No
<u>Spatial Memory</u>		
1. Highly accurate in ake recovery	Yes	No
2. Highly accurate in radial maze	Yes	No
3. Highly accurate in operant test	No-----PJ----->	No
<u>Brain Structure</u>		
1. Large hippocampus	No -----PJ----->	No
<u>Nesting</u>		
1. Large, insulated nest	Yes	No
2. Nest in winter	Yes	No
3. Feed seeds to nestlings	Yes	No
4. Male has incubation patch	No -----PJ----->	No

A reoccurring pattern in the results from our various experiments was the specialization gradient whereas species most dependent on their seed caches were most specialized in morphology, behavior, physiology, and psychology, particularly in spatial memory ability. In this specialization gradient Clark's nutcrackers and pinyon jays demonstrated the most accurate spatial memory, and the Mexican and western scrub jay showed only modest spatial memory. The evidence reviewed above suggests that the differences among scrub jays, Mexican jays and pinyon jays represent divergence while the similarities between nutcracker and pinyon jays represent a case of convergence. According to this view seed caching behavior has evolved in the family Corvidae at least twice, once in the Old World and once in the New World. The pinyon jay appears to be a nutcracker "want-to-be."

The degree of convergence between Clark's nutcrackers and pinyon jays is intriguing in terms of the kinds of and degrees of adaptations. The three tables are designed to show the different types of traits that show divergence and convergence among the four seed caching species of corvids.

VIII. Summary

The cognitive abilities of the seed caching species reveals some interesting patterns of adaptations. The responds of the four species to the presence of pinyon pine seeds differs dramatically. Two species show a major integration of adaptations in all aspects of their lives, while two other species show only modest adaptations for this habit. These adaptations all build on one another. For example, the caching of thousand of seeds would be wasteful if the cache forgot the locations of the caches, or placed them where other animals could easily find them.

Of interest here is the fact that only the nutcracker has a larger than expected hippocampus. The other seed specialist, the pinyon jay does not (Basil et al., 1996). Thus, either the hippocampus does extra duty or other areas of the brain have been recruited to aid in the memory for seed caches in the pinyon jay. However, new evidence suggests that hippocampus size does not correlate with spatial memory ability.

Another example of the integration of these adaptations is the life history trait of early breeding by nutcrackers and pinyon jays in response to a large crop of pine seeds. Breeding in February and March would be highly ineffective if the breeders did not build large well insulated nest to counter the cold weather, and effectively locate caches (even through deep snow). The energy from these seeds provides the reproductive energy to form eggs, provides heat for incubation and brooding, and provides food for the nestlings. To utilize this food nestlings must have the physiological ability to digest these pine seeds. Many more examples of this integration could be given for these seed caching species. In conclusion, cognitive abilities are interlinked with all other characteristics of the species to form an integrated adaptive suite of characters that contributes to the biological fitness of the species possessing these suites.

IX. Afterword

Trees that are stressed because of low soil moisture are particularly susceptible to infestation by bark beetles. Due to the combination of moisture stress and beetle attack, hundreds of thousands (possibly millions) of pinyon and ponderosa pine trees are dying on our study area (Figure 41, 42).

Also, there has been no cone crop in the past four years. This massive mortality event coupled with the lack of pine cone production in trees that are still alive, poses a severe selective event for all the resident birds and could have especially serious fitness consequences for the seed caching corvids. One could predict, based on the specialization gradient described above, that the nutcracker and pinyon jays will be most heavily impacted and the western scrub jay and Mexican jay would be affected to a lesser extent. This situation is presently being monitored.



Figure 41. Dead pinyon pine that is at least 150 years old.



Figure 42 (Right). Dead ponderosa pines. One live pinyon pine in far left.

X. References

- Abbot, H.G. (1962). The seed preferences of mice and voles in the Northeast. *Journal of Forestry*, 60, 97-99.
- Balda, R.P. (1980). Recovery of cached seeds by a captive *Nucifraga caryocatactes*. *Zeitschrift fur Tierpsychologie*, 52, 331-346.
- Balda, R.P. (1980). Are seed caching systems co-evolved? *Acta XVII Congr. International Ornithology*, 2, 1185-1191.
- Balda, R.P. (1987). Avian impacts on pinyon-juniper woodlands. In L. Everett (Ed.) *Proceedings of the pinyon-juniper conference* (No. 7, pp. 525-533). General Technical Report (INT-215). Reno, NV: U.S. Forest Service.
- Balda, R.P. (2002). Pinyon jay (*Gymnorhinus cyanocephalus*). In A. Poole, & F. Gill (Eds.), *The birds of North America* (No. 605). Philadelphia, PA: The Birds of North America, Inc.
- Balda, R.P., & Bateman, G.C. (1971). Flocking and annual cycle of the pinyon jay. *Condor*, 75, 287-302.
- Balda, R.P., & Bateman, G.C. (1972). The breeding biology of the pinyon jay. *Living Bird*, 11, 5-42.
- Balda, R.P., & Kamil, A.C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, 38, 486-495.
- Balda, R.P., & Kamil, A.C. (1992). Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Animal Behaviour* 44, 761-769.
- Balda, R.P., & Kamil, A.C. (1998). The ecology and evolution of spatial memory in corvids of the southwestern USA: The perplexing Pinyon Jay. P. Balda, I.M. Pepperberg, & A.C. Kamil (Eds.), *Animal Cognition in Nature* 7 (pp. 33-66). London, UK: Academic Press.
- Balda, R.P., Kamil, A.C., & Bednekoff, P.A. (1996). Predicting cognitive capacity from natural history: Examples from four species of corvids. In E. Ketterson & V. Nolan (Eds.), *Current Ornithology* (pp.33-66). Plenum Press, New York.
- Balda, R.P., & Turek, R.J. (1984). The cache-recovery system as an example of memory capabilities in Clark's nutcracker. In H. L. Roitblat, T.G. Beaver, & H.S. Terrace (Eds.), *Animal Cognition* (pp. 513-532). London, UK: Erlbaum Associates.
- Balda, R.P., & Wiltschko, W. (1991). Caching and recovery in scrub jays: Transfer of sun-compass directions from shaded to sunny areas. *Condor*, 93, 1020-1023.
- Basil, J.A. (1993). Neuroanatomical and behavioral correlates of spatial memory in Clark's nutcrackers. Unpublished PhD. Dissertation, University of Massachusetts.
- Basil, J.A., Kamil, A.C., Balda, R.P., & Fite, K.V. Differences in hippocampus volume among food storing corvids. *Brain, Behavior and Evolution*, 47, 156-164.
- Bateman, G.C., & Balda, R.P. (1973). Growth, development, and food habits of young pinyon jays. *Auk*, 90, 39-61.
- Bednekoff, P.A., & Balda, R.P. (1996a). Social caching and observational spatial memory in pinyon jays. *Behaviour*, 133, 807-826.
- Bednekoff, P.A., & Balda, R.P. (1996b). Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour*, 52, 833-839.

- Bednekoff, P.A., & Balda, R.P. (1997). Clark's nutcracker spatial memory: Many errors might not be due to forgetting. *Animal Behaviour*, 54, 691-698.
- Bednekoff, P.A., Balda, R.P., Kamil, A.C., & Hile, A.L. (1997). Long term spatial memory in four seed caching corvid species. *Animal Behaviour*, 53, 335-341.
- Bendire (1895). Life histories of North American birds. *U.S. National Museum Bulletin*, 3.
- Benkman, C.W., Balda, R.P., & Smith, C.C. (1984). Adaptations for seed dispersal and the compromises due to seed predation in limber pine. *Ecology* 65: 632-642.
- Bennett, A.T.D. (1993). Spatial memory in a food storing corvid. I. Near tall landmarks are primarily used. *Journal of Comparative Physiology A*, 173, 193-207.
- Bock, W.J., Balda, R.P., & Vander Wall, S.B. (1973). Morphology of the sublingual pouch and tongue musculature in Clark's nutcrackers. *Auk*, 90, 491-519.
- Brown, J.L. (1994). Mexican jay (*Aphelocoma ultramarina*). In A. Poole, & F. Gill (Eds.), *The birds of North America*, no.118. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington D. C.
- Burnell, K.L., & Tombback, D.F. (1985). Steller's jays steal gray jay caches: Field and laboratory observations. *Auk*, 102, 417-491.
- Chen, B. (2000). Differential spatial memory by male and female pinyon jays. Unpublished M.S. thesis. Northern Arizona University, Flagstaff.
- Cheng, K. (1988). Some psychophysics of the pigeon's use of landmarks. *Journal of Comparative Physiology A*. 162, 815-826.
- Cheng, K., & Sherry, D. F. (1992). Landmark-based spatial memory in birds (*Parus atricapillus* and *Columba livia*): The use of edges and distances to represent spatial positions. *Journal of Experimental Psychology: Animal Behavior Processes*, 106, 331-341.
- Cheng, K., & Spetch, M.L. (1998). Mechanisms of landmarks use in mammals and birds. In S. D. Healy (Ed.), *Spatial representation in animals*. Oxford: Oxford University Press.
- Cheng, K., Collett, T.S., Pickard, A., & Wehner, R. (1987). The use of visual landmarks by honeybees: Bees weight landmarks according to their distance from the goal. *Journal of Comparative Physiology A*, 161, 469-475.
- Christensen, K.M., & Whitham, T.G. (1993). Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds. *Ecology*, 74, 2270-2278.
- Crocq, C. (1978). Ecologie du Casse-noix (*Nucifraga caryocatactes L.*) dans les Alpes Francaises du sud: Ses relations avec L'Arolle (*Pinus cembra L.*). Unpublished PhD, L'Univerite d'Aix-Marseille, Marseille, France.
- Giuntoli, M., & Mewaldt, L.R. (1978). Stomach contents of Clark's nutcrackers collected in western Montana. *Auk*, 95, 595-598.
- Goodyear, A.J., & Kamil, A.C. (2004). Clark's nutcrackers (*Nucifraga columbiana*) and the effects of goal landmark distance on overshadowing. *Journal of Comparative Psychology*, 118, 258-264.
- Gould-Beierle, K.L., & Kamil, A.C. (1996). The use of local and global cues by Clark's nutcrackers, *Nucifraga columbiana*. *Animal Behaviour*, 52, 519-528.
- Gould-Beierle, K.L., & Kamil, A.C. (1998). Use of landmarks in three species of food-storing corvids. *Ethology*, 104, 361-378.
- Gould-Beierle, K.L., & Kamil, A.C. (1999). The role of proximity in landmark use by Clark's nutcrackers. *Animal Behaviour*, 58, 477-488.
- Johnson, H.C. (1900). The breeding home of the Clark's nutcracker. *Condor*, 2, 49-52.
- Johnson, L.S., Marzluff, J.M., & Balda, R.P. (1987). Handling of pinyon pine seeds by Clark's nutcracker. *Condor*, 89, 117-125.
- Jones, J.E., & Kamil, A.C. (2001). The use of relative and absolute bearings by Clark's nutcrackers, *Nucifraga columbiana*. *Animal Learning & Behavior*, 29, 120-132.
- Kamil, A.C. (1988). A synthetic approach to the study of animal intelligence. In D.W. Leger (Ed.), *Nebraska symposium on motivation: Comparative perspectives in modern psychology* (Vol. 35, pp. 230-257). Lincoln, Nebraska: University of Nebraska Press.
- Kamil, A.C., & Balda, R.P. (1990). Spatial memory in seed caching corvids. In G.H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 26, pp. 1-25). New York: Academic Press.
- Kamil, A.C., & Cheng, K. (2001). Way-finding and landmarks: The multiple-bearings hypothesis. *Journal of Experimental Biology*, 204, 103-

- Kamil, A.C., & Jones, J.E. (1997). Clark's nutcrackers learn geometric relationships among landmarks. *Nature*, 390, 276-279.
- Kamil, A.C., & Jones, J.E. (2000). Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, 26, 439-453.
- Kamil, A.C., Goodyear, A.J., & Cheng, K. (2001). The use of landmarks by Clark's nutcrackers: First tests of a new model. *Journal of Navigation*, 54, 429-435.
- Kamil, A.C., Balda, R.P., & Good, S. (1999). Patterns of movement and orientation during caching and recovery by Clark's nutcrackers (*Nucifraga columbiana*). *Animal Behaviour*, 57, 1327-1335.
- Kamil, A.C., Balda, R.P., & Olson, D.J. (1994). Performance of four seed-caching corvid species in the radial maze analog. *Journal of Comparative Psychology*, 108, 385-393.
- Lanner, R.M. (1981). *The pinyon pine: A natural and cultural history*. Reno, Nevada: University of Nevada Press.
- Ligon, J.D. (1978). Reproductive interdependence on the pinyon jay and pinyon pines. *Ecological Monographs*, 48, 111-126.
- Ligon, J.D., & Martin, D.J. (1974). Pinyon seeds assessment by the pinyon jay, *Gymnorhinus cyanocephalus*. *Animal Behaviour*, 22, 421-429.
- Marzluff, J.M., & Balda, R.P. (1992). The Pinyon jay: Behavioral ecology of a colonial and cooperative corvid. London, U.K.: T. & A.D. Poyser.
- Merriam, C.H. (1890). Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. In *North American Fauna* (No.3, I-vii, pp.1-136). U.S. Department of Agriculture.
- de los Monteros, A.E., & Cracraft, L. (1997). Intergeneric relationships of the New World jays inferred from cytochrome *b* gene sequences. *Condor*, 99, 490-502.
- Morris, R.G.M. (1981). Spatial localisation does not require the presence of local cues. *Learning and Motivation*, 12, 239-260.
- Olson, D. J. (1991). Species differences in spatial memory among Clark's nutcrackers, scrub jays, and pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 17, 363-376.
- Olson, D. J., Kamil, A.C., Balda, R.P., & Nims, P.J. (1995). Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*, 109, 173-181.
- Peterson, A.T. (1993). Adaptive geographical variation in bill shape of scrub jays (*Aphelocoma coerulescens*). *American Naturalist*, 142, 508-527.
- Pitelka, F.A. (1951). Speciation and ecologic distribution of American jays of the genus *Aphelocoma*. *University of California Publications in Zoology*, 50, 195-463.
- Romonchuk, W.J. (1995). The role of memory in cache-recovery in Clark's nutcrackers and pinyon jays. Unpublished PhD dissertation, Northern Arizona University, Flagstaff, AZ.
- Schopmeyer, C.S. (1974). Seeds of wood plants in the United States. In *Agriculture, Handbook* (No. 540, pp. 196-197). Washington D.C.: U.S.D.A. Forest Service.
- Shulzitski, J. (1999). Sex differences in the spatial memory ability of mated pinyon jays. Unpublished MS thesis, Northern Arizona University, Flagstaff, AZ.
- Spetch, M.L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 166-181.
- Stegmann, B.K. (1934). On the ontogeny of the nutcracker (Kedrovka) (trans. L. Kelso). *Dolk. Akad. Nauk. SSSR*, 24, 267-269.
- Stotz, N.G., & Balda, R. P. (1995). Cache and recovery behavior of wild pinyon jays in Northern Arizona. *Southwest Naturalist*, 40, 180-184.
- Tombback, D. (1980). How nutcrackers find their seed stores. *Condor*, 82, 10-19.
- Tombback, D. (1983). Nutcrackers and pines: Coevolution or coadaptation? In M.H. Nitecki (Ed.), *Coevolution* (pp. 179-223). Chicago, IL: University of Chicago Press.
- Tombback, D. (1998). Clark's Nutcracker (*Nucifraga columbiana*). In A. Poole & F. Gill (Eds.), *The birds of North America* (No. 331). Philadelphia, PA: The Birds of North America, Inc.

Turcek, F.J., & Kelso, L. (1968). Ecological aspects of food transportation and storage in the Corvidae. *Communications in Behavioral Biology, Part A*, 1, 277-297.

Vander Wall, S.B. (1982). An experimental analysis of cache recovery in Clark's nutcracker. *Animal Behaviour* 30, 84-94.

Vander Wall, S.B. (1990). *Food hoarding in animals*. Chicago, IL: University of Chicago Press.

Vander Wall S.B., & Balda, R.P. (1977). Co-adaptation of the Clark's nutcracker and pinyon pine for efficient seed harvest and dispersal. *Ecological Monographs*, 47, 89-111.

Vander Wall, S.B., & Balda, R.P. (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. *Zeitschrift für Tierpsychologie*, 56, 217-242.

Vander Wall, S.B., & Hutchins, H.E. (1983). Dependence of Clark's nutcrackers (*Nucifraga columbiana*) on conifer seeds during the post-fledging period. *Canadian Field-Naturalist*, 97, 208-214.

Vander Wall, S.B., Hoffman, S.W., & Potts, W.K. (1981). Emigration behavior of Clark's nutcrackers. *Condor*, 83, 162-170.

Westcott, P.W. (1964). Invasion of Clark's nutcrackers and pinyon jays into southeastern Arizona. *Condor*, 66, 441.

Wiltschko, W., & Balda, R.P. (1989). Sun compass orientation in seed caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology*, 164, 717-721.

Wiltschko, W., Balda, R.P., Jahnle, M., & Wiltschko, R. (1999). Sun compass orientation in seed-caching corvids: Its role in spatial memory. *Animal Cognition*, 2, 215-221.

Zusi, R.L. (1987). A feeding adaptation of the jaw articulation in new world jays (Corvidae). *Auk*, 104, 665-680.



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