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Clark's nutcracker spatial memory: The importance of large, structural cues

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ABSTRACT

Clark's nutcrackers, *Nucifraga columbiana*, cache and recover stored seeds in high alpine areas including areas where snowfall, wind, and rockslides may frequently obscure or alter cues near the cache site. Previous work in the laboratory has established that Clark's nutcrackers use spatial memory to relocate cached food. Following from aspects of this work, we performed experiments to test the importance of large, structural cues for Clark's nutcracker spatial memory. Birds were no more accurate in recovering caches when more objects were on the floor of a large experimental room nor when this room was subdivided with a set of panels. However, nutcrackers were consistently less accurate in this large room than in a small experimental room. Clark's nutcrackers probably use structural features of experimental rooms as important landmarks during recovery of cached food. This use of large, extremely stable cues may reflect the imperfect reliability of smaller, closer cues in the natural habitat of Clark's nutcrackers.

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1. Introduction

Clark's nutcrackers, *Nucifraga columbiana*, are roughly 130–140 g corvids that live in alpine environments in montane regions in the western USA and Canada. A single nutcracker will cache an estimated 22,000–33,000 pine seeds in 5000–6000 separate locations in an autumn with a good seed crop (Vander Wall and Balda, 1977, 1981, see also Vander Wall, 1990, p. 304). The best available evidence indicates that Clark's nutcrackers rely upon cached food for 80–100% of their energy intake during winter and also for breeding during the late winter (Vander Wall and Balda, 1977, 1981). Clark's nutcrackers in nature accurately recover caches for at least 9 months after caching (Vander Wall and Hutchins, 1983). They have caches available to recover throughout this long period because they cache in a variety of habitats. Their caching is most conspicuous on open, windswept slopes where many nutcrackers may cache at the same time (Tomback, 1978; Vander Wall and Balda, 1977). These areas are the least snow covered parts of the mountains and nutcrackers probably must rely on these areas in order to survive the worst winter storms (Vander Wall and Balda, 1977). Nutcrackers also cache many seeds in dense forests near their breeding territories. Nutcrackers provision their nestlings with seeds from caches (Mewaldt, 1956) and provisioning is obviously easier if the caches are near to the nest. Finally, nutcrackers cache seeds above treeline in the alpine tundra. Nutcrackers recover these caches into the summer and bring their dependent fledglings to these alpine areas (Vander Wall and Hutchins, 1983). Caches apparently "keep" longer in these environments because both rodent foraging and sprouting potential are reduced and Clark's nutcrackers continue to recover and consume cached seeds through the post-fledgling period (Vander Wall and Hutchins 1983).

Laboratory experiments have demonstrated that Clark's nutcrackers use spatial memory to relocate their caches (see review by Kamil and Balda, 1990). They accurately relocate cache sites without relying on cues emanating from seeds, fixed rules for placing caches, nor retracing routes (Kamil and Balda, 1990). Furthermore, nutcrackers can remember cache locations for long periods. In the laboratory, nutcrackers recovered caches they had made 285 days previously with a level of accuracy that was nearly as high as that with which they recovered caches made only 10 days beforehand (Balda and Kamil, 1992, see also Bednekoff et al., 1997). This long-lasting, highly accurate spatial memory is thought to be a cognitive adaptation for seed storing by Clark's nutcrackers (Balda and Kamil, 1989, 1992; Balda et al., 1996; Kamil and Balda, 1990).

Other studies have examined what sorts of spatial cues Clark's nutcrackers remember about cache sites. The details of the substrate surrounding the cache site do not seem to be important: In experiments in aviaries with sand or dirt floors, raking the substrate between caching and recovery did not cause nutcrackers to

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be any less accurate in recovering their caches (Balda, 1980; Balda and Turek, 1984; Vander Wall, 1982). In experiments where either sand-filled cups or wooden plugs can fill holes in a wooden floor, nutcrackers recover their caches accurately even when the pattern of available cups is dramatically different during recovery than during caching sessions (Kamil et al., 1993). Thus, Clark's nutcrackers do not rely upon substrate details to recover their caches.

Two early studies conducted in aviaries with sand or dirt floors tested how nutcrackers use objects when locating their caches. Both studies found that nutcrackers often, but not always, shifted their digging when objects were manipulated. In the first study, when objects were moved 20 cm in one direction, two nutcrackers directed 52 probes at sites correct according to the shifted landmarks, nine probes at original cache positions, and five at intermediate positions (Vander Wall, 1982, Experiments 3 & 4). Although these results show a clear effect of nearby objects, nutcrackers probed for some caches in their original locations even though all nearby objects had been moved (Vander Wall, 1982). The second study was part of a series of trials conducted with a single Clark's nutcracker (Balda and Turek, 1984). In this series, no objects were present on the floor during the first trial, objects were present for a second trial, these objects were removed between caching and recovery during a third trial, and all objects were moved 40 cm between caching and recovery in a fourth trial. During the fourth trial, the nutcracker recovered 8 caches in their original positions, 4 in positions correct for the shifted objects, and did not recover 15 caches (Balda & Turek, 1984). No probes at intermediate positions were reported. Although interpreted somewhat differently at the time, both of these studies show that nutcrackers often shift the full distance that objects are moved and sometimes do not shift at all. In these results, shifting with the moved objects clearly indicates that nutcrackers used the objects as cues but relocating the original cache sites despite nearby objects being shifted indicates that nutrcrackers remember spatial cues other than these objects.

Thus Clark's nutcrackers use objects near the site as landmarks to some degree, but they also use some cues in addition to the objects placed on the floor by researchers. A clue to the identity of these other cues was revealed when research in our laboratory shifted from a small (3.4 m × 3.4 m) to a purpose-built large (15.3 m × 9.1 m) experimental room (Balda and Kamil, 1992). Although Clark's nutcrackers continued to relocate cached seeds with levels of accuracy far better than expected by chance, their accuracy levels were generally lower than researchers had seen previously in the small experimental room (see Balda and Kamil, 1989; Balda et al., 1986; Kamil and Balda, 1985). Below we describe two experiments designed to test whether nutcracker recovery accuracy depended upon the sorts of objects we placed in this room, on the overall appearance of the room, and on overall room structure. The second experiment directly tested if Clark's nutcrackers perform differently on cache-recovery tasks conducted in different experimental rooms. After presenting our experiments, we will discuss the results in light of a series of studies of spatial cue use by nutcrackers that were searching for food hidden by the experimenters.

2. General methods

2.1. Birds & bird care

All nutcrackers were wild caught adults of unknown age and sex. Eight birds began Experiment 1 and ten birds began Experiment 2. All nutcrackers had cached and recovered pinyon pine (*Pinus edulis*) seeds in sand-filled cups during previous studies in the laboratory. Birds were housed individually in metal cages 0.51 m wide × 0.51 m deep × 0.72 m high. They maintained on a constant 10:14 light:dark cycle with a daily diet of parrot pellets, sunflower seeds, turkey starter, and Tenebrio larvae. Nutcrackers were deprived of all food for 24 h before each experimental session but always had access to fresh water and to ground oyster shell as a calcium supplement. Powdered vitamins were added to the food at least twice per week and birds were weighed twice per week.

2.2. Apparatus

These experiments were conducted in two experimental rooms within the Avian Cognition Laboratory at Northern Arizona University. The large experimental room was 15.3 m long × 9.1 m wide × 2.8 m high (Fig. 1a). Its raised floor contained 330 holes (5.5 cm diameter) arranged in 15 rows (labeled A–O) and 22 columns (1–22). Rows were spaced 55.9 cm apart and columns 60.5 cm apart, except for columns 11 and 12, which were 128.3 cm apart. Six 2 m high perches were spaced around the edge of the large room. The relatively small room was 3.4 m long × 3.7 m wide × 2.6 m high (Fig. 1b). The floor of this room was perforated with 237 holes in a grid with 17 columns (labeled A–N) and 14 rows. Holes were 5.5 cm in diameter and separated from each other by 21 cm. Each hole could be fitted with a wooden plug or a sand-filled paper cup (4 cm deep). A 1 m tall feeding platform was always present in the center of each room. Each room contained rocks, bricks, and boards of various shapes and sizes, and posters on each wall. Birds entered and exited the room through a porthole in the wall. While they were in the experimental rooms, birds were observed through one-way glass windows. Each caching session was followed by two recovery sessions 7 and 9 days afterwards. In each recovery session, birds were allowed to recover half of their caches. All sessions were ended by turning out the lights in the experimental room. During each second recovery session, nutcrackers could probe again at sites from which they had recovered the caches during the first recovery session. These probes were recorded as revisits but were not counted as errors because nutcrackers retain some memory for cache locations for days or weeks after they have recovered the contents of those caches (Balda et al., 1986; Kamil and Balda, 1985; Kamil et al., 1993).

2.3. Analyses

Because the three sets of analyses we report below follow the same procedure, we report that general procedure here before the individual experimental details. In each experiment, birds were divided into two squads of equal size and each individual bird completed all treatments. The two squads completed the treatments in opposite orders. The experiments tested for within subject changes in reaction to the treatments and all *F*-ratios reported below are from analyses of variance with subject (bird) nested in squad (order) and cross-factored with treatment. As none of the squad effects or the treatment by squad interactions approached statistical significance, they will not be reported nor discussed below. The only obvious consequence of keeping squad in the analyses is to reduce the denominator degrees of freedom – instead of 7 degrees of freedom for 8 subjects we report 6 degrees of freedom for 8 subjects in two squads of 4 birds each.

In random search we would expect accuracy to equal the number of caches to be found divided by the number of holes available for searching. This calculation is straightforward for the first recovery session. For the second session we excluded the sites of caches already recovered as neither caches to be found nor simple errors. For example, in a first caching session a nutcracker might be searching for eight caches among 154 holes. Chance here would be 8/154, which is 0.052. For the second session, the nutcracker would be looking for four caches among 150 holes (not counting the sites of the four caches already recovered). Here chance would be 4/150,