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The fine-grained spatial abilities of three seed-caching corvids

Brett M. Gibson
University of New Hampshire

Alan Kamil
University of Nebraska - Lincoln, akamil1@unl.edu

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BRETT M. GIBSON
University of New Hampshire, Durham, New Hampshire

and

ALAN C. KAMIL
University of Nebraska, Lincoln, Nebraska

We used a psychophysical method to examine the ability of three corvid species to discern fine-grained spatial information. Nutcrackers, pinyon jays, and scrub-jays were required to discriminate the distance between two landmarks on a computer screen in an operant chamber. All three species were able to discriminate between arrays that differed by 20 mm; the discrimination gradients for scrub-jays and pinyon jays were sharper than those for nutcrackers, however. The results suggest that differences in spatial memory among these species are not related to differences in fine-grained perception.

Three corvid birds, the Clark's nutcracker (*Nucifraga columbiana*), pinyon jay (*Gymnorhinus cyanocephalus*), and Western scrub-jay (*Aphelocoma californica*) live in the southwestern United States and cache pine seeds each fall. These three species differ in their morphological adaptations for making caches and their dependence upon the recovery of caches for survival during the winter. The Clark's nutcracker lives in high coniferous forests at altitudes of up to 3,200 m above sea level. During a 3-week period in the early fall, nutcrackers cache as many as 33,000 pine seeds (Balda, 1987) in thousands of spatially unique locations up to 22 km away from the harvesting site (see Balda & Kamil, 1998, for a review). Nutcrackers have a sublingual pouch that allows them to transport up to 90 seeds during each caching trip (Bock, Balda, & VanderWall, 1973). During the course of the harsh alpine winter, nutcrackers are almost exclusively dependent upon the recovery of the seeds from the hidden caches as energy resources for reproduction and survival (VanderWall & Balda, 1981).

The pinyon jay lives in ponderosa pine woodlands at a somewhat lower elevation (1,700–2,100 m) than the nutcracker. This bird caches fewer seeds (20,000; Balda, 1987) and travels less distance from the harvesting to the caching sites (11 km) than does the nutcracker (Balda & Kamil, 1998). Pinyon jays have a distensible esophagus that allows them to transport up to 39 seeds to a cache site (VanderWall & Balda, 1981). Pinyon jays, like nutcrackers, are also dependent upon the recovery of caches for their survival during the winter (VanderWall & Balda, 1981).

The Western scrub-jay also lives 1,700–2,100 m above sea level in pinyon-juniper woodlands, but it only caches up to 6,000 seeds each season (Balda, 1980). These birds have no specialized morphological structures for transporting seeds from the harvesting to the caching sites (Balda & Kamil, 1998). The Western scrub-jay is not dependent upon the recovery of pine seeds from hidden caches for survival, as other sources of food are available to this bird during the winter (VanderWall & Balda, 1981).

Over the past two decades, converging empirical evidence has indicated that there is a strong correlation between the dependence of these three species upon the recovery of hidden caches and their spatial memory. When tested in a large room in a laboratory, nutcrackers and pinyon jays are more accurate than Western scrub-jays in returning to locations where they have made caches (Balda & Kamil, 1989). Likewise, Kamil, Balda, and Olson (1994) found that nutcrackers acquired an open-room analogue of the radial-maze task more quickly and more accurately than did scrub-jays.

The spatial relationships between one or more surfaces (e.g., landmarks) in the environment and a hidden goal would appear to be contained in the memory for the location of the hidden goal (for reviews, see Cheng & Spetch, 1998; Gallistel, 1990; Healy, 1998; Shettleworth, 1998). Many of these spatial memories are encoded in the hippocampus (e.g., Clayton & Lee, 1998; Hampton & Shettleworth, 1996a, 1996b; Sherry, Jacobs, & Gaulin, 1992; Sherry & Vaccarino, 1989; Squire, 1992). Indeed, many studies have indicated a strong positive relationship between hippocampal volume and dependence upon food recovery (e.g., Basil, Kamil, Balda, & Fite, 1996; Healy & Krebs, 1992; Krebs, Sherry, Healy, Perry, & Vaccarino, 1989).

The aforementioned behavioral experiments with corvids strongly suggest that Clark's nutcrackers have a

greater capacity for storing and/or retaining spatial information than do either pinyon jays or scrub-jays. The results from these same studies may also reflect more generalized differences in perception (e.g., Macphail & Bolhuis, 2001), however. Species that are more dependent upon the recovery of caches may process information differently than less dependent species (e.g., Cheng & Sherry, 1992). For example, the perceptual systems of food-caching species (e.g., nutcrackers) may be more likely to encode spatial cues that could be used to identify the location of a goal than are species less dependent upon the recovery of hidden food for survival. Brodbeck and Shettleworth (1995) trained black-capped chickadees (a food-storing species) and dark-eyed juncos (a nonstoring species) to find a lone baited feeder among an array of four feeders. The feeder that contained the hidden food could be identified by its color, by its geometry relative to the other feeders, or by its spatial location in the global testing environment. Notably, the chickadees primarily used the geometric location of the feeder in the environment, whereas the juncos tended to use all three cues about equally often.

One possibility, then, is that the differences reported between nutcrackers, pinyon jays, and scrub-jays on some spatial memory tasks may also be due to differences in the spatial resolution of the information these three species can encode into or retrieve from memory. Thus, nutcrackers, pinyon jays, and scrub-jays may differ in the scale or quality of the geometric information that each species can maximally encode and that can be specified in their spatial representations. Indeed, even small differences in visual acuity or perceptual features, such as the ability to discriminate geometric information such as distance or heading, may lead to meaningful differences in the ability to encode or relocate a small hidden goal, like a cache (Kamil & Cheng, 2001). One way to determine whether these three species differ in the resolution of the spatial information they can use would be to examine the psychophysical ability of each species to discriminate geometric information.

Recently, Biegler, McGregor, Krebs, and Healy (2001) required food-storing coal tits (*Parus ater*) and nonstoring great tits (*Parus major*) to discriminate between two circles presented on a computer screen. A white circle (16-mm diameter) appeared during testing, and a single peck cleared it from the screen. Following a retention interval, the white circle reappeared at the same location on the screen, and another circle simultaneously appeared at a novel location. The birds were required to peck the circle that appeared in the novel location; the distance between the circles was adjusted incrementally across trials, and discrimination gradually became more difficult. The resolution of the spatial discriminations made by coal tits and great tits was comparable following relatively short retention intervals, but coal tits performed better than great tits following longer retention intervals. These results suggest that differences in spatial memory between food-storing and nonstoring animals

are not due to differences in memory resolution or visual acuity (since both species performed comparably following a short retention interval), but rather to differences in memory persistence. However, little work has examined the psychophysical scale at which other seed-storing and nonstoring species, such as corvids, might make comparable spatial discriminations. In addition, although parids and corvids would appear to have common selective pressures for remembering the location of hidden food, the mechanisms that they use to achieve such apparently comparable results on tests of spatial memory may be quite different (e.g., based on memory capacity vs. spatial resolution).

In the following experiment, we used a psychophysical method to examine the scale at which nutcrackers, pinyon jays, and scrub-jays make fine-grained discriminations of the spatial information provided by an array of two landmarks presented on a computer screen. If the differences in spatial memory that have been documented for these species reflect more general differences in spatial cognition or perception, then nutcrackers might have a better psychophysical ability than either pinyon jays or scrub-jays to detect differences in very fine-grained geometric information.

METHOD

Animals

Four adult birds of each species—the Clark's nutcracker, pinyon jay, and scrub-jay, all of which were trapped in the wild and subsequently housed at the University of Nebraska at Lincoln—were used in this study. The birds had free access to water and were maintained between 80% and 85% of their ad-lib weight. The birds were experimentally naive at the time of testing. Half pieces of pine nuts were used as reinforcers for nutcrackers and pinyon jays, and grubs were used for scrub-jays. Each type of reinforcement has been documented (e.g., Olson, 1991) to be exceptionally motivating and is consistent with the food types primarily encountered by the birds in their natural environment.

Apparatus

Training and testing were conducted in a rectangular operant chamber. A high-resolution computer monitor that displayed computer-generated images was placed outside the chamber behind a 25 × 30-cm opening created in one of the short ends of the chamber. A touch screen (EloTouch, Fremont, CA) was mounted on the interior of the chamber over the opening and was used to record the Cartesian position of pecks made to stimuli presented on the computer monitor. A vertically adjustable perch was positioned 10 cm away from the base of the touch screen; the birds could reach the entire screen with their beaks. A feeder (Davis Universal Feeder, Model 310) delivered single rewards into a food well that was centered on the front wall below the computer monitor. A houselight dimly illuminated the chamber; white noise was filtered into the chamber through a speaker located in the room.

Procedures

The birds were initially trained, using the procedure of successive approximations, to peck at a small red disk or "landmark" (5 mm in diameter) that appeared on the screen. An invisible "hot area" 15 mm in diameter was centered over the disk. Pecks that fell within the perimeter of the hot area were identified as "hitting" the landmark. Three consecutive pecks to the hot area cleared the land-

mark from the screen and resulted in a reward. In a second phase of training, the trial sequence proceeded as described above, except that a white disk (5 mm in diameter) appeared on the screen with the red landmark after the third peck was delivered to the landmark's hot area (Figure 1). This white disk served as the second landmark of a two-landmark array. For two birds from each species, the white landmark was located directly to the left of the red landmark, and for the other two birds, it always appeared to the right of the red landmark. Like the red landmark, the white disk also had a 15-mm hot area. Two pecks to the hot area of the white landmark cleared both landmarks from the screen and resulted in a reward. To eliminate the use of all cues other than the landmarks (e.g., the border of the monitor), the anchor point for the position of the array moved to a randomly determined screen position from trial to trial. The horizontal distance between the two landmarks, the interlandmark distance (ILD), varied from trial to trial.

Next, discrimination training began, in which we examined whether the birds could make fine discriminations of the distance between two points by rewarding responses to the white landmark when the distance between the red and white landmarks was less than 50 mm (S+ condition) and not rewarding responses when the distance between the landmarks was greater than 50 mm (S− condition). Specifically, the red landmark defined one end of an invisible correct region (Figure 1) extending 50 mm from the center of that landmark. Following three pecks to the hot area of the red landmark, the white landmark appeared either to the left or to the right. The ILD between the red and white landmarks in the array could be 20, 30, 40, 60, 70, or 80 mm. The number of pecks directed at the hot area of the white landmark was then recorded for a 10-sec fixed interval (FI). Pecking at the white landmark was defined as being "correct" when the array ILD (measured from the center of each landmark) was less than 50 mm, whereas this behavior was "incorrect" when the array ILD was greater than 50 mm. Hence, there were three arrays that were shorter than the criterion of 50 mm (S+ = 20, 30, or 40 mm) and three that were longer than the criterion (S− = 60, 70, or 80 mm). Because the white landmark was positioned to the right of the red landmark for two of the four birds from each species, the direction in which the birds had to respond to the white stimulus was balanced within each species. All other procedures were the same.

The first peck to the hot area of the white landmark after the 10-sec FI following a correct response cleared the landmarks from the screen and resulted in the delivery of a food reward. The first peck after the 10-sec FI following an incorrect response only resulted in the landmarks being cleared from the screen. An intertrial interval (ITI) with a mean of 15 sec (range 10–20 sec) ensued. It was expected that the rate of pecking at the white landmark during the FI would increase when the distance between the landmarks was shorter
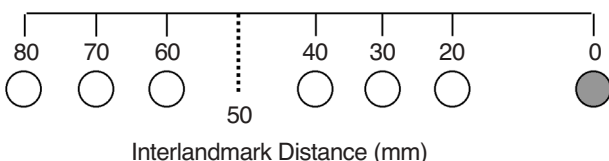

Figure 1. The dark circle indicates the position of the red landmark, and the unfilled circles indicate positions of the white landmark on the computer screen for 2 of the birds in each group (the white landmark appeared to the right of the red landmark for the other 2 birds). The white landmark was separated from the red landmark by one of six interlandmark distances (20, 30, 40, 60, 70, and 80 mm) during the course of testing. The criterion distance of 50 mm is indicated by the vertical dashed line; the diagram is not drawn to scale.

than the 50-mm criterion and decrease when the distance was greater.

Each daily session of discrimination training consisted of 8 warm-up, 32 correct, and 32 incorrect block-randomized trials. The data from the warm-up trials were not used in the analysis. The presentation of each of the ILDs was randomized and balanced within each session. We continued discrimination training until (1) the discrimination ratio (see measures below) for each bird was above 70% and (2) mean discriminative performance for each group approached asymptote. The birds were trained in this way to ensure that individuals reached a reasonable level of discriminative performance and that the species as a group had achieved a maximal level of performance. Although some birds reached the 70% criterion earlier than others, such differences should have had little impact, since all of the birds were at asymptote at the end of discrimination training. This criterion for performance ensured that by the end of discrimination training, differences in the ability of the species to discriminate between the shorter and longer sets of arrays reflected differences in psychophysical factors rather than in learning about the discrimination procedure. Discrimination training continued for a total of 60 sessions; the sessions were arranged into 12 blocks (5 trials/block) for the analysis described below.

Measures and Analyses

Three measures of performance were used in three separate sets of analyses. The first measure was a discrimination ratio that reflected the proportion of pecks made during the FI on trials when the array was shorter than the criterion distance (S+ condition) to the total number of pecks made during the FI to all arrays during the session. This measure was averaged across blocks of testing and was used in the analysis below.

The ability of each species to discriminate between each of the six landmark arrays was assessed using a percentage score. This measure was calculated each session for each of the six ILDs. Each score was determined by calculating the number of pecks delivered during the FI following each of the six ILDs. Each of these values was then divided by the sum of all pecks delivered during the FI across all trials in a session. The percentage scores for each array type were then averaged across sessions and subjected to the analysis below.

The final measure was used to examine the distribution of pecks across the FI separately for S+ and S− trials for each species. The 10-s FI for S+ and S− trials was split into five consecutive 2-sec bins, and the number of pecks in each bin during each type of trial was recorded across the session. The total number of pecks made during each of the S+ and S− trials was also recorded. The bin with the maximum number of pecks for each trial type was identified for the session, and the number of pecks in each of the five bins was divided by this maximal value for the S+ and S− trials, respectively. This procedure produced five bin indexes that indicated how pecks were distributed across the FI for both S+ and S− trials for each species. These data were then used in the analysis below.

RESULTS

During the course of discrimination training, birds in each of the three species improved steadily in their ability to discriminate between landmark arrays that were shorter and longer than the criterion distance (Figure 2A). The ability of nutcrackers, pinyon jays, and scrub-jays to make such discriminations was comparable during the course of acquisition. The average discrimination ratio scores for each of the three species approached asymptote by Block 10 of testing.
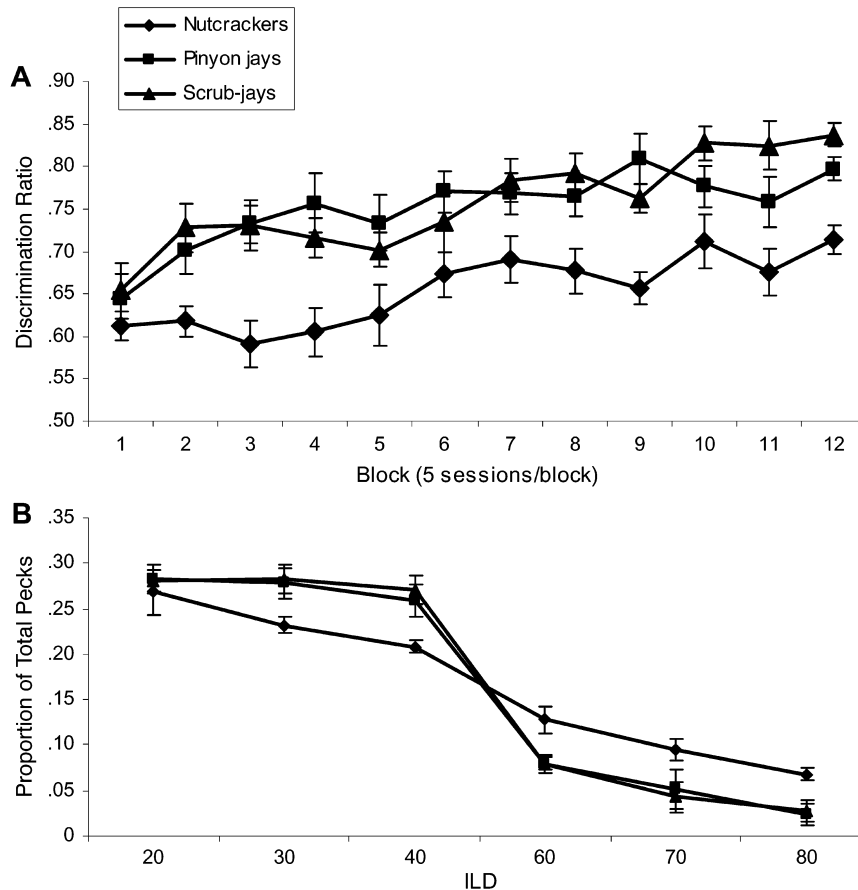
Figure 2. (A) Mean discrimination ratio scores (error bars = _SEM_) shown across blocks of testing for all three species. (B) Discrimination gradients for each of the three species. The gradients were based on the proportion of pecks the birds made during the last block when each of the six array interlandmark distances (ILDs) was presented.

To test these observations, an analysis of variance (ANOVA) was conducted with block as a repeated variable, species as a between-groups variable, and the discrimination ratio as a dependent measure. Alpha was set at .05 for the determination of reliable effects for all of the analyses described here. The analysis revealed a significant effect of block [$F(11,99) = 9.13$] but no reliable difference in discriminative performance among the three species [$F(2,9) = 2.36$]. Fisher least significant difference (LSD) comparisons indicated that performance was significantly poorer during each of the first two blocks than during any of the last three blocks (all $ps < .05$). The interaction between block and species was not significant [$F(22, 99) < 1$].

We used the data from the last block (when performance appeared to be at asymptote for each species) for constructing and analyzing the discrimination gradients for each species. Figure 2B displays the mean discrimination gradients for each of the ILDs during the last block of the experiment. The gradients for the scrub-jays and pinyon jays were similar and demonstrated a particularly sharp drop between arrays (ILDs of 40 and 60 mm)

that bordered the criterion distance of 50 mm. The discrimination gradient for nutcrackers, in contrast, tended to be flatter and showed a shallower drop around the 50-mm criterion than did those for the other two species. An ANOVA was conducted with array ILD as a repeated variable, species as a between-groups variable, and the proportion score for each array ILD as a dependent measure. The results from this analysis indicated a robust difference in discriminative performance among the arrays across species [$F(5,45) = 143.01$]. The birds delivered significantly more pecks to each of the three arrays that were shorter than 50 mm (20, 30, and 40 mm) than to the three arrays that were longer than the 50-mm criterion (60, 70, and 80 mm) (all $ps < .05$; Fisher LSD tests were used for comparisons).

Another ANOVA indicated a significant interaction between species and array ILD [$F(10,45) = 3.22$]. Notably, all three species reliably discriminated between arrays (ILDs of 40 and 60 mm) nearest the criterion distance (50 mm), although scrub-jays and pinyon jays were reliably better than nutcrackers in making this discrimination (all $ps < .05$). Scrub-jays were significantly bet-

ter than nutcrackers at identifying whether each of four arrays (ILDs of 20, 40, 60, and 70 mm; all $ps < .05$) was larger or smaller than the criterion, whereas pinyon jays were better than nutcrackers at discriminating whether three of the six arrays (ILDs of 30, 40, and 60 mm; all $ps < .05$) were larger or smaller than the criterion.

As can be seen in Figure 3A, pinyon jays and scrub-jays tended to distribute their pecks evenly across each of the five bins of the FI during S+ trials (Figure 2C). In

contrast, nutcrackers made very few pecks during the onset of the FI and increased their rate of pecking as the FI progressed. To evaluate these observations, an ANOVA was performed with bin as a repeated variable, species as a between-groups variable, and the discrimination index as a dependent measure (again data from the last block of discrimination training were used). The analysis indicated significant effects of species [$F(2,9) = 7.96$] and bin [$F(2,9) = 11.82$]. The analysis also indicated a reliable
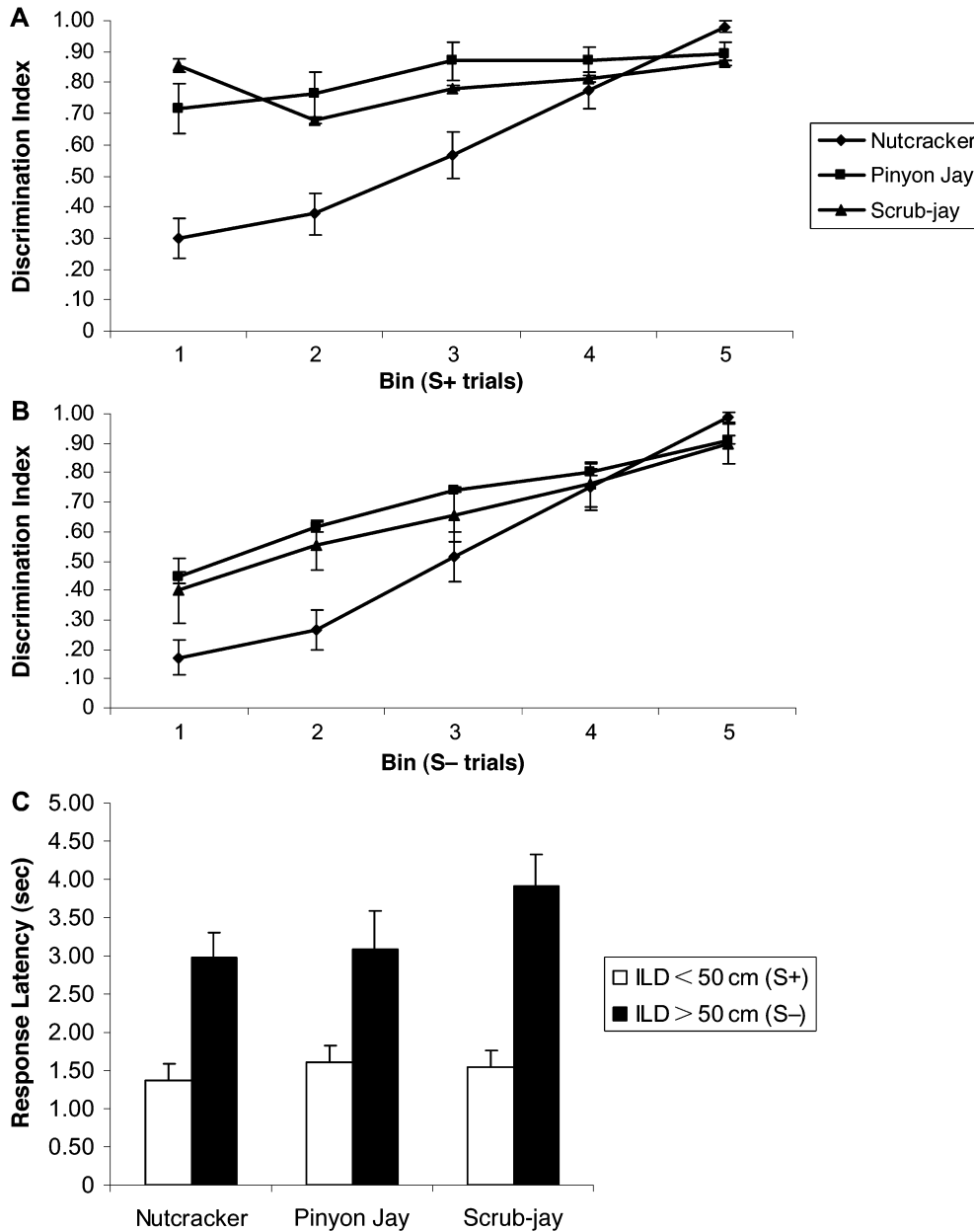

Figure 3. (A and B) The mean discrimination index scores (error bars = *SEM*), indicating the proportion of pecks made by the birds during each bin of the FI for each of the three species during the last block of discrimination training, for (A) S+ trials, in which the interlandmark distance (ILD) was less than 50 mm, and (B) S− trials, in which the ILD was greater than 50 mm. (C) The mean latency of the first peck following the conclusion of the 10-sec FI for all three species during S+ and S− trials (last block of discrimination training).

interaction between species and bin [$F(8,36) = 4.75$]. Tukey HSD comparisons indicated that pinyon jays and scrub-jays delivered a larger percentage of pecks across the first two bins than did nutcrackers (all $ps < .05$) but that the three species had statistically indistinguishable bin index scores during the last two bins of the FI (all $ps < .05$).

The discrimination index scores for the three species during S− trials appeared more comparable across the five bins of the FI (Figure 3B). An ANOVA identical to that reported for the S+ trials was conducted (using data from the last block of discrimination training). This analysis indicated reliable differences for species [$F(2,9) = 5.17$] and bin [$F(2,9) = 36.41$]. Notably, and in contrast to the S+ trials, the ANOVA failed to indicate a reliable interaction between species and bin [$F(8,36) = 2.03$].

Figure 3C displays the average latency for the birds' first response to the white stimulus following the conclusion of the 10-sec FI during S+ and S− trials (this response terminated the trial). A visual inspection of this figure indicates that the average response latencies were comparable for all three species for both S+ and S− trials. We conducted an ANOVA using trial type (S+/S−) as a repeated variable, species as a between-groups variable, and response latency as a dependent measure (again using data from the last block of discrimination training). The results of this analysis indicated a robust effect of trial type [$F(1,9) = 47.97$] but failed to indicate a difference in response latency between the species [$F(2,9) = 1.36$]. There was no interaction between species and trial type [$F(2,9) = 1.14$].

DISCUSSION

In the present experiment, nutcrackers, pinyon jays, and Western scrub-jays were able to distinguish accurately between landmark arrays that differed by as little as 20 mm in length. This scale of resolution is impressive and previously undocumented for these birds. The discrimination gradients observed for Western scrub-jays and pinyon jays were significantly sharper than those for nutcrackers. That is, both the Western scrub-jays and pinyon jays were better at discriminating interlandmark distances that were closer to the threshold than were the nutcrackers. This pattern of results may be considered surprising, since the differences in spatial memory observed for these species might have been expected to be correlated with other aspects of the three birds' spatial cognitive abilities.

The results from the present study were notably different from those reported by Biegler et al. (2001), who found that food-storing coal tits and nonstoring great tits did not differ in their ability to discriminate fine-grained spatial information when a memory component was minimal (see the introduction). A variety of studies have documented that food-storing corvids and parids (see the introduction) perform better on a variety of spatial tasks in comparison with counterparts that are less dependent upon the recovery of hidden food for survival. However, the similar selective pressure that these two lines encountered may have had very different effects on the perceptual and cognitive abilities of these two distinct lineages. Thus, although the recovery of hidden food for survival would appear to have supported the evolution of an improved memory for spatial information for food-storing parids and corvids, this common selective pressure may not have resulted in the evolution of other shared adaptations.

Notably, Macphail and Bolhuis (2001) have recently argued that apparent differences in spatial memory between storing and nonstoring species may actually be due to differences in perceptual ability rather than spatial memory. According to their account, the salience of spatial cues may be greater for food-storing than for nonstoring species; when an animal encodes where it stored a cache, nonstoring species may use nonspatial cues (such as the color of the cache location), whereas spatial species may use geometric information. These perceptual filters would then feed information into quite comparable central learning and memory systems. The results from our study, however, indicate that the perceptual system of scrub-jays (a species less dependent upon cache recovery) is more refined for spatial tasks than that of nutcrackers (a species more dependent upon cache recovery) for some types of spatial information. Thus, support for a perceptual account as an alternative explanation for apparent differences in spatial memory is limited.

It remains unclear why scrub-jays and pinyon jays would have reliably sharper discrimination gradients than nutcrackers. Both Western scrub-jays and pinyon jays steal caches (e.g., Emery & Clayton, 2001), whereas nutcrackers are less sensitive to and rarely encounter pilfering of their caches. Perhaps the visuospatial memories that may be required for Western scrub-jays and pinyon jays to pilfer the caches of conspecifics were a selective force that led to the evolution of finer-grained visual acuity for these birds. In addition, evolution may have favored sharper perceptual skills in scrub-jays because they are relatively more dependent upon locating and tracking mobile and sometimes cryptic insects for their diet than are nutcrackers. One further possibility is that although the differences in the abilities of these three species to discriminate fine-grained spatial cues in the present experiment are reliable, they may not have been driven by specific differences in the ecologies of these birds.

It is notable that the tests of spatial memory described in the introduction (e.g., open-room cache recovery) have all required birds to use spatial cues on a relatively larger scale than was required in the present study. The scale of the spatial cues that were discriminated in the present task appears more consistent with the scale of the spatial cues used in the studies of episodic memory reported by Clayton and Dickinson (e.g., 1998, 1999). In those studies, scrub-jays cached and recovered food items from the wells of sand-filled ice cube trays that were only a few centimeters apart. The landmarks that specified the

location of the hidden goals in those studies were only a few centimeters from the goal locations, and the scale of this geometric information was more consistent with the distances that were discriminated in the present experiment. Thus, fine-grained spatial tasks may be more favorable for Western scrub-jays and pinyon jays than for nutcrackers, particularly when these tasks do not require a large memory component.

It is also notable that the time course of the distribution of pecks across the 10-sec FI was quite different for the three species under investigation. Pinyon jays and scrub-jays tended to distribute their pecks evenly across the 10-sec FI during S+ trials, whereas nutcrackers tended to make most of their pecks just prior to the termination of the FI. This finding might suggest that nutcrackers are better at discriminating temporal relationships than either pinyon jays or scrub-jays. The pattern of results might also be explained by more general differences in motivation among the species. A single peck was required to terminate either an S+ or S− trial after the 10-sec FI. A highly motivated bird may peck more frequently toward the end of the FI, so that it can terminate the current trial and advance more rapidly to the next S+ trial, thereby increasing its rate of reward. Because nutcrackers cache and recover many thousands of pine seeds, they might be expected to terminate trials more rapidly (i.e., distribute more pecks during the end of the trial) than either scrub-jays or pinyon jays.

Previous operant research with these species (e.g., Olson, 1991) has indicated that all three are highly motivated to complete operant tasks like the one used in the present study. The data in our experiment allow us to address this issue more directly. If nutcrackers are more motivated than either scrub-jays or pinyon jays to maximize their rate of reward, then they should not only peck more frequently during the end of the trial, but the latency of their first peck after the FI (which determines when the trial will end) should have been shorter on both types of trials. This was not the case, however (Figure 3C), suggesting that the differences in the time courses of pecking shown in Figure 3A may be due to differences in temporal judgments rather than motivation. Although temporal factors would appear to play an important role for any animal that caches (Clayton & Dickinson, 1999), the pattern of results suggests that scrub-jays and pinyon jays are relatively poorer than nutcrackers at discriminating temporal relationships (i.e., determining when the FI would terminate). An extensive comparative analysis of the ability of food-storing and nonstoring species to make temporal discriminations has not been conducted, and further empirical work in this domain would be of interest.

In keeping with the psychophysical method (Chaplin & Krawiec, 1968), the fine-grained spatial abilities of these three species could be compared at an even finer scale. Reducing the ILD so that the landmark arrays became even more similar to each other (e.g., ILDs of 47 and 53 mm) and the criterion (50 mm) would increase the difficulty of the discrimination. Eventually, this procedure

should yield arrays that the birds are incapable of distinguishing between, thereby isolating the absolute threshold of discrimination. Such an approach was used during a second experiment (ILDs of 72, 68, 62, and 56 mm, and 46, 42, 38, and 32 mm), but many of the birds (2 scrub-jays, 1 pinyon jay, and 2 nutcrackers) failed to complete experimental sessions and were dropped from the study, or died due to illness. The loss of these birds made a meaningful comparative analysis of the data from this second experiment challenging.

The psychophysical method that was used in the present set of experiments was useful in identifying the ability of three corvid species to discriminate fine-grained spatial information. Future studies designed to determine the absolute threshold of discriminating spatial information by these three species would be of interest. The application of the method used here would appear to be a useful tool for investigating the fine-grained spatial abilities of a wide variety of animals.

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