

Qadri, M.A.J., Leonard, K., Cook, R.G. et al. Examination of long-term visual memorization capacity in the Clark's nutcracker (*Nucifraga columbiana*). *Psychon Bull Rev* (2018). <https://doi.org/10.3758/s13423-018-1439-4>

Examination of Long-Term Visual Memorization Capacity in the Clark's Nutcracker
(*Nucifraga Columbiana*)

Muhammad A.J. Qadri¹, Kevin Leonard², Robert G. Cook¹, Debbie M. Kelly²

Department of Psychology, Tufts University¹

Department of Psychology, University of Manitoba²

Running head: Nutcracker Visual Memory Capacity

Corresponding author:

Muhammad A.J. Qadri
Department of Psychology
Tufts University
490 Boston Ave
Medford, MA 02155, USA
Phone: 617 627-5606, Fax: 617 627-3181
Email: Muhammad.Qadri@tufts.edu

Abstract

Clark's nutcrackers exhibit remarkable cache recovery behavior, remembering thousands of seed locations over the winter. No direct laboratory test of their visual memory capacity, however, has yet been performed. Here, two nutcrackers were tested in an operant procedure used to measure different species' visual memory capacities. The nutcrackers were incrementally tested with an ever-expanding pool of pictorial stimuli in a two-alternative discrimination task. Each picture was randomly assigned to either a right or left choice response, forcing the nutcrackers to memorize each picture-response association. The nutcrackers' visual memorization capacity was estimated at a little over 500 pictures, and the testing suggests effects of primacy, recency, and memory decay over time. The size of this long-term visual memory was less than the approximately 800-picture capacity established for pigeons. These results support the hypothesis that nutcrackers' spatial memory is a specialized adaptation tied to their natural history of food-caching and recovery and not to a larger long-term general memory capacity. Furthermore, despite millennia of separate and divergent evolution, the mechanisms of visual information retention seems to reflect common memory systems of differing capacities across the different species tested in this design.

Clark's nutcrackers (*Nucifraga columbiana*) are renowned for storing and recovering large numbers of seed caches that are critical to surviving the winter (Tomback, 1980). Nutcrackers can even recover seeds from caches buried in snow which occludes the local visual cues present when originally cached. This apparently large spatial memory has made nutcrackers of particular comparative interest. Their cache-recovery ability is cited regularly as one of the best examples of an evolved specialized cognitive capacity. As a result, it ranks among the best evidence supporting an adaptive, as opposed to a generalist, framework for thinking about the evolution and organization of cognition (Balda & Kamil, 2002; Bitterman, 1975; Shettleworth, 1984; Thorndike, 1898). This latter issue directly connects to the longer standing debate about the organization of human intelligence (Binet, Simon, & Terman, 1980; Gardner, 1985; Spearman, 1904; Sternberg, 1977; Thurstone, 1924). Further understanding how cognitive processes diversified in non-human species will provide greater perspective on human cognitive evolution.

The cognitive specialization hypothesis gains support from numerous spatial memory studies demonstrating that the cache-recovery capacity of nutcrackers exceeds those of other closely-related corvids (e.g. Balda & Kamil, 1989). Operant short-term memory tasks have revealed that nutcrackers can better remember spatial information than visual information (Olson, Kamil, Balda, & Nims, 1995). Further, wild-caught nutcrackers have enlarged hippocampal formations (Capaldi, Robinson, & Fahrback, 1999) or a greater number of neurons in the hippocampus (Basil, Kamil, Balda, & Fite, 1996; Gould et al., 2013) in comparison to less cache-reliant species (Capaldi et al., 1999).

An alternative account is that these memory abilities are not unique to spatial information or cache recovery, however, but instead reflect the operation of larger general-purpose memory or cognitive capacity. For instance, Clark's nutcrackers possess many other advanced skills like

abstract concept learning (Magnotti, Katz, Wright, & Kelly, 2015), mirror-self recognition (Clary & Kelly, 2016), inferential reasoning (Clary & Kelly, 2013; Tornick & Gibson, 2013) and situationally-specific cache protection strategies (Clary & Kelly, 2011). Furthermore, corvids in general, though not nutcrackers specifically, have been found to possess superior tool-use abilities (Emery & Clayton, 2004). These data suggest a greater degree of generalized intelligence, opening the possibility that their renowned spatial memory stems from a larger general-purpose memory system. For the purposes of this paper, these two accounts are labeled the *specialized memory* and *generalized memory* hypotheses, respectively.

Although the long-term memory capacity of nutcrackers has been directly evaluated in the laboratory, generating a sufficient number of controlled caching sites to sufficiently challenge their spatial memory has been difficult (Balda & Kamil, 1992). The large estimates of their spatial memory capacity have instead been derived from indirect calculations from natural observations (Balda & Kamil, 1992). Therefore, whether nutcrackers have a large, specialized spatial memory or simply a larger capacity to store and use information of all types is an open question.

Our understanding and measurement of the long-term memory abilities of several species has recently been advanced using a relatively new testing procedure. The long-term visual memory capacity of two pigeons (*Columba livia*), two baboons (*Papio papio*), and one human (*Homo sapiens*) has been examined using comparable operant procedures (Cook, Levison, Gillett, & Blaisdell, 2005; Fagot & Cook, 2006; Voss, 2009). In this procedure, the observer is required to associate randomized right and left responses to an increasingly large pool of successively introduced pictures. The pictures' content is unrelated to their correct choice assignments, so only memorized left/right associations can be used to be correct. Accuracy with these memorized

items over time then provides estimates for the number of simultaneous picture-response associations that can be maintained. For pigeons, a limit of approximately 800 items was found. For baboons and humans, no limit was reached during testing even after learning 3500 to 5000 items for baboons and 3400 items for the single human.

This experimental procedure for measuring long-term visual association formation enables the examination of nutcrackers' memory capacity directly and its comparison to established values for pigeons, baboons, and humans. If, on the one hand, nutcrackers have a large generalized memory capacity, their measured capacity should exceed the pigeons and perhaps approach the primates. This result would be consistent with the *generalized memory* account and suggest nutcrackers are not specifically adapted for cache recovery. If, on the other hand, they possess specialized spatial memory mechanisms devoted to just caching, then this operant visual procedure should not tap into that ability. In that case, their measured capacity might look more like the non-caching pigeons. This latter outcome would be consistent with *the specialized memory* account.

Here, two nutcrackers were tested continuously with the same memory procedure and pictures as previously used (Cook et al., 2005; Fagot & Cook, 2006). The primary question of interest centered on estimating the size of their visual memory capacity and comparing to other known results. We additionally examined their speed of learning, choice reaction time, lag effects, primacy/recency effects, and the proportion of stimuli learned in one trial to examine the operation of the memory mechanisms involved.

Methods

Animals

Two wild-caught male nutcrackers (Cornelius and Gabby) were tested. Both were naïve to visual operant testing but had participated in spatial cognition studies over the prior 12 years. The University of Manitoba's Animal Care Committee approved all procedures (protocol #F10-029).

Apparatus

The nutcrackers were tested in a custom-built touchscreen chamber. Stimuli were presented on an LCD monitor (ThinkVision L171p, resolution 1024 × 768) located just behind a 32 × 27 cm infrared Open-Frame viewing window (Elo CarrollTouch). A ceiling light illuminated the chamber at all times, except during time-outs. White noise masked external sounds. A food reward wheel rotated to provide a single mealworm for correct choices. All experimental events were controlled by a computer (Lenovo M600) connected through a USB digital I/O panel (Phidgets Inc.).

All picture stimuli were 20 cm × 13 cm in size (480 × 300 pixels) and were the same as used in prior tests (Cook et al., 2005; Fagot & Cook, 2006). The pictures consisted of landscapes, objects, and abstract photography as drawn from different commercial image collections and the Internet.

Procedure

The testing procedures were as similar as possible to those used with the baboons and pigeons. Trials started with a peck to a 3.5 cm white circle. This circle was immediately replaced by a centrally located picture stimulus. After five pecks to it, the picture was removed and yellow choice stimuli appeared on the left (plus sign) and right (circle) sides of the display. A peck to the correct choice for the preceding picture resulted in a mealworm reward. A peck to the incorrect choice caused the trial to repeat after a brief, dark timeout. Such correction trials were

excluded from the data analyses, except in computing the lag function. A 5-s inter-trial interval was used.

Birds were presented with a 100-trial daily session, testing a mixture of old and new items. New-item trials involved two presentations of 30 recently introduced pictures, which were repeated across sessions until the nutcrackers reached criterion. The correct responses to these stimuli were randomly and permanently assigned to the left or right choices at their introduction. The learning criterion was 80% or better performance on the new-items for two consecutive sessions. Once this criterion was attained, this set of pictures was moved to the pool of old-items and a new set of 30 novel pictures was introduced (only 20 new pictures were used for the first 18 sets). Each session's old-item trials were made from randomly-selected pictures from the ever-expanding pool of previously learned picture–response associations acquired from memorizing the prior sets. This incremental process of adding sets of pictures continued for 399 sessions for Cornelius (acquiring 58 sets prior to an unrelated health issue) and 734 sessions for Gabby (acquiring 76 sets prior to stopping in light of unchanging capacity estimates).

Results

Both nutcrackers successfully memorized large numbers of picture-response associations over testing. At the end, Cornelius had an old-item pool containing 1500 pictures, whereas Gabby's pool contained 2040 pictures. Although both birds initially started near 90% accuracy with old items, accuracy declined as increasingly more sets of items were included. Over the final ten sets of testing, Cornelius (67.5%, bootstrapped bias-corrected and accelerated (BCa) 95% confidence interval $CI_{95\%} = [65.9\%, 69.6\%]$) and Gabby (65.1%, $CI_{95\%} = [63.3\%, 66.3\%]$) correctly responded to the randomly-selected old items from their respective pools of learned

stimuli. Figure 1A shows this gradual decline as a function of the number of items in the old-item pool.

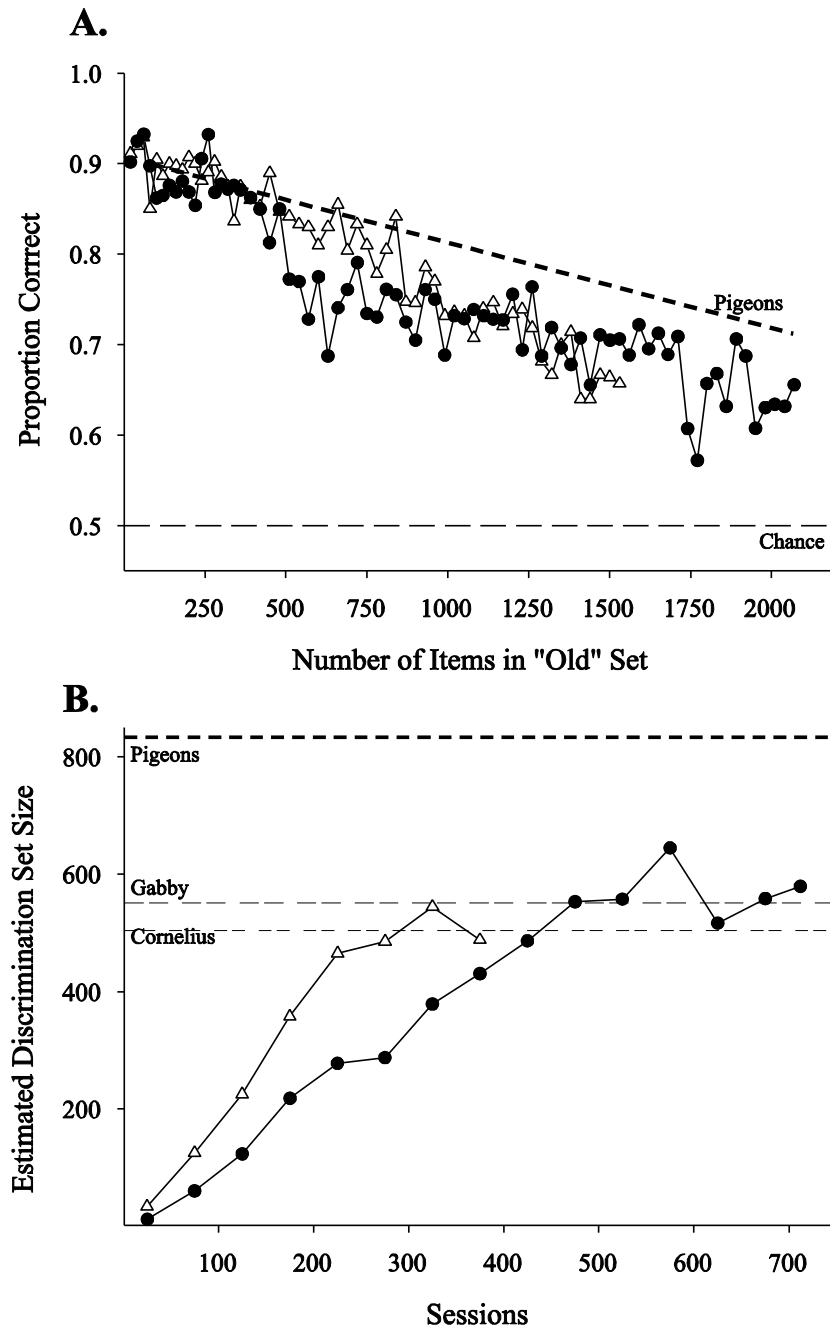


Figure 1. Proportion correct on memorized items over the experiment as a function of the number of items memorized (A) and the estimated memory set size as a function of sessions in the experiment (B; see text for details of this latter calculation). In both panels, the closed triangles are the results for Cornelius and the open circles are those for Gabby. The thick, short-dashed line represents the mean pigeon results from Cook et al. (2005). In panel A, the thin dashed line represents chance performance. In panel B, the thin dashed lines represent the mean

estimated discrimination set size estimates from the last three blocks for each bird. Note that Cornelius' and Gabby's last blocks only contain 49 and 34 sessions, respectively, whereas the remaining blocks contain 50 sessions.

Cook et al. (2005) employed a simple all-or-none model of memory to estimate the number of fully memorized items. In this model, pictures are either fully memorized and accessible at time of choice, or they are completely inaccessible and require a guess. The number of fully memorized items can then be estimated by determining what proportion of correct responses (i.e., 100% accuracy) and random guesses (i.e., 50% accuracy) would yield the observed level of accuracy. This unpretentious model provides a ready metric for evaluating the minimal memorization capacities of an observer. These results are displayed in Figure 1B in 50-session blocks. The estimated memory set sizes for both nutcrackers steadily increased with additional items, until they eventually plateaued towards the final stages of testing. The estimates over the final three blocks were 504 ($CI_{95\%} = [475.9, 532.4]$) items for Cornelius and 551 ($CI_{95\%} = [497.8, 595.5]$) items for Gabby.

The speed with which the sets of new-items were learned stayed constant during the experiment, despite reduced old-item accuracy with increasing memory loads. The numbers of sessions both subjects completed were each divided into five approximately equal sets for this analysis. The first quintile of the experiment seemed to require slightly more sessions for both subjects to learn the first sets of new-items, perhaps because of unfamiliarity with operant testing. Averaging the data after the first 10 new-item sets revealed that Cornelius averaged about 6.5 ($CI_{95\%} = [6.06, 6.92]$) sessions to acquire a typical set whereas Gabby averaged 9.1 ($CI_{95\%} = [8.63, 9.62]$) sessions. A mixed-model analysis of these data (fixed effect of quintile, random effect of bird; using R package nlme) found no significant change during the experiment, $F(1,7) = 3.1, p = .123; \alpha = .05$, for this and all remaining tests.

Within the new-item acquisitions, we examined the frequency of items learned with a single exposure (Cook & Fagot, 2009). Items were designated as “one-trial learning” items if after the first exposure, the bird responded correctly for the next ten exposures (i.e., exposures 2-11). The nutcrackers learned, on average, 17.3% of the stimuli with a single exposure (Cornelius 17.7%, $CI_{95\%} = [15.8, 19.6]$; Gabby 17.0%, $CI_{95\%} = [15.4, 18.6]$). Additionally, one-trial learning was more prevalent when the first exposure was rewarded rather than punished. For Cornelius and Gabby, these occurred at a 2.5:1 rewarded:punished rate ($CI_{95\%} = [1.94, 3.25]:1$) and a 4.1:1 rate ($CI_{95\%} = [3.10, 5.26]:1$), respectively. The proportion of these one-trial learning items did not change over the course of the experiment (fixed effect of quintile, random effect of item nested within bird, $\chi^2(1) = 0.6, p > .250$; using R package lme4).

The prior comparative research identified that the time between successive stimulus presentations affected accuracy. Figure 2A plots the nutcrackers’ accuracy against the number of intervening stimulus presentations (including correction trials) between successive stimulus presentations in the last half of the experiment. Both nutcrackers performed more accurately for recently tested stimuli, with decreasing accuracy as the intervening duration between tests increased (Cornelius slope = -11.5×10^{-6} , $p = .004$, $R^2 = .47$; Gabby slope = -7.65×10^{-6} , $p = .009$; $R^2 = .63$).

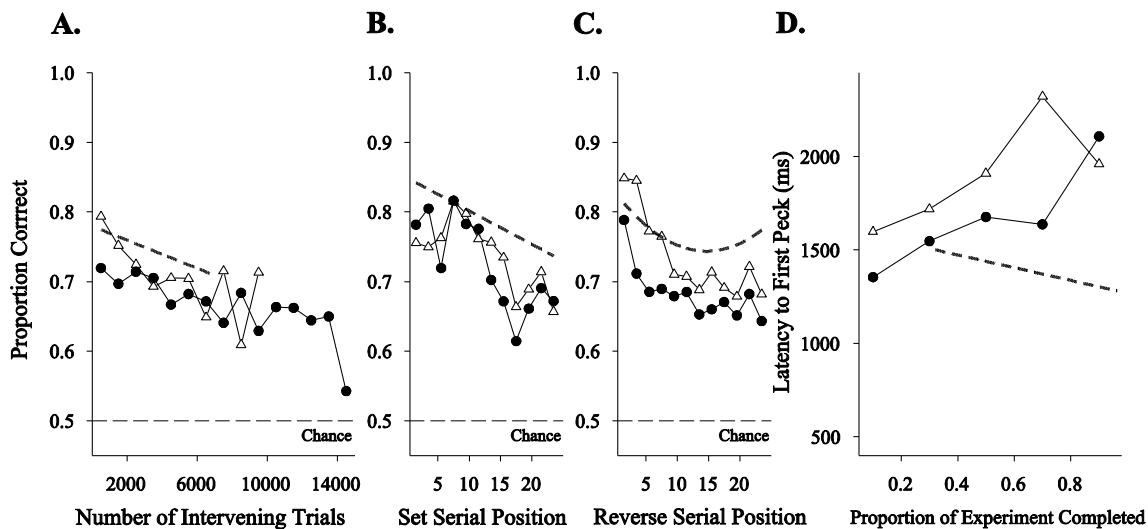


Figure 2. Proportion correct as a function of number of intervening trials between presentation during the last half of the experiment (lag; A), proportion correct during the last half of the experiment for the first 24 stimulus sets as a function of the serial position of when they were learned (serial position; B), proportion correct during the last half of the experiment for the most recent 24 stimulus sets as a function of how long ago they were learned (reverse serial position; C), and latency to the first peck as a function of the proportion of the experiment completed (RT; D), with corresponding comparisons to pigeon results (depicted by heavy dotted lines; Cook et al., 2005). In all panels, triangles show results for Cornelius, and circles are for Gabby. The thin dashed lines in A, B, and C represent chance performance. In panel A, although there were instances of more than 14,000 intervening trials for Gabby and more than 10,000 intervening trials for Cornelius, these data are omitted because of their sparsity.

We next examined whether the nutcrackers' memory was susceptible to primacy and recency learning effects. Figure 2B and 2C address primacy and recency, respectively, by depicting accuracy during the last half of the experiment for the first and last 24 stimulus sets learned according to their serial position. The earliest sets learned and the most-recently learned sets showed high accuracy, and as the amount of primacy or recency decreases, accuracy is reduced by approximately ten percentage points. Fitting upward-opening quadratic functions to these data confirms the curves display the expected boosts from primacy (Cornelius overall $R^2 = .54$; Gabby $R^2 = .61$) and recency (Cornelius overall $R^2 = .91$; Gabby $R^2 = .76$) as compared to items memorized during the middle of the experiment.

Finally, we also evaluated the choice time the nutcrackers needed to respond to the pictures. For pigeons, this choice time was captured by measuring the latency to the first peck of the

picture. This was done because the spatial location of the first peck to the pictures was highly predictive of final choice. This was also true of the nutcrackers' pecking behavior to the pictures. When examining spatially-directed pecking (pecks greater than 50 pixels from the midline of the picture (Cornelius 96.3% of choices; Gabby 87.7%), the side of the first peck reliably predicted the subsequent choice response 90% of the time (Cornelius 93.1%; Gabby 86.1%). Thus, like pigeons, the nutcrackers seemingly made their choice "decision" by the time of their first peck to the picture. Whereas this choice time measure decreased over the experiment for the pigeons, the nutcrackers, however, showed the opposite pattern (Figure 2D). The first peck choice latency slowly increased from near 1500 ms during the first quintile of the experiment to near 2000 ms by the last quintile. A linear mixed-model analysis modeling choice time as a combination of time during the experiment (in quintiles), accuracy, and stimulus set (i.e., old- or new-item; all as fixed effects; with a random effect of subject; using R package nlme) confirmed this significant effect of time over the experiment, $F(1, 35) = 47.8, p < .001$, partial R^2 for GLMM $R^2_p = 0.49$ (see footnote 1). Accuracy was also a significant predictor of first peck latency $F(1, 35) = 12.2, p = .001, R^2_p = 0.20$, with incorrect responses estimated to be 211 ms slower than correct responses.

Discussion

Clark's nutcrackers exhibited overall lower long-term visual memory capacity than previously established with pigeons. The estimated asymptotic memory capacity for the two nutcrackers (≈ 530) was less than that found for pigeons (≈ 830 ; see Figure 1; cf. Cook et al., 2005). Even with measurement error, the nutcrackers' long-term pictorial memory is at best the same or smaller than pigeons' when tested almost identically. Therefore, the nutcrackers' extraordinary caching and recovery abilities are not due to having a larger generalized memory

capacity. If these behaviors were supported by general-purpose memory, their capacity to learn picture-response associations should have measurably exceeded those of a non-caching bird, like the pigeon. If anything, the pigeons were slightly better. This result offers further support for the specialized memory hypothesis, in which the cache recovery ability of this bird species is rooted in a memory system that has evolved differentially for storing spatial information relevant to its niche.

Beyond comparable visual memory capacities, the results in Figure 2 point to other similarities in the long-term memory systems of these two avian species. Both species show evidence of memory decline, with more recently seen stimuli supporting better accuracy than stimuli with larger test-retest lags. Besides this recency effect, both bird species also show recency and primacy learning effects, where the earliest and latest sets learned generally support better performance than those learned in between. Additionally, neither species required additional time to learn new sets of pictures despite increasing memory loads of old items. Given the nature of caching and recovering seeds, we thought the nutcrackers might show a greater degree of “one-trial learning.” The nutcrackers’ average of 17.3% of stimuli learned in one trial, however, is not better than the pigeons’ 20.8%. These shared properties are good evidence that the memory systems tapped by this task operate in fundamentally similar ways. One possible difference was reflected in choice reaction time. For the nutcrackers, RT increased with extended testing, whereas for the pigeons (and primates), this measure decreased over testing. Whether this reflects differences in memory search mechanisms or other aspects of the task, such as automaticity or procedural learning, is an open question.

Although consistent with the specialized memory hypothesis, considering other reasons why the nutcrackers were not better than the pigeons is sensible. One possibility is that the pigeons’

response (head poke) was separated from the stimulus presentation apparatus (touchscreen), which could support stronger spatial representations. Additionally, the pigeons were relatively young and experimentally naïve, in contrast to the nutcrackers who had been in the laboratory for 12 years. Beyond possible cognitive effects of aging, one study has shown that chickadees' hippocampus size (and therefore presumably function) diminishes with less than two months of captivity (Tarr, Rabinowitz, Imtiaz, & DeVogd, 2009). In the absence of any natural caching behavior during their captivity (during which, however, they participated in spatial memory experiments), our nutcrackers' capacity for memorizing large amounts of information, visual or not, might have diminished. Another possibility lies in the task. Because the stimulus information is spatially irrelevant and the choice outputs are spatially redundant and highly repetitive, the spatial parts of the task are not as varied as during caching in the wild. When caching, contexts and sequences may aid visual memory for cache locations, and the variability of spatial response locations may greatly reduce proactive interference (Lewis & Kamil, 2006; Olson et al., 1995). Finally, nutcrackers choose their caching locations in the wild, which may result in a "generation effect" that boosts memory (Kornell & Terrace, 2007; Slamecka & Graf, 1978). These factors were unavailable here. Perhaps by varying or providing more spatial response outputs or different encoding contexts the nutcrackers might have exhibited more robust and generalized visuo-spatial memory abilities. Of course, the same would hold for the pigeons, who shared these same potential disadvantages.

Nonetheless, this evidence indicates that the archetypal caching species' memory does not rival a common, non-caching bird species'. In comparing the four species now tested within this same memory task (humans, baboons, pigeons, and nutcrackers), the basic operation of their retention mechanisms seems substantially conserved. Despite millennia of separate and divergent

evolution, the mechanisms of visual information retention in each species seems to reflect the common operation of a large durable memory system that can be searched in parallel, with the most frequently repeated or most recent items being best retained. The only clear difference is that the two primate species have a several-fold larger pictorial memory capacity than the two avian species.

These findings contribute to the ongoing debate about the nature of human and nonhuman animal intelligence. Although definitions of intelligence vary, the results indicate that long-term memory capacity is not strongly related to complex cognition. Presumably, a larger memory store might permit greater retention of more experience and information and allow the abstract relations among items or subsets of items to be discovered or connected. There is wide support for corvids having more cognitive flexibility than pigeons. For example, corvids consistently solve more complex problems in the laboratory than pigeons (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007; Magnotti et al., 2015). The same is true in comparisons of human and baboon problem solving. Yet as measured in the current memory task, neither of these more “advanced” problem-solving species exhibited dramatically greater memory capacity than its less “advanced” brethren. This suggests that problem solving, cognitive flexibility, and intelligence resides elsewhere than in the long-term memory organization of the avian and primate nervous systems.

Footnote 1: Proper effect sizes for linear mixed effect models are currently an active area of applied research. We used the marginal R^2_{GLMM} , and report the ratio of the factor's variation accounted for (determined by dropping it from the model) to sum of the factor's variation and the model's unexplained variation. This parallels the method of computing eta-squared in traditional ANOVA analyses.

References

- Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, *38*(3), 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. (2002). Spatial and social cognition in corvids: An evolutionary approach. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 129-133). Cambridge, MA: MIT Press.
- Basil, J. A., Kamil, A. C., Balda, R. P., & Fite, K. V. (1996). Differences in hippocampal volume among food storing corvids. *Brain, Behavior & Evolution*, *47*(3), 156-164.
- Binet, A., Simon, T., & Terman, L. M. (1980). *The development of intelligence in children*. Nashville, Tenn.: Williams Printing Co.
- Bitterman, M. E. (1975). The comparative analysis of learning. *Science*, *188*(4189), 699-709.
doi:10.1126/science.188.4189.699
- Bluff, L. A., Weir, A. A. S., Rutz, C., Wimpenny, J. H., & Kacelnik, A. (2007). Tool-related cognition in new Caledonian crows. *Comparative Cognition & Behavior Reviews*, *2*, 1-25. doi:10.3819/ccbr.2008.20001
- Capaldi, E. A., Robinson, G. E., & Fahrback, S. E. (1999). Neuroethology of spatial learning: The birds and the bees. *Annual Review of Psychology*, *50*(1), 651-682.
doi:10.1146/annurev.psych.50.1.651

- Clary, D., & Kelly, D. M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). *Animal Cognition*, *14*(5), 735-744. doi:10.1007/s10071-011-0408-3
- Clary, D., & Kelly, D. M. (2013). Are Clark's nutcrackers (*Nucifraga columbiana*) able to discriminate knowledge states of human experimenters during an object-choice task? *Evolutionary Psychology*, *11*(3), 147470491301100310. doi:10.1177/147470491301100310
- Clary, D., & Kelly, D. M. (2016). Graded mirror self-recognition by Clark's nutcrackers. *Scientific reports*, *6*, 36459. doi:10.1038/srep36459
- Cook, R. G., & Fagot, J. (2009). First trial rewards promote 1-trial learning and prolonged memory in pigeon and baboon. *Proceedings of the National Academy of Sciences*, *106*, 9530-9533. doi:10.1073/pnas.0903378106
- Cook, R. G., Levison, D. G., Gillett, S. R., & Blaisdell, A. P. (2005). Capacity and limits of associative memory in pigeons. *Psychonomic Bulletin & Review*, *12*(2), 350-358. doi:10.3758/BF03196384
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, *306*(5703), 1903.
- Fagot, J., & Cook, R. G. (2006). Evidence for large long-term memory capacities in baboons and pigeons and its implication for learning and the evolution of cognition. *Proceedings of the National Academy of Science*, *103*, 17564-17567.
- Gardner, H. (1985). *Frames of mind :the theory of multiple intelligences*. New York: Basic Books.

- Gould, K. L., Gilbertson, K. E., Hrvol, A. J., Nelson, J. C., Seyfer, A. L., Brantner, R. M., & Kamil, A. C. (2013). Differences in relative hippocampus volume and number of hippocampus neurons among five corvid species. *Brain, Behavior and Evolution*, *81*(1), 56-70.
- Kornell, N., & Terrace, H. S. (2007). The generation effect in monkeys. *Psychological Science*, *18*(8), 682-685. doi:10.1111/j.1467-9280.2007.01959.x
- Lewis, J. L., & Kamil, A. C. (2006). Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana*. *Journal of experimental psychology. Animal behavior processes*, *32*(4), 407-418. doi:10.1037/0097-7403.32.4.407
- Magnotti, J. F., Katz, J. S., Wright, A. A., & Kelly, D. M. (2015). Superior abstract-concept learning by Clark's nutcrackers (*Nucifraga columbiana*). *Biology Letters*, *11*(5). doi:10.1098/rsbl.2015.0148
- 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*(2), 173-181.
- Shettleworth, S. J. (1984). Natural History and Evolution of Learning in Nonhuman Mammals. In P. Marler & H. S. Terrace (Eds.), *The Biology of Learning: Report of the Dahlem Workshop on the Biology of Learning Berlin, 1983, October 23–28* (pp. 419-433). Berlin, Heidelberg: Springer Berlin Heidelberg.
- Slamecka, N. J., & Graf, P. (1978). The generation effect: Delineation of a phenomenon. *Journal of Experimental Psychology: Human Learning and Memory*, *4*(6), 592-604. doi:10.1037/0278-7393.4.6.592

- Spearman, C. (1904). "General intelligence," objectively determined and measured. *The American Journal of Psychology*, 15(2), 201-292. doi:10.2307/1412107
- Sternberg, R. J. (1977). *Intelligence, information processing, and analogical reasoning :the componential analysis of human abilities*. Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Tarr, B. A., Rabinowitz, J. S., Imtiaz, M. A., & DeVoogd, T. J. (2009). Captivity reduces hippocampal volume but not survival of new cells in a food-storing bird. *Developmental Neurobiology*, 69(14), 972-981. doi:10.1002/dneu.20736
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Monographs: General and Applied*, 2(4). doi:10.1037/10780-000
- Thurstone, L. L. (1924). *The nature of intelligence*. London: Routledge.
- Tomback, D. F. (1980). How nutcrackers find their seed stores. *Condor*, 82, 10-19.
- Tornick, J. K., & Gibson, B. M. (2013). Tests of inferential reasoning by exclusion in Clark's nutcrackers (*Nucifraga columbiana*). *Animal Cognition*, 16(4), 583-597. doi:10.1007/s10071-013-0595-1
- Voss, J. L. (2009). Long-term associative memory capacity in man. *Psychonomic Bulletin & Review*, 16(6), 1076-1081. doi:10.3758/pbr.16.6.1076

Author Notes

This research was supported by grants from the National Eye Institute (#RO1EY022655 - RGC) and the Natural Sciences & Engineering Research Council of Canada #312379-2009 – DK). E-mail: Muhammad.Qadri@tufts.edu. Home Page: www.pigeon.psy.tufts.edu.