

RESEARCH PAPER

Individual and social factors affecting the ability of American crows to solve and master a string pulling task

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Abstract

Crows and other birds in the family Corvidae regularly share information to learn the identity and whereabouts of dangerous predators, but can they use social learning to solve a novel task for a food reward? Here, we examined the factors affecting the ability of 27 wild-caught American crows to solve a common string pulling task in a laboratory setting. We split crows into two groups; one group was given the task after repeatedly observing a conspecific model the solution and the other solved in the absence of conspecific models. We recorded the crows' estimated age, sex, size, body condition, level of nervousness, and brain volume using DICOM images from a CT scan. Although none of these variables were statistically significant, crows without a conspecific model and large brain volumes consistently mastered the task in the minimum number of days, whereas those with conspecific models and smaller brain volumes required varying and sometimes a substantial number of days to master the task. We found indirect evidence that body condition might also be important for motivating crows to solve the task. Crows with conspecific models were no more likely to initially solve the task than those working the puzzle without social information, but those that mastered the task usually copied the method most frequently demonstrated by their knowledgeable neighbors. These findings suggest that brain volume and possibly body condition may be factors in learning new tasks and that crows can use social learning to refine their ability to obtain a novel food source, although they must initially learn to access it themselves.

KEYWORDS

American crow, body condition, brain volume, *Corvus brachyrhynchos*, social learning, string pulling task

1 | INTRODUCTION

Most vertebrates regularly encounter novel situations throughout their lives, and their ability to successfully navigate them directly benefits their survival and fitness (Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole & Quinn, 2011; Wetzel, 2017). Assessing how to acquire and process novel foods is one such challenge faced by many species, particularly generalists. There are many opportunities for individuals from social species to observe conspecific behavior,

and those capable of using information obtained via social learning to improve their foraging efficiency and solve novel problems would have an advantage over those that cannot (Galef & Giraldeau, 2001; Rieucou & Giraldeau, 2011). One way that researchers can tease apart aspects of a species' capacity to decipher novel situations is to measure their ability to solve novel tasks of varying complexities; by modifying this approach to include other conspecifics, researchers can also test whether individuals learn the task by watching others interact with it.

Aside from social learning and information sharing, there are a variety of individual factors that are known to contribute to problem-solving ability, but motivation is perhaps the most overarching factor. An animal's motivation can be affected by hunger and associated body condition; hungry animals will be more motivated and devote more time and attention to a task with a food reward compared to well-fed individuals (Birch, 1945). An animal's temperament can affect its motivation: neophobia, for example, inhibits problem-solving (Benson-Amram & Holekamp, 2012) such that animals with greater degrees of neophobia are more reluctant to approach an unfamiliar object and require additional time before they attempt a novel task compared with bolder individuals (Heinrich, 2000; Heinrich, Marzluff, & Adams, 1995). Age might also affect motivation; juveniles tend to more persistently interact with the task due to playfulness (Vince, 1958), although older animals are more cognitively developed and have amassed experience, which may be applicable to the novel task (Mason & Harlow, 1961).

Large brains are demonstrably advantageous in many species (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016; Deaner, Isler, Burkart, & Schaik, 2007); therefore, brain volume might affect an individual's ability to solve novel problems. Domestic dog breeds (*Canis lupus familiaris*) with larger brains perform better in cognitive tasks (Horschler et al., 2019), although there may be confounding factors stemming from other differences between breeds, such as body size or temperament. Additionally, large-brained guppies (*Poecilia reticulata*) had a higher survivorship than small-brained conspecifics, though this effect was limited to females (Kotrschal et al., 2015), suggesting that an individual's sex may also be a confounding factor when examining the effect of brain size. Alternatively, brain volume may not be as important as other factors; the brain is a complex organ, and aspects such as neuronal density, neuronal counts, or the relative size or complexity of specific circuits within the brain may be better indicators of the advantages that developed brains provide (Healy & Rowe, 2006; Jardim-Messeder et al., 2017; Olkowicz et al., 2016).

Crows and other members of family Corvidae (corvids) are widely regarded as among the most intelligent bird species (Emery & Clayton, 2004; Lambert, Jacobs, Osvath, & Bayern, 2019); many are capable of long-term human facial recognition (Marzluff, Walls, Cornell, Withey, & Craig, 2010), understanding and responding to reward inequity (Wascher & Bugnyar, 2013), assessing risk (Dufour, Broihanne, & Wascher, 2019), tracking and remembering the actions of others (Bobrowicz & Osvath, 2019), manufacturing rudimentary tools (Caffrey, 2000; Hunt, 1996; Shumaker, Walkup, & Beck, 2011; Uomini & Hunt, 2017), and potentially possessing a theory of mind (Bugnyar, Reber, & Buckner, 2016; Clayton, Dally, & Emery, 2007; Ostojic, Shaw, Cheke, & Clayton, 2013, though see Van der Vaart, Verbrugge, & Hemelrijk, 2012). Corvids are also capable of social learning; American crows (*Corvus brachyrhynchos*) learn new dangers and keep track of predators by observing conspecific behavior (Cornell, Marzluff, & Pecoraro, 2011; Marzluff, DeLap, & Haycock, 2015; Swift & Marzluff, 2015), while New Caledonian crows (*Corvus moneduloides*) and common ravens (*Corvus corax*) obtain information

on how to acquire food socially (Heinrich, Marzluff, & Marzluff, 1993; Holzhaider, Hunt, & Gray, 2010; Sierró, Loretto, Szpl, Massen, & Bugnyar, 2019). Crows possess many of the characteristics required for high intelligence: They have high annual survivorship (Kilham, 1990; Marzluff & Neatherlin, 2006), live in fission–fusion social groups (Cornell et al., 2011), and possess a large brain relative to their body size (Marzluff & Angell, 2007; Portmann, 1946). These qualities allow crows to amass and draw upon a great deal of experience (via individual and social learning) over the course of their long lives.

A common behavioral test given to birds to gauge their problem-solving ability is the string pulling task: Out-of-reach food is suspended from a perch by a string, and the subject must devise a method to retrieve it (Jacobs & Osvath, 2015; Thorpe, 1943). There is considerable debate concerning whether birds use insight (here defined as the use of mental visualization to suddenly solve a specific novel task without the incremental progression of trial-and-error learning nor pre-programmed instinctual responses) or other processes, such as operant conditioning or positive reinforcement, to solve the string pulling task (Heinrich, 1995; Heinrich & Bugnyar, 2005; Shettleworth, 2012; Taylor et al., 2010). However, because the task does not resemble anything most birds would encounter in the wild, a naïve bird must learn a new strategy to solve it rather than rely on experience (Jacobs & Osvath, 2015). The most common solution is for the bird to “reach down from the perch, pull up on the string, place the pulled-up loop of string onto their perch, step on the loop with one foot, release the string from the bill, then reach down and pull up more string, etc., so that the food is drawn into reach” (Heinrich, 1995), hereafter referred to as the string pull method. While common ravens are usually able to solve the task using a string pull method on their first try (Heinrich, 1995), American crows typically require training before they can retrieve the food this way, although naïve crows have been observed solving the task by flying up and grabbing the food from the string while airborne (Heinrich, 1999).

Here, we expand on Heinrich's work with American crows by asking which factors (if any) affect the birds' abilities to solve the string pulling task. We wondered if crows: (a) used social learning to aid their ability to solve this novel task and (b) whether individual factors (such as sex, age, motivation, or brain volume) affect the crows' ability to solve the task. Other bird species can learn how to acquire food from novel sources by watching knowledgeable conspecifics (Aplin, Sheldon, & Morand-Ferron, 2013), and American crows have demonstrated that they can acquire novel information by observing the behavior of other crows (Cornell et al., 2011). If crows can use social learning to solve novel tasks, then we predict that crows with a conspecific model will be more successful at solving and learning the task compared to crows without a model. Additionally, we predict that crows with the model will be more likely to adopt the method demonstrated to them by the model. If individual factors influence task performance, we make the following predictions: older, calmer individuals with lower body condition (smaller body mass than expected for a given body size, see Methods below) and larger brain volumes (either absolute or relative to body size) will be more likely to initially solve the task and will master

it in less time compared with younger, nervous individuals with higher body condition and smaller brain volumes.

2 | METHODS

2.1 | Capturing and housing crows

We captured wild American crows as they departed a large communal roost at various locations in Seattle, Bothell, and Woodinville WA. We lured birds from flocks with bread and trapped them using a net launcher. We captured 27 subadult and adult crows (16 males and 11 females), which we categorized as being in their second year of life ($n = 15$ subadults) or older ($n = 12$ adults) by a combination of plumage color and feather wear (Emlen, 1936), as well as coloration of their mouth lining (fully black in birds older than two years). Due to potential differences in behavior and cognitive development, we released birds in their first year of life immediately upon capture. We caught birds outside of the breeding season and held them for several months each of three years (10 crows from Feb. to Mar. 2016, 9 from Oct. to Dec. 2017, and 8 from Sep. to Nov. 2018).

We kept captured crows in a protected outdoor aviary at the University of Washington, Seattle. The crows were housed individually and assigned to each cage randomly. The aviary contained 10 adjacent cages separated by wire mesh; crows could see and hear their immediate neighbors (and potentially birds beyond their immediate neighbors' cages) but could not leave their own cage. Because the cages were arranged in a line, the birds at each end of the aviary ($n = 2$ for each year, $N = 6$ total) only had a single neighbor, but the remaining crows all had two neighbors ($N = 21$). Each cage measured 1.8 m wide \times 2.1 m tall \times 2.4 m deep and contained three perches, each approximately 1.2–1.5 m above the ground. The perch configuration was identical for each cage, and each bird was given the task within their own cage.

Crows were fed once per day and had full access to their food bowl for at least 6 hr. The 2016 group of crows was given a large amount of food immediately after participating in tasks within experiments described below, and their uneaten food was not removed until the following morning. Because half the birds in the 2016 group never solved the task (see Results below), we modified the food availability during subsequent years; the 2017 and 2018 groups received less food, were not fed until 2–3 hr after their task was completed, and had any uneaten food taken away later that evening. Theoretically, the 2017 and 2018 birds were more highly motivated by hunger to solve the tasks we describe compared with the 2016 group.

2.2 | String pulling task

We suspended a preferred food item (a small piece of fried chicken) from the center of the perch nearest to the cage door using sisal rope twine. Even at full string length, the food remained approximately 1 m above the ground and 50 cm away from the cage walls.

We gave crows the task within their cage, and they had the remainder of the day to solve it. We removed the food from unsolved tasks the following morning. When the task was first introduced to a crow, the food was suspended 45 cm below the perch; we called this the “Naïve Full” stage. The purpose of the Naïve Full stage was to determine whether and how crows can solve the task at full length without any prior training. The amount of time Model crows (defined below) spent in the Naïve Full stage varied from 3 days (2016 and 2017 cohorts) to 7 days (2018 cohort). Observer crows in 2016 spent up to 16 days in this stage, but this was reduced to 7 days in 2017 and 2018. After the Naïve Full stage was completed, the string length was shortened so that the food was tied directly to the perch (string length 0 cm) within easy reach of the crow; this was the start of the “Learning” stage. During this stage, we lengthened the string by 7.5 cm each day if the crow previously succeeded in retrieving the food and reduced the string length by 7.5 cm each day if the crow failed. Once the string length reached 15 cm, the crows could not directly reach the food. We considered a crow to have mastered the task when it succeeded consistently enough to increase the string length back to 45 cm (minimum six successes); all subsequent trials with the string back at full length were part of the “Mastery” stage.

We assigned crows to a role as Model ($n = 13$) or Observer ($n = 14$) at random based on their cage number (odd vs. even). We immediately gave the Model group crows access to the task. The Observer crows did not initially have access to the task but could freely observe both of their Model neighbors as they interacted with the task (Observer crows housed in an end cage were only directly adjacent to a single Model, $n = 4$). Crows in the Observer group were only given access to the task after at least one of their Model neighbors had solved it seven times after reaching the Mastery stage.

The crows utilized a variety of strategies to solve the task, which we combined into three broad categories: attacking string, food intercept, and string pulling (Figure 1). Each of the three broad categories includes several specific methods, which we list from most to least common. Attacking string occurs when the crows retrieve the food by knocking it to the ground and includes the specific methods “string break,” where the crow breaks the string at the base of the perch; and “shake free,” where the crow's efforts to break/manipulate the string cause the food to slip free of the knot and fall to the ground. Food intercept occurs when the crow intercepts the hanging food from midair without interacting with the string and includes the specific methods “fly up and grab,” where the crow starts on the ground and flies up to the food; “drop down and grab,” where the crow starts at the perch and intercepts the food as it drops to the ground; and “cling and grab,” where the crow clings to the side of the cage and jumps outward toward the food. String pulling occurs when the crow pulls the hanging food toward itself and includes the specific methods “pull, step, pull,” where the crow string pulls while remaining stationary; “side pull,” where the crow string pulls while moving laterally along the perch; and “swing and catch,” where the crow manages to swing the food within reach. During the beginning of the Learning stage, the string length was short enough (<15 cm) that the crows could

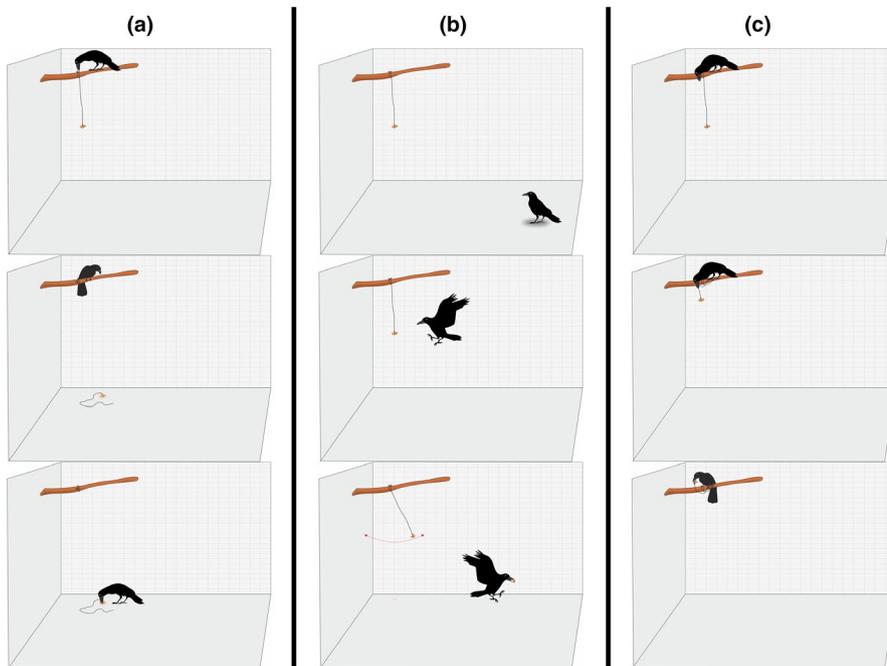


FIGURE 1 Illustration of the three general methods used by the crows to solve the string pulling task: (a) attacking string, (b) food intercept, and (c) string pulling [Colour figure can be viewed at wileyonlinelibrary.com]

directly grab the food from the perch—we called this the “within reach” method. Because this method was only possible for a limited amount of time and required relatively little cognitive ability to solve, we omitted it from all analysis which examines the methods used. Because they were wild caught, the crows were never tame enough to attempt the task while any experimenters were present, so we determined each crow's method of solving the task by reviewing video from a surveillance system.

2.3 | Individual measures

In addition to a crow's role as Model or Observer, we measured the following attributes of each bird: age (1- to 2-year-old = “sub-adult,” older = “adult”), body condition, culmen length, level of nervousness, sex, and brain volume (both absolute and relative to body size). We calculated the crows' body condition ($n = 26$) by extracting the residuals from a regression of their body weight upon capture (although see Discussion below for shortcomings to this method) against their culmen length (mm from the distal tip of the bill to the base of the feathers, $n = 26$). We determined each bird's level of nervousness by standing 2 m away from each bird's cage while staring at a fixed point within the cage (not at the crow) and counting the bird's movements for 60 s. We assigned a numerical value based on the bird's perceived urgency to each move; walking along the perch = 0.5, while flying/hopping to another perch = 1. We obtained two such measurements for each bird (the first within two weeks of capture and the second within two weeks of release) and averaged them.

To determine the sex of the crows, we extracted approximately 20 μ l samples of blood from each bird via the brachial artery and stored them at -80°C . We used a QIAGEN[®] DNeasy[®] Blood &

Tissue Kit to isolate genomic DNA from each blood sample and then amplified the target genes (CHD1-W and CHD1-Z) using polymerase chain reaction (PCR). We conducted agarose gel electrophoresis on the PCR product; males contain two Z chromosomes and produce a single band in the gel between 400 and 450 bp, whereas females contain a Z and a W chromosome and therefore produce an additional band in the gel between 300 and 325 bp (Griffiths, Daan, & Dijkstra, 1996).

As part of a related experiment, we imaged all but two crows ($n = 25$) in a Siemens Inveon PET/CT system, and we used the resulting CT images to calculate crow total brain volume (Figure 2). We anesthetized (isoflurane) crows and secured them to a multimodality bed before conducting a 15 min microPET scan, followed by a CT scan in the docked and coregistered microCT scanner. The CT field of view was 7.9 cm \times 13.3 cm and included the entire brain with a slice thickness of approximately 0.1 mm. We used open-source DICOM viewer Horos version 3.2.1 (Horos, 2019) to analyze the CT images and calculate brain volume. Brain segmentation was done using Horos's threshold-based 2D region of interest (ROI) utility on approximately 40% of the relevant slices. We edited these ROIs by hand before the software added interpolated ROIs on the missing slices. The generated ROIs were then inspected before we calculated the final volume (cm^3) with the built-in utility. As some of the brain segmentation is done manually and is thus subject to user bias, two researchers (L.T.P and A.L.L) independently analyzed several of the CTs; their findings differed by a very small amount ($0.82\% \pm 0.62\%$, $n = 11$); thus, we discounted user bias as minimal. To account for the allometric association of brain volume to body size (Figure 3), we extracted the residuals from a regression of brain volume and culmen length ($n = 24$) and used these residuals as a measure of relative brain volume during analysis in addition to raw absolute brain volume.

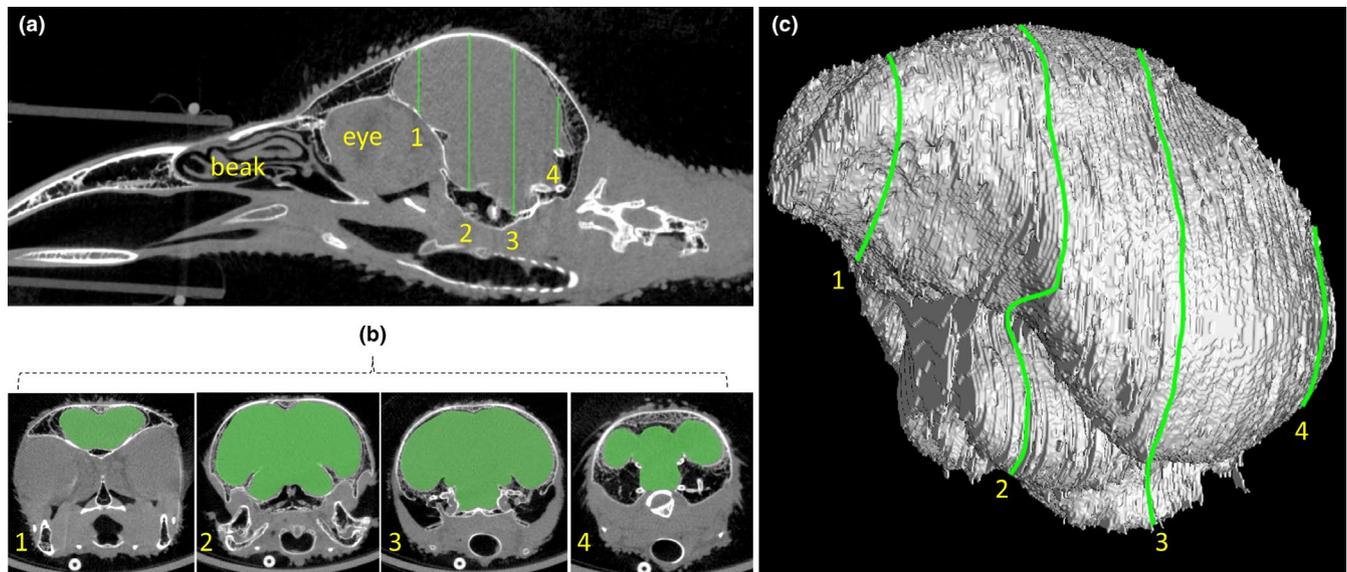


FIGURE 2 DICOM image output from CT scan of a crow's head. For all viewpoints, the same regions of interest (indicated by numbers) are highlighted in green. (a) Medial slice of head from sagittal viewpoint. (b) Sample slices from axial viewpoint progressing from anterior to posterior position within head. (c) 3D model of brain volume generated by the regions of interest from approximately 260 axial slices [Colour figure can be viewed at wileyonlinelibrary.com]

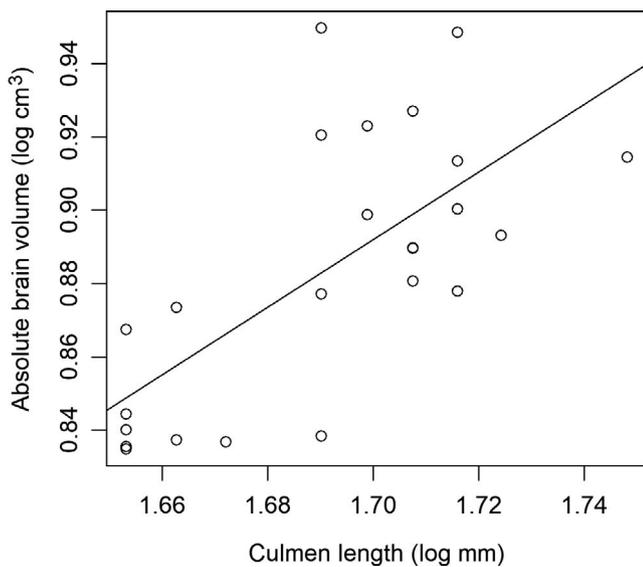


FIGURE 3 Relationship between log-transformed absolute brain volume (cm^3) and body size (represented by culmen length, mm) of captive crows

2.4 | Analyses

We conducted all statistical analyses using RStudio version 1.0.136 (RStudio Team, 2016). Because we examined eight different variables using a limited sample size, we constructed models using each single variable (along with an accompanying null model) and used AICc to determine which were most consistent with the data. We considered models to be competitive if they were within 2 AICc of the model with lowest AICc (Burnham & Anderson, 1998). As we obtained many variables which could be correlated with each other (such as sex and culmen length; Clark, James, & Morari, 1991), we tested correlation via

Pearson's r . We used generalized linear models to compare the individual factors affecting the crows' likelihood of solving the task during the Naïve Full stage (limiting this analysis to the first three days to account for the variable amount of time the different groups spent in this stage) and the time it took the successful crows to reach Mastery (progress fully through the Learning stage). We examined whether the methods used by the crows and those used by their neighbors affected their likelihood of success with Fisher's exact tests.

We examined the congruency in methods used by the Models and Observers' by treating their similarity as a binomial and as a continuous variable. Because most Observer crows had two Model neighbors directly adjacent to them, which may have demonstrated different or the same methods, we considered the Observer to have copied a Model if it adopted either demonstrated method as its own. We conducted a binomial test (single tail because we predicted the observers would copy their neighbors with assumed probability 0.333 because there were three potential methods) to determine whether the Observers and the Models used the same primary method more often than expected by chance. We assumed the most frequently used method was the primary method for this test. To account for all methods used by Observers and Models, we combined each of the three general methods' proportion of use by both the Observer and its Model to create a continuous "difference index" using the following equation:

$$\frac{|\alpha_{\text{Obs AS}} - \alpha_{\text{Mod AS}}| + |\alpha_{\text{Obs FI}} - \alpha_{\text{Mod FI}}| + |\alpha_{\text{Obs SP}} - \alpha_{\text{Mod SP}}|}{2}$$

where AS, FI, and SP stand for the three general methods (attacking string, food intercept, and string pulling, respectively) and α_{Obs} and α_{Mod} are the proportion of successful trials where the Observer or Model used that method to solve the task. The index returns a value

TABLE 1 Correlation matrix of the variables we obtained from the crows

	Relative brain volume (n = 24)	Absolute brain volume (n = 25)	Body condition (n = 26)	Culmen length (n = 26)	Nervousness (n = 27)	Sex (n = 27)	Age (n = 27)
Absolute brain volume (n = 25)	$r = .74$ $t_{22} = 5.23$ $p < .001$						
Body condition (n = 26)	$r = -.043$ $t_{22} = -0.20$ $p = .84$	$r = .005$ $t_{22} = 0.025$ $p = .98$					
Culmen length (n = 26)	$r = .00017$ $t_{22} = 8.2 \times 10^{-4}$ $p = .99$	$r = .67$ $t_{22} = 4.21$ $p < .001$	$r < .001$ $t_{24} < 0.001$ $p = 1$				
Nervousness (n = 27)	$r = .29$ $t_{22} = 1.44$ $p = .16$	$r = .14$ $t_{23} = 0.67$ $p = .51$	$r = -.51$ $t_{24} = -2.92$ $p = .007$	$r = -.038$ $t_{24} = -0.19$ $p = .85$			
Sex (n = 27)	$t_{22} = 1.05$ $p = .30$	$t_{23} = 4.86$ $p < .001$	$t_{24} = 0.25$ $p = .80$	$t_{24} = 8.13$ $p < .001$	$t_{25} = 0.10$ $p = .92$		
Age (n = 27)	$t_{22} = 0.36$ $p = .72$	$t_{23} = 0.91$ $p = .37$	$t_{24} = -0.007$ $p = .99$	$t_{24} = 0.75$ $p = .46$	$t_{25} = -0.16$ $p = .87$	$t_{25} = 0.08$ $p = .93$	
Social role (n = 27)	$t_{22} = -1.55$ $p = .14$	$t_{23} = -1.90$ $p = .07$	$t_{24} = -0.09$ $p = .93$	$t_{24} = -1.29$ $p = .21$	$t_{25} = -0.51$ $p = .62$	$t_{25} = -1.85$ $p = .08$	$t_{25} = 0.93$ $p = .36$

Note: We calculated Pearson's correlation coefficient when comparing two continuous variables and reported t-score and p-values for all comparisons for all variables. Notable correlations are bolded.

between 0 and 1, where 0 means the two birds solved the task using the exact same proportion of methods, and 1 means the two birds had absolutely no overlap in methods used. For example, if the Observer and Model both exclusively used the food intercept method, the difference index would be $\frac{|0-0|+|1-1|+|0-0|}{2} = 0$, which reflects that both birds are perfectly aligned in method choice. If the Observer evenly preferred the food intercept and string pulling methods while the Model evenly preferred the attacking string and food intercept methods, the difference index would be $\frac{|0-0.5|+|0.5-0.5|+|0.5-0|}{2} = 0.5$, showing that there was 50% overlap in the methods used by the two birds. If the Observer exclusively used attacking string and the Model evenly used food intercept and string pulling methods, the difference index would be $\frac{|1-0|+|0-0.5|+|0-0.5|}{2} = 1$, demonstrating that the two birds used completely different methods. Although the index does not have a critical threshold for statistical significance (such as <0.05 for p -value) and tends to bias toward 1 (minor differences in the sample size of Observers and Models can only increase the score rather than decrease it), we present the difference index as a relative measure of method choice similarity instead of statistical tests of individual Model and Observer congruence (e.g., chi square) because the repeated choice of methods by a particular bird is not independent of one another.

Because it is possible that the Observers copied the exact method most commonly used by their Model neighbors to solve the task, we examined the use of specific, rather than general, methods using the six different methods the crows could use to solve the task during the Mastery stage (none of the crows used the cling and grab or swing and catch specific methods during this stage). As above, we calculated difference indices for the use of exact methods by Observers and Models and used an exact binomial test to determine whether the crows are copying their neighbors. To reflect the six possible methods, we set the probability that crows copied their models due to chance to be 0.167.

2.5 | Ethical note

We captured, housed, and tested all crows (including PET/CT scans) in accordance with the Institutional Animal Care and Use Committee of the University of Washington (IACUC; protocol number 3077-01), Federal Fish and Wildlife Permit MB761139-0, and State of Washington Scientific Collection Permit 14-010. All were released back into the wild at the conclusion of the study.

3 | RESULTS

3.1 | General

Our captive crows varied in size (culmen length: $\bar{X} + SD = 49.5 + 3.08$ mm, $n = 26$), body condition ($0.00 + 38.15$ g, $n = 26$), level of nervousness ($29.11 + 11.99$ movements/min, $n = 27$), and absolute brain volume (Figure 3; $7.68 + 0.64$ cm³, $n = 25$), although compensating for body size reduced the variation in brain

volume somewhat (relative brain volume: $0.00 + 0.48$ cm³, $n = 24$). The level of nervousness displayed by the crows did not significantly change over time (first measure: $29.74 + 13.14$ movements/min, second measure: $28.48 + 13.62$ movements/min, $t_{26} = 0.55$, and $p = .59$). The crows were well fed during their time in captivity and gained a significant amount of weight by the time they were released (capture: $400 + 46.16$ g, release: $442.4 + 59.77$ g, $t_{26} = -5.67$, and $p < .001$). While the Model birds were given the task within eight days of capture ($1.45 + 2.93$ days), the Observers had to wait several weeks ($19.07 + 5.21$ days) before they were given the task.

Our calculated crow brain volumes were larger than the endocranial volumes reported by Iwaniuk and Nelson (2002) (endocranial volume: $7.17 + 0.55$ cm³), yet smaller than the brain volumes reported by Mlikovsky (2003) (endocranial volume: 8.7 cm³, SE not provided). These discrepancies are likely due to differences in measurement technique and demonstrate that our virtual measurements are comparable to physical measurements of the brain.

Among the eight variables we obtained from the crows, we observed five cases where variables were strongly correlated, and two additional cases where there was notable correlation (Table 1). Absolute brain volume and relative brain volume are, unsurprisingly, highly correlated ($t_{22} = 5.23$, $p < .001$). Three of the variables (absolute brain volume, culmen length, and sex) are closely tied to the size of the bird and are all highly correlated with one another as a result; males have larger absolute brain volumes ($t_{23} = 4.86$, $p < .001$) and culmen lengths ($t_{22} = 8.13$, $p < .001$) than females, and birds with long culmen lengths had correspondingly large brains ($t_{22} = 4.21$, $p < .001$). Additionally, birds with poorer body condition were more nervous than those in good condition ($t_{24} = -2.92$, $p = .007$). The Model group contained more males ($t_{25} = -1.85$, $p = .08$) and had somewhat larger absolute brain volumes ($t_{23} = -1.90$, $p = .07$) than the Observer group, although this was due to chance as we randomly assigned birds to their cages (and therefore, social role) prior to determining their sex and brain volume.

3.2 | Initial access to task

Many of the crows initially struggled to obtain the food hung at full length from the perch; only nine Models and four Observers solved the task within the first three days. However, eight additional crows learned to solve the task after the first three-day period; three Observers given additional time in the Naïve Full stage solved it, and one Observer and four Models solved it during the Learning stage. In total, 21 of 27 birds were successful. The crows became increasingly successful at solving the task as they gained experience with it; all successful birds were nearly twice as likely to solve the task on any given day during the Mastery stage than during the Naïve Full stage (Naïve Full probability of solving: $\bar{X} + SE = 0.47 + 0.9$, Mastery: $0.91 + 0.04$, $t_{20} = 4.82$, $p < .001$). Although almost all crows in the 2017 and 2018 cohorts learned to solve the task, only five of the crows we captured in 2016 solved it (all from the Model group). These birds had better overall body condition upon capture than both the 2017 ($t_{23} = 3.32$, $p = .003$) and the 2018 ($t_{23} = 3.35$, $p = .003$) cohorts.

Almost all the crows that succeeded during the entire Naïve Full stage ($n = 16$) used an attacking string ($n = 5$) or food intercept ($n = 9$) method when they solved the task for the first time. The crows' social role significantly affected their method choice during this stage (Fisher's exact test, $p = .037$), with crows in the Model group preferring food intercept while Observer crows preferred the other two methods (Table 2). Contrary to our expectations, three crows from 2018 used a string pull method during the Naïve full stage; one male Model switched to this method after first solving the task using food intercept, and two female Observers used this method to solve the task for the first time. Afterward, all three birds immediately adopted string pulling as their primary method. Although one of the females had a notably small culmen (46 mm) and poor body condition (38 g lower than expected, given culmen length), the remaining attributes of the three string pullers were within one standard deviation of the mean for the rest of the crows.

The most commonly used method by the birds in the Model group did not significantly affect their Observer neighbors' likelihood of solving the task during the entire Naïve Full stage (Fisher's exact test; $p = .48$; Table 3), nor did it influence the general method used by the successful Observers (Fisher's exact test; $p = 1.0$; Table 3). Even after lumping the "copy/did not copy" data from all four possibilities for methods demonstrated by their neighbors (Table 3) into a single category, we found that successful Observers were not significantly more likely than expected by chance to adopt a method used by their Model neighbors (Exact binomial test, $p = .54$).

Of the eight individual variables we modeled, social role best accounted for the likelihood of a crow succeeding during its first three days with the task, although it only garnered 42% of the weight of evidence and was not substantially better than the null model (Table 4). Specifically, the crows in the Observer group were *less* likely than their neighbors to solve the task during this stage (Models: $\bar{X} = 0.75$ likelihood success, Observers: 0.33 likelihood success, $z_{23} = -1.98$, $p = .048$). This relationship persisted, albeit not as intensely, even after we removed the 2016 group to control for the abysmal performance of that year's Observers (Models: 0.88, Observers: 0.44, $z_{16} = -1.72$, $p = .086$).

3.3 | Learning and mastery

After the Naïve Full stage ended, we trained the crows to consistently solve the task using a string pulling method (time required: $\bar{X} + SE = 7.9 + 0.73$ days). Of the eight individual variables we modeled, social role, absolute brain volume, relative brain volume, and body condition best explained the number of days it took for a successful

TABLE 2 The most common method used by crows in each social group that solved the task during the Naïve Full stage

Primary method choice during Naïve Full stage	Model	Observer
Attacking string	1	4
Food intercept	7	1
String pulling	1	2

crow to progress through the Learning stage and reach the Mastery stage (Table 5), although none of them were significant at the $p = .05$ level, nor substantially better than the null model. Specifically, crows in the Model group, birds with larger brain volumes (both absolute and relative to their body size), and those with good body condition tended to reach Mastery in fewer days than Observers, small-brained birds, and those with poor body condition (Figure 4). The effect was strongest for social role; Observers on average required an additional 2.5 days more than the Models ($z_{18} = 1.879$, $p = .06$). Absolute brain volume was also notable; gaining 1 cm³ of brain volume decreased the mean time required to master the task by 1.88 days ($z_{18} = -1.746$, $p = .08$). The models for relative brain volume (gaining 1 cm³ relative to body size decreased time required by 1.77 days; $z_{18} = -1.379$, $p = .168$) and body condition (gaining 1 g decreased time required by 0.02 days; $z_{18} = -1.286$, $p = .199$) were weaker and appear to be primarily driven by a few individuals (three small-brained birds and three poor body condition birds, respectively, see Table S1). The only competitive multivariate models combined social role/body condition and absolute brain volume/body condition, but neither performed the single variate models (Table 5). Altogether, the six competitive models cumulatively garnered 52% of the weight of evidence, but none were substantially better than the null model (Table 5).

Many of the crows showed flexibility in method preference; a significant number of birds changed their most frequently used method after they progressed out of the Naïve Full stage (Fisher's exact test; $p = .013$), with more than half of the crows adopting the string pulling method as their primary method overall (Figure 5). Although the methods employed by the Model birds did not affect the likelihood that neighboring Observers would succeed overall (Fisher's exact test; $p = .5$; Table 6), those that did succeed were significantly more likely to adopt their Model neighbor's primary method as their own (Exact binomial test, $p = .003$; Table 6) after they entered the Mastery stage. This effect persisted even after removing the two Observers that were exposed to two differing favorite methods by their neighbors (Exact binomial test, $p = .018$) to account for them having a greater probability of copying one of the demonstrated methods by chance alone.

During the Mastery stage, six of the eight successful Observers used nearly identical general methods as one of their Model neighbors to solve the task (difference index < 0.25, Table 7). All but two successful Observers most frequently used a string pull method, but the two that did not (Observer crows 4 and 5) closely matched their neighbors' use of a food intercept method (Table 7), even though our training emphasized string pulling and Observer crow 4's other neighbor (Model crow 3) overwhelmingly solved via string pulling. Another Observer (crow 3) used a wider variety of methods and had a difference index of nearly 0.5 with both of its neighbors, even though all three crows in that group most frequently solved with a string pull method. Only one Observer avoided using the same method as its neighbor (Table 6); that same bird (crow 8) was one of the three crows that began using a string pull method to solve the task prior to receiving any training, and it continued to exclusively use that method during the Mastery stage, whereas its Model only used attacking string or food intercept methods (difference

TABLE 3 A comparison of the most common methods used by the Observer crows' neighbors during the entire Naïve Full stage, and whether the Observer crows' most commonly used method was the same or different as their neighbors' during this stage

Naïve full stage only	Solved task		
	Same method as neighbor	Different method from neighbor	Failed to solve task
Neighbors primarily used different methods	1	1	3
Neighbor(s) primarily used String pulling	1	2	2
Neighbor(s) primarily used Food Intercept	0	2	1
Neighbor(s) primarily used Attacking string	0	0	1
Total	2	5	7

Note: During the Naïve Full stage, the Observers' primary method was identical to their first method. If the neighbors used different methods, we checked whether the Observer used either of the two modeled methods.

TABLE 4 Individual variable model selection for a crow's likelihood of succeeding during the first three days after gaining access to the task ($n = 24$). Intercept, coefficient, and *SE* estimates are given in logit scale

Model	Δ AICc	W_i	Intercept \pm SE	Coefficient \pm SE	p
Social role (model/observer) ^a	0.00 ^b	0.40	1.10 \pm 0.67	-1.79 \pm 0.91	.048
Null model	1.95	0.15	0.17 \pm 0.41		
Body condition	2.44	0.12	0.14 \pm 0.43	-0.016 \pm 0.01	.204
Relative brain volume	3.48	0.07	0.18 \pm 0.42	+0.83 \pm 0.93	.371
Sex (female/male) ^a	3.79	0.06	-0.22 \pm 0.67	+0.63 \pm 0.85	.461
Absolute brain volume	3.83	0.06	-3.37 \pm 5.07	+0.46 \pm 0.66	.480
Age (adult/subadult) ^a	4.17	0.05	0.34 \pm 0.59	-0.34 \pm 0.82	.682
Nervousness	4.29	0.05	-0.08 \pm 1.19	+0.008 \pm 0.04	.822
Culmen	4.33	0.04	-0.10 \pm 6.67	+0.005 \pm 0.14	.969

Note: Best-fit model and competing models ($<2 \Delta$ AICc) are highlighted in gray.

^aBinomial variable coefficients are for Observer (social role), Male (sex), and Subadult (Age).

^bAICc = 33.34

index = 1, Table 7). In addition to matching the general methods demonstrated by their neighbors, Observers were also more likely than expected by chance to copy one of the six specific methods modeled by their neighbors (Table S2). Five of the eight successful Observers copied the most frequently demonstrated specific method (Table S2; Binomial $p = .005$). Five Observers were at least 50% similar to their neighbors in their choice of method and three mirrored their neighbors nearly perfectly (difference index < 0.15 ; Table S3). One Observer (Observer crow 2) had two Models that used different specific methods (Model crow 1 used pull, step, pull, and Model crow 2 preferred side pull; Table S3) and that Observer utilized both demonstrated methods to solve the task.

4 | DISCUSSION

While multiple studies have examined the role that cultural transmission, experience, and other individual factors play in an individual's ability to solve novel tasks (Beck, 1973; Holzhaider et al.,

2010; Jacobs & Osvath, 2015; Roth, LaDage, & Pravosudov, 2010; Tomasello, Davis-Dasilva, CamaK, & Bard, 1987; Von Bayern, Heathcote, Rutz, & Kacelnik, 2009), fewer studies have simultaneously examined which of multiple factors best determine an individual animal's ability to solve such a task (though see Cole, Cram, & Quinn, 2011 and Papp, Vincze, Preiszner, Liker, & Bókony, 2015). Here, we expand on Heinrich's, 1999 research on American crows by examining which individual and social factors in a long-lived, social animal have the greatest impact on their ability to solve a string pulling task.

4.1 | Observers less motivated than models

Contrary to our predictions, crows that observed their neighbors master a task were not more likely to initially solve the task and took longer to master it than did crows without access to such information. The Observers performed measurably worse than the birds in the Model group.

TABLE 5 Model selection for time required for a successful crow to progress through the Learning stage and reach the Mastery stage ($n = 19$)

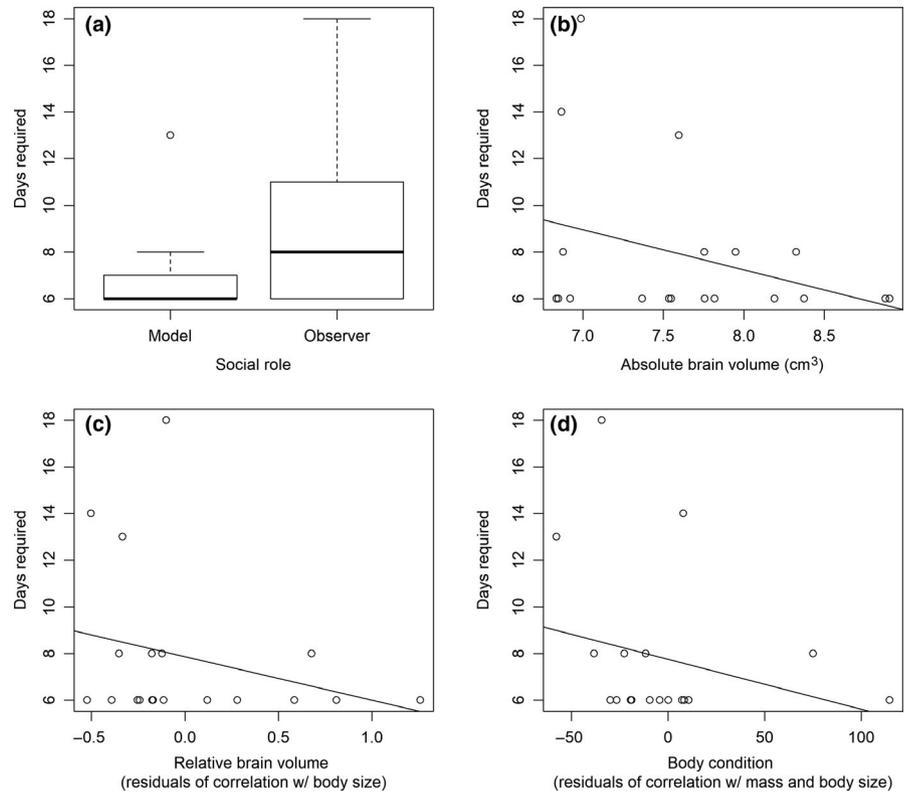
Model	Δ AICc	W_i	Intercept \pm SE	Coefficient 1 \pm SE	p	Coefficient 2 \pm SE	p	Coefficient 3 \pm SE	p	Coefficient 4 \pm SE	p
Social role ^a	0.0 ^b	0.15	1.93 \pm 0.11	0.31 \pm 0.16	.060						
Abs. brain volume	0.35	0.12	3.78 \pm 0.98	-0.23 \pm 0.13	.081						
Null model	0.96	0.09	2.06 \pm 0.08								
Rel. brain volume	1.47	0.07	2.06 \pm 0.08	-0.26 \pm 0.19	.168						
Body condition	1.71	0.06	2.04 \pm 0.08	-0.003 \pm 0.002	.199						
Social role ^a + body condition	1.79	0.06	1.93 \pm 0.11	0.28 \pm 0.17	.09	-0.002 \pm 0.002	.31				
Abs. brain volume + body condition	1.85	0.06	3.64 \pm 0.98	-0.21 \pm 0.13	.10	-0.003 \pm 0.002	.26				
Sex ^a	2.03	0.05	2.17 \pm 0.12	-0.20 \pm 0.16	.229						
Culmem	2.04	0.05	3.71 \pm 1.37	-0.034 \pm 0.028	.230						
Social role ^a + abs. brain volume	2.05	0.05	3.01 \pm 1.21	0.21 \pm 0.21	.28	-0.14 \pm 0.15	.37				
Social role ^a + rel. brain volume	2.24	0.05	1.95 \pm 0.11	0.26 \pm 0.18	.15	-0.16 \pm 0.20	.44				
Rel. brain volume + body condition	2.43	0.04	2.04 \pm 0.08	-0.26 \pm 0.19	.16	-0.003 \pm 0.002	.18				
Age ^a	2.98	0.03	2.01 \pm 0.11	0.12 \pm 0.16	.480						
Abs. brain volume + rel. brain volume	3.19	0.03	3.67 \pm 1.52	-0.21 \pm 0.20	.29	-0.03 \pm 0.29	.93				
Nervousness	3.43	0.03	2.02 \pm 0.23	0.001 \pm 0.007	.845						
Social role ^a + rel. brain volume + body condition	4.25	0.02	1.95 \pm 0.11	0.22 \pm 0.18	.23	-0.18 \pm 0.20	.38	-0.003 \pm 0.002	.28		
Social role ^a + abs. brain volume + body condition	4.27	0.02	2.98 \pm 1.21	0.18 \pm 0.20	.36	-0.13 \pm 0.15	.38	-0.002 \pm 0.002	.32		
Abs. brain volume + rel. brain volume + body condition	5.03	0.01	3.29 \pm 1.55	-0.16 \pm 0.20	.42	-0.08 \pm 0.29	.78	-0.003 \pm 0.002	.25		
Social role ^a + abs. brain volume + rel. brain volume	5.27	0.01	2.77 \pm 1.73	0.22 \pm 0.20	.28	-0.11 \pm 0.22	.64	-0.06 \pm 0.29	.85		
Social role ^a + abs. brain volume + rel. brain volume + body condition	7.90	0.00	2.53 \pm 1.76	0.19 \pm 0.20	.35	-0.07 \pm 0.23	.74	-0.11 \pm 0.30	.72	-0.003 \pm 0.002	.30

Note: Intercept, coefficient, and SE estimates are given in log scale. Best-fit model and competing models ($<2 \Delta$ AICc) are highlighted in gray. Multivariate models are constructed using only the variables from competing models.

^aBinomial variable coefficients are for Observer (social role), Male (sex), and Subadult (Age).

^bAICc = 96.56

FIGURE 4 The four leading variables for explaining the days required for a crow to progress through the learning stage and reach mastery: (a) social role, (b) absolute brain volume, (c) relative brain volume, and (d) body condition



We believe this apparent lack of social learning was due to the Observers being less motivated to retrieve the food—they spent roughly three weeks in captivity before being given the task, during which their body condition improved from regular food access. The 2016 group supports this hypothesis: they performed objectively worse (none of the Observers from that cohort ever solved the task), yet their initial body condition was greater (possibly due to their being captured later in the non-breeding season) than the groups

from subsequent years. Furthermore, the statistical model containing body condition was one of the competitive models for predicting the amount of time required for a crow to reach the Mastery stage and was the most highly ranked of the non-competitive models for predicting the likelihood of initial success. Unfortunately, because we did not extract daily weights from the birds (we used weight on day of capture to calculate body condition) we cannot directly compare the body condition of Models vs. Observers when each group first gained access to the task—future studies should consider regularly measuring the body condition of their study species as they attempt the task.

In addition to better body condition, the Observer crows may have been less motivated due to learning the routine of captivity. While the Model birds were newly captured from the wild (and still uncertain of when their next meal would come) when they were first given the task, the Observers had likely learned that food would be delivered at some point each day. While we attempted to motivate them by removing their food bowls prior to giving them the task, after several days we noticed that the crows had started caching food throughout their cage. Whether as a result of the natural corvid instinct to cache (Jacobs et al., 2014), or in anticipation of their food bowl being removed (Emery, 2004), this caching behavior ensured that most crows had continuous access to food and were therefore less motivated to retrieve the hanging chicken (Birch, 1945).

Finally, the Model group contained more males and a higher mean absolute brain size compared with the Observer group. This is due to chance, as we assigned crows to cages randomly at the beginning of the study and did not determine sex or brain volume

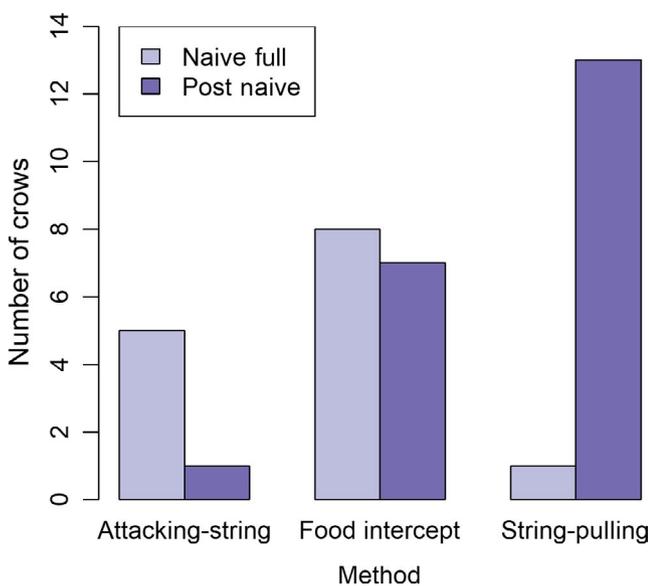


FIGURE 5 A comparison of the number of crows that most frequently used each method during the Naive Full stage and afterward [Colour figure can be viewed at wileyonlinelibrary.com]

Overall	Solved task		Failed to solve task
	Same method as neighbor	Different method from neighbor	
Neighbors primarily used different methods	2	0	3
Neighbor(s) primarily used String pulling	4	0	1
Neighbor(s) primarily used Food Intercept	1	1	1
Neighbor(s) primarily used Attacking string	0	0	1
Total	7	1	6

TABLE 6 A comparison of the most common general methods used by the Observer crows' neighbors during the Mastery stage, and whether the Observer crows utilized the same or different primary method as their neighbors (or failed to solve the task). If the neighbors used different methods, we checked whether the Observer used either of the two modeled methods

TABLE 7 A comparison of how often each general method was used during the Mastery stage by the eight successful Observers and the Model birds they were adjacent to. Crows on the edge of the aviary only had a single neighbor, while the rest had two. Many of the Models were included more than once in this comparison, as they were adjacent to two successful Observers. Difference Index scores near to 0 indicate close alignment of method choice between the Observer and that Model, whereas scores close to 1 indicate the two birds were highly dissimilar in method choice

Group	Birds	# Trials total	# Success attacking string	# Success food intercept	# Success string pulling	Difference index
1	Obs 1	15	0	0	15	
	Mod 1	42	6	0	35	0.15
2	Obs 2	11	0	0	11	
	Mod 1	42	6	0	35	0.15
	Mod 2	39	1	0	34	0.03
3	Obs 3	22	3	8	11	
	Mod 2	39	1	0	34	0.47
	Mod 3	42	2	0	39	0.45
4	Obs 4	21	0	20	1	
	Mod 3	42	2	0	39	0.95
	Mod 4	31	0	29	1	0.01
5	Obs 5	9	0	7	1	
	Mod 4	31	0	29	1	0.09
6	Obs 6	18	0	0	16	
	Mod 5	38	0	38	0	1.00
	Mod 6	38	0	9	29	0.24
7	Obs 7	16	1	0	15	
	Mod 6	38	0	9	29	0.24
	Mod 7	38	3	0	35	0.02
8	Obs 8	18	0	0	18	
	Mod 8	37	13	23	0	1.00

until the study had concluded. Although the crows' sex did not affect any of the conditions we measured, absolute brain volume might play a role in the amount of time a successful crow needs to master the task. Therefore, it is possible that the superior performance of the Model group compared with the Observer group may be due, in part, to the higher mean absolute brain volume of that group.

4.2 | Social learning

Although they did not master the task more rapidly, nor have a higher likelihood of initially solving it, the crows in the Observer group were more likely to copy the general and specific method most frequently used by their neighbors. This suggests that crows can use social learning to hone their technique *after* they have independently

learned to solve the task. The ability to use social learning to refine a foraging technique would allow an observer to capitalize on a conspecific's innovation to improve its own foraging efficiency. Crows are certainly capable of this; carrion crow (*Corvus corone*) use of vehicles as nutcrackers is transmitted via social learning throughout Japan (Nihei & Higuchi, 2001). The crows were already capable of cracking the nuts by repeatedly dropping them on a hard surface, but those that copy the “car nutcracker” method demonstrated by conspecifics can save both time and energy.

Our social learning results may have been limited by the crows' individual housing, a precaution taken to reduce social inhibition (Marzluff & Heinrich, 1991) and to accurately monitor individual food consumption. Most research into corvid social learning allow the model and observer to freely interact with each other in a single chamber (Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007; Clayton et al., 2007; Fritz & Kotrschal, 1999). It is possible that the American crows might have had more success learning the string pull task socially if they had been allowed to interact with one another in a similar fashion. This could be considered in future studies. Additionally, the crows may be more likely to copy individuals of a particular social class (such as their mate or kin, see Clayton & Emery, 2007), and we do not know the prior relationships (if any) our study animals shared prior to capture.

4.3 | Brain volume

Our findings that American crows with smaller absolute brain volumes tended to have greater variability in the time required to master the task supports the hypothesis that larger brains are advantageous for complex cognitive tasks (Deaner et al., 2007). Brain tissue is metabolically expensive to grow and maintain (Aschoff, Günther, & Kramer, 1971; Hofman, 1983), and thus, we would expect large brains to provide a proportionally greater benefit than their costs to overcome selection pressure. The variation in brain volume in our results and those reported by Iwaniuk and Nelson (2002) are comparable, indicating that the brain volume of American crows can vary in size by up to 8% between individuals. This variation would offer an avenue for natural selection to favor large or small-brained individuals under differing constraints; appropriate given that American crows are human commensal species that live in dynamic environments with ample opportunities to discover novel food sources (Kilham, 1990).

However, there are significant caveats to claiming that within-species whole brain volume can be used to predict task performance. Primary among these caveats is that none of the models we used to compare each measured factor against the crows' likelihood solving or learning the task were substantially better than the null model, which severely limits our ability to apply our findings generally. Additionally, most of the brain regions responsible for higher-order cognitive tasks (such as the nidopallium and mesopallium) are located in the forebrain (Emery & Clayton, 2004), a specific area we did not measure. Furthermore, our method for calculating brain volume does not account for neuron density, which varies between and

within species (Collins, Airey, Young, Leitch, & Kaas, 2010; Lange, 1975; Olkowicz et al., 2016), and even within brain regions of a single individual (Collins et al., 2010).

Despite these caveats, there are numerous studies supporting brain volume as a predictor of cognitive ability. Recent research has emerged demonstrating the importance of neuronal counts over other brain-related metrics (such as relative brain volume or cortex/pallium mass) in predicting a species' cognitive capability (Herculano-Houzel, 2017; Jacobs, Kabadayi, & Osvalth, 2019; Jardim-Messeder et al., 2017), with brain size being an appropriate predictor of neuron number (Marhounová, Kotrschal, Kverková, Kolm, & Němec, 2019). Additionally, a close association has been found between brain size and neuron count for the regions in the brain involved with cognition, such as the telencephalon (Marhounová et al., 2019). We have demonstrated that the absolute brain size of American crows varies among individuals and provides some evidence that individuals with larger brain volumes tend to consistently require less time to master the task. While this might suggest that large-brained individuals contain greater neuronal counts compared with smaller-brained individuals of a similar size (supporting the theory that neuronal counts are a predictor of cognitive ability), factors such as neuronal size and density must also be considered (Herculano-Houzel, 2017; Herculano-Houzel, Messeder, Fonseca-Azevedo, & Pantoja, 2015) both of which are currently unknown for American crows.

4.4 | Method choice

The methods used by the crows throughout the study matched earlier (Heinrich, 1999) observations: while naive crows rarely pulled the string to initially solve the task (preferring instead to intercept the food from the air or attack the string), most crows readily switched to string pulling with experience and training. Compared with other methods, string pulling requires less aerial agility (especially challenging for larger birds) than food interception and less physical strength (especially challenging for smaller birds) than attacking the string. We regularly observed three crows from 2017 and two from 2018 that would first use a string pull method to retrieve the food, but afterward would begin attacking the empty string until it broke. This may be a form of play behavior for bored captive crows. Contrary to expectations (Heinrich, 1999), we found that some American crows are capable of using a string pull method without training, although we only observed three birds accomplish this and were unable to identify any characteristic which might be responsible.

Crows in the Model group overwhelmingly preferred the food intercept method when they were first given the task, whereas the Observer crows strongly preferred the other methods (Table 2). We do not believe that this discrepancy was caused by social learning (most successful Observers did not *initially* copy their neighbors' favorite method), but it could have been caused by the additional time the Observers spent in captivity prior to being given the task. While the aviary cages were spacious enough to allow limited flight, the crows did not receive nearly as much exercise in captivity as

they would in the wild (for perspective, we resighted one of our studies crows on a territory 24 km away from the roost where we initially captured her). If their flight muscles had atrophied to some degree, then intercepting the food from the air would become relatively more difficult than the other two methods.

The training we gave the crows during the Learning stage preferentially emphasized the string pulling method; by shortening the string, we made that method both easier to learn and perceive, and more efficient to perform than the other two methods. We did not change the difficulty of the attacking string method (the string material remained constant), and we increased the difficulty of the food intercept method by bringing the string closer to the perch relative to the ground. This is the most probable explanation for why most crows switched to using the string-pull method after beginning the Learning stage and presents a competing reason for why most Observers copied the method frequently demonstrated by their Model neighbors. However, three lines of evidence suggest that social learning was involved. First, while six of the eight successful Observers did preferentially use the string-pull method to solve the task after mastering it, only five of them had a neighbor that used that method. Second, of the seven Observers that favored the same method as their neighbors, two preferred the Food Intercept method, even though one of them had a second neighbor that opted to use the string-pull method. (Table 7). Third, in addition to adopting the most commonly modeled method of problem-solving, after mastering the task the variety of general and specific methods used by most Observers closely matched the frequency of method use by their Model neighbors (difference index, Tables 7 and S3).

There is much disagreement over whether birds solve the string pulling task using spontaneous insight-like processes, or more methodical processes such as operant conditioning (Heinrich, 1995; Heinrich & Bugnyar, 2005; Shettleworth, 2012; Taylor et al., 2010). Our results favor the hypothesis that most crows learn to string pull using operant conditioning. Specifically, during the Learning stage, the crows learned to use a string pull method by receiving immediate positive reinforcement; the shortened string length meant that a single reach down and pull sequence brought the food within or almost within reach of the hungry crow, motivating it to continue its behavior. However, some crows may use other methods, as evidenced by the three crows that learned to use a string pull method without going through any training. These three crows may have discovered the method via social learning or an insight-like process, although we have no way of knowing if they had any prior life experiences that would have prepared them to use this method.

4.5 | Brain volume calculation

Our method of using DICOM from CT scans to calculate the brain volume of crows generated a mean estimate that was within the endocranial volumes calculated by Iwaniuk and Nelson (2002) and Mlikovsky (2003), demonstrating that our virtual approach is comparable to direct estimation. The advantage of our approach is that no

animals were sacrificed, and brain volume was unaffected by post-mortem fluid/blood pressure loss.

4.6 | Caveats

Because we wanted to maximize the opportunities for an Observer crow to see their Model neighbors work the task, we did not partition the cages into pairs or otherwise block any bird's view of their conspecifics. While this meant that crows could observe both of their immediate neighbors, it also meant that they could potentially see the birds beyond their neighboring cages. Because the additional distance and layers of wire mesh would make it more difficult to see the details of distant bird's activities, coupled with the poorer performance of Observers compared with Models, we do not believe this to be a major confounding factor.

Despite our efforts to ensure every year's group of crows experienced the same conditions, we were inconsistent with the amount of time the crows were given to attempt to solve the task during the Naïve Full stage (caused by temporal constraints from a different experiment), forcing us to limit our analysis to the first three days of task access. Additionally, we captured the 2016 crows later in the non-breeding season than subsequent years' cohorts, which may have played a role in their poor performance.

Our findings that brain volume and body condition are weakly correlated with learning time are primarily driven by three individuals (Figure 4b–d); if we remove them from the analysis, the effect vanishes completely. While we could disregard a single outlier, multiple individuals that span a range of sizes, ages, and genders (Table S1) behaving similarly indicate a possible effect of brain volume and body condition that could be investigated in future studies.

Finally, our inability to detect social learning may be due to our experimental setup. We used wild-caught rather than captive-reared crows for our study; while this ensured that the factors we measured were representative of the wild crow population in our area, it also meant that our setup was less optimal than a typical cognitive study and may have added unnecessary variation to the data and the crows' performance. For example, many studies examining social learning record and/or standardize additional variables, such as the relationship of the tutor/observer dyad, the amount of time the observers watch the demonstrators, how much time the demonstrator spent working on the task, and whether the observer had a preferred demonstrator (Hoppitt & Laland, 2008; Nielsen, Subiaul, Galef, Zentall, & Whiten, 2012). Social status also influences Corvid behavior (Miyazawa, Seguchi, Takahashi, Motai, & Izawa, 2019), but we did not know what (if any) social relationship our crows had with each other prior to capture, and we had no opportunity to learn while they were captive because the birds were housed individually and had limited ability to interact. The crows remained wary of humans, so we had to observe them remotely via surveillance cameras; the video resolution was good enough to ascertain which method the crows used to solve the task, but not enough to determine how long the crows were actively watching

others interact with the task. This lack of standardization may be responsible for our crows' lackluster performance compared with other studies which examined corvid problem-solving (Heinrich & Bugnyar, 2005; Jacobs & Osvath, 2015). However, our setup was sufficient in demonstrating some aspects of social learning, such as the propensity of Observers to copy their neighbors most frequently modeled solution.

5 | CONCLUSION

In conclusion, our results suggest that motivation (caused by hunger and associated body condition) is the most important factor in determining the ability of American crows to solve a string-pull task, although absolute brain volume and social learning may also play a role. Crows tested a few days after capture were more likely to initially solve the task compared with crows that were given the task after several weeks of captivity. This same group of crows also required consistently fewer days to master the task compared with the group tested after several weeks, but bigger-brained birds also mastered in consistently less time compared with the crows with smaller brains. Contrary to our expectations, the only effect of social learning we found was that crows given the opportunity to watch conspecifics solve the task tended to change their method to copy the solution demonstrated by their knowledgeable neighbors, although our inability to detect additional examples of social learning might be due to our experimental setup inadvertently stymying the crows' ability to learn socially. Finally, we also found that absolute brain volume was a better predictor of an individual's capacity to solve novel tasks than was relative brain volume. We encourage future researchers to take a holistic approach when examining cognition, as there are a variety of factors which may play a role in an individual's ability to solve problems.

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REFERENCES

- Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, *85*(6), 1225–1232. <https://doi.org/10.1016/j.anbehav.2013.03.009>
- Aschoff et al., 1971Aschoff, J., Günther, B., & Kramer, K. (1971). *Energiehaushalt und temperaturregulation*. Munich, Germany: Urban & Schwarzenberg.
- Beck, B. B. (1973). Observation learning of tool use by captive Guinea baboons (*Papio papio*). *American Journal of Physical Anthropology*, *38*(2), 579–582. <https://doi.org/10.1002/ajpa.1330380270>
- Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*, *113*(9), 2532–2537. <https://doi.org/10.1073/pnas.1505913113>
- Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095.
- Birch, H. G. (1945). The role of motivational factors in insightful problem-solving. *Journal of Comparative Psychology*, *38*(5), 295. <https://doi.org/10.1037/h0059937>
- Bobrowicz, K., & Osvath, M. (2019). Social context hinders humans but not ravens in a short-term memory task. *Ethology*, *2019*, 1–15. <https://doi.org/10.1111/eth.12971>
- Bugnyar, T., Reber, S. A., & Buckner, C. (2016). Ravens attribute visual access to unseen competitors. *Nature Communications*, *7*, 10506. <https://doi.org/10.1038/ncomms10506>
- Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K., & Heinrich, B. (2007). Ravens judge competitors through experience with play caching. *Current Biology*, *17*(20), 1804–1808. <https://doi.org/10.1016/j.cub.2007.09.048>
- Burnham, K. P., & Anderson, D. R. (1998). *Model selection and inference: A practical information-theoretical approach*. New-York, NY: Springer-Verlag.
- Caffrey, C. (2000). Tool modification and use by an American Crow. *The Wilson Bulletin*, *112*(2), 283–284. [https://doi.org/10.1676/0043-5643\(2000\)112\[0283:TMAUBA\]2.0.CO;2](https://doi.org/10.1676/0043-5643(2000)112[0283:TMAUBA]2.0.CO;2)
- Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F., & Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour*, *85*(1), 19–26. <https://doi.org/10.1016/j.anbehav.2012.10.005>
- Clark, R., James, P., & Morari, J. B. (1991). Sexing adult and yearling american crows by external measurements and discriminant analysis (Determinación del sexo de adultos y aves de un año de *Corvus brachyrhynchos* mediante medidas externas y análisis discriminativo). *Journal of Field Ornithology*, *62*(1), 132–138.
- Clayton, N. S., Dally, J. M., & Emery, N. J. (2007). Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 507–522.
- Clayton, N. S., & Emery, N. J. (2007). The social life of corvids. *Current Biology*, *17*(16), R652–R656. <https://doi.org/10.1016/j.cub.2007.05.070>
- Cole, E. F., Cram, D. L., & Quinn, J. L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, *81*(2), 491–498. <https://doi.org/10.1016/j.anbehav.2010.11.025>
- Cole, E. F., & Quinn, J. L. (2011). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1168–1175.
- Collins, C. E., Airey, D. C., Young, N. A., Leitch, D. B., & Kaas, J. H. (2010). Neuron densities vary across and within cortical areas in primates. *Proceedings of the National Academy of Sciences*, *107*(36), 15927–15932. <https://doi.org/10.1073/pnas.1010356107>

- Cornell, H. N., Marzluff, J. M., & Pecoraro, S. (2011). Social learning spreads knowledge about dangerous humans among American crows. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1728), 499–508.
- Deaner, R. O., Isler, K., Burkart, J., & Van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, 70(2), 115–124. <https://doi.org/10.1159/000102973>
- Dufour, V., Broihanne, M.-H., & Wascher, C. A. F. (2019). Corvids avoid odd evaluation by following simple rules in a risky exchange task. *Ethology*, 2019, 1–12. <https://doi.org/10.1111/eth.12994>
- Emery, N. J. (2004). Are corvids 'feathered apes'. *Comparative Analysis of Minds*, 181, e213.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, 306(5703), 1903–1907.
- Emlen, J. T. (1936). Age determination in the American crow. *The Condor*, 38(3), 99–102. <https://doi.org/10.2307/1363907>
- Fritz, J., & Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. *Animal Behaviour*, 57(4), 785–793.
- Galef, B. G. Jr, & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, 61(1), 3–15. <https://doi.org/10.1006/anbe.2000.1557>
- Griffiths, R., Daan, S., & Dijkstra, C. (1996). Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263(1374), 1251–1256.
- Healy, S. D., & Rowe, C. (2006). A critique of comparative studies of brain size. *Proceedings of the Royal Society B: Biological Sciences*, 274(1609), 453–464. <https://doi.org/10.1098/rspb.2006.3748>
- Heinrich, B. (1995). An experimental investigation of insight in common ravens (*Corvus corax*). *The Auk*, 994–1003. <https://doi.org/10.2307/4089030>
- Heinrich, B. (1999). *Mind of the Raven*. New York, NY: Cliff Street Books.
- Heinrich, B. (2000). Testing insight in ravens. In C. Heyes, & L. Huber (Eds.), *Vienna series in theoretical biology. The evolution of cognition* (pp. 289–305). Cambridge, MA: The MIT Press.
- Heinrich, B., & Bugnyar, T. (2005). Testing problem solving in ravens: String-pulling to reach food. *Ethology*, 111(10), 962–976. <https://doi.org/10.1111/j.1439-0310.2005.01133.x>
- Heinrich, B., Marzluff, J., & Adams, W. (1995). Fear and food recognition in naive common ravens. *The Auk*, 112(2), 499–503. <https://doi.org/10.2307/4088740>
- Heinrich, B., Marzluff, J. M., & Marzluff, C. S. (1993). Common ravens are attracted by appeasement calls of food discoverers when attacked. *The Auk*, 110(2), 247–254.
- Herculano-Houzel, S. (2017). Numbers of neurons as biological correlates of cognitive capability. *Current Opinion in Behavioral Sciences*, 16, 1–7. <https://doi.org/10.1016/j.cobeha.2017.02.004>
- Herculano-Houzel, S., Messeder, D. J., Fonseca-Azevedo, K., & Pantoja, N. A. (2015). When larger brains do not have more neurons: Increased numbers of cells are compensated by decreased average cell size across mouse individuals. *Frontiers in Neuroanatomy*, 9, 64. <https://doi.org/10.3389/fnana.2015.00064>
- Hofman, M. A. (1983). Energy metabolism, brain size and longevity in mammals. *The Quarterly Review of Biology*, 58(4), 495–512. <https://doi.org/10.1086/413544>
- Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learning & Behavior*, 38(3), 206–219. <https://doi.org/10.3758/LB.38.3.206>
- Hoppitt, W., & Laland, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior*, 38, 105–165.
- Horos (Version 3.2.1) [Computer Software] (2019). Retrieved from <https://horosproject.org/download>
- Horschler, D. J., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2019). Absolute brain size predicts dog breed differences in executive function. *Animal Cognition*, 22(2), 187–198. <https://doi.org/10.1007/s10071-018-01234-1>
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379(6562), 249. <https://doi.org/10.1038/379249a0>
- Iwaniuk, A. N., & Nelson, J. E. (2002). Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology*, 80(1), 16–23. <https://doi.org/10.1139/z01-204>
- Jacobs, I., Kabadayi, C., & Osvath, M. (2019). The development of sensorimotor cognition in common ravens (*Corvus corax*) and its comparative evolution. *Animal Behavior and Cognition*, 6(3), 194–212. <https://doi.org/10.26451/abc.06.03.04.2019>
- Jacobs, I. F., & Osvath, M. (2015). The string-pulling paradigm in comparative psychology. *Journal of Comparative Psychology*, 129(2), 89. <https://doi.org/10.1037/a0038746>
- Jacobs, I. F., Osvath, M., Osvath, H., Mioduszevska, B., von Bayern, A. M., & Kacelnik, A. (2014). Object caching in corvids: Incidence and significance. *Behavioural Processes*, 102, 25–32. <https://doi.org/10.1016/j.beproc.2013.12.003>
- Jardim-Messeder, D., Lambert, K., Noctor, S., Pestana, F. M., de Castro Leal, M. E., Bertelsen, M. F., ... Herculano-Houzel, S. (2017). Dogs have the most neurons, though not the largest brain: Trade-off between body mass and number of neurons in the cerebral cortex of large carnivorous species. *Frontiers in Neuroanatomy*, 11, 118. <https://doi.org/10.3389/fnana.2017.00118>
- Kilham, L. (1990). *The American crow and the common raven* (No. 10). College Station, TX: Texas A&M University Press.
- Kotrschal, A., Buechel, S. D., Zala, S. M., Corral-Lopez, A., Penn, D. J., & Kolm, N. (2015). Brain size affects female but not male survival under predation threat. *Ecology Letters*, 18(7), 646–652. <https://doi.org/10.1111/ele.12441>
- Lambert, M. L., Jacobs, I., Osvath, M., & von Bayern, A. M. (2019). Birds of a feather? Parrot and corvid cognition compared. *Behaviour*, 156(5–8), 505–594.
- Lange, W. (1975). Cell number and cell density in the cerebellar cortex of man and some other mammals. *Cell and Tissue Research*, 157(1), 115–124. <https://doi.org/10.1007/BF00223234>
- Marhounová, L., Kotrschal, A., Kverková, K., Kolm, N., & Němec, P. (2019). Artificial selection on brain size leads to matching changes in overall number of neurons. *Evolution*, 73(9), 2003–2012. <https://doi.org/10.1111/evo.13805>
- Marzluff, J. M., & Angell, T. (2007). *In the company of crows and ravens*. New Haven, CT: Yale University Press.
- Marzluff, J. M., DeLap, J. H., & Haycock, K. (2015). Population variation in mobbing Ospreys (*Pandion haliaetus*) by American crows (*Corvus brachyrhynchos*). *The Wilson Journal of Ornithology*, 127(2), 266–270.
- Marzluff, J. M., & Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders: An experimental analysis of social foraging. *Animal Behaviour*, 42(5), 755–770. [https://doi.org/10.1016/S0003-3472\(05\)80121-6](https://doi.org/10.1016/S0003-3472(05)80121-6)
- Marzluff, J. M., & Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biological Conservation*, 130(2), 301–314. <https://doi.org/10.1016/j.biocon.2005.12.026>
- Marzluff, J. M., Walls, J., Cornell, H. N., Withey, J. C., & Craig, D. P. (2010). Lasting recognition of threatening people by wild American crows. *Animal Behaviour*, 79(3), 699–707. <https://doi.org/10.1016/j.anbehav.2009.12.022>
- Mason, W. A., & Harlow, H. F. (1961). The effects of age and previous training on patterned-strings performance of rhesus monkeys. *Journal of Comparative and Physiological Psychology*, 54(6), 704. <https://doi.org/10.1037/h0044686>

- Miyazawa, E., Seguchi, A., Takahashi, N., Motai, A., & Izawa, E.-I. (2019). Different patterns of allopreening in the same-sex and opposite-sex interactions of juvenile large billed crows (*Corvus macrorhynchos*). *Ethology*, 2019, 1–12. <https://doi.org/10.1111/eth.12992>
- Mlikovsky, J. (2003). Brain size and forearm magnum area in crows and allies (Aves: Corvidae). *Acta Societatis Zoologicae Bohemicae*, 67(1–4), 203–211.
- Nielsen, M., Subiaul, F., Galef, B., Zentall, T., & Whiten, A. (2012). Social learning in humans and nonhuman animals: Theoretical and empirical dissections. *Journal of Comparative Psychology*, 126(2), 109. <https://doi.org/10.1037/a0027758>
- Nihei, Y., & Higuchi, H. (2001). When and where did crows learn to use automobiles as nutcrackers. *Tohoku Psychologica Folia*, 60, 93–97.
- Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, 113(26), 7255–7260. <https://doi.org/10.1073/pnas.1517131113>
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the National Academy of Sciences*, 110(10), 4123–4128. <https://doi.org/10.1073/pnas.1209926110>
- Papp, S., Vincze, E., Preiszner, B., Liker, A., & Bókony, V. (2015). A comparison of problem-solving success between urban and rural house sparrows. *Behavioral Ecology and Sociobiology*, 69(3), 471–480. <https://doi.org/10.1007/s00265-014-1859-8>
- Portmann, A. (1946). Études sur la cerebralisation chez les oiseaux. I. *Alauda*, 14, 2–20.
- Rieucou, G., & Giraldeau, L. A. (2011). Exploring the costs and benefits of social information use: An appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 949–957.
- Roth, T. C., LaDage, L. D., & Pravosudov, V. V. (2010). Learning capabilities enhanced in harsh environments: A common garden approach. *Proceedings of the Royal Society B: Biological Sciences*, 277(1697), 3187–3193.
- RStudio Team. (2016). RStudio: integrated development for R. RStudio, Inc. Boston, MA. Retrieved from <http://www.rstudio.com/>
- Shettleworth, S. J. (2012). Do animals have insight, and what is insight anyway? *Canadian Journal of Experimental Psychology/Revue Canadienne De Psychologie Expérimentale*, 66(4), 217. <https://doi.org/10.1037/a0030674>
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. Baltimore, MD: JHU Press.
- Sierro, J., Loretto, M.-C., Szpl, G., Massen, J. J. M., & Bugnyar, T. (2019). Food calling in wild ravens (*Corvus corax*) revisited: Who is addressed? *Ethology*, 2019, 1–10. <https://doi.org/10.1111/eth.12991>
- Swift, K. N., & Marzluff, J. M. (2015). Wild American crows gather around their dead to learn about danger. *Animal Behaviour*, 109, 187–197. <https://doi.org/10.1016/j.anbehav.2015.08.021>
- Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R., & Gray, R. D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS ONE*, 5(2), e9345. <https://doi.org/10.1371/journal.pone.0009345>
- Thorpe, W. H. (1943). A type of insight learning in birds. *British Birds*, 37, 29–31.
- Tomasello, M., Davis-Dasilva, M., CamaK, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, 2(2), 175–183. <https://doi.org/10.1007/BF02436405>
- Uomini, N., & Hunt, G. (2017). A new tool-using bird to crow about. *Learning & Behavior*, 45(3), 205–206. <https://doi.org/10.3758/s13420-017-0262-5>
- Van der Vaart, E., Verbrugge, R., & Hemelrijk, C. K. (2012). Corvid re-caching without 'theory of mind': A model. *PLoS ONE*, 7(3), e32904. <https://doi.org/10.1371/journal.pone.0032904>
- Vince, M. A. (1958). "String-pulling" in birds. (2) differences related to age in greenfinches, chaffinches and canaries. *Animal Behaviour*, 6(1–2), 53–59.
- Von Bayern, A. M., Heathcote, R. J., Rutz, C., & Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Current Biology*, 19(22), 1965–1968. <https://doi.org/10.1016/j.cub.2009.10.037>
- Wascher, C. A., & Bugnyar, T. (2013). Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS ONE*, 8(2), e56885. <https://doi.org/10.1371/journal.pone.0056885>
- Wetzel, D. P. (2017). Problem-solving skills are linked to parental care and offspring survival in wild house sparrows. *Ethology*, 123(6–7), 475–483. <https://doi.org/10.1111/eth.12618>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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