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Raptors' Natural History Influences Their Response to the String-Pull Task

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Largely due to the small number of individuals in captivity, birds of prey remain an understudied, but promising group for animal cognition research. Variations on the classic string-pulling task have been applied across species to evaluate abilities such as associative learning, means-end understanding, and insight problem solving. Previous research has examined only a few species of raptor on the task such as the Harris's hawk (*Parabuteo unicinctus*), great grey owl (*Strix nebulosa*), and turkey vulture (*Cathartes aura*). Here, we explored how 1-3 individuals from each of seven raptor species (turkey vulture; barn owl, *Tyto alba*; western screech owl, *Megascops kennicottii*; eastern screech owl, *M. asio*; red-tailed hawk, *Buteo jamaicensis*; Swainson's hawk, *B. swainsoni*; and Harris's hawk) responded to a standardized vertical apparatus. Our goal was to replicate, diversify, and extend the literature by documenting how these different species approached the same problem. Two strings were tied around a perch, one of which was baited. Birds underwent multiple 60-min trials. At least one bird from four of the seven species retrieved the food reward. Three individuals retrieved the food consistently across trials, including the first recorded solving by a western screech owl. Birds displayed diverse apparatus-directed behaviors and solving methods which supported our predictions regarding sociality and predation method. We frame our findings as a roadmap for future researchers studying physical problem-solving by raptors.

Keywords: bird of prey, comparative cognition, natural history, raptor, string-pull task

Typically comprised of hawks, owls, eagles, falcons, and vultures, raptors (i.e., birds of prey) are a collection of bird orders that descended from a predatory ancestor and maintained a raptorial lifestyle (McClure et al., 2019). Most raptors are opportunistic predators, with vultures being a notable scavenger exception (Venable, 1996). Raptors tend to have altricial young and experience an extended juvenile period as well as long lifespans, features that have been connected to cognitive abilities like self-control in mammals (Chiappa et al., 2018). Despite these links, raptors remain a group of animals that has been severely understudied in empirical animal cognition research. Definitions of cognition vary, leading to well-established challenges (e.g., Abramson, 2013). For our purposes, we consider cognition to be "the ways in which animals take in information about the world through the senses, process, retain and decide to act on it" (Shettleworth, 2001, p. 278). This includes domains such as perception, memory, social learning, problem-solving, and others.

Raptors possess high brain encephalization values, a metric associated with problem solving and tool use abilities in other species (see van Overveld et al., 2022). Indeed, as a group, raptors' encephalization is comparable to some parrots' and corvids' (see van Overveld et al., 2022, Figure 1 for reference), birds which are considered especially advanced in the realm of physical problem solving (Auersperg et al., 2011; Taylor et al., 2010). Previous reports of natural raptor behavior describe flexible and innovative feeding techniques, possible evidence of cooperative problem solving (e.g., Nicolakakis et al., 2003), and tool use (e.g., van Lawick-Goodall & van Lawick-Goodall, 1966), among other abilities. Such behaviors are common in mammals and birds known for their impressive problem-solving abilities, further implicating raptors as a strong candidate group for research.

To date, only a handful of studies have empirically investigated raptors' abilities to solve problems. Their findings support what is predicted by neural correlates and field observations described earlier. In one study, five wild caught chimango caracaras (*Milvago chimango*) successfully solved a puzzle box with four compartments opened via different physical actions (i.e., lifting, sliding, pushing, and pulling; Biondi et al., 2008). All five of the caracaras successfully opened at least two of the compartments of the box, and each subject eventually opened all four. The authors framed their findings around both ecological relevance (e.g., natural feeding technique of scratching with talons) and flexible generalization of learned behaviors (e.g., similar lid-flipping of humans' waste baskets by caracaras living in urban areas). What is unknown is how other raptor species might perform on this task, as the small body of literature has resulted in minimal replication across diverse raptor species on one standardized apparatus.

String-Pull Task

The string-pulling task is one of the most common tests of physical cognition given its simple set-up. In its simplest form, the task consists of one baited string with food that is out of reach tied to the end, requiring the subject to pull on the string to retrieve the food. Mammals have been primarily tested on horizontal strings and birds on vertical ones (see Obozova & Zorina, 2013; Danel et al., 2019 for exceptions). As recent research suggests, the basic task is only able to successfully assess associative processes around perceptual motor feedback learning (Jacobs & Osvath, 2015). Variations of the task, however, have been designed to assess means-end understanding and even insightful problem solving (e.g., Jacobs & Osvath, 2015). One common variation is the parallel strings version, in which two strings are presented, with one baited, which provides information on goal-directed behavior. Other variations include the "contact and connection" versions of the task, where one string is not connected to a reward, allowing for testing of means-end understanding, and the coiled condition, where coiling the string near the reward prevents visual feedback from influencing the choice of strings (e.g., Danel et al., 2019).

To date, more than 100 mammalian and bird species have been tested (Jacobs & Osvath, 2015). Among birds, successful string-pulling has been observed in various corvids (Heinrich & Bugnyar, 2005; Hofmann et al., 2016; Manrique et al., 2017; Taylor et al., 2010), parrots (Krasheninnikova et al., 2013; Krasheninnikova & Wanker, 2010) and some passerines (Cole et al., 2011; Seibt & Wickler, 2006). One commonly reported method of vertical solving by birds is the pull-step-pull method, where a bird pulls on the string with the beak, secures it with a foot, and then repeats this sequence with loops of the string until the food is reached. Until more recently, some avian researchers treated this method as a "gold standard" indicator of advanced cognition when observing new species on the task (e.g., Colbert-White et al., 2013; Heinrich, 1995). However, the speed and efficiency associated with pulling and stepping can just as easily be explained by associative processes as insightful ones (e.g., Taylor et al., 2010), leading to controversy surrounding what the task can actually measure.

Three previous studies have examined three different raptor species' abilities to solve variations on the string-pulling task. Colbert-White et al. (2013) tested one captive-bred Harris's hawk (*Parabuteo unicinctus*), a social hunting species, using both a baited and control string. The hawk solved within 8 min on its first trial, and latencies to solve decreased over time, clearly demonstrating learning. According to Colbert-White et al. (2013), the hawk's performance (i.e., solving times and solving behaviors used) was on par with other species tested on the task including crows, ravens, and parrots, providing further evidence that some raptors may have similar physical problem-solving abilities to these more well-studied species.

Ellison et al. (2015) presented a single string task to six turkey vultures (*Cathartes aura*), a social species, with mixed success. Three of the subjects solved the task and solved progressively faster over time. To encourage participation, birds uninterested in the task were paired with a conspecific during testing, which resulted in evidence of social learning, with one vulture solving only after watching a conspecific. Finally, using a single string horizontal variation, Obozova and Zorina (2013) observed twelve communally-living great grey owls (*Strix nebulosa*), a solitary species, six of which were successful. The subjects were also tested using the contact variation in which one of the two strings was unattached to a visible piece of meat. Only one owl consistently avoided pulling this string.

While the results of these three studies demonstrated that the focal species could solve the string-pulling task (i.e., reach the food), comparisons of performance across the species, as well as conclusions about the cognitive domains being assessed, are difficult to make given the diverse methodologies and life histories of the subjects (see Table 1). Furthermore, each of these studies focused only on one species, making it impossible to explore how problem solving behavior is influenced by the various ecological pressures raptors face.

Table 1
Comparison of Raptor String-Pull Studies

	Colbert-White et al. (2003)	Ellison et al. (2015)	Obozova & Zorina (2013)
Species (N)	<i>Parabuteo unicinctus</i> (1)	<i>Cathartes aura</i> (6)	<i>Strix nebulosa</i> (12)
Sociality	Social	Social	Solitary
Feeding Style	Predatory	Scavenging	Predatory
Life History	Captive-bred, injured, flown	3 captive-bred; 3 wild-caught injured	Captive
Housing	Single	Communal	Communal
Human Interaction	High	Mixed	Unknown
String-Pull Method	Vertical	Vertical	Horizontal
Control String	Rock	None	Unattached bait
Testing Location	Solitary	Solitary or 1 conspecific	Communal
Trials Visible to Other Subjects	N/A	Sometimes	Yes
Number of Trials	8	15-40	At least 2
Length of Trials	30 min	15 min	Unrestricted
% of Trials Successful	100%	50%	50% single string; 20% control string condition

Note. Obozova and Zorina (2013) presented their single-baited string task apparatus to marked group-housed birds and returned each hour to rebait strings when necessary. Subjects had unrestricted time between 5:00 p.m. – 12:00 a.m. to approach and interact with the apparatus.

Natural History Frameworks

Evidence across multiple species has shown sociality to be associated with increased encephalization in the brain, which is often linked to cognitive flexibility (Shultz & Dunbar, 2010). The social intelligence hypothesis posits that primates living in complex social groups may need to be more cognitively nimble to effectively interact with group members (Dunbar, 1998; Humphrey, 1976). Successful group living involves navigating and maintaining complex social relationships which can require a variety of skills (e.g., memory, decision making, impulse control, reconciliation) and the evolution of such complex prosocial abilities may have expanded cognition more broadly into other domains.

Though the social intelligence hypothesis was originally developed using data from primates, social avian species tend to outperform nonsocial ones on certain tasks. For example, while all three species were successful at a reversal learning task, the social pinyon jay (*Gymnorhinus cyanocephalus*) outperformed both Clark's nutcrackers (*Nucifraga columbiana*) and western scrub jays (*Aphelocoma californica*), two nonsocial species (Bond et al., 2007). Given the nature of the task, being able to shift to a new “rule” (i.e., previously unrewarded option is now rewarded) could have parallels to the constantly changing social dynamics of group living. This pattern also holds within species as well. Compared to those living in smaller social groups, Australian magpies (*Gymnorhina tibicen*) living in larger social groups had better performance across four tasks including associative learning and spatial memory tasks (Ashton et al., 2018). Moreover, the authors asserted that the observed differences could not be attributed to any characteristic measured other than group size.

Methods of engagement with the environment broadly have also been presented as mechanisms that can facilitate the evolution of cognitive abilities like spatial memory, value-based decision making and self-regulation (Miltion, 1988; Rosati, 2017). The ecological intelligence hypothesis is a collection of observations connecting ecological natural history to cognition. For example, one theory posits that diet influences the evolution of different cognitive domains. According to DeCasien et al. (2017), frugivores tend to have sophisticated cognition due to their need to identify ripeness and remember where edible food is located. In support of this, these authors showed that brain size in primates was indeed correlated with eating fruit, which they concluded illustrates a connection to the sharpening of cognition in relevant domains over time.

Foraging methods within and between species may also contribute to differences in cognition. For example, hunting coyotes showed more boldness, less neophobia and greater persistence toward a cognitive task compared to scavenging coyotes (*Canis latrans*) (Parsons et al., 2022). Broadly, species with high boldness and a low neophobia perform better on problem solving tasks perhaps due to an increased willingness to engage with the unfamiliar (Audet et al., 2016; Benson-Amram & Holekamp, 2012; Guenther & Brust, 2017). Further, though there is little evidence that predatory species trend towards having larger brains than their prey, predators—more than scavengers or grazers—would likely benefit from being able to flexibly plan and dispatch unpredictable moving targets while hunting (Benson-Amram et al., 2022).

Current Study

In their review, Krashennikova et al. (2020) highlight two issues in contemporary comparative cognition research: a lack of large-scale diversity of species tested and weak comparability of findings across studies due to inconsistent methods. Here, we replicate, diversify, and extend current raptor physical problem-solving literature by using one standardized string-pulling set-up and data analysis method to test seven different species of the same three orders assessed by Colbert-White et al. (2013), Ellison et al. (2015), and Obozova and Zorina (2013). The apparatus was a vertical one that included an unbaited string in order to assess holistic exploration of the apparatus rather than to draw explicit conclusions around means-ends or insight. Instead, by examining multiple species of raptor and eliminating common inconsistencies such as trial length, vertical vs. horizontal strings, operational definitions for *solving*, and behaviors coded, we aimed to provide future researchers with a roadmap for better understanding the kinds of behaviors that could be expected from raptors in physical problem-solving tasks involving food. This is accomplished using natural history as a framework for prediction and interpretation.

Among raptors, there are several social species including the turkey vulture and Harris's hawk (Bednarz, 1988; Hagler et al., 2022; van Overveld et al., 2020; Vogel, 1950). We predicted that these species would be more likely than the nonsocial raptors to retrieve the food reward due to enhanced physical cognition predicted by the social intelligence hypothesis (Dunbar, 1998; Humphrey, 1976). Additionally, while some raptors hunt for food, others are scavengers or even a hybrid between the two. Therefore, we predicted a commonality between species' predation styles and the kinds of physical interactions with the apparatus they had and/or solving methods they used. Specifically, we expected to see the hawks and owls, both of which are hunting predators, to engage with the apparatus using behaviors associated with actively dispatching prey such as flying or grasping at parts of the apparatus. Conversely, the scavenging turkey vultures were predicted to use behaviors like string pulls and shield interactions when interacting with the apparatus, behaviors which are associated with extraction (i.e., similar to how they might work on a carcass). We also saw this as an opportunity to possibly replicate Ellison et al.'s (2015) novel finding of string swallowing by the turkey vultures, a behavior that the authors reported was reminiscent of their natural feeding behavior.

Method

Subjects

Two turkey vultures (*Cathartes aura*, TV), three Harris's hawks (*Buteo jamaicensis*, HH), and one each of red-tailed hawk (*Buteo jamaicensis*, RT), Swainson's hawk (*Buteo swainsoni*, SH), barn owl (*Tyto alba*, BO), western screech owl (*Megascops kennicottii*, WS), and eastern screech owl (*Megascops asio*, ES) were tested between June and August 2022 (see Table 2 for bird names and demographics). Availability and regulations following an avian flu outbreak limited the sample sizes. Birds were housed and tested individually at three facilities: Lindsay Wildlife Experience (Walnut Creek, CA), WildCare (San Rafael, CA), and West Coast Falconry (Marysville, CA), with the first two being wildlife rehabilitation centers housing unreleasable animals, and the latter being a falconry institution. Birds were fed and cared for by their home institutions. All previously-injured birds had no known brain damage.

Table 2
Demographics and Life History

Bird	Species	Age (years)	Sex	Location	History/Use	Injuries	Trials	Approx. Height (cm)
Lord Richard	Turkey Vulture	48	Male	LWE	Born in captivity. Used as handled ambassador. Can free fly.	None	6	70
Vlad	Turkey Vulture	~37	Male	WildCare	Born in wild, but imprinted in first few months. Was once a handled ambassador.	None	5	70
Saguaro	Harris's Hawk	5	Male	LWE	Born in captivity. Used as handled ambassador. Target trained and can free fly.	None	6	50
Havek	Harris's Hawk	2	Male	WCF	Born in wild, but captured and unable to be returned. Used as falconry bird.	None	3	50
Teeka	Peruvian Harris's Hawk	11	Female	WCF	Born in captivity. Used as falconry bird	None	3	50
Odin	Swainson's Hawk	>23	Male	LWE	Born in wild, but eye injury prevented release. Used as handled ambassador.	Left eye removed	6	50
Cora	Red-Tailed Hawk	8	Female	WCF	Born in captivity. Originally falconry bird but now ambassador due to vision loss	Right eye vision loss	3	50
Tyto	Barn Owl	>18	Male	LWE	Born in wild but suffered wing injury preventing release. Used as handled ambassador. Can free fly.	Wing injury	3	30
Cypress	Western Screech Owl	~5	Female	LWE	Born in wild, but in captivity since ~3 days old. Imprinted. Used as handled ambassador. Flight trained.	None	6	20
Wee Hamish	Eastern Screech Owl	5	Male	WCF	Born in captivity. Used as animal ambassador.	None	5*	20

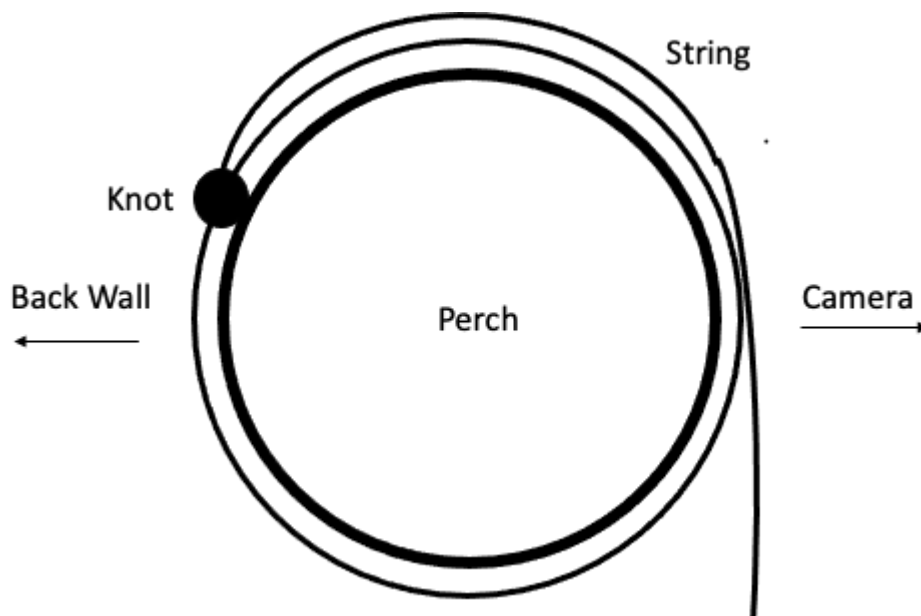
Note: LWE = Lindsay Wildlife Experience, WCF = West Coast Falconry, "Approx." = Approximate. Heights represent estimated length from bill to tail (Cornell Lab of Ornithology, 2019).
*Last two suffered from video corruption

Vlad (TV), Saguro (HH), and Hamish (ES) were tested in their overnight aviaries and Lord Richard (TV), Havek (HH), Teeka (HH), Cora (RT), Odin (SH), and Tyto (BO) were tested alone in communal aviaries. Cypress (WS) underwent her first trial in a communal aviary before moving to her more familiar overnight aviary to promote interaction with the task. Vlad (TV) was tested in an aviary open to the public, while the other birds were tested in aviaries with reduced access; however, for all birds less than 10 people passed by during a trial. Aviaries were rectangular enclosures with wire mesh walls on 1-4 sides.

Apparatus

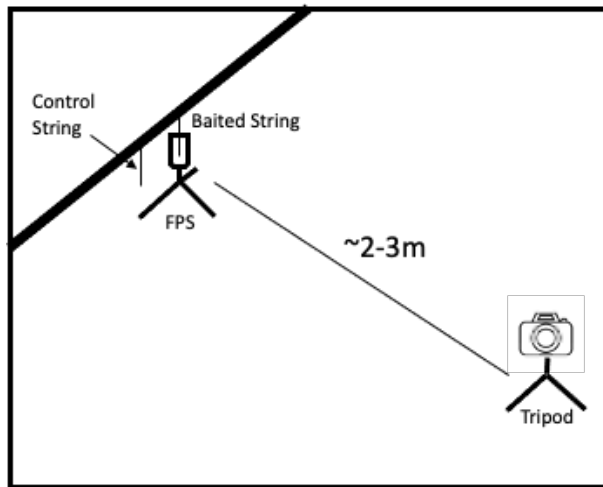
Two pieces of 4 mm diameter braided nylon paracord (hereafter referred to as “string”) were tied around the perch in the bird’s testing aviary, hanging vertically downward approximately 20 cm apart. The distance between the strings was the same for all animals to ensure both strings were within similar range of each other, regardless of species size. The unbaited string was always on the left to make procedures easier for keepers at different facilities to follow. Strings were tied so that they draped over the top of the perch, anchored by a knot placed at the back of the perch (see Figure 1), and were approximately 30 cm from the top of the perch to the meat (~20 cm for Screech Owls). One string was baited with a previously frozen piece of meat (mouse, quail or chicken, ~10 g for Screech Owls and ~20 g for the larger birds). The control string was baited with a similarly sized rock (~20 g). The control string was introduced to examine how the subjects interacted with different parts of the apparatus and if apparatus-directed behaviors were merely exploratory or focused on the food reward. A food protection stand (FPS) was constructed to prevent access to the baited string from beneath the perch. The stand consisted of a metal tripod base with a clear plastic shield attached to the top that surrounded the meat (shield 20 cm tall, 8 cm diameter for Screech Owls, shield 25 cm tall, 11 cm diameter for all other birds). Two 4.5 kg weighted bags filled with rice were placed on the base of the FPS to prevent it from falling. Trials were recorded by a Sony Handycam HDR-PJ540 attached to a tripod placed against a wall of the aviary 2-3 m from the perch (see Figure 2).

Figure 1
Arrangement of String Attachment to the Perch



Note. Knot was placed on the back of the perch facing away from the camera.

Figure 2
Example Experimental Set up in an Aviary



Note. FPS = Food protection stand

Procedure

To increase motivation, birds were tested around their normal feeding time (i.e., their previous meal was at least 12 hr prior to testing). Subjects were acclimated to the FPS and the recording equipment for between 30 and 60 min before each trial, depending upon the keeper's schedule. The two strings were then tied to a perch in the aviary while a second keeper prevented the bird from accessing the perch. Trials began when the bird was either placed on the perch or allowed access to the entire aviary. If the bird showed no attention toward the apparatus after the first 60-min trial, on subsequent trials, the reward was held in its line of sight before being placed in the FPS at the beginning of a trial. All birds except Saguaro (HH) and Lord Richard (TV) needed this procedure after the first trial. Trials ended when the bird successfully retrieved the meat or 60 min elapsed, whichever happened first. A bird "solved" the task when it grasped the meat in its beak or foot, regardless of the method used to access it. Each bird completed 3-6 trials which occurred with 3-14 days in between trials, depending on the institution's availability to test. Trial 4 for Saguaro and 4 and 5 for Hamish suffered from video corruption, eliminating behavioral data. However, CS observed Saguaro's sessions out of view and recorded solve time. The study and all procedures described were approved by the home institution's Institutional Animal Care and Use Committee (Protocol #PS22004).

Behavioral Coding and Data Analysis

Recorded trials were coded using Behavioral Observation Research Interactive Software (BORIS, Friard & Gamba, 2016). An ethogram adapted from Colbert-White et al. (2013) included effective and ineffective behaviors for solving the task (see Table 3). Gaze toward the apparatus was also recorded for each trial and was defined as a downward head tilt toward the apparatus from the perch where the strings were tied. Latency to solve was defined as the time from when the bird visually attended to the apparatus to when the food was grasped with a foot or beak, with attention to the task being the first gaze or interaction toward the apparatus. An additional measurement, latency to engage, was defined as the time from the bird having access to the apparatus to when the bird first attended to the task. Nine (20%) random trials were coded by an outside observer with κ ranging from 0.64 to 1.00 (average $\kappa = 0.74$). Discrepancies were discussed until a consensus was reached.

Table 3
Ethogram of Coded Behaviors

Behavior	Description	Type
String grab foot/beak	Grabbing the string with the bird's foot/beak	Effective
String pull foot/beak	Pulling the string with the foot/beak	Effective
String release foot/beak	Releasing the string held by foot/beak	Effective
String hold static/moving	Holding the string without moving the body for a few moments/ Holding the string while moving the body	Effective
Step on string	Stepping on the string and securing it underneath the foot	Effective
Reward grab foot/beak	Grabbing the meat with the foot/beak	Effective
Missed grab foot/beak	Missing either the string or the meat when grabbing with the foot/beak	Ineffective
Shield interaction	Touches plastic shielding around meat	Ineffective
String interaction	Touches string but does not grab or pull	Ineffective
Flying strike	Strikes shielding while flying or dropping	Ineffective
Misstep	Attempts to step on the string but misses and does not secure string beneath foot	Ineffective
Rock string interaction/pull	Touches string with rock on it or pulls on string with rock	Ineffective
Movement Perch	Moving along the perch	Other
Movement leaving/arriving	Leaving the perch/landing on the perch	Other
Out of view	Not in view of the camera	Other
Start of trial	Bird is placed on perch or released in aviary	Other
Initial interest	First attention directed toward the apparatus for the trial	Other

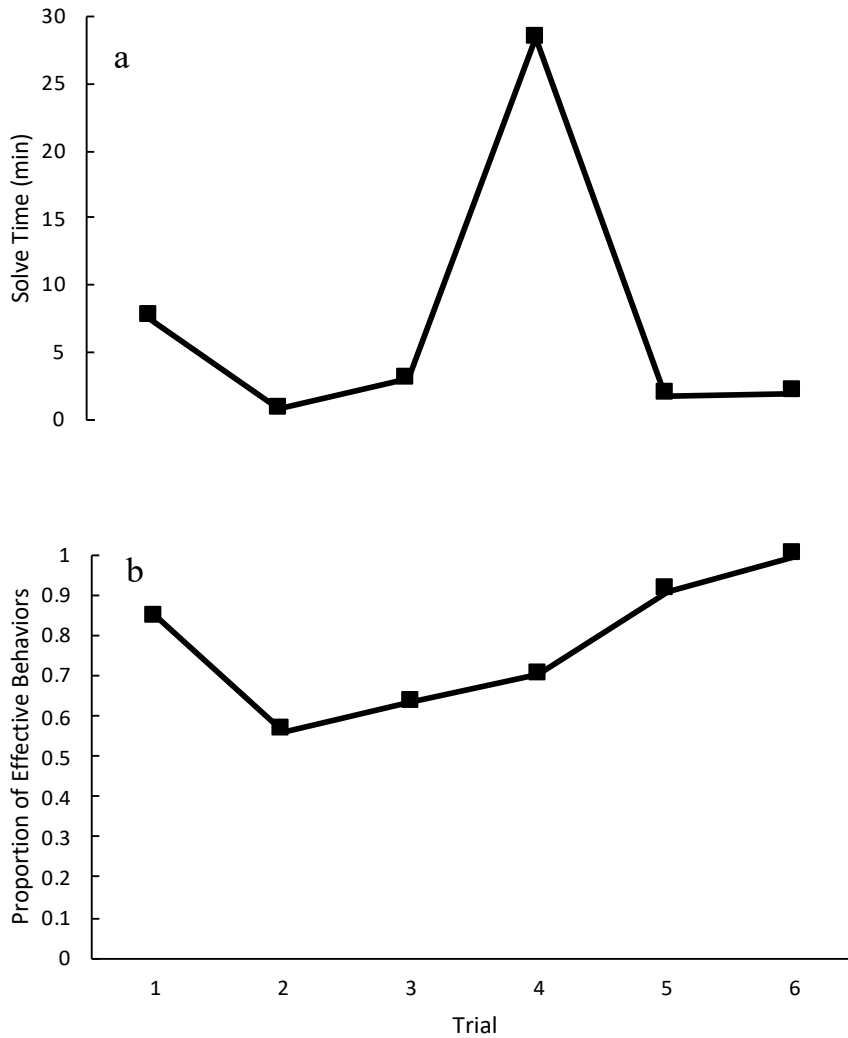
Results

Turkey Vultures

Lord Richard retrieved the meat during all six of his trials, with his first solving occurring in 7.5 min during trial one. Additionally, his solve times decreased across the trials, with all times being under 30 min. Further, the proportion of effective to ineffective behaviors he used while solving increased (see Figure 3). Lord Richard showed interest in solving immediately during all six trials with latency to engage of 0 min. Vlad solved only during his third (latency to solve = 2.15 min, latency to engage = 51 min) and fourth trials (latency to solve = 0.5 min, latency to engage = 32 min). During the first and fifth trials he directed no attention to the apparatus, while in the second trial, he attended to the meat-baited string for 2 min with no attempts to physically interact with the apparatus. Both vultures interacted with the unbaited string on one occasion. Lord Richard pulled at it during his fourth trial after pulling the baited string into close proximity to the unbaited string, and Vlad tugged on the unbaited string available above the perch during his third trial prior to solving.

Figure 3

Solve Time and Proportion of Effective Behaviors by Lord Richard



Note. (a) Solve time (min) for Lord Richard the Turkey Vulture decreased across the trials. (b) The proportion of effective to ineffective behaviors used while solving steadily increased over time after trial 1.

Both vultures solved using a pull-step-pull method, pulling on the string with their beaks and securing the string to the perch with their feet (see Supplementary Video 1). While Vlad exclusively used this method, Lord Richard also solved using a combination method of securing the string in his beak and turning from facing the front to the side of the perch until he could place the reward on it. Starting with trial 4, he used this method exclusively, never again stepping to secure the string to the perch. (see Supplementary Video 2).

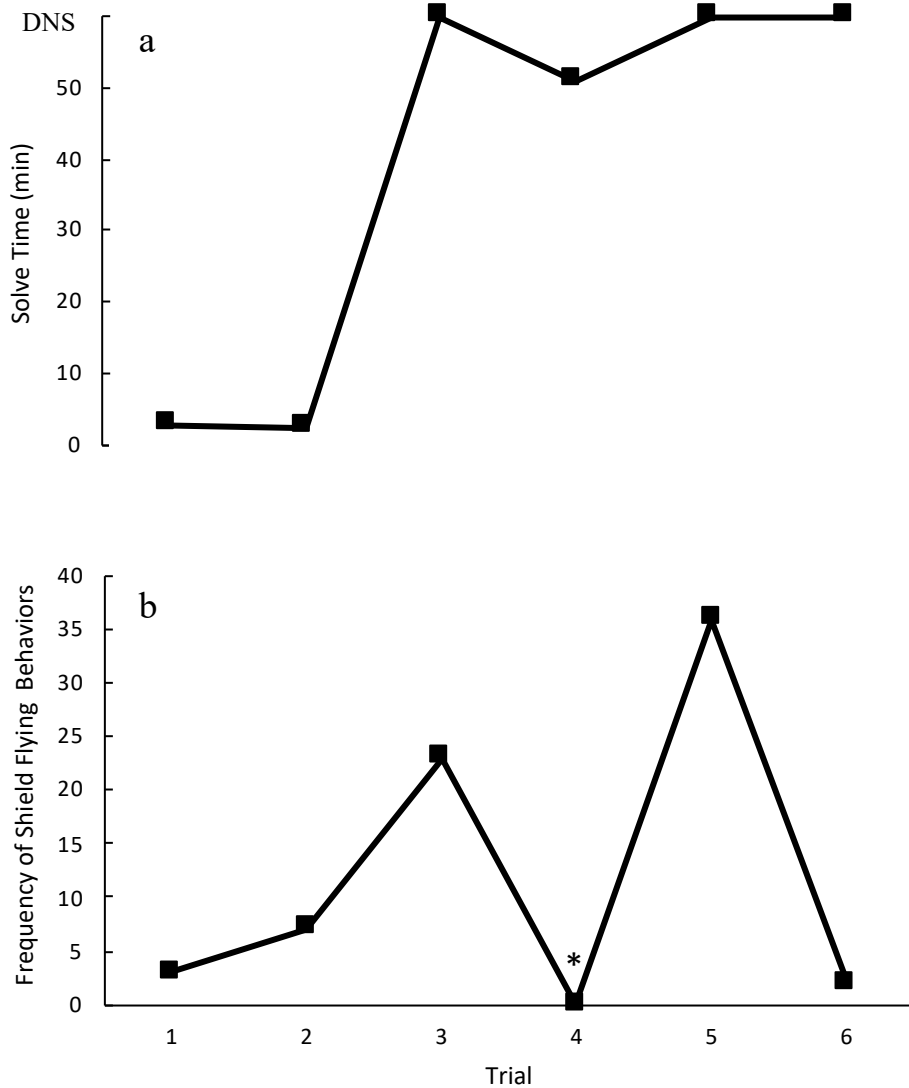
Both Lord Richard (trial 4) and Vlad (trials 1, 2, 3, 4) exhibited a behavior of tearing at the weighted bags securing the FPS. The vultures stood atop or near the bags and ripped upward with their beaks gripping the edge of the bags. Vlad demonstrated this behavior on all trials, starting during the solve phase of his first trial while Lord Richard only did this during the solve phase of his fourth trial. As Lord Richard tore at the weighted bag during trial 4, his solve time was longer than other trials, while his ratio of effective behaviors remained stable. This tearing behavior was not observed in any of the other species tested.

Harris's Hawks

All three Harris's Hawks exhibited exploratory behaviors toward the apparatus by gazing at it from different locations in the aviary and from on the perch above the meat. Teeka however, made no attempts to physically interact with the apparatus during any of her three trials. Havek also exhibited no physical interaction with the string but did attempt to reach the meat by flying at the plastic shielding around the food three times during trial 3.

Saguaro solved during 3 of his 6 trials. On the first and fourth trials, Saguaro solved them by flying into the plastic shielding with enough force to knock the meat out from the shielding and then subsequently flying and grabbing the meat with his talons (see Supplemental Video 3). During his second trial, he grasped the string as close to the meat as he could before grabbing it with his opposite foot while hovering right above the FPS (see Supplemental Video 4). Because the reward rarely popped out of the shielding when struck, Saguaro's solve times and success in solving varied across trials (Figure 4a). Persistence in attempting to solve using this shield striking behavior was seen across the trials after his success with the method in trial one (Figure 4b).

Figure 4
Solve Times and Persistence of Shield Flying Behavior by Saguaro



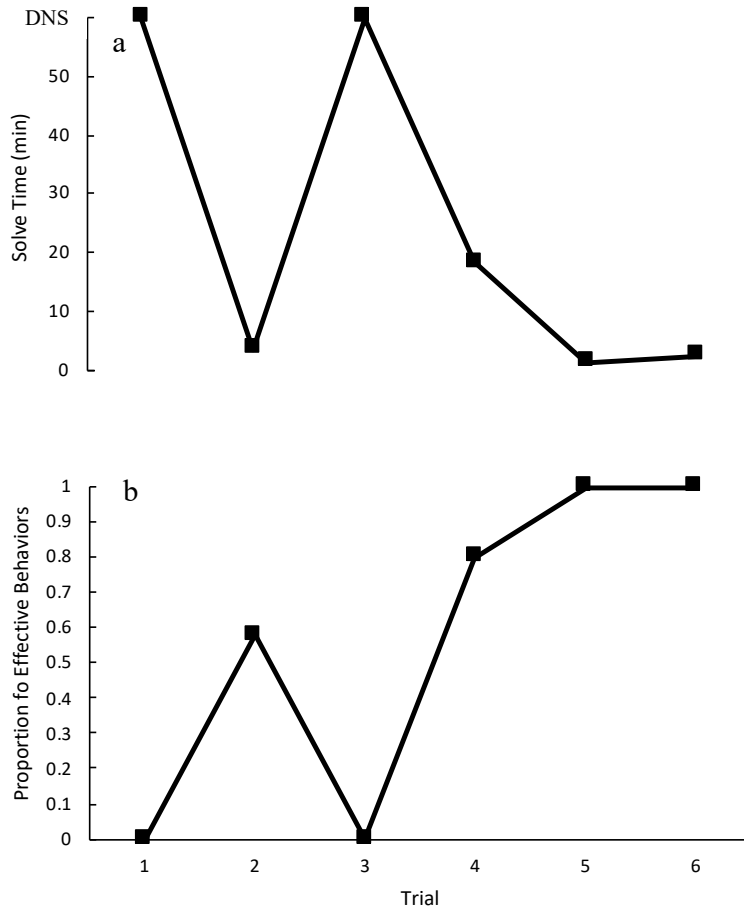
Note. (a) Solve times (min) varied across trials for Saguaro the Harris's Hawk. DNS = did not solve by the 60 min time limit. (b) Persistence of the flying into the shield behavior was shown across all trials. * denotes video recording error occurred for this trial so it was not included in analysis.

Screech Owls

Hamish solved the task during on his third trial, out of five trials (latency to solve = 2 min, latency to engage = 0.33 min) after exhibiting no attempts to physically interact with the apparatus in trials 1 and 2. To solve during trial 3, he landed inside the FPS and grasped the string with his feet before flying out and removing the food from the shielding. He then flew and yanked the reward from the string (see Supplemental Video 5).

Cypress solved the task in under 20 min during trials 2, 4, 5, and 6, while directing no attention to the apparatus in trials 1 and 3 (see Figure 5a). Over the trials, she utilized an increasing proportion of effective behaviors to ineffective behaviors when solving (see Figure 5b). An approximation of the step-pull-step method was used to solve by Cypress, involving gripping and pulling the string first with her beak, then reaching down with her foot to grip and hold the string, then pulling again with her beak (see Supplemental Video 6).

Figure 5
Solve Times and Proportion of Effective Behaviors by Cypress



Note. (a) Solve times (min) for Cypress the Western Screech-Owl varied generally over time. (b) The proportion of effective to ineffective behaviors she used increased over time beyond trial 3 where no attempts were made toward the apparatus.

Barn Owl, Swainson’s Hawk, and Red-tailed Hawk

Odin (SH) showed no attention to the apparatus during his 6 trials. Tyto (BO) engaged in a single instance of attention directed toward the reward at the very beginning of his second of three trials. Cora (RT) directed attention toward the apparatus from perches in the aviary including on the perch above the food. However, she did not physically interact with the apparatus during any of her three trials with the exception of one attempted reward grab with her beak 9 mins into trial 1.

Discussion

Four of the seven species of raptors tested solved the task according to our definition of accessing the food reward. The turkey vultures and western screech owl solved the task consistently and used traditional string-based methods. One Harris's hawk and the eastern screech owl accessed the meat infrequently and without utilizing the string. The other species displayed little attention to the task.

Whereas Colbert-White et al.'s (2013) Harris's hawk solved the task using a pull-step-pull method in all eight trials, our sole successful Harris's hawk, Saguaro, solved by flying into the FPS. Colbert-White et al.'s (2013) hawk had previous experience using baited string lures when being flown as a falconry bird; Saguaro did not. Individual history and personality have strong influences on cognition (Thorton & Truskanov, 2022). Being previously flown involving food on string lures may have caused Colbert-White et al.'s (2013) hawk to develop certain cognitive traits that mediated exploration, boldness, and transfer of learning from one seemingly irrelevant experience to our novel problem. This difference in the two hawks' behavior illustrates why reporting as much life history information as possible about subjects is critically important in small-*n* cognition research to more accurately interpret findings.

Natural history impacts what kinds of stimuli will best draw an organism's attention and informs how it will react to stimuli, as well as what kinds of associations are built among stimuli (i.e., learning) in the environment. From here, we turn to two natural history features relevant to our focal species and show how these features align with the behaviors we observed.

Sociality

As predicted, the social species (i.e., Harris's hawks and turkey vultures) demonstrated more participation in attending to the task (i.e., engaged with the apparatus in 65% of trials compared to 39% pooled across all trials). However, social species had equal success in actually retrieving the reward as the non-social species. For example, the non-social, solitary western screech owl solved more frequently than the only Harris's hawk to solve the task, which we did not predict.

Examining observational learning of the bird species in our study may shed further light onto the interplay between sociality and ability to solve the string-pulling task in raptors. In Ellison et al. (2015), one of the turkey vultures solved after watching a conspecific, and in Obozova and Zorina (2013), the tested owls were in a communal aviary and may have learned to solve the task via observation. In our study, birds did not have access to a conspecific solving the task and so observational learning was impossible. Observational learning is relatively common and can lead to pervasive changes in the behavior of group members (Thorton & Truskanov, 2022). The social species tested in our study may be more adept at learning from another bird and this impact of sociality on solving behavior was not present in our study. Furthermore, sociality may influence performance on non-social cognitive tasks depending upon whether it is tested with conspecifics. For example, individuals of one social bird species, orange-winged Amazons (*Amazona amazonica*), performed equally well when tested individually or in a social group on a string-pull discrimination task, but individuals tested alone took significantly longer to engage with the apparatus (Krasheninnikova & Schneider, 2014). Thus, engagement with the task in previously tested raptor species may have been facilitated somehow by the presence of group members during testing and is an opportunity for future work.

Predation Method

We observed strong evidence of apparatus-directed behaviors which aligned with species-specific predation methods, supporting our second prediction. The most common ineffective behavior the Harris's hawks displayed was flying into the protective shielding and scraping their feet against the plastic as if to grasp the food. This rapid, highly aggressive, reflexive behavior is similar to that of a hunting hawk capturing prey mid-air and may have been prompted by the hunting drive to quickly dispatch prey. While this would suggest that the hawks' behavior was guided by naturally-elicited hunting behaviors, we do acknowledge that what we classified as an "ineffective," mechanistic behavior may have been intentional haptic exploration. Krasheninnikova et al. (Supplemental Information, 2020) described a curious behavior of parrots in Kabadayi et al.'s (2017) problem solving study touching the tube apparatus with their beaks and tongue, which they initially considered to be failures, but were more likely examples of haptic exploration. While Colbert-White et al.'s (2013) Harris' hawk had prior experience with food attached to strings, our Harris' hawks may have required additional trials to fully explore the apparatus haptically before attempting to solve.

The turkey vultures' apparatus-directed behavior may have been influenced by its natural predation style of scavenging. First, the birds were very attentive to manipulating the string, which Ellison et al. (2015) attributed to how wild turkey vultures pull intestines out of a carcass. In fact, Ellison et al.'s (2015) birds solved by swallowing the string and moving it down their beaks using their tongue. While neither of our vultures solved using this technique, Vlad did engage in the string-swallowing behavior after solving in one trial. Thus, the birds may have been biologically predisposed to use feeding-like behaviors during their interactions with the apparatus. In addition to pulling at intestines, vultures typically manipulate food with their beaks to probe and tear pieces from carcasses, a behavior that requires strong beak dexterity, but little foot grasping (Shimmel, 2020; Smith et al., 2002). As such, Vlad and Lord Richard solved using a combination of either pulling and stepping or moving along the perch to access the reward. Over time, Lord Richard refined this technique away from relying on foot movements, to instead pivoting his body so the reward could be placed on the perch. This change in solving style may have stemmed from mobility challenges caused by the lack of dexterity in vultures' feet.

While hunting birds may have reduced neophobia which is correlated with more advanced cognition (Parsons et al., 2022), vultures are afforded longer time to explore and interact with a carcass due to its immovable nature. Over time, the scavenging niche could have expanded areas of the brain associated with behavioral and cognitive flexibility or innovation that authors like van Overveld et al. (2022) highlighted in their recommendation of vultures as candidates for future animal cognition research.

Despite what appeared to be intentional apparatus-directed behaviors by the turkey vultures, one behavior stood out as worthy of further consideration. The rice bag tearing behavior was reminiscent of how turkey vultures might tear open a carcass. Initially, we posited that this behavior could have been novel object exploration that was reinforcing and thus repeated. However, the first instance of the tearing behavior by both vultures occurred only after the introduction of the reward on the string, not during the habituation phase, suggesting the behavior was elicited by the presence of the food (see Timberlake's, 1993, behavior systems theory). That is, the bag tearing appears to be an elicited displacement behavior reminiscent of, for example, cats engaging in social body rubbing against the walls inside a puzzle box only when humans were in the room (Moore & Stuttard, 1979). Similarly, the look and smell of the food reward may have triggered instinctual, carcass-interaction behaviors like tearing with the beak.

Cypress the western screech owl used a combination of securing and manipulating the apparatus with both her feet and beak when solving. Flexible use of both feet and beak to solve was also observed in Obozova and Zorina's (2013) great grey owls. As hunting birds, screech owls eat a combination of rodents, reptiles, and arthropods, as well as some other small animals (Gehlbach & Stoleson, 2010). To capture such a diverse range of prey, these animals use a combination of hunting both with their feet and beak (Sutton, 1929). With this dual dexterity, Cypress may have been predisposed to coordinate her feet and beak in concert while solving the task. Additionally, western screech owls have been recorded scavenging in the wild, a behavior also observed in other owl species (Allen et al., 2019; Allen & Taylor, 2013). While it is unknown how prevalent this scavenging is, the flexibility to both scavenge and hunt may have led to increased flexibility and therefore strong performance on the task.

Challenges with the String-Pulling Task

The string-pulling paradigm has changed little since the first documented string pull study by Shepherd in 1915. Since then, it has been applied to over 100 bird and mammal species (Jacobs & Osvath, 2015). Here, we observed that features of natural history may influence both methods of engaging with the apparatus and solving behavior, illustrating natural history cannot be divorced from any conversations about developing tasks or comparing cognitive abilities across species on that task. Our findings illuminate two major issues with the task's frequent use: a conflating of what the task is measuring and confounds resulting from natural history. We expand on both in turn.

Variations on the string-pulling task have historically been credited with assessing associative learning as well as means-end understanding and insight (Jacobs & Osvath, 2015; Obozova & Zorina, 2013). While the turkey vultures and the western screech owl solved the task quickly, especially Vlad who solved the task in just over 2 min, all three birds made many ineffective behaviors on their first trial. Thus, perceptual motor feedback learning, where birds repeated behaviors that made the food come physically closer until they reached it, may better explain their behavior than more complex means-end or insight, especially given our apparatus was not able to assess this type of understanding. We encourage future work aimed at such an assessment with raptors.

Finally, while the string-pulling task can provide important information about cognition in animals, it suffers from a lack of ecological relevance across all taxa, an issue that has been raised by both mammal and avian researchers, alike (e.g., Danel et al., 2019; Halsey et al., 2006; Magat & Brown, 2009). The same apparatus design is used to test birds ranging from corvids (Taylor et al., 2010) to keas (*Nestor notabilis*; Werdenich & Huber, 2006) with conclusions drawn about cognitive differences that often ignore natural history. Because of the minimally-modified use of the string-pulling task across taxa, conclusions about cognition drawn from task performance are confounded by the task itself being outside of the range of normal behaviors the species evolved to emit in its environment. In our study, we recognize that the task had less ecological relevance for the naturally hunting birds like the Harris's hawks, which would quickly strike their prey in the wild, not needing to undergo sequences of sequential steps or beak-usage to access it. While some hawks may solve the task, perhaps with an advantage of generalized learning (e.g., Colbert-White et al., 2013), our hawks' ability to solve was likely impacted by the lack of ecological relevance when compared to species like the turkey vultures, which are not predisposed to speed, and may have more readily engaged in some of the behaviors needed to solve the task. Our work with diverse raptors further illustrates the importance of developing tasks with individual species rather than groups in mind—regardless of how similar the species in the group are considered to be—when assessing problem solving and other cognitive abilities in raptors.

Conclusions

In light of our findings, we offer two considerations for future animal cognition research: keeping natural history at the forefront of interpretation when applying common tasks to a new species and a call to expand work with lesser-studied avian taxa.

We are not the first to impress the importance of centering natural history when developing methods and interpreting findings (e.g., Balda et al., 1996; Thornton & Truskanov, 2022). Due to the large impacts of natural history on behavior, factors such as sociality, biomechanics, diet, and foraging method need to be taken into account. For the string-pulling task, the most commonly-reported method of solving by birds is the pull-step-pull method, with performance on the task—and therefore conclusions about cognition—often being measured against this method (Jacobs & Osvath, 2015). Unfortunately, this technique is only possible for birds with feet and beaks built for dexterous manipulation of the string and for whom these sorts of behaviors are biologically and ecologically relevant. Thus, the pull-step-pull is not the way many bird species would or could solve the task, if at all. We encourage thoughtful modifications on commonly-used tasks that can even the playing field in the event comparisons across species are the end-goal.

When applying standardized methods to new species, we encourage a practice made famous in Breland and Breland's (1961) famous piece, *The Misbehavior of Organisms*, in which the Brelands carefully documented errors and unexpected behaviors then connected those “failures” to the animals' natural tendencies. By reporting, for example, our turkey vultures' bag-shredding behavior, we provided yet another example of the nuanced interaction between cognition and biology. This reveals additional information about the complexity of learning employed by an individual to solve a cognitive task.

Animal cognition research can also be improved broadly by greater focus and attention paid to studying a larger variety of species, allowing a more holistic view of how various pressures can shape the evolution of cognition. By expanding to test multiple individuals across taxa, settings, and populations (where life history is clearly documented) and also reporting null findings as well as behavioral idiosyncrasies, we can identify patterns and fill in phylogenetic gaps in what cognition looks like across species. Krasheninnikova et al. (2020) offer an earnest charge to researchers to conduct these sorts of large-scale systematic assessments. While larger sample sizes within individual studies are ideal, this can be difficult to achieve with certain species such as raptors, due to logistical challenges. Still, we agree with Krasheninnikova et al. (2020) and argue that information from even one or a few individuals can be valuable as a “proof of concept” for how a particular species behaves. For example, we have demonstrated here for the first time that the western screech owl can solve the string-pull task, something that was previously unknown and expands our knowledge of owl cognition. It is our hope that our use of a standardized task, transparency, collaboration across facilities, and attention to species' individual and natural history serve as a guide and reference for future work with raptors and other species.

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References

- Abramson, C. I. (2013). Problems of teaching the behaviorist perspective in the cognitive revolution. *Behavioral Sciences*, 3(1), 55–71. <https://doi.org/10.3390/bs3010055>
- Allen, M. L., & Taylor, A. P. (2013). First record of scavenging by a Western Screech-Owl (*Megascops kennicottii*). *The Wilson Journal of Ornithology*, 125(2), 417–419. <https://doi.org/10.1676/12-176.1>
- Allen, M. L., Ward, M. P., Južnič, D., & Krofel, M. (2019). Scavenging by owls: A global review and new observations from Europe and North America. *Journal of Raptor Research*, 53(4), 410–418. <https://doi.org/10.3356/0892-1016-53.4.410>
- Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, 554(7692), 364–367. <https://doi.org/10.1038/nature25503>
- Audet, J.-N., Ducatez, S., & Lefebvre, L. (2016). The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27(2), 637–644. <https://doi.org/10.1093/beheco/arv201>
- Auersperg, A. M. I., Bayern, A. M. P. von, Gajdon, G. K., Huber, L., & Kacelnik, A. (2011). Flexibility in problem solving and tool use of Kea and New Caledonian Crows in a multi access box paradigm. *PLOS ONE*, 6(6), e20231. <https://doi.org/10.1371/journal.pone.0020231>
- Balda, R. P., Kamil, A. C., & Bednekoff, P. A. (1996). Predicting cognitive capacity from natural history: Examples from four species of corvids. In V. Nolan & E. D. Ketterson (Eds.), *Current Ornithology* (pp. 33–66). Springer. https://doi.org/10.1007/978-1-4615-5881-1_2
- Bednarz, J. C. (1988). Cooperative hunting Harris' Hawks (*Parabuteo unicinctus*). *Science*, 239(4847), 1525–1527. <https://doi.org/10.1126/science.239.4847.1525>
- Benson-Amram, S., Griebing, H. J. & Sluka, C. M. (2022). The current state of carnivore cognition. *Animal Cognition*, 1–22. <https://doi.org/10.1007/s10071-022-01709-2>
- 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. <https://doi.org/10.1098/rspb.2012.1450>
- Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2008). Experimental assessment of problem solving by *Milvago chimango* (Aves: Falconiformes). *Journal of Ethology*, 26(1), 113–118. <https://doi.org/10.1007/s10164-007-0035-2>
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, 121, 372–379. <https://doi.org/10.1037/0735-7036.121.4.372>
- Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*, 16(11), 681–684. <https://doi.org/10.1037/h0040090>
- Chiappa, P., Singh, S., & Pellicer, F. (2018). The degree of altriciality and performance in a cognitive task show correlated evolution. *PLOS ONE*, 13(10), e0205128. <https://doi.org/10.1371/journal.pone.0205128>
- Colbert-White, E. N., McCord, E. M., Sharpe, D. I., & Fragaszy, D. M. (2013). String-pulling behaviour in a Harris's Hawk *Parabuteo unicinctus*. *Ibis*, 155(3), 611–615. <https://doi.org/10.1111/ibi.12040>
- Cole, E. F., Cram, D. L., & Quinn, J. L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. *Animal Behaviour*, 81, 491–498. <https://doi.org/10.1016/j.anbehav.2010.11.025>
- Cornell Lab of Ornithology (2019). *All about birds*. <https://www.allaboutbirds.org/guide>
- Danel, S., von Bayern, A. M., & Osiurak, F. (2019). Ground-hornbills (*Bucorvus*) show means-end understanding in a horizontal two-string discrimination task. *Journal of Ethology*, 37, 117–122. <https://doi.org/10.1007/s10164-018-0565-9>
- DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, 1(5), Article 5. <https://doi.org/10.1038/s41559-017-0112>
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, 6(5), 178–190. [https://doi.org/10.1002/\(SICI\)1520-6505\(1998\)6:5<178::AID-EVAN5>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
- Ellison, A. M., Watson, J., & Demers, E. (2015). Testing problem solving in turkey vultures (*Cathartes aura*) using the string-pulling test. *Animal Cognition*, 18(1), 111–118. <https://doi.org/10.1007/s10071-014-0782-8>
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- Gehlbach, F. R., & Stoleson, S. H. (2010). Western Screech-Owl (*Megascops kennicottii*). In Jean-Luc Cartron (Ed.), *Raptors of New Mexico* (pp. 511–523). University of New Mexico Press. <https://www.fs.usda.gov/research/treesearch/36268>

- Guenther, A., & Brust, V. (2017). Individual consistency in multiple cognitive performance: Behavioural versus cognitive syndromes. *Animal Behaviour*, *130*, 119–131. <https://doi.org/10.1016/j.anbehav.2017.06.011>
- Hagler, S. J., Gibbons, A., Bednarz, J. C., Clark, W. S., & Bonter, D. N. (2022). Nest provisioning and sociality at Harris's Hawk nests in south Texas. *Journal of Raptor Research*, *56*(2), 161–170. <https://doi.org/10.3356/JRR-21-39>
- Halsey, L. G., Bezerra, B. M., & Souto, A. S. (2006). Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? *Animal Cognition*, *9*, 229–233. <https://doi.org/10.1007/s10071-006-0016-9>
- Heinrich, B. (1995). An Experimental Investigation of Insight in Common Ravens (*Corvus corax*). *The Auk*, *112*(4), 994–1003. <https://doi.org/10.2307/4089030>
- 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>
- Hofmann, M. M., Cheke, L. G., & Clayton, N. S. (2016). Western scrub-jays (*Aphelocoma californica*) solve multiple-string problems by the spatial relation of string and reward. *Animal Cognition*, *19*(6), 1103–1114. <https://doi.org/10.1007/s10071-016-1018-x>
- Humphrey, N. (1976). The Social Function of Intellect. In Paul Patrick Gordon Bateson and Robert Aubrey Hinde (Ed.), *Growing Points in Ethology* (pp. 303–317). Cambridge University Press. https://www.researchgate.net/publication/275519041_The_Social_Function_of_Intellect
- Jacobs, I. F., & Osvath, M. (2015). The string-pulling paradigm in comparative psychology. *Journal of Comparative Psychology*, *129*(2), 89–120. <https://doi.org/10.1037/a0038746>
- Kabadayi, C., Krasheninnikova, A., O'Neill, L., van de Weijer, J., Osvath, M., & von Bayern, A. M. P. (2017). Are parrots poor at motor selfregulation or is the cylinder task poor at measuring it? *Animal Cognition*, *20*(1), 1137–1146. <http://dx.doi.org/10.1007/s10071-017-1131-5>
- Krasheninnikova, A., Bräger, S., & Wanker, R. (2013). Means–end comprehension in four parrot species: Explained by social complexity. *Animal Cognition*, *16*(5), 755–764. <https://doi.org/10.1007/s10071-013-0609-z>
- Krasheninnikova, A., Chow, P. K. Y., & von Bayern, A. M. P. (2020). Comparative cognition: Practical shortcomings and some potential ways forward. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, *74*(3), 160–169. <https://doi.org/10.1037/cep0000204>
- Krasheninnikova, A., & Schneider, J. M. (2014). Testing problem-solving capacities: Differences between individual testing and social group setting. *Animal Cognition*, *17*(5), 1227–1232. <https://doi.org/10.1007/s10071-014-0744-1>
- Krasheninnikova, A., & Wanker, R. (2010). String-pulling in spectacled parrotlets (*Forpus conspicillatus*). *Behaviour*, *147*, 725–739. <https://doi.org/10.1163/000579510X491072>
- Magat, M., & Brown, C. (2009). Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1676), 4155–4162. <https://doi.org/10.1098/rspb.2009.1397>
- Manrique, H. M., Molina, A.-B. C., Posada, S., & Colell, M. (2017). Vertical string-pulling in green jays (*Cyanocorax yncas*). *Behavioural Processes*, *140*, 74–80. <https://doi.org/10.1016/j.beproc.2017.04.004>
- McClure, C. J. W., Schulwitz, S. E., Anderson, D. L., Robinson, B. W., Mojica, E. K., Therrien, J.-F., Oleyar, M. D., & Johnson, J. (2019). Commentary: Defining raptors and birds of prey. *Journal of Raptor Research*, *53*(4), 419–430. <https://doi.org/10.3356/0892-1016-53.4.419>
- Milton, K. (1988). *Foraging behaviour and the evolution of primate intelligence*. Clarendon Press.
- Moore, B. R., & Stuttard, S. (1979). Dr. Guthrie and *Felis fomesiticus* Or: Tripping over the cat. *Science*, *205*(4410), 1031–1033. <https://doi.org/10.1126/science.572990>
- Nicolakakis, N., Sol, D., Lefebvre, L. (2003). Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, *65*, 445–452. <https://doi.org/10.1006/anbe.2003.2085>
- Obozova, T. A., & Zorina, Z. A. (2013). Do great grey owls comprehend means–end relationships? *International Journal of Comparative Psychology*, *26*(3), 197–201. <https://doi.org/10.46867/ijcp.2013.26.03.04>
- Parsons, M. A., Garcia, A., & Young, J. K. (2022). Scavenging vs hunting affects behavioral traits of an opportunistic carnivore. *PeerJ*, *10*, e13366. <https://doi.org/10.7717/peerj.13366>
- Rosati, A. G. (2017). Foraging cognition: Reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. <https://doi.org/10.1016/j.tics.2017.05.011>
- Seibt, U., & Wickler, W. (2006). Individuality in problem solving: String pulling in two *Carduelis* species (Aves: Passeriformes). *Ethology*, *112*(5), 493–502. <https://doi.org/10.1111/j.1439-0310.2005.01172.x>
- Shepherd, W. T. (1915). Tests on adaptive intelligence in dogs and cats, as compared with adaptive intelligence in rhesus monkeys. *The American Journal of Psychology*, *26*(2), 211–216. <https://doi.org/10.2307/1413250>
- Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal Behaviour*, *61*(2), 277–286. <https://doi.org/10.1006/anbe.2000.1606>

- Shimmel, L. (2020). Diurnal Raptors. In Rebecca S. Duerr & Laurie J. Gage (Ed.). *Hand-Rearing Birds* (pp. 329–343). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781119167792.ch20>
- Shultz, S., & Dunbar, R. (2010). Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proceedings of the National Academy of Sciences*, *107*(50), 21582–21586. <https://doi.org/10.1073/pnas.1005246107>
- Smith, H. R., DeGraaf, R. M., & Miller, R. S. (2002). Exhumation of food by turkey vulture. *Journal of Raptor Research*, *36*, 165.
- Sutton, G. M. (1929). Insect-catching tactics of the screech owl (*Otus asio*). *The Auk*, *46*(4), 545–546. <https://doi.org/10.2307/4076209>
- 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>
- Thornton, A., & Truskanov, N. (2022). The role of natural history in animal cognition. *Current Opinion in Behavioral Sciences*, *46*, 101154. <https://doi.org/10.1016/j.cobeha.2022.101154>
- Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105–128. <https://doi.org/10.1901/jeab.1993.60-105>
- van Lawick-Goodall, J., & van Lawick-Goodall, H. (1966). Use of tools by Egyptian vultures *Neophron percnopterus*. *Nature*, *212*, 1468–1469. <https://doi.org/10.1038/2121468a0>
- van Overveld, T., Blanco, G., Moleón, M., Margalida, A., Sánchez-Zapata, J. A., de la Riva, M., & Donázar, J. A. (2020). Integrating vulture social behavior into conservation practice. *Ornithological Applications*, *122*(4), 1–20. <https://doi.org/10.1093/condor/duaa035>
- van Overveld, T., Sol, D., Blanco, G., Margalida, A., & de la Riva, M. (2022). Vultures as an overlooked model in cognitive ecology. *Animal Cognition*, *25*, 495–507. <https://doi.org/10.1007/s10071-021-01585-2>
- Venable, N. J. (1996). *Birds of Prey*. West Virginia University Extension Services.
- Vogel, H. H. (1950). Observations on social behavior in Turkey Vultures. *The Auk*, *67*(2), 210–216. <https://doi.org/10.2307/4081214>
- Werdenich, D., & Huber, L. (2006). A case of quick problem solving in birds: String pulling in keas, *Nestor notabilis*. *Animal Behaviour*, *71*(4), 855–863. <https://doi.org/10.1016/j.anbehav.2005.06.018>

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