Anim Cogn
DOI 10.1007/s10071-014-0782-8

ORIGINAL PAPER

Testing problem solving in turkey vultures (*Cathartes aura*) using the string-pulling test

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Received: 18 February 2014 / Revised: 14 May 2014 / Accepted: 25 June 2014

Abstract To examine problem solving in turkey vultures (*Cathartes aura*), six captive vultures were presented with a string-pulling task, which involved drawing a string up to access food. This test has been used to assess cognition in many bird species. A small piece of meat suspended by a string was attached to a perch. Two birds solved the problem without apparent trial-and-error learning; a third bird solved the problem after observing a successful bird, suggesting that this individual learned from the other vulture. The remaining birds failed to complete the task. The successful birds significantly reduced the time needed to solve the task from early trials compared to late trials, suggesting that they had learned to solve the problem and improved their technique. The successful vultures solved the problem in a novel way: they pulled the string through their beak with their tongue, and may have gathered the string in their crop until the food was in reach. In contrast, ravens, parrots and finches use a stepwise process; they pull the string up, tuck it under foot, and reach down to pull up another length. As scavengers, turkey vultures use their beak for tearing and ripping at carcasses, but possess large, flat, webbed feet that are ill-suited to pulling or grasping. The ability to solve this problem and the novel approach used by the turkey vultures in this study may be a result of the unique evolutionary pressures imposed on this scavenging species.

Keywords Turkey vulture · *Cathartes aura* · Cognition · String-pulling

Introduction

Selective pressures affect how animals acquire food, locate suitable habitat, maintain social bonds and avoid predation (McLean 2001; Sol et al. 2002; Emery and Clayton 2004; Turner et al. 2006; Roth et al. 2010). One of the greatest ecological drivers of cognition may be the ability to locate food. Many optimal foraging models predict animals can increase foraging efficiency by responding to cues that help predict the spatial and temporal distribution of their food (Shettleworth 1984; Devault et al. 2003; Overington et al. 2008). Animals that exploit patchy resources are subject to unique challenges (Devault et al. 2003) and the ability to recall the location, quantity and quality of a temporary food source (such as a fruiting tree or a carcass), helps ensure energetically-efficient foraging (McLean 2001; Overington et al. 2008). For example, the frugivorous African grey parrot (*Psittacus erithacus*) and Florida scrub jay (*Aphelocoma coerulescens)* rely on patchy food resources, and both display higher-order cognitive abilities (Clayton and Dickinson 1999; Pepperberg 1987, 2013). The selective pressure imposed upon scavengers may be one factor contributing to the selection of higher cognitive function in some species (McLean 2001).

The cognitive traits of scavenging corvid species such as the American crow (*Corvus brachyrhynchos*) and Common raven (*Corvus corax*) have been well documented but one of the largest groups of scavenging birds, the vultures, have

Electronic supplementary material The online version of this article (doi:10.1007/s10071-014-0782-8) contains supplementary material, which is available to authorized users.

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largely been overlooked in cognitive research (Heinrich 1995; Heinrich and Bugnyar 2005; Tebbich et al. 2007; Taylor et al. 2009; Afework et al. 2011). In fact, relatively little is known about the cognition of raptors when compared to the large body of work on passerine species (Colbert-White et al. 2013). Organisms may display similar cognitive traits because of shared ancestry, or as a result of similar ecological pressures (Van Horik and Emery 2011), consequently examining poorly-known species that share similar ecological roles with well-studied species may provide clues about the cognitive abilities of the lesser-known species (Balda et al. 1996). Thus exploring the cognitive abilities of other scavenging birds, may add to our understanding of ecological forces that shape cognition.

Few cognitive studies been conducted on raptors, including New and Old World vultures, despite anecdotal and experimental evidence of higher cognitive ability in some species (Witoslawski and Hanson 1963; Sazima 2007; Colbert-White et al. 2013). Egyptian vultures (*Neophron percnopterus*) use rocks as tools to break open ostrich eggs and have also been observed using twigs to "rake" wool from a sheep shearing enclosure to use as nesting material (van Lawick-Goodall and van Lawick-Goodall 1966; Stoyanova et al. 2010). Chimango caracaras (*Milvago chimango*), a social scavenging species from South America, and Harris's hawk (*Parabuteo unicinctus*) have both demonstrated the ability to solve simple problem-solving tasks (Biondi et al. 2010; Colbert-White et al. 2013). Black vultures (*Coragyps atratus*) in Brazil have learned that plastic bags may contain garbage and routinely open bags left on the beach by beach-goers (Sazima 2007). The ability to use tools, solve problems and recognize novel food items suggests that at least some raptor species are capable of complex cognitive processes.

Turkey vultures (*Cathartes aura*), a New World vulture, are only distantly related to Old World vultures and other Falconiformes. It is not yet understood if New and Old World vultures arose from a common ancestor or if their behavioral and physical similarities are evolutionarily convergent, resulting from shared feeding strategies (Slack et al. 2007). Turkey vultures are subject to many of the same ecological pressures as North American scavenging corvids. Turkey vultures and corvids occur in numerous and variable habitats across North and South America (Houston 1994; Balda et al. 1996; Van Horik and Emery 2011) and although turkey vultures are obligate scavengers, both turkey vultures and corvids are generalists consuming mammals, birds, reptiles and fish (Houston 1994; Kirk and Houston 1995; Devault et al. 2003; Sekercioglu 2006; Platt and Rainwater 2009). Generalists, needing to recognize and retain information about multiple food types, may require greater cognitive abilities than specialists (Reader and Laland 2002). Finally, both turkey vultures and corvids are social (Clayton and Emery 2007); turkey vultures roost communally and display social dominance (Houston 1994; Kirk and Houston 1995; McVey et al. 2008; Evans and Sordahl 2009). Social living is thought to require increased cognition because of the complex behaviours needed to maintain group dynamics (Clayton and Emery 2007; Emery et al. 2002). The feeding ecology and social behaviour parallels between corvids and turkey vultures, and evidence of high cognitive ability in other raptor species, provides a basis for exploring cognition in turkey vultures.

To compare cognition among species researchers must use methods that balance ecological relevance with experimental control and reproducibility but still allow for generalization (Balda et al. 1996; Van Horik and Emery 2011). The string-pulling task is one of the most common tests used in comparative psychology and has been given to more than 130 species of birds and mammals in over 180 studies. The test has been used to examine various mechanisms of cognition such as insight, physical cognition, instinct and associative learning (Wasserman et al. 2013). When given to avian species, the simplest version of the test consists of a reward (usually food) suspended by a length of string which is attached to the underside of a perch. The food cannot be retrieved from the ground or by flying directly at it (Heinrich and Bugnyar 2005). Variations of this test with increased complexity, such as the addition of unbaited strings, can test an animal's understanding of the problem (Heinrich and Bugnyar 2005; Seibt and Wickler 2006; Krasheninnikova and Wanker 2010; Wasserman et al. 2013). Numerous observations of pulling-like behaviour in nature, such as vultures pulling at intestines, suggest that the test is ecologically relevant for some species (Houston 1994). More importantly, the test is easy to reproduce and can be used to compare the behaviour of distantly-related species.

Few cognitive studies have been conducted on vulture species. We tested the hypothesis that turkey vultures are capable of solving problems. To do this we challenged captive vultures with the basic string-pulling task. Given the selection pressures that scavengers such as vultures and corvids share, we predicted that turkey vultures, like corvids, would be capable of solving the string pulling task. If successful, this work would provide the foundational evidence of cognitive ability in turkey vultures and hopefully encourage the application of advanced string-pulling problems to test the species' understanding of the problem.

Materials and methods

General methods

The trials for this study took place at Pacific Northwest Raptors (PNWR) in Duncan, British Columbia (BC), Canada, the North Island Wildlife Rescue Association (NIWRA) in Errington, BC and the Grouse Mountain Wildlife Refuge (GMWR), Vancouver, BC. Six turkey vultures were used in this study. At PNWR, three hand-reared turkey vultures were used: Judge Dredd, Jury and Phoenix were 7, 3 and 2 years old, respectively. All three birds were hatched and raised in captivity. These birds were on public display in a shared aviary and interacted with trainers during daily flying demonstrations. The three birds were determined to be male by genetic testing. In contrast, the two vultures at NIWRA were injured wild birds rehabilitated but deemed non-releasable: Vladimir was about 2 years old, whereas Igor, admitted as an adult, had been at the centre for 15 years. In the wild, turkey vultures live for about 15 years and up to 30 years in human care (Palmer 1988), so Igor was quite old. The birds shared an aviary and were on public display but did not interact with humans except for a yearly physical exam. At GMWR, the hand-reared vulture, Frank, was 3 years old. Frank was not on public display but participated in three daily flying demonstrations and interacted with trainers. Igor, Vladimir and Frank were never tested genetically, and since turkey vultures are not sexually dimorphic it was not possible to determine their sex. Unlike other falconry birds, the vultures were not trained using baited lures and as such, had no experience with a food reward attached to string.

At PNWR and GMWR, birds were weighed daily and maintained at weights determined by animal care personnel. At NIWRA, care personnel were unable to weigh the birds and feeding amounts were estimated based on behaviour. Birds were typically fed day-old chicken chicks and quail meat in the morning, with the exception of experimental trial days. On these days the birds were not fed in the morning. Records were maintained of food fed during experimental trials, to ensure that all birds received their daily allotment of food. If birds did not receive their daily allotment of food during the course of the experimental trials, the remainder was fed no sooner than 3 h after trials ended.

This study and the experimental procedures outlined were approved by the Vancouver Island University Animal Care Committee (Animal Use Protocol #2012-01-TR).

String-pulling

A small eye hook was installed in the underside of a perch in the vulture aviary at PNWR, NIWRA and GMWR. A 60 cm length of 3 mm nylon string with a piece of quail or chicken meat (25–30 g) attached at its end was tied to the eye hook. All six vultures were tested with the string-pulling task. A Kodak Zi8 video camera removed the need for an observer to be within sight of the birds, with the exception of Frank where an observer, inside the aviary recorded behaviours with a Sony Handycam DCR-SR80.

Experimental procedure

During a trial, each bird was given 15 min to solve the string-pulling task. The trial ended when the food was successfully retrieved or 15 min had elapsed (Heinrich and Bugnyar 2005). A trial was deemed successful when the vulture pulled the string and ingested the attached food and unsuccessful when a vulture did not ingest the food. A total of 40 trials were carried out for birds that successfully solved the task (modified from Heinrich and Bugnyar 2005). Birds that were unsuccessful were given 15 trials to solve the task. If after 15 trials they were still unable to solve the task, and were unwilling to approach the string, the birds were given up to 15 one-hour acclimation periods to see if they would overcome their hesitance. These acclimation periods were not included in the analyses.

Vultures were given between 1 and 15 trials per day and trials were conducted at random times between 09:00 and 15:00 over the course of a 22 day period. With the exception of Igor and Vladimir, the vultures were held in an area just outside of the aviary prior to the start of the trial, so they were not present when the string was baited and were unable to view this process.

When possible, vultures were separated and approached the string-pulling task alone. However, when a bird was reluctant to approach the string, even after a period of acclimation, a second vulture was introduced into the aviary. At PNWR and NIWR, the birds exhibited a strict dominance hierarchy. At PNWR, Phoenix was the most dominant, followed by Jury and lastly Judge Dredd. At NIWRA, Igor was dominant over Vladimir. As the birds at PNWR were housed together, we thought the reintroduction of a subordinate bird would help dominant birds overcome their caution.

Statistical analysis

For successful birds, a significant reduction in the time taken to solve the string pulling task was taken to indicate that a vulture had had improved its technique.

If vultures successfully completed the string-pulling problem, a one-tailed Spearman's rank correlation test was used to test if time required to solve the string-pulling task decreased over the 40 trails and the vultures had learned to understand the problem and improve their technique.

A Chi square contingency table was used to determine if the behavioural approach to solve the string-pulling problem differed significantly among birds. A difference in approach was assumed to suggest the birds learned to solve the problem by applying different techniques. The videos

Table 1 The four common behaviours recorded in the string-pulling trials conducted with turkey vultures

Behaviour	Description
1. Look at the food	The bird pauses and looks at the hanging food from the ground or perch. This is done with a turned head so that one eye is focused on the food
2. Walk along perch	The bird walks or paces along the perch that has the food hanging down
3. Tear/nibble string	The bird reaches down and grasps the string in its beak. It may jerk its head in a sideways motion (tear) or rapidly open and close its beak over the string (nibble)
4. Pull up string	The bird reaches down and takes the string in its beak. It teases the string through its beak until the food is within reach

of ten randomly-chosen trials for each successful bird were reviewed and four commonly observed behaviours were chosen for comparison (Heinrich and Bugnyar 2005) (Table 1). The frequency (and order) of occurrence for each of the four behaviours was recorded. Statistical analyses were performed on the frequency data using NCSS 2007 (Hintze 2007). All the assumptions of the Chi square test were met (Zar 2010).

Results

Three of the six birds successfully completed the string-pulling problem. Two birds (Judge Dredd and Frank) solved the problem on the first trial (5 and 3.4 min respectively). A third bird (Phoenix) was unsuccessful in the first 9 trials but solved his first trial after closely observing the actions of Judge Dredd while standing beside him on the perch, and subsequently completed the task in 6.3 min. Although Jury approached the string, he did not complete the task despite 15 h of acclimation. The two birds at NIWRA (Igor and Vladimir) did not solve the string-pulling task and avoided the string despite 15 h of acclimation. Both birds examined the string from the ground, and the perch although Igor never stood directly above the string. Vladimir explored the string on one occasion, and reached forward to nibble at the string before jumping away.

The three vultures that solved the string-pulling problem did so using a method not described in other avian species (Online Resource 1). The vultures teased the string through their beak using their tongue, and may have stored the string in their crop until the food was within reach. A Spearman's correlation was used to determine the relationship between trial number and time to solve. All three vultures showed a significant decrease in the time required to solve (Judge Dredd, Spearman's: $r_s = -0.68$, $n = 40$, $p < 0.0005$; Phoenix, Spearman's: $r_s = -0.58$, $n = 40$, $p < 0.0005$; Frank, Spearman's: $r_s = -0.67$, $n = 40$, $p < 0.0005$) (Fig. 1).

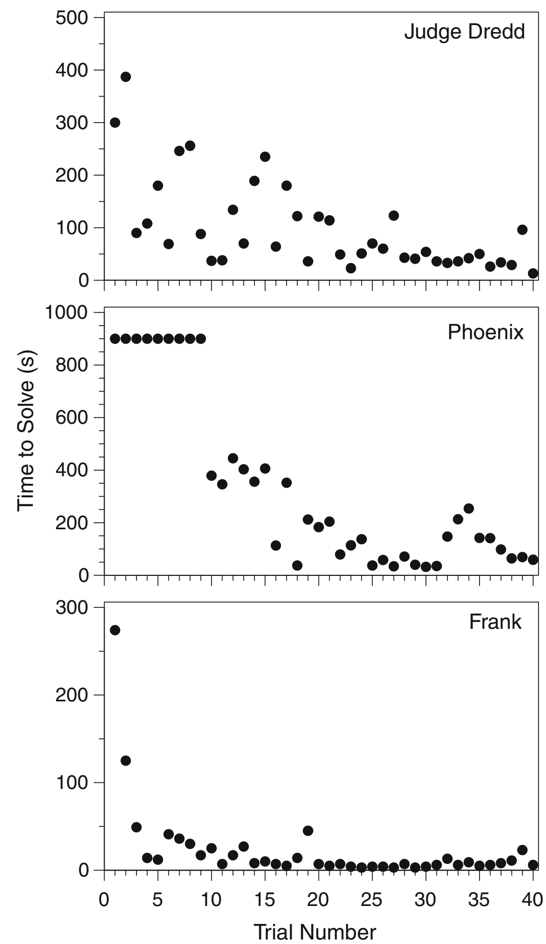

Fig. 1 Time required to solve the string-pulling task decreased significantly over the 40 trials for all three successful vultures (Judge Dredd, Spearman's: $r_s = -0.68$, $n = 40$, $p < 0.0005$; Phoenix, Spearman's: $r_s = -0.58$, $n = 40$, $p < 0.0005$; Frank, Spearman's: $r_s = -0.67$, $n = 40$, $p < 0.0005$)

During their attempts to complete the string-pulling task, the birds exhibited a number of exploratory behaviours (Colbert-White et al. 2013) such as looking at the food from the ground or from the perch, walking along the perch, nibbling or tearing at the string, and drawing the string up through their beak (Table 2). The birds never attempted to fly at the food directly. Although the three successful birds used the same technique of bringing the string up through their beak, the birds varied significantly in their approach to the task ($\chi^2 = 24.8$, $df = 6$, $p < .001$) (Tables 2, 3). Igor and Vladimir were not included in this analysis as they never attempted to solve the problem. Their acclimation periods were characterized by some exploratory behavior, pacing along the ends of the perch, but never above the string, and flying to the ground or other

Table 2 Frequency of behaviours performed in ten randomly chosen trials of the string-pulling trials conducted with turkey vultures

Behaviour	Judge Dredd	Phoenix	Frank
Look at the food	10	16	0
Walk along perch	9	7	0
Tear at string	24	37	10
Pull up string	25	9	13
Total	68	69	23
Total success	10	8	10

Table 3 Sequence of behaviours used by three turkey vultures to solve the string-pulling task in ten randomly chosen trials

Individual	Trial number	Time to solve	Behaviour
Judge Dredd	2	6:50	3-3-3-4-3-2-1-4-3-4-1-4-4-1-4-1-3-4-1-3-3-3-4-4
	4	1:37	2-1-2-1-2-3-2-4
	10	1:21	2-3-2-3-2-4-4
	13	1:07	4-1-3-3-1-3-3-4-4
	17	2:20	4-4-4-4-2-2-2-4
	25	0:51	3-4
	26	1:10	3-3-3-4-4-4
	38	0:18	2-4
	39	0:21	2-4
	40	2:17	4-1-4-4-3-3-3-3-4-4
Phoenix	5	Did not solve	2-1-2-1
	8	Did not solve	1-3-3-3-2-1-3-1-1-2-3-3-3-5-3-3-3-3-1-2-1-3-2-1
	13	6:57	1-1-3-3-3-3-3-1-3-3-3-3-3-4-4
	24	0:35	1-2-4
	25	0:53	3-3-3-3-4
	27	1:10	3,3,4
	29	0:28	1-3-3-4
	35	2:11	3-3-3-3-4
	37	1:02	1-3-4-4
	40	0:51	1-3-4
Frank	6	0:41	3-3-4-4-4
	7	0:36	3-3-4-3-3-3-3-4
	9	0:17	4
	19	0:04	4
	22	0:07	3-4
	24	0:03	4
	27	0:03	4
	30	0:04	4
	38	0:03	4
	39	0:07	3-4

Description of the numbered behaviours are provided in Table 1

perches to examine the string. Jury was not included in this analysis because he was unsuccessful but his attempts were dominated by tearing at the string.

Discussion

In this study the string-pulling task was used to assess the problem-solving abilities of turkey vultures. Three out of six vultures completed the string-pulling problem and successfully retrieved the food. The birds retrieved the food in a novel manner. The vultures used their tongues to pull the string through their beak, possibly storing the string in their crop until they could reach the food. In contrast, ravens (Heinrich and Bugnyar 2005), finches (Seibt and Wickler 2006), keas (*Nestor notabilis*) (Werdenich and Huber 2006), Harris's hawk (Colbert-White et al. 2013) and many other birds use a stepwise process that involves pulling up the string, tucking it under foot, and reaching down to pull up another length to retrieve the suspended food. As scavengers, turkey vultures use their beak for tearing and gulping food, but possess large, flat, webbed feet that are poorly suited to pulling or grasping (Houston 1994; Wink 1995). Without the ability to press the string to the perch, the vultures appear to have utilized the feeding behaviour they commonly use to pull intestines and other viscera from their prey, to solve the string-pulling problem.

The successful birds took less time to acquire the food between earlier and later trials (Fig. 1) suggesting that, like corvids (Heinrich and Bugnyar 2005) and other birds of prey (Colbert-White et al. 2013), the vultures abandoned ineffective behaviours and learned to improve their technique. In addition to improving time to solve, two of the vultures (Judge Dredd and Frank) solved the problem without apparent need for trial-and-error learning. In contrast, Phoenix solved the problem only after observing Judge Dredd retrieve the food.

During the first string-pulling trials, Phoenix did not investigate the string. When Judge Dredd was placed in the aviary, Phoenix dominated the perch when Judge Dredd attempted to retrieve the food. With Judge Dredd present, Phoenix's early attempts to solve the problem were characterized by tearing at the string, pacing the perch and examining the string from different angles. After a number of unsuccessful attempts, Phoenix allowed Judge Dredd to return to the perch and retrieve the food. During the trials in which Phoenix allowed Judge Dredd to solve the problem, Phoenix stood directly beside Judge Dredd on the same perch and lowered his head to the level of Judge Dredd's as he reached for the string. During these trials, Phoenix's gaze remained on Judge Dredd's head, rather than the food moving closer, suggesting he was observing the technique, rather than the reward. After observing Judge Dredd several times, Phoenix subsequently adopted the same method used by Judge Dredd to retrieve the food. Interestingly, Sazima (2007) has also noted that social learning and imitation likely contribute to the novel foraging strategies observed in black vultures. While we did not design this study to test for social learning, the observation is nonetheless interesting and should be explored with future research.

These results suggest that, compared to other birds, turkey vultures rely on their mouthparts rather than their feet to complete this standard test. Furthermore turkey vultures may be capable of social learning. Corvids such as rooks (*Corvus frugilegus*), common ravens and New Caledonian crows (*Corvus moneduloides*) have also shown evidence of social learning (Clayton and Emery 2005). The ability to learn from conspecifics may help scavengers and other generalist species locate and exploit patchy and temporally available food sources. High cognitive function and the ability to share information may be an important trait in many species of scavenging birds (Clayton and Emery 2007). Unfortunately, little research has been conducted on social behaviour in turkey vultures and, although they are observed in communal roosts of up to a hundred birds, the nature of social behaviour in turkey vultures is largely unknown (McVey et al. 2008).

Neither of the vultures at NIWRA completed the string-pulling task. The two vultures flew to the perch to examine the hanging food, and one bird flew to the ground and other perches to look at the food from different angles, but after 15 one-hour acclimation periods, the birds had only physically investigated the string on one occasion. On the ninth acclimation period, the meat was placed, still attached to the string, on top of the perch to see if the birds would investigate the testing materials. Vladimir flew to the perch and attempted to retrieve the meat. The meat fell from the top of the perch and was partially hanging over the side. Vladimir reached for the string that was looped around the perch, and pulled the meat to within reach but did not ingest it. This was the only occasion that a vulture at NIWRA physically interacted with the string.

In this study, four of six vultures were hesitant to approach the string pulling apparatus introduced into their aviaries. Hesitant or nervous behaviours were characterized by flying away to far corners of the aviary, avoiding the experimental perch, pacing (either away from or on the ends of the experimental perch but not above the string), hissing and jumping or flying away from the string if/when approached. At PNWR and NIWRA, the most dominant bird (Phoenix and Igor, respectively) was most reluctant to approach the experimental set-up. Phoenix appeared curious but nervous and would not immediately approach the string placed in the aviary. At NIWRA, Igor, although the more dominant bird never moved closer to the string until Vladimir had approached first. Neither Phoenix, Jury nor Igor approached the string until a less dominant bird had explored it first.

A similar pattern was documented in ravens by Heinrich (1999). Dominant ravens appeared to allow the other birds to assume the risk of assessing a novel and potentially dangerous situation. Similarly, dominant vultures were most cautious, and did not approach the testing apparatus until a less dominant bird had explored the item first. Fear of the unknown may be an adaptation to the dangers associated with scavenging; fearful or cautious birds survive. This should be considered when designing cognitive studies (Evans and Sordahl 2009; Kirk and Houston 1995) as longer acclimation periods may be required before the birds can overcome their neophobia. We had not anticipated such strong neophobic behaviours in some of the birds, otherwise all birds would have been given acclimation periods prior to trials.

The results of this study suggest turkey vultures use existing behaviours to solve new problems. Turkey vultures feed almost exclusively on carrion and depend upon spatially and temporally patchy food. Locating and exploiting such resources may require cognitive skills similar to those described in other avian scavengers, frugivores and nut eating birds (Clayton and Dickinson 1999; Pepperberg 1987, 2013). Additionally since turkey vultures specialize on feeding on soft viscera and scraps at carcass sites (Hertel 1994), it is likely that their novel approach to the string-pulling problem, gathering the string in their crop until the food was accessible, is a function of their feeding methodology and weak feet. The vultures at PNWR exhibited a behaviour similar to string pulling when fed day old chick carcasses. The chick carcasses had a yolk sac and when the other raptors fed, the yolk was torn open and often dripped or fell to the ground; whereas vultures drew the yolk out in long strings and delicately consumed the yolk sacs in a manner similar to the way they pulled and stored string.

Turkey vultures thus used a unique method to complete the string pulling task, showed apparent evidence of social learning, reduced the time needed to complete the string pulling task, and displayed a response to novel objects, similar to that seen in ravens. While these results may not be evidence of causal reasoning, further research is needed to understand the cognitive mechanisms that turkey vultures use when problem solving. Recent studies have suggested string-pulling success is the result of positive perceptual feedback and not reasoning. That is, as the reward is pulled closer the behaviour is reinforced and the animal continues the behaviour until the reward is within reach (Taylor et al. 2010; Seed and Boogert 2013). To see if turkey vultures are applying means—end understanding or responding to perceptual feedback, transfer tasks, such as adding an unbaited string beside the reward string, or using a design that restricts visual feedback during string-pulling would be required. It is hoped that the results of this study stimulate studies of cognition in vultures or other species adapted to scavenging.

Acknowledgments We would like to thank Dr. Elliott Marchant for acting as a consultant during this project. We would also like to thank Gill and Robyn Radcliffe of Pacific Northwest Raptors, Julie Mackey of the North Island Wildlife Rescue and Devin Manky of the Grouse Mountain Wildlife Refuge for allowing us to work with their vultures, and for their continued support and enthusiasm. We would also like to thank Ron Ydenberg for funding the research at Grouse Mountain for his helpful insights and discussion. This study was funded by the Biology Department at Vancouver Island University.

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