Olfactory Discrimination in a Captive Turkey Vulture

(*Cathartes aura*)

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Abstract

Birds are not known for their sense of olfaction; in fact, until recently it was thought that all birds had a markedly poor sense of smell in comparison to mammals. Recent studies, however, have proven otherwise. Although only a select few birds species have been found to rely heavily on olfaction for food and nest location, a sense of olfaction is by no means absent in birds. There have been numerous studies on avian olfaction but to date there have been no studies directly testing a turkey vulture's ability to use olfaction in a discrimination task, and the methods employed in other studies on this subject are inconclusive. By utilizing a behavioral olfactory discrimination task, this study aims to test a thirteen-year-old captive turkey vulture's use of his sense of olfaction to discriminate between visually identical unscented and peppermint scented containers. In a preliminary study, Stan performed well above chance levels during every session of a visual discrimination task. Similarly, results of an olfactory discrimination task indicate that Stan chose the correct container (scented with peppermint extract) significantly more often than the unscented container. Although a right side bias was initially observed and although Stan adopted a win-stay-lose-shift strategy, those strategies were eliminated with the introduction of negative punishment. Stan was successfully able to use olfaction as cue to earn a food reward; however, he did not appear to develop an effective discrimination learning set and he did not generalize well from one stimulus type to another. These results suggest that wild turkey vultures may also be able to use odorants as a cue to find food or discriminate between carrion at different stages of decomposition,

and that they may be similarly predisposed to use simple heuristics (i.e., win-stay-lose-shift) when faced with cognitive challenges.

Olfactory Discrimination in a Captive Turkey Vulture (*Cathartes aura*)

Vision and audition dominate as the primary senses used by birds in foraging, social interactions, and orientation. Their exquisitely diverse plumage, their ability to thrive within the three dimensional world offered by flight, and the complexity and diversity of their vocalizations confirm that vision and audition are likely the dominant senses of most avian species; however, the body of knowledge encompassing avian olfaction has begun to grow, revealing the role of olfaction in the lives of an increasing number of bird species.

History of Avian Olfaction Research:

The modern history of research into avian olfaction is (for the most part) one of pioneering female scientists (specifically Bernice Wenzel and Betsey Bang) who have paved the way to investigation of an otherwise neglected avian sense (Bang & Wenzel 1985; Birkhead, 2012). However, much earlier John James Audubon was the first to conclude that turkey vultures utilized their olfactory sense to locate food, though he came to these conclusions through a series of poorly designed experiments (Birkhead, 2012). Audubon's flawed methodology went unnoticed and despite anatomical evidence to the contrary, his conclusions were considered valid and untested until Betsey Bang and Stanley Cobb's comprehensive comparative study of avian olfactory anatomy.

Bang and Cobb's results transformed the study of avian olfaction from one of neglect at best to one of wide-open potential for new investigations. In their first study, Bang and Cobb (1968) described the olfactory ratio (the ratio of the diameter of the olfactory bulb to the diameter of the cortex, expressed by Bang & Cobb as percentages)

in 108 different avian species. The birds with the largest olfactory ratios had the largest olfactory bulbs; the assumption was that larger size meant a greater likely role for the olfactory sense in these birds. Apterygiformes (kiwis) (34%) and Procellariiformes (albatrosses, petrels and shearwaters, storm petrels, and diving petrels) (29%) had the highest mean olfactory ratio, and of all of the birds in the study, snow petrels (*Pagodroma nivea*) (37%) had the highest olfactory ratio followed closely by kiwis (*apteryx australis*) (34%). Psittaciformes had the lowest mean olfactory ratio percent (8%). The olfactory ratios measured by Bang and Cobb fit in well with what was known about the behavior of these particular species. For example, it is not surprising that a nocturnal, ground dwelling bird like the kiwi would have a high olfactory ratio, since the selection pressures of this particular niche would be for a sense that does not require light.

Bang and Cobb's 1968 study documented the extent of olfactory systems in avian species. However, their simple method of calculating relative ratios based on the diameter of the olfactory bulb and the diameter of the overall avian cortex proved to be problematic. This method failed to take into consideration the three-dimensional structure of the olfactory bulb, an error that led to a number of false conclusions that were resolved by subsequent research described below.

Evolution of Avian Olfaction:

It is important to ask how and why olfaction might have evolved in birds, and to answer these questions one must look to theropod dinosaurs. Recently, olfactory bulb size was compared between fossils of theropod dinosaurs and living birds (Zelenitsky,

Therrien, Ridgely, McGee, & Witmer, 2011). The results were unexpected. In general, the olfactory ratio *increased* from theropod dinosaurs to Neornithines. Psittacines (with one exception—the Kakapo (*Strigops habroptila*)) were the only exception to that trend (Hagelin 2004). From an evolutionary perspective, a superior sense of olfaction would likely provide a selective advantage to nocturnal birds, ground-dwelling birds, and birds whose food sources are particularly odiferous. Kiwis and kakapos are among the ground-dwelling, nocturnal birds with superior senses of olfaction and vultures of the genus *Cathartes* and Procellariiformes are also birds with particularly odiferous food preferences that would favor development of a superior olfactory sense (Nevitt et al., 2008; Wenzel, 1968). While the lifestyles of all of these birds are somewhat different, the selection pressures for a heightened sense of olfaction are likely very much the same. Somewhere in the evolutionary history of each of these species, individuals experienced selection pressures such that birds with heightened senses of olfaction were better able to forage, navigate, and/or engage in social interactions with one another. Zelenitsky et al. (2011) have shown that these transitions likely occurred at particular points during avian evolution – specifically during the evolution of non-avian maniraptors (a clade containing all dinosaurs that are evolutionarily more similar to modern birds than to other dinosaurs) and during the evolution of early Neornithines (modern birds).

Evidence for Olfaction in Species Other than *Cathartid* Vultures:

Olfaction is already used as one of several cues to navigation in Columbiformes (pigeons and doves) and in certain Procellariiform species; however, the importance of olfactory navigational cues in Columbiformes is a topic of contention. It seems as though

visual cues and magnetic cues (in that order) are used preferentially in distance navigation by these species. The birds draw on visual cues to navigate through familiar environments in close proximity to home and magnetic and olfactory cues are used primarily during long distance navigation through unfamiliar landscapes (Keeton 1974; Beason 2005). For example, homing pigeons treated with zinc-sulfate (a compound that induces reversible anosmia (a lack of functioning olfaction)) were unable to orient towards their home roost when they were released. Both the control birds and the experimental birds oriented homeward when released from short distances; however, the experimental birds were unable to do so when released from distances of 54-70km away from their home roost (Guilford et al., 1998). Similar findings have been documented by others (Benvenuti & Gagliardo, 1996). Interestingly, Columbiforms were among the birds with the lowest olfactory ratios in Bang and Cobb's comparative study, highlighting the potential risks associated with using anatomy only to assess olfactory abilities in birds (Bang & Cobb 1968; Birkhead, 2012).

Procellariiformes (such as shearwaters and petrels) forage and navigate through featureless stretches of open ocean, but they do not appear to use a magnetic sense for navigation as do pigeons (Bonadonna et al, 2003; Bonadonna et al., 2005); therefore, it was proposed that Procellariiformes rely on olfactory cues for foraging, navigation, and homing. This hypothesis was tested in Cory's shearwaters (*Calonectris diomedea*) – one of several Procellariiform species that nests in burrows and returns to those burrows in the dark of night. Controls were sham-treated with saline solution and experimental birds were treated with zinc-sulfate. After treatment the birds were released a short distance away from their nest burrows and collected again at the nest site. As expected, birds that

had been treated with zinc-sulfate were unable to locate their burrows, indicating that olfaction plays a significant role in wayfinding in this species (Benvenuti, Ioale, & Massa, 1993). In a similar study, Bonadonna and Bretagnolle (2001) tested olfactory homing abilities in nine petrel species. They compared the burrowing, surface-nesting, and crevice-nesting petrels and found that burrow-nesting petrels and crevice-nesting petrels that returned to their nest sites at night were unable to locate their nest sites when anosmia was induced by plugging their nostrils or by treating them with zinc-sulfate. In comparison, diurnal, surface-nesting birds' homing abilities were unimpaired by anosmia.

Not only do certain species of Procellariiformes utilize their sense of olfaction to orient to and locate their nest sites, but some species use olfactory cues when foraging through vast stretches open ocean. It was by sheer coincidence that Gabrielle Nevitt stumbled upon the olfactory seascape that Procellariiformes such as the wandering albatross (*Diomedea exulans*) are likely using as a cue to locate food and to navigate. Dimethyl sulfide (DMS) is a chemical compound given off by krill. The olfactory receptors of many Procellariiform species are sensitive to DMS, and since the diet of Procellariiforms consists of krill and animals that eat krill, it was hypothesized that DMS may be a cue for the presence of a food resource (Rajchard, 2008; Nevitt, 2008; Nevitt & Bonadonna 2005). To test this hypothesis, Antarctic prions (*Pachyptila desolata*) were fitted with removable heart rate monitors and exposed to DMS at natural concentrations. DMS increased heart rates in these birds, suggesting that they were capable of detecting the substance. In another study, wandering albatrosses were fitted with tracking devices and stomach temperature monitors to measure food intake. Results revealed that albatrosses did not fly straight to a food resource as one would expect of a bird using

visual cues to locate food, but instead flew in a meandering, crisscrossed pattern downwind of a food resource according to the DMS seascape produced by krill (Nevitt & Bonadonna 2005; Nevitt 2008). These results strongly suggested that wandering albatrosses and other Procellariiformes use DMS as an olfactory cue for food location.

Assuming that the olfactory ratios for birds computed by Bang and Cobb (1968) and based on anatomical data have any merit, the results of Nevitt and Bonadonna (2005) Bonadonna and Bretagnolle (2001) and Benvenuti et al. (1993) are not surprising. Procellariiformes have some of the highest olfactory ratios of the 108 bird species that were examined by Bang and Cobb.

A number of bird species that were previously thought not to have a strong sense of olfaction are now known to use olfaction in their daily lives to some degree. Psittacines (with the exception of the kakapo) historically have not been thought to have much of a functional olfactory sense. In Bang and Cobb's (1968) comparative study, Psittacines had the lowest olfactory bulb ratios of all 108 bird species, and in a more recent genetic study, Psittacines had the lowest number of olfactory receptor genes of all nine bird species tested (Steigler Fidler, Valcu, & Kempenaers, 2008). However, recent studies have challenged the anatomical data as necessarily indicative of olfactory ability. For instance, a pair of captive yellow-backed chattering lorries (*Lorius garrulous flavopalliat*) were tested for their olfactory discrimination abilities by placing a scented cotton ball above a nectar-containing dish scented with one of three odorants (palmarosa, patchouli, or geranium) and an unscented cotton ball above a dish of water. Within approximately 100 trials, both birds selected the nectar-containing dish at greater than chance levels, suggesting that olfactory cues could be used by this species as an indicator

of food (Roper, 2003). The degree to which wild Psittacines use odorants as a cue for food location has yet to be determined, but based on these results it is clear olfaction could play a larger role in the lives of Psittacines than previously realized.

Similarly, several sources assert that Passeriformes (often referred to as perching birds or songbirds) do not have a particularly “well-developed” sense of olfaction (Bang & Cobb 1968; Mennerat et al., 2005); however, it is unclear what “well-developed” truly means. The term “well-developed” suggests that there is some standard that passerines do not meet, but again, that standard is not clearly defined. Recent research suggests that bird species that were previously thought not to have a “well-developed” sense of olfaction are capable of using olfactory cues for food location, nest location, or in social interactions. Even though olfactory ratios as defined by Bang and Cobb are generally accurate predictors of olfactory prowess, a small olfactory ratio does not indicate the absence of olfactory capabilities.

European starlings (*Sturnus vulgaris*) are Passeriformes, and although Bang and Cobb did not provide an olfactory ratio for European starlings, one can assume that as members of the passerine group (Passeriformes), starling olfactory ratio is likely to be low. However, European starlings have been shown to use olfactory cues when choosing preferred nesting materials (Gwinner & Berger, 2008). Starling nests were either scented with milfoil (a preferred natural starling nest material) or vanilla. When males in the study reached breeding age they were given the choice between milfoil and vanilla scented nest material, and all of the birds chose milfoil scented nest material. In another condition, males were presented with vanilla scented or unscented nest material. Males that had been exposed to vanilla as nestlings showed a marked preference for vanilla-

scented nest material, whereas males that had been exposed to milfoil as nestlings showed no preference for either material. Not only do adult starlings discriminate between nesting material on the basis of olfactory cues but also the scent of the nest in which they were raised appears to prime them to choose nest material with a certain scent as adults (Gwinner & Berger, 2008). Other research has shown that finches (birds with some of the lowest olfactory ratios) are able to use olfactory cues to locate their nest sites (Krause & Caspers, 2012), and that mallard ducks (*Anas platyrhynchos*), Japanese quail (*Coturnix japonica*), certain auklet (*Cerorhinca*) species, and ring doves (*Streptopelia risoria*) use olfactory cues in mate selection, nestling recognition, and reproductive behaviors (Balthazart & Taziaux, 2009).

While many misconceptions still exist about avian olfaction as a result of Audubon's first experiments on the olfactory abilities of turkey vultures, the results of the research described above highlight the potential importance of olfactory cues within the avian order. Even those birds with low olfactory ratios and few olfactory receptor genes appear to be capable of using olfaction to some extent whether it be for food location, navigation, nest site location, nest material selection, reproduction, or mate selection. Turkey vultures are no exception, despite the results of Audubon's first study of avian olfaction.

Turkey Vulture Ecology:

Turkey vultures are large, soaring birds that are typically observed using thermal currents to gain altitude. They have adapted to soaring at low altitudes where odorants from carrion can more easily be detected and where visual cues are more likely to be

present. When soaring, they seem to teeter unsteadily on their outstretched five-foot long wings positioned in the shape of a “v.” It is on these currents that odorants also travel, reaching the sensitive olfactory receptors of a turkey vulture’s nose (Kirk & Mossman, 1998; Smith & Paselk 1986).

In New England, turkey vultures are partial migrants, having only recently colonized the region. A few appear to be permanent residents and most only grace us with their presence in the sky when ambient air temperatures begin to warm, leaving again in the fall as temperatures drop. Migrants arrive to nest between March and April and depart between late August and early November for their wintering grounds in the southern United States and South America. The habitat throughout which turkey vultures are found is usually hilly and forested (Kirk & Mossman, 1998).

Turkey vultures typically prefer to nest far from human habitation, and their nest sites include but are not limited to rocky outcrops, caves, burrows dug by mammals, and hollow logs. Very little is done in the way of nest construction. Monogamous pairs occupy the nest site at least two weeks before nesting, and during this time the male vulture performs a number of courtship behaviors before copulation occurs. Both the male and female vultures incubate the eggs, which are typically laid in clutches of two. Incubation lasts an average of twenty-eight days with eggs hatching one to two days apart. Brooding responsibilities are shared by both parents, who feed the nestlings by regurgitation one to two times per day. Nestlings continue to be fed by their parents until twelve weeks of age. For turkey vultures, fledging is a process that takes between one and three weeks, beginning with short flights to and from the nest site or to and from nearby food sources. At twelve weeks of age, turkey vultures leave their nest sites for

communal roosts and are no longer dependent on their parents for food (Kirk & Mossman, 1998). They continue to perfect their foraging and flying skills by observing other vultures and by trial and error learning.

Although pairs of turkey vultures nest apart from one another, they roost communally in groups that usually consist of up to one hundred birds. In areas where their range overlaps with the range of black vultures (*Coragyps atratus*), turkey vultures are often observed roosting with black vultures. Unlike black vultures, which do occasionally prey on live or dying animals, turkey vultures are almost exclusively scavengers. They feed primarily on small rodents but have been observed feeding on larger carrion as well as fish, reptiles, and amphibians. Turkey vultures, since they are opportunistic scavengers, will adapt to available food sources at any given location throughout their range. Their primary source of foraging competition comes from black vultures, which are significantly more aggressive than turkey vultures, in addition to intra-specific competition (Kirk & Mossman., 1998; Coleman & Fraser 1987; Kelly, Sparks, DeVault, & Rhodes, 2007). This competition (intra-specific in particular) was likely a selection pressure during the evolutionary history of turkey vultures. It is probable that vultures with a superior sense of olfaction (by way of a larger olfactory bulb and larger and more complex nasal conchae) were able to more quickly find carrion; therefore, they were better able to compete for food resources with black vultures or other competitors (Buckley, 1996; Kirk & Mossman 1998).

Anatomical Evidence of Olfaction in Turkey Vultures:

In addition to their preference for small carrion, turkey vultures also prefer fresh carrion. At this point, it would be prudent to begin discussing how they might be discriminating fresh carrion from putrid carrion by describing what is known about the olfactory abilities of turkey vultures. Of the 108 bird species analyzed in Bang and Cobb's 1968 study, turkey vultures were ranked ninth, with an olfactory bulb ratio percent of 28.7%, meaning that the length of the olfactory bulb made up 28.7% of the length of the brain in relation to each cerebral hemisphere. If one knew nothing about turkey vulture behavior, one might nonetheless infer from this measurement that olfaction plays a significant role in some aspect of turkey vulture life.

Bang (1964) compared the nasal organs of the turkey vulture to the nasal organs of the black vulture and three other vulture species. A number of key differences were found, and these differences highlight the olfactory prowess of turkey vultures. Bang found that turkey vultures' nostrils were significantly larger than the nostrils of black vultures. Each of these features allows for greater airflow, and the airflow is optimal for thermal currents to push air upward into the turkey vultures' nostrils. There were also notable differences between the turbinate bones of turkey vultures and those of black vultures. There are three turbinate bones in a vulture's nasal cavity: the atrial turbinate bone, the maxillary turbinate bone, and the posterior turbinate bone. The primary function of the atrial and maxillary turbinate bones is to filter, humidify, and warm incoming air as it passes over the respiratory mucosa lining each of these bones. The posterior turbinate bone is lined with olfactory epithelium. Along with other supporting cells, the olfactory epithelium is lined with olfactory cells, whose dendrites project into a

sea of cilia coating the surface of the olfactory epithelium, and Bowman's glands, which serve to secrete mucus in order to dissolve odorants and to continue to moisten the air passing through the posterior turbinate bone. The more surface area that there is over which odorants can pass, the greater the chance that they will connect with an olfactory receptor protein on the dendrite of an olfactory cell.

Plates 4 and 5 of Bang's 1964 study compare sagittal cross-sections of turkey vulture and black vulture skulls. In these cross-sections, one can see that the maxillary turbinate bone is reduced in turkey vultures and enhanced in black vultures. The reason for this discrepancy in size between the maxillary turbinate bone and consequent respiratory mucosa of the turkey vulture and that of the black vulture is unknown, but the important difference between these two species having to do with olfaction is illustrated when one looks at the posterior turbinate bone. On plates 6 and 7, cross-sections of the posterior nasal turbinate bone of each vulture species are compared. The difference is rather obvious, even to an untrained eye. The posterior turbinate of the turkey vulture is complex and offers significantly more surface area for odorants to be absorbed in the mucus and received by olfactory receptors within the olfactory epithelium. Black vultures' posterior turbinate bone are quite simple in comparison and offer far less surface area through which odorants can be absorbed. Again, even if one knew nothing about turkey vulture behavior, given this significant difference related to the anatomy of the olfactory "machinery" in each species, one can surmise that turkey vultures have something that black vultures do not, and that "something" could possibly be a keen olfactory sense; however, this conclusion cannot be based solely on anatomical evidence,

and in the following sections I will describe additional, non-anatomical evidence of olfaction in turkey vultures.

Physiological Evidence of Olfaction in Turkey Vultures:

What data are there, if any, that turkey vultures actually use their sizable olfactory epithelium to detect odors? In one study, electrophysiological recordings of bulbar activity were taken by surgically implanting three electrodes into the olfactory bulb of a turkey vulture and recording the activity in response to pure air versus particular odorants. Respiratory and heart rate measurements were also taken and they were recorded by implanting pins subcutaneously into thigh and the pectoral area of the vulture. Spindle bursts (bursts of electrical activity from the neurons in which the electrodes are implanted) increased in response to the presented olfactory stimuli along with increases in respiration and heart rate, especially when the stimulus presented was pyridine at low concentration. Not only do these results indicate that neurons in a turkey vulture's olfactory bulb are excited by a number of odors, but they do indicate that there are specific carrion-associated odors to which the response of these cells is heightened (Wenzel & Sieck, 1972).

A similar study in 1986 measured only the heart and respiratory rates of four turkey vultures in response to odors that are associated with decomposition. These odors included butanoic acid, ethanethiol, and trimethylamine. Mean change in heart rate was the highest at a concentration of 1×10^{-5} M for all odorants, and the mean change in heart rate was the highest for butanoic acid (Smith & Paselk, 1986). In this study, the authors also created a model for potential odor dispersion from a carcass in relation to the size of

the carcass and the moles of odorant released per day. Based on this model, even at low altitudes (as low as 71m above the carcass) odorant concentrations are predicted to be extremely low (between 1×10^{-10} M and 1×10^{-12} M). These concentrations would seem to be below the olfactory thresholds of turkey vultures, which would suggest that these birds are not able to use olfaction as a cue for the location of food. However, since there are a number of other odorants released from decomposing carrion, it is possible that the three chosen for testing in this particular study are not used by turkey vultures as cues for food location. As reviewed above, there is anatomical and behavioral evidence to the contrary. It is possible that this study reflects the methodological difficulties of testing olfaction and the difficulties in determining a reliable model for odorant dispersion in nature. A modified replication of this study is required to determine the merit of its results – especially pertaining to the model created for odorant dispersion, which failed to take into consideration environmental factors like temperature and humidity.

Other Evidence for Olfaction Use by Turkey Vultures:

Other evidence of for the use of olfaction in by turkey vultures has been found in the field by observing and testing the behavior of wild turkey vultures. The majority of these studies involve burying or otherwise obstructing carrion from the view of turkey vultures so that they have to rely exclusively on their sense of olfaction to locate hidden carcasses. In one such study, chicken carcasses were placed in a line 200-400m apart from one another underneath the tree canopy so that they were not visible above the canopy. After one day, turkey vultures arrived to feed at the carcasses. By day three they had located and consumed meat from 71 of the 74 carcasses. Given the density of the

forest canopy, it was very unlikely that turkey vultures were using anything but their sense of olfaction to find the hidden carrion. Additional evidence supporting this conclusion comes from the fact that although the birds were seen on the first day soaring above the canopy under which the carrion was hidden, they were unable to detect it until it decayed further and those odorants traveled into the air (Houston, 1986).

In another set of studies, turkey vulture olfaction was tested in a number of clever ways. In one case a fake deer decoy was placed in an open field in sight of turkey vultures. The birds soared over it but never descended to feed. Researchers then replaced the decoy carcass with a real deer carcass in the same location and after two days turkey vultures soared over the carcass and descended to feed on it (Wetmore, 1965). They also placed carcasses that varied in size into several visually identical boxes with ventilation and exhaust fans to allow odors to escape from the top of the boxes. This study was followed by one in which perforated boxes of carrion were hidden from view in locations where the air currents were consistent. In all of the experiments described, the turkey vultures circled over the boxes but did not descend to investigate. Similarly, turkey vultures have been observed circling over areas in which ethyl mercaptan has leaked out of natural gas lines but they do not land to search for food (Wetmore, 1965; Houston, 1986). These observations suggest that turkey vultures rely both on their sense of olfaction and on their acute vision to locate carrion and to determine whether or not the source of an odorant is a potential food resource.

There is also evidence to suggest that turkey vultures use their sense of olfaction to locate carrion that has been buried. In one instance a woodchuck (*Marmota monax*) had been buried about thirty centimeters underground in a field in Connecticut, and even

though there was no evidence of the burial (the soil had been plowed after the burial) and there were no turkey vultures seen during the burial, two days later a turkey was observed circling overhead, landing on the spot where the woodchuck was buried, digging until the carcass was exposed, and consuming parts of the carcass (Smith, DeGraaf, & Miller, 2002).

Evidence for Olfaction in Other Members of the Genus *Cathartes*:

There are two additional vulture species belonging to the genus *Cathartes*; Greater yellow-headed vultures (*Cathartes melambrotus*) and lesser yellow-headed vultures (*Cathartes burrovianus*). As with turkey vultures, observational evidence suggests that greater yellow-headed vultures use their sense of olfaction to locate food. For instance, greater yellow-headed vultures have been observed consuming carrion located under dense tree canopy in Rio Xingu, Pará, Brazil. Presumably it was impossible for the vultures to see the carrion when they were soaring above the tree canopy, so it is probable that they had used olfactory cues to find the carcasses (Rajchard, 2008; Graves, 1992). Although these other Cathartid species have not been studied as extensively as the turkey vulture, anecdotal and observational evidence suggests that they too have a sense of olfaction, which they use along with their sense of vision to aid in locating food.

Documenting Sensory Abilities in Captivity: The Use of Discrimination Learning Tasks:

The way by which the turkey vulture in this study was tested for his olfactory abilities was through the use of a discrimination learning task. In discrimination learning task, an animal is presented with two or more stimuli that vary in some presumably

discriminable dimension, and is allowed to choose between them. The animal is rewarded for choosing only one of these stimuli. If the animal is capable of detecting the key feature that discriminates this rewarded stimulus from the others, it should change its behavior over time in a way that maximizes its getting a reward. Thus, successful discrimination learning requires that the animal have the ability to detect the stimulus quality that is varying between stimulus options. Because of this, one can use discrimination tasks as a behavioral indicator of whether or not an animal can detect a given stimulus (an odor, an object, a sound, etc.) or variations in stimulus quality (amplitude, intensity, etc.).

Especially in two-choice discrimination tasks, positional effects are often observed when the animal first begins learning such a task. Often an animal will continue to choose the stimulus on either the right or the left regardless of whether or not that choice is correct (Vallortigara & Rogers, 2005). Such right or left side biases are often idiosyncratic, generally consistent within an individual (Casey & Sleight, 2001; McGreevy & Rogers, 2005), and in some cases, within a species (i.e., Schwarting & Borda, 2005).

As an animal begins learning the task, the next strategy it often employs is a “win-stay-lose-shift” strategy (Fellows, 1967). For example, if the animal chooses the stimulus on the left and that choice is correct, it will choose the stimulus on the left again in the next trial. If the animal chooses the stimulus on the left and that choice is incorrect, it will choose the stimulus on the right in the next trial. As long as a choice that the animal makes is associated with a reward, it will repeat that choice, and shift to the other choice once the original choice is no longer rewarded. Fundamental side biases and initial

heuristic strategies such as win-stay-lose-shift must be overcome before the animal is able to show that it is capable of discriminating the stimulus quality of interest.

Discrimination learning is a process that requires an animal to figure out on its own what stimulus or stimulus quality will earn it a reward. Animals that are familiar with discrimination tasks usually develop a discrimination learning set. A learning set is evidenced by the animal's ability to use previously learned behaviors to solve subsequent problems (Macphail, 1987). This means that the animal performs better on a discrimination learning task with each subsequent exposure to the task. Presumably, an animal that has developed a discrimination learning set "knows" that one stimulus in an unfamiliar set will earn it a reward, so it just has to determine which stimulus that is. Furthermore, an animal that has developed a discrimination learning set might also be able to generalize the concept of discrimination from one kind of stimulus (visual) to another (olfactory). In my study I hoped to develop a discrimination learning set in a captive turkey vulture (*Cathartes aura*) by first introducing him to numerous visual discrimination tasks prior to introducing an olfactory discrimination task.

My Study:

The purpose of the present study was to test the ability for a captive turkey vulture (Stan) (n=1) to discriminate between odorants in order to receive a food reward. Since this study tested only one subject, it is essentially a proof-of-concept study that mainly generated descriptive results. If Stan was able to discriminate between a container scented with peppermint (an arbitrarily chosen scent) and an unscented container, then he should have performed above criterion (50% correct) when all trials are taken into

consideration. In this study, I endeavored to determine whether a captive turkey vulture could use his sense of olfaction to discriminate between an unscented container and a container scented with peppermint extract. To date, there have been no behavioral studies such as this one examining the evidence for olfactory discrimination in turkey vultures. The results contribute to our understanding of whether or not wild turkey vultures are able to use olfactory cues to locate food and to discriminate between carrion at different stages of composition.

Methods

Subject:

The subject of this study was a thirteen-year-old male turkey vulture (*Cathartes aura*) named “Stan.” At the time of the study, Stan was housed at the EcoTarium in Worcester, MA, an interpretive nature center that displays live animals.

As a first year bird, Stan was found emaciated and unable to fly with a broken right wing. He was rehabilitated and trained to be used in educational programs but it was determined that he was not suited for the lifestyle of an education bird. During this time, he was housed in the mews of a falconer in Vermont. At five years old he was brought to the EcoTarium. He is in an outdoor enclosure where he is on exhibit for the public to see. I began training him two years ago to touch a target, to go to and remain at a station, and to get on a scale using positive reinforcement training techniques. Prior to the olfactory discrimination task described later in this manuscript, he was trained to perform a visual discrimination task.

Visual Discrimination Task:

Two objects (a large green plastic dog toy in the shape of a child's jack, and a rubber rainbow-colored ball) were used to begin the visual discrimination task. The green jack was arbitrarily chosen as Stan's first target object. The green jack was presented, and Stan was bridged with the word "good" and rewarded with a piece of meat if he made any movement toward the jack and finally if he touched the jack with his beak. When he was consistently touching the jack with his beak every time it was presented, a new object (a rainbow ball) was added. I held the rainbow ball in one hand and the jack in the other hand, presenting the objects so that they were equidistant from Stan and so that they were level with the perch on which he was standing. The side (right or left) on which the jack was presented was varied, although not systematically. Stan responded by touching his beak to the object of his choice. When Stan was choosing the target object in 90% of the trials during two consecutive training sessions, the alternative object (for instance, in the first set of trials, the rainbow ball) became the new target object, the original target object was retired, and another novel object was introduced. In each case, Stan's task was to identify and touch the more familiar object, obtaining a food reward if done correctly. The procedure was repeated, and the previous target object was replaced with a new object when the vulture chose the target object in 90% of the trials during three consecutive training sessions.

Each time a new object was introduced, the vulture was desensitized to that object by pairing movement toward the new object with a reward until the vulture was touching his beak to the new object each time it was presented. This procedure was repeated with seven different objects of varying shapes, sizes, textures and colors. The purpose of the

procedure was to develop a discrimination learning set in Stan, in anticipation of asking him to perform a similar set of tasks using olfactory cues only.

Preparation of the Olfactory Discrimination Task:

Latex gloves were worn at all times when handling any item used in the olfactory discrimination task. Cardboard paper towel or toilet paper tubes were cut to 7 cm in length, and four tubes were used during each training session. Four paper towels were cut to be 30 cm in length and four paper towels were also used during each training session. A piece of masking tape was placed on the bottom of each of two red, circular containers, and the containers were placed tape-side down, 45 cm apart on a black plastic tray. (The purpose of the tape was to secure the containers to the plastic tray and limit their movement). Each paper towel was folded lengthwise into the shape of a rectangle that was about 7 cm wide and 30 cm long. A photograph of this setup can be found on page 58). Two of the four rectangular paper towels were scented with 0.5mL liquid peppermint extract. Peppermint extract was drawn up from its container with a 1.0mL syringe and spread evenly along the length of each paper towel. The rectangular paper towels were each rolled up into the shape of a cylinder and placed into the cardboard tubes. One cardboard tube with a scented paper towel was placed into a container on either the left or right side of the tray based on random numbers that were generated as described in the following paragraph. Another cardboard tube containing an unscented paper towel section was placed into the remaining container.

For each trial, an online random numbers generator (<http://www.random.org/integers/>) determined the arrangement of the containers on the

tray. Peppermint was designated as “1” and the empty container was designated as “2.” For each trial, numbers were generated using this application, and whichever number (1 or 2) was generated first was placed on the left for that trial. An even number of trials was chosen for each training session so that the tube scented with peppermint and the empty tube were placed on the right or left side for the same number of trials. If necessary, I forced the side on which a certain container was placed to ensure that the scented article was presented on the left and right the same number of times.

Olfactory Discrimination Procedure:

Upon entering Stan’s enclosure, I cued him to move to his station by pointing to the station on his perch and saying the word “station” as I pointed. (This behavior had been trained in previous training sessions). If Stan moved to the station, he was bridged with the word “good” (in a clear and consistent tone) and rewarded with a small piece of meat. In these cases, the olfactory discrimination procedure was conducted on a high perch closest to the back of Stan’s enclosure. However, if the vulture was on the ground when I entered his enclosure, the procedure was conducted on a perch near the front of his enclosure.

Once Stan was on a suitable perch, the tray with the olfactory discrimination objects was presented to him. I held the tray up towards Stan so that he was making a choice from the center of the tray and the tray was level with the perch on which he was standing. Stan was allowed to choose a container after a five second wait period during which the tray was placed underneath him just out of his reach, and he indicated his choice by biting the cardboard tube or by putting his head into the container of his choice.

If Stan chose the correct container (the container with peppermint extract) he was bridged with the word “good” and he was given a small piece of meat as a reinforcer. If he chose incorrectly, negative punishment (in the form a “time out” from earning a reinforcer) was used. I remained silent and took the tray out of Stan’s sight for 20-30 seconds. No verbal or food reinforcer was given. Halfway through each training session, the cardboard tubes were replaced with a new set of tubes so that the vulture could not use a visual cue, as the tube he chose most often became dirty from his contact with them.

After each trial, I moved out of the vulture’s sight to rearrange the containers in the correct location on the tray as determined by the random numbers generator, and Stan was allowed to choose again. This was repeated until I ran out of meat or until the vulture lost interest in the task. More often than not, I ran out of meat before Stan became disinterested.

When Stan was choosing the target scent of peppermint in 90% of the trials during three consecutive training sessions, a new scent was introduced and that became the new target scent. In each case, Stan’s task was to identify and touch the container with the target scent. The procedure was repeated, and the previous target scent was replaced with a new scent when the vulture chose the correct scent in 90% of the trials during three consecutive training sessions. During each session, distraction ratings from one to four were given depending on the number of people inside and outside of the exhibit and on Stan’s previous experience with those people. The distraction ratings are defined as follows: DR1: No visitors, alone in exhibit while training; DR2: One to three visitors outside of his exhibit, alone in exhibit while training; DR3: Four to six visitors outside of his exhibit and/or unfamiliar person in his exhibit while training and/or

familiar person with whom the vulture has had primarily neutral or positive interactions;
 DR4: Over six visitors outside of his exhibit and/or a familiar person with whom the vulture has had primarily negative interactions.

Data Analysis:

Since this was a descriptive, proof-of-concept study with only one subject, very few statistical analyses were performed. Five unpaired Student's t-tests were performed. Two were performed to compare the mean number of choices Stan made across all trials of the scented or unscented containers, and of the left or right containers. An additional t-test was performed to compare the mean number of incorrect choices Stan made across all trials before and after introducing negative punishment as part of training, and two were performed to determine whether or not Stan was using a win-stay, lose-shift strategy before and after I had introduced negative punishment. The percent of correct choices for each session was calculated for both the olfactory discrimination task and the visual discrimination task. These values were calculated to determine how Stan's performance was changing over time. In addition, a linear regression was calculated. Preliminary analyses suggested that Stan's performance was negatively affected by colder temperatures, so the linear regression was performed in order to determine whether or not there was a correlation between temperature and Stan's performance on the olfactory discrimination task.

Results

Visual Discrimination:

Stan performed above chance levels (50% correct) during every session. In 19 out of 27 sessions Stan performed well above chance at 80% correct or above. He was 100%

correct during at least one session before the introduction of a new object with the exception of the introduction of a cheeseburger dog toy. During the session before the addition of the cheeseburger dog toy, 80% of Stan's choices were correct (Figure 1). Stan's performance did not increase with the introduction of each new target object, but remained high across all new conditions. For each combination of objects the average percent correct ranged between 80% and 96% (Figure 2).

Olfactory Discrimination:

For the first seven sessions Stan fluctuated between performing just above and just below chance. During these trials there was no consequence for making an incorrect choice, and Stan seemed to be exhibiting a right side bias. During the eighth session I began using negative punishment by giving Stan a time out from the opportunity to earn a reward when he made an incorrect choice. Though the results of introducing negative punishment were not statistically significant when comparing the number of correct and incorrect choices before and after introducing negative punishment, there was a visible difference in Stan's overall performance as seen in Figure 7. He made fewer incorrect choices after the introduction of negative punishment than he did before the introduction of negative punishment. In addition, there was a significant difference between the mean number of times Stan chose the correct container on a certain side and chose the container on that same side in the following trial ($p=0.0005$) or chose incorrectly on a certain side and then switched to choosing the other side in the following trial ($p=0.0002$) before and after introducing negative punishment. These data suggest that adding

negative punishment for incorrect choices significantly affected Stan's win-stay-lose-shift strategy.

After his seventh session, Stan's performance increased from 50% to 93% correct. He continued performing above chance levels until the seventeenth session during which the vet tech was present. During this trial he performed below chance levels (43% correct), and in the next session after having five days off from training his performance fell even further below chance levels (25% correct). He performed above chance in the following three trials, but fell well below chance to 16% correct during his last session in which two other people besides me were in his enclosure during the training session (Figure 3).

In order to determine what might have been causing Stan's decreased performance during particular sessions, I looked at the effects of temperature and distractions on his performance. In determining whether temperature affected Stan's performance I found that the line of best fit showed a slight negative correlation between correct choices and higher temperatures. The R^2 value for the regression line was - 0.07974 (Figure 5). I also found that Stan performed best at a distraction rating of 2 (one to three visitors outside of his exhibit, trainer alone in exhibit while training). His performance decreased at distraction ratings of 3 (four to six visitors outside of his exhibit and/or unfamiliar person in his exhibit while training and/or familiar person with whom the vulture has had primarily neutral or positive interactions) and 4 (over six visitors outside of his exhibit and/or a familiar person with whom the vulture has had primarily negative interactions) (Figure 6).

Discussion

Visual Discrimination:

Because Stan performed above chance levels during every test session, it can be said that he was able to learn a visual discrimination task. He was able to discriminate between objects of varying shapes, sizes, textures, and colors. However, I cannot say that he learned the concept of a discrimination learning set. If he had been learning about visual discrimination as a task in and of itself, then I would expect Stan's performance to have increased with each new object.. Generally, the results of this study do not show this trend. However, in four out of the five individual sessions in which a new target object was introduced, Stan chose the new object within the first two trials. Stan's performance with each object seemed to be dependent his initial reaction to the object and the time I spent introducing him to the object. For instance, at the start of the study, I spent two training sessions desensitizing him to the green jack (his first target object) and shaping the behavior of having him touch the object with his beak. When I introduced the second object (the rainbow ball) and allowed him to choose between the two, he had already been consistently touching the green jack on its own for two training sessions, so it is not surprising that he started out with such a high percentage of correct choices during the first session with both objects. I did not spend as much time introducing him to any of the other objects by themselves, they were always paired with another object and Stan had to choose between those two objects. If I saw that he was exhibiting signs of nervousness about a particular object (i.e., moving away from the object when it was presented, unwillingness to move towards the object when it was presented), I took the time to desensitize him to that object. Otherwise the first time Stan saw a new object it was

paired with another object that Stan had already seen. This could explain why his performance fluctuated during the first sessions with the rainbow ball, the red Kong toy, the tennis ball, and the cheeseburger dog toy.

Nonetheless, Stan's overall success rate with a visual discrimination task was high. This good performance was not surprising. Like hawks, falcons, and eagles, turkey vultures are bifoventate, having a central and a temporal fovea (Jones et al., 2007). The fovea is pit at the back of the eye which functions as a focal point for vision and in which only cone cells are present. Having two foveae allows turkey vultures to use vision as a cue for food location even from high altitudes, but olfaction may also be used as cue when food is obscured from view.

Olfactory Discrimination:

The results of my study indicate that Stan was successfully able to discriminate between a container scented with peppermint and an unscented container. Between sessions eight and sixteen Stan performed well above chance on this task (Figure 3), at a level similar to when he was performing the visual discrimination task. These are the sessions in which proof of concept was shown. Taken as a whole, however, Stan's performance on the olfactory discrimination task was not as consistently good as was his performance on the visual discrimination tasks. These data suggest that Stan did not generalize well from a visual discrimination task to an olfactory discrimination task (Figures 1 & 3). I believe that the reduced performance in the olfactory task (compared to the visual task) can be explained by several other factors, though, that do not have to do

with an inability to generalize from one type of task to another. I discuss these factors in the “limitations and possible confounds” section of my discussion below.

Measures were taken during the course of the study to try to reduce Stan’s use of guessing or heuristics such as win-stay-lose-shift. Negative punishment in the form of taking away Stan’s opportunity to earn a reward for a short period of time. Prior to using negative punishment, there was no consequence to Stan for making an incorrect choice. Following any incorrect answer, he was immediately allowed to choose again with the containers in the same position on the tray as they were when he made his first choice. In this case Stan would choose the container that he had not initially chosen and he would still earn a reward. This initial protocol most likely resulted in the adoption of the “win-stay-lose-shift” strategy that he was observed to employ for determining the location of the scented container. For example, if at first he chose the container on the right and that choice was incorrect, in the next trial he would choose the container on the left. If at first he chose the container on the right and that choice was correct, he would choose the container on the right in the following trial. While it was interesting that he adopted this strategy (it shows a clear, cognitive reasoning approach to solving the problem of how to get a reward as opposed to trial and error guessing), it prevented him from learning the olfactory discrimination task, because what he was attending to was likely not the odor but which side seemed to be “paying” in a particular trial. After introducing negative punishment there was a marked increase in Stan’s performance and a decrease in the number of times he used the win-stay, lose-shift strategy. These results strongly suggest that the introduction of negative punishment enhanced Stan’s performance on an olfactory discrimination task.

In the first several training sessions Stan also seemed to have a right side bias; however, that bias was also eliminated when negative punishment was introduced and a comparison between the mean number of choices he made of the right and left sides produced results that were not statistically significant, indicating that by the end of the study he did not have a right or left side bias.

Since Stan was successfully able to discriminate between a scented and an unscented container, it is possible that wild turkey vultures possess a similar ability not only to discriminate between the presence and absence of an odor but also to discriminate between two different odors. In the wild this could translate to turkey vultures possibly being able to discriminate between carrion at various stages of decomposition. Numerous sources have shown that turkey vultures prefer fresh carrion and that the birds make this choice while they are circling overhead and not after they have taken their first bite of a putrid carcass (Houston, 1986). It is possible that the birds get information about the freshness of a carcass from both olfactory and visual cues, relying primarily on olfaction when carrion is obscured from view.

Turkey vultures' ability to discriminate between the presence and absence of a carrion related odor would be adaptive, because of the competition they face from other vultures and from scavenging mammals. As stated in the introduction, turkey vultures' primary competition comes from black vultures, which are smaller but more aggressive than turkey vultures and from members of their own species. Individual turkey vultures with a particularly keen sense of olfaction to detect carrion-related odors – especially when that carrion was hidden from view – would arrive at a food source before black vultures and before their conspecifics could discover it. Ultimately this would provide a

selective advantage to those birds that were able to arrive first at a food source, outcompeting black vultures and other carcass competitors.

Limitations and Possible Confounds:

There are a number of limitations to using a single, captive subject in a study of this nature. Although Stan was flying and scavenging for at least five months before he was found with a wing injury, he has been in captivity for the majority of his life. In stark contrast to wild turkey vultures, Stan has led a relatively structured and predictable life since his move to the EcoTarium at the age of five. He is fed 140 grams of deceased mice every day, and on the days he is being trained he is given 100 grams of mice and 40-60 grams of ground horsemeat. This level of predictability likely has a muting effect on Stan's foraging strategies. It is normal for his wild counterparts to go for several days without food and to gorge on a carcass in light of the uncertainty they face with regard to the future availability of food resources. This is not the case for Stan. Not only does he have the luxury of a predictable food schedule, but also his food is almost always exposed in plain sight on a tray. On occasion his food is given to him in a foraging toy in which the food is hidden; however, the foraging toy in and of itself is enough of a visual cue to let him know where his food is, since the toy only appears when food is hidden in it. He does not have to use his sense of olfaction to know that food is hidden in a foraging toy. Surely his sense of olfaction has not disappeared, but until this study, it is a fairly safe assumption that he has not been required to use his sense of olfaction as a method for obtaining food while in captivity.

There are six different compounds that make up the peppermint oil used in this study, none of which are structurally similar to ethyl mercaptan, one of the chemicals that give decaying carcasses their characteristic, foul-smelling odor. All of the compounds within peppermint extract consist of an aromatic group and a side chain, whereas ethyl mercaptan (a key component in the smell of decaying flesh) is a two-carbon chain ending in a sulfhydryl group. In addition, peppermint extract is not behaviorally relevant to a vulture. New world vultures are attracted to carrion-related odors, and so they would have no instinctive reason to pay attention to an odor like peppermint if their olfactory receptors could detect it at all. However, the results of this study suggest that turkey vultures do have the ability to detect the compounds in peppermint extract. Although peppermint was not the ideal choice as a target scent, detecting the odor associated with peppermint was made behaviorally relevant to Stan by pairing it with a favored food reinforcer. Stan had the incentive to attend to the peppermint odor because doing so resulted in obtaining a high value food reward. Although in the context of Stan's captivity it became behaviorally relevant for him to detect this odor, the lack of any endogenous or "natural" relevancy for this scent could have affected the efficacy and speed with which he acquired the ability to successfully complete a peppermint identification task. If I were to repeat this study, I would choose an odorant (like ethyl mercaptan) that was behaviorally relevant to turkey vultures.

Odor is extremely difficult to control in an outdoor environment. Wind, temperature, and humidity are among the many factors simultaneously affecting an odor's concentration and dispersal in the air. In order to allow for Stan to put his beak into each container, the containers were left open; therefore, the odorant could disperse

freely into the air depending on the factors described above. On any given day wind, temperature, and humidity were different, so the rate, direction, and concentration at which the odor dispersed also differed. Although I hypothesized that Stan's performance would increase as the temperature increased, this was not the case. The slight negative correlation between higher temperatures and Stan's performance indicated that it was somewhat more difficult for Stan to detect odorants on a warm day. These results were not statistically significant; rather, they merely suggest a trend. The humidity was typically higher on warm days, so perhaps the presence of more water molecules in the air prevented the odorant from dispersing as it would have on a cool, dry day.

Stan was also faced with a number of potential distractions during any given training session. It is not surprising that Stan's performance was the worst when a level 3 or a level 4 distraction rating was given. The results suggest that Stan was not able to concentrate on the task at hand when there were over six visitors outside of his exhibit or when a person with whom he had primarily negative interactions was present. When a level 4 distraction rating was given, the latter was usually the case, and the vet tech at the EcoTarium was usually the person in the exhibit with us during those training sessions. Since the vet tech's job is to catch and restrain Stan for veterinary procedures, it is understandable that Stan's performance was adversely affected when she was present. He clearly must associate her with particularly negative events, and as a result, he was consistently distracted by her presence. Unexpectedly, Stan seemed to perform best when a distraction rating of 2 was given. This meant that he and I were alone in the exhibit, but there were one or two visitors outside of his exhibit. There are several possible explanations for these results. First, on these occasions visitors often asked me questions

in between trials. This allowed for a short pause between trials during which Stan could do what he wanted. Perhaps these short breaks were beneficial. Since Stan is used to visitors coming and going, it is unlikely that his behavior changed as a direct result of the presence of visitors; however, it is more likely that my behavior changed. Under the scrutiny of a small audience, perhaps I was more precise and methodical about how I conducted each trial. Despite the fact that I tried to be as consistent as possible with how I presented the odorants to Stan, there is always a chance that I could have been influencing his behavior.

Future Research:

There are several directions in which this study could be taken should I decide to replicate it or expand it in the future. First, it would be beneficial to increase the number of subjects in my study. Although testing a single subject has its benefits, I would need to significantly increase my sample size in order to have results that would be generalizable to all turkey vultures. As I said in the previous section, if I were to replicate the study I would choose a carrion-related odor that was behaviorally relevant to turkey vultures. Those odors could include ethyl mercaptan, amyl acetate, or pyridine, all of which have been proven in previous studies to elicit a physiological response in turkey vultures. Additionally, I would prefer to conduct the study indoors in as small an enclosure as the bird is comfortable in order to control odorant dispersal.

My original intention was to conduct an olfactory discrimination task with Stan using real carrion that had been left out to decompose for specific periods of time. If I found that Stan was able to discriminate between carrion at varying stages of

decomposition, it would have given me reason to believe that wild turkey vultures could do the same and that they were basing their decision to eat a particular carcass on olfactory cues. Should I have the ability to revisit work like this in the future, I would like to do so using this original plan.

It would also be interesting to determine whether or not individual turkey vultures had significantly different degrees of olfactory sensitivity. In Betsey Bang's 1964 study of turkey and black vulture nasal anatomy, she notes that turkey vultures forage in "loose" flocks, circling about a mile apart from one another in search of food. When one vulture locates food, the others follow. Since turkey vultures watch their conspecifics to locate a food source, it would be fascinating to see whether two adaptive foraging strategies prevail in turkey vulture population. It would be challenging, but not impossible, to observe wild turkey vultures foraging and to determine if there were particular birds that were always finding food first and birds that were always following the food locator to the carcass. What would be more difficult is measuring the olfactory abilities of each of those birds. These kinds of strategies persist throughout nature, particularly when it comes to mating. In cuttlefish, two mating strategies persist – one in which larger males prevail by outcompeting small males for mates and the other in which small males disguise themselves as female cuttlefish, allowing them to get close to large, male cuttlefish unnoticed and to mate with females while the large male is distracted (Norman et al., 1999). Both strategies are equally adaptive so both strategies persist. In a similar way, I think that turkey vultures could have two different but successful foraging strategies – one based on olfaction and the other based on an awareness of conspecifics.

If my hypothesis is correct, it could provide at least one reason as to why some of the data on olfaction in turkey vultures is somewhat inconclusive.

Conclusion:

Vultures play a significant but underrated role in keeping ecosystems healthy. By rapidly consuming carcasses they prevent the transmission of potentially harmful bacteria to slower-arriving mammalian hosts like rats, and in so doing they prevent the spread of disease to humans and other animals. Their importance in nutrient cycling and disease prevention was best illustrated when vultures were virtually eliminated from ecosystems in Africa and India due to accidental poisoning. Eliminating vultures caused a number of ecological and health-related problems for humans and animals alike (Beasley, Olson, & DeVault, 2012). Though there is nothing particularly groundbreaking about studying olfactory discrimination in turkey vultures, it is beneficial to continue adding to the body of knowledge about vultures and their role in their respective ecosystems. This study and future studies of vulture foraging strategies will not only benefit vultures themselves but also will benefit humans who unknowingly rely on them to serve as the clean-up crew of the world's ecosystems.

Turkey vultures are relatively unique in the bird world if they indeed have the ability to use olfactory cues to locate food. Continued research is required to determine the extent to which these birds use visual and/or olfactory cues in foraging; however, this field of research has moved forward significantly since Audubon claimed that turkey vultures were unable to use their sense of olfaction.

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Figure Legends

Figure 1: The percent of correct choices made by Stan in each session is illustrated in this figure. Labels indicate the sessions in which a new object was introduced. The bolded line at 50% indicates chance level for a two choice discrimination task.

Figure 2: The percent of correct choices versus incorrect choices made by Stan in each session is illustrated in this figure. Each set of two bars indicates combination of objects from which Stan was choosing. The first object in the label is the target object, and the bolded line at 50% indicates chance level for a two choice discrimination task.

Figure 3: The percent of correct choices made by Stan in each session is illustrated in this figure. Labels indicate the sessions where a notable event could have contributed to his decreased or enhanced performance on the olfactory discrimination task. The bolded line at 50% indicates chance level for a two choice discrimination task.

Figure 4: Illustrated in this figure is the mean number of choices Stan made of either the peppermint scented container or the unscented container and of either the container on the left or the container on the right. An unpaired Student's t-test determined that the means were significantly different in the peppermint and unscented conditions ($p=0.0027^*$), but the means were not significantly different in the left and right conditions ($p=0.3859$).

Figure 5: The effect of temperature on Stan's performance is illustrated in this scatter-plot. The line of best fit shows a slight negative correlation between correct choices and higher temperatures. The R^2 value for the regression line was 0.07974. All sessions were conducted between December 2012 and January 2013.

Figure 6: This figure shows the mean number of correct choices for each distraction rating. The distraction ratings are defined as follows: DR1: No visitors, alone in exhibit while training; DR2: One to three visitors outside of his exhibit, alone in exhibit while training; DR3: Four to six visitors outside of his exhibit and/or unfamiliar person in his exhibit while training and/or familiar person with whom the vulture has had primarily neutral or positive interactions; DR4: Over six visitors outside of his exhibit and/or a familiar person with whom the vulture has had primarily negative interactions.

Figure 7: Illustrated in this graph is the mean number of choices made in each condition before and after the introduction of negative punishment. When the mean numbers of correct and incorrect choices before and after the introduction of negative punishment were compared, the results were not statistically significant. The difference between the number of incorrect choices before and after the introduction of negative punishment was almost statistically significant ($p=0.0508$).

Figure 8: This graph illustrates the effect of introducing negative punishment on Stan's choice to use a win-stay-lost-shift strategy. There was a very statistically significant

difference between the mean number of times Stan won and stayed ($p=0.0005$) or lost and shifted ($p=0.0002$) before and after introducing negative punishment.

Figure 9: This is a photograph of the setup of the olfactory discrimination study.

Figures

Figure 1:

Figure 2:

Figure 3:

Figure 4:

Figure 5:

Figure 6:

Figure 7:

Figure 8:

Figure 9: