OLFACTORY SENSITIVITY OF THE TURKEY VULTURE (*CATHARTES AURA*) TO THREE CARRION-ASSOCIATED ODORANTS

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ABSTRACT.—The Turkey Vulture (*Cathartes aura*) is generally thought to rely on olfactory cues to locate carrion. Because vertically rising odorants are dispersed rapidly by wind turbulence, we predict that Turkey Vultures should be highly sensitive to these chemicals to detect them at foraging altitudes.

Olfactory thresholds to three by-products of animal decomposition (1×10^{-6} M for butanoic acid and ethanethiol, and 1×10^{-5} M for trimethylamine) were determined from heart-rate responses. These relatively high thresholds indicate that these odorants are probably not cues for foraging Turkey Vultures. Odorant thresholds, food habits of Turkey Vultures, and the theoretical properties of odorant dispersion cast some doubt on the general importance of olfaction in food location by this species. *Received 23 September 1985, accepted 3 March 1986.*

THE sensory modality by which Turkey Vultures (*Cathartes aura*) locate carrion has been debated by naturalists for nearly 140 years (see Stager 1964 for review). Most of the controversy concerned whether olfaction or vision was the more important sense, although other theories included an "occult" sense (Beck 1920), the noise of carrion-eating rodents, or the noise of carrion-eating insects (Taber 1928, Darlington 1930) as attracting Turkey Vultures to their prey.

Cathartes aura is now known to possess an anatomically well-developed and physiologically functional olfactory system. Comparative anatomical studies indicate that the relative size of the Turkey Vulture olfactory bulb is the eighth largest of 108 avian species reported by Bang and Cobb (1968). The olfactory tubercle in this species is scrolled and lined with an epithelium innervated by the olfactory nerve (Bang 1960, 1971; Stager 1964). Single-unit neural responses have been recorded from the olfactory epithelial receptors (Shibuya and Tucker 1967), and heart- and respiratory-rate changes are known to occur when vultures are presented with olfactory stimuli (Wenzel 1965, Wenzel and Sieck 1972). In 1938 the Union Oil Company discovered that natural gas leaks could be traced by injecting ethanethiol into gas lines and patrolling the lines for Turkey Vultures that, ostensibly, were attracted to the mercaptan (Stager 1964). Stager (1964: 56) concluded from anatomical examinations and field tests that the Turkey Vulture "possesses and utilizes a well developed olfactory food locating mechanism."

If Turkey Vultures rely on olfactory cues to find food, foraging altitudes and search patterns should be a function of their ability to respond to concentration gradients formed by carrion odorants emitted during decomposition. Numerous mathematical models predict odorant concentrations along Cartesian coordinates downwind from the odorant source. Most commonly used is the Gaussian gas dispersion model, which assumes that the concentration gradient is normally distributed in three dimensions (Strom 1976). Odorant concentrations at a given point in space decrease with respect to an increase in the parameters that affect odorant dispersion. Because wind is the principal dispersing agent for gases released into the atmosphere (Bossert and Wilson 1963), the model predicts that dispersion of a given odorant concentration is greatest in the direction of the prevailing wind (x-axis). Because the interaction of wind shear with the ground produces turbulence, dispersion is least along the vertical axis above the emission source (z-

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axis). Bossert and Wilson (1963) applied the Gaussian model to an analysis of olfactory communication in animals and provided maxima solutions for the extent of odorant dispersal along the x- and z-axes as a function of an animal's olfactory threshold. These solutions describe the maximum downwind distance (x_{max}) and altitude (z_{max}) for an odorant concentration that is above the threshold level of an animal responding to olfactory cues.

Although it is generally accepted that Turkey Vultures locate carrion from olfactory cues, olfactory thresholds to carrion-associated odorants have not been reported for this species. Presumably, their olfactory thresholds are low enough for them to detect carrion odorants at foraging altitudes. Solutions for x_{max} and z_{max} provide a model that can be used to examine the likelihood of specific carrion odorants serving as olfactory cues to foraging Turkey Vultures.

We determined approximate olfactory response thresholds to three odorants (butanoic acid, ethanethiol, and trimethylamine) associated with animal decomposition. Butanoic acid has the characteristic odor of rancid fat and is a by-product of protein, carbohydrate, and fat decomposition (Wells 1907). Several thiols, including ethanethiol, are formed from the breakdown of sulfur-containing amino acids (Wells 1907) and are the compounds used commercially to give natural gas its odor. Trimethylamine has a "fishy" odor and is released during muscle tissue decomposition (Grey and Lea 1969). In addition to the association of these odorants with animal decomposition, both ethanethiol and butanoic acid are known to elicit olfactory responses in the Turkey Vulture (Stager 1964, Wenzel and Sieck 1972).

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Response thresholds to olfactory stimuli were determined by continuous monitoring of a vulture's heart rate before and during the presentation of three concentrations of ethanethiol (ethyl mercaptan), trimethylamine, and butanoic acid (n-butyric acid). Our method was a modification of the technique employed by Wenzel (1965) and Wenzel and Sieck (1972). Each of four Turkey Vultures was repeatedly tested with three dilutions of each test odorant [1×10^{-7}, 1×10^{-6}, and 1×10^{-5} moles odorant/liter air (M), calculated at STP, for butanoic acid and trimethylamine, and 1×10^{-8}, 1×10^{-7}, and 1×10^{-6} M for ethanethiol; these concentrations were chosen from a preliminary screening of a wide range of odorant dilutions]. Odorant dilutions were presented in order of increasing concentration, with a control odorant consisting of distilled water randomly inserted within each dilution series. A minimum of 5 min elapsed between presentations of test dilutions. All three chemical odorants were used during each trial, with the order of presentation determined randomly. To minimize mixing the odorants, an exhaust fan was used for a minimum of 15 min between presentations of the different chemicals. A total of 66 trials was run using each odorant dilution series; individual sample sizes for the four vultures were 15, 16, 17, and 18 trials.

Heart rates were determined by electrocardiography (ECG). Differences in heart rate were determined by comparing the number of beats in 5-s intervals both before and after the odorant reached the bird (0 s). Net changes were established by adding the difference in the number of beats between the time intervals 0-5 s and −5 to 0 s, to the difference in the number of beats between the time intervals 5-10 s and 0-5 s. A Kruskal-Wallis analysis was used to compare heart-rate changes within treatments to determine whether the data from individual birds could be pooled. The Wilcoxon two-sample test compared heart-rate changes associated with each odorant concentration against changes recorded during the presentation of the control. Significant ($P < 0.05$) changes in heart rate between the control and odorant dilutions were interpreted as indicators of olfactory thresholds.

The Turkey Vultures used in this study were adults of unknown sex and age. Three of the four had sustained permanent wing injuries and were obtained from raptor rehabilitation centers or other researchers; there was no evidence that these injuries had affected the olfactory sense of these animals. The fourth bird was physically sound and had been raised in captivity. All four birds were maintained on a daily diet of meat and were weighed biweekly to monitor their health. Considerable time was spent habituating the vultures to the olfactometer and the ECG equipment. Test sessions always preceded daily feedings. Birds were not tested until minimal heart rates had been achieved. To minimize odorant habituation and stress, the birds were not tested more than once every three days.

Olfactometer.—The olfactometer was a modification of the simple injection olfactometer described by Moulton (1973). Our system vaporized dilute odorant into an air stream to achieve the desired odorant concentration. Diluted odorants were drawn from 15-ml ampules by a peristaltic pump at 2.9×10^{-6} l/s through 0.51-mm (ID) standard pump tubing and allowed to drip onto a glass "T" via a 20-gauge stainless steel hypodermic needle inserted through a rubber diaphragm. The glass T was wrapped with nichrome wire and electrically heated to give an instantaneous vaporization of the odorant. A regulated and calibrated airflow (3.9×10^{-2} l/s) connected to the glass T carried the vaporized odorant to a mixing chamber.

The mixing chamber was constructed from a glass powder funnel attached to a 58 × 99-mm glass tube with a perforated Plexiglas baffle placed at the junction of the funnel and glass tube. The mixing chamber was positioned through a hole in the front of a closed compartment (63 × 33 × 30 cm, constructed from plywood) in which the test bird was placed, and adjusted for optimal placement around the vulture's head. A muffin fan exhausted odorants from the compartment into an outside vent.

After each test session the mixing chamber, glass T, and animal compartment were washed with soapy water, rinsed with distilled water, and dried. The apparatus was then reassembled, and compressed air was allowed to flow through the system for at least 60 min.

Heart-rate monitoring system.—Heart rates were recorded with an ECG assembled from two preamplifiers wired in series and connected to a strip-chart recorder. The first preamplifier filtered and amplified signals between 0.3 and 10 Hz; the second preamplifier boosted the filtered signal. Electrodes for the ECG were constructed from 22-gauge × 25-mm stainless steel hypodermic needles soldered to shielded wire. Two electrodes were placed subdermally on either side of the pectoral region near the axilla. A ground electrode was placed subdermally on the vulture's back.

GAS DISPERSION MODEL

The Gaussian form of the various atmospheric gas dispersion equations (as modified by Bossert and Wilson 1963) was used to evaluate olfactory threshold values as functions of maximal downwind and altitude distances from a hypothetical carcass. Relevant solutions for the maxima are:

$$x_{\max} = \left(\frac{2Q}{K\pi C_y C_z u}\right)^{\frac{1}{2}-n}$$

and

$$z_{\max} = C_z\left(\frac{2Q}{K\pi C_y C_z u \mathrm{e}}\right)^{\frac{1}{2}},$$

where $x_{\max}$ and $z_{\max}$ are distances (cm) downwind and above the threshold level of an animal responding to the odorant. Q is the rate of odorant emission from a source in molecules/s, K is the threshold response in molecules/cm^3, C_y and C_z are diffusivity constants equal to 0.4 and 0.2 cm$^{1/8}$, respectively (see Sutton 1953), u is wind speed in cm/s, and n is a constant equal to 0.25 for wind speeds between 100 and 500 cm/s. Because empirical measures of Q for decomposing carcasses are unavailable, we assumed values of Q between 1 and 20 moles/day ($7 \times 10^{18} - 1.4 \times 10^{20}$ molecules/s) as plausible estimates. For butanoic acid (88 g/mole), Q represents a daily carcass mass loss between 88 and 1,760 g. For rodent-size carcasses, we suggest that these estimates for emission rates are likely to be high. Because $x_{\max}$ and $z_{\max}$ vary directly with the rate of odorant emission, however, our estimates of Q result in excessive odorant dispersion distances and, thus, provide a cautious test of our hypothesis. Similarly, wind speed was conservatively assumed to be 100 cm/s because odorant dispersion distances vary inversely with wind speed.

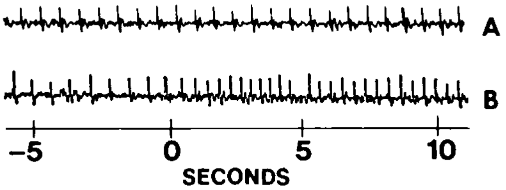
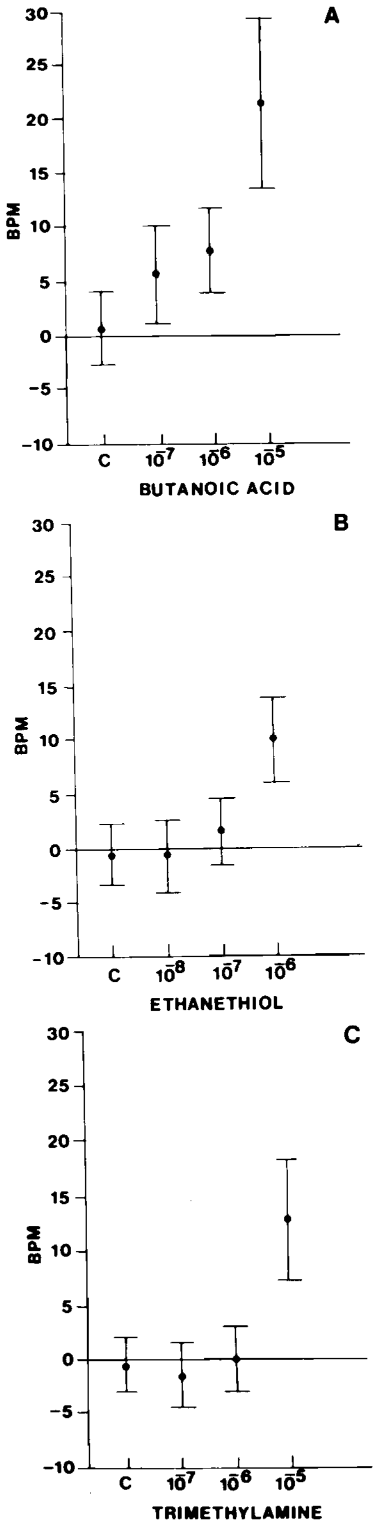


Fig. 1. Sample ECG records showing (A) no net change in heart rate following stimulation with distilled water, and (B) a net heart-rate change of 4 beats following stimulation with 1×10^{-6} M ethanethiol.

RESULTS AND DISCUSSION

The rationale for inferring olfactory responses from changes in heart rate is that the presentation of a novel stimulus to an animal tested in a homeostatic environment results in a group of autonomic nervous system responses (Wenzel 1971). These generally include changes in heart and respiratory rates but may involve other autonomic actions (Uno and Grings 1969). Wenzel (1973) demonstrated that the heart-rate response in pigeons decreases significantly after bilateral sectioning of the olfactory nerve. Monitoring heart-rate changes to study olfactory perception in birds has been used in several investigations (Neuhaus 1963; Wenzel 1965, 1973; Wenzel and Sieck 1972). Although these studies were not designed to determine threshold levels, Schmidt (1975) used heart- and respiratory-rate changes to determine olfactory thresholds in three species of neotropical bats. Similarly, respiratory-rate changes were used to evaluate olfac-



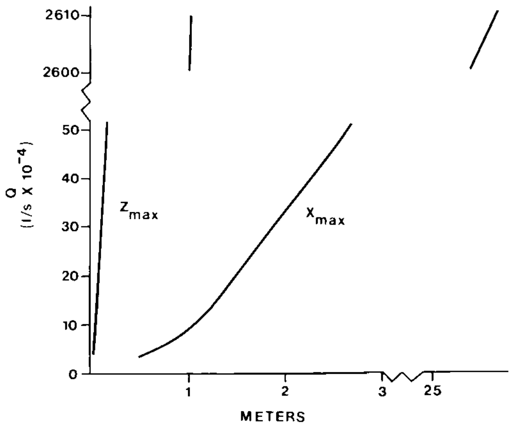


Fig. 3. The relationship between x_{max} and z_{max} for different odorant emission rates (Q). Calculations were based on an olfactory threshold (K) of 1×10^{-6} M and a wind speed of 100 cm/s.

tory thresholds in Black-billed Magpies (*Pica pica*) and pigeons (*Columba* sp.; Snyder and Peterson 1979). Zeaman and Wegner (1954) determined that heart-rate responses were as accurate indicators of threshold levels as verbal responses in auditory-perception studies of humans.

All presumptive olfactory responses were associated with an increase in heart rate (Fig. 1). Because changes in heart rate were consistent within treatments across all birds used in this study, the data were pooled for the pair-wise comparisons between controls and diluted odorants. A significant ($P < 0.008$) mean heart-rate increase of 6.8 beats per minute (BPM) was recorded at 1×10^{-6} M for butanoic acid, although nearly significant ($P < 0.09$) changes were observed at 10^{-7} M (Fig. 2A). Threshold concentrations were less ambiguous for ethanethiol and trimethylamine. A mean heart-rate increase of 10.3 BPM ($P < 0.0001$) indicated a threshold response to 1×10^{-6} M ethanethiol (Fig. 2B). Trimethylamine concentrations of 10^{-5} M resulted in a significant ($P < 0.01$) mean heart-rate increase of 13 BPM (Fig. 2C).

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Fig. 2. Mean heart-rate changes for odorant concentrations of three by-products of carrion decomposition. Solid circles represent mean heart-rate changes. Vertical lines through the means indicate 95% confidence intervals. C indicates controls.

TABLE 1. Predicted olfactory thresholds (K) at various maximum altitudes (z_{max}) and odorant emission rates (Q). Values of Q are given in different units for comparative purposes. Values of Q above the line are assumed to represent plausible emission rates. Those below the line are obviously high but are included for comparison. Calculations are for a wind speed of 100 cm/s.

Q		K		
l/s	Moles/day	$z_{max} = 3$	$z_{max} = 10$	$z_{max} = 60$
2.6×10^{-4}	1	1.5×10^{-10}	1.3×10^{-11}	3.8×10^{-13}
5.2×10^{-4}	2	3.0×10^{-10}	1.3×10^{-11}	3.8×10^{-13}
7.4×10^{-4}	3	4.3×10^{-10}	3.8×10^{-11}	1.1×10^{-12}
1.3×10^{-3}	5	7.6×10^{-10}	6.8×10^{-11}	1.9×10^{-12}
2.6×10^{-3}	10	1.5×10^{-9}	1.4×10^{-11}	3.8×10^{-12}
5.2×10^{-3}	20	3.0×10^{-9}	2.7×10^{-10}	7.6×10^{-12}
2.6×10^{-2}	100	1.5×10^{-8}	1.3×10^{-9}	3.7×10^{-11}
2.6×10^{-1}	1,000	1.5×10^{-7}	1.3×10^{-8}	3.7×10^{-10}
2.6	10,000	1.5×10^{-6}	1.3×10^{-7}	3.8×10^{-9}

GAS DISPERSION MODEL

The extent to which atmospheric turbulence near the ground impedes the vertical rise of odorants at given concentrations is reflected in the considerably steeper slope of z_{max} relative to x_{max} (Fig. 3). For an olfactory threshold of 1×10^{-6} M and what is probably a high odorant emission rate (20 moles/day), z_{max} extends only to 0.17 m above the source. If Turkey Vulture olfactory thresholds to butanoic acid and ethanethiol are 1×10^{-6} M, this analysis suggests that they should be able to detect these odorants only at exceedingly low altitudes. Furthermore, the odorant concentration at 1 m is above threshold only if the emission rate is impossibly high (2.6 l/s; Fig. 3). For butanoic acid, this emission rate yields an exceptional daily carcass mass loss of 8.8×10^5 g.

Solving the z_{max} equation in terms of the threshold value and setting z_{max} at various altitudes between 3 and 60 m suggests that olfactory thresholds between 1×10^{-10} and 1×10^{-12} M are necessary to detect any carrion-associated odorant for emission rates between 1 and 20 moles/day (Table 1). Although these odorant concentrations are considerably lower than the threshold values for Turkey Vultures, they are within the perceptual range of humans and some bats. Humans respond to butanoic acid and ethanethiol at concentrations as low as 1×10^{-11} M (Phelps 1976) and to 1×10^{-10} M trimethylamine (Zwaardemaker 1926). Schmidt (1975) reported olfactory thresholds of the vampire bat (*Desmodus rotundus*) to butanoic acid as 1.5×10^{-10} to 1.5×10^{-11} M.

OLFACTORY CUES AND FOOD LOCATION

Stager's (1964) anatomical investigations of the olfactory organ and innovative field studies of the possible ecological role of the Turkey Vulture olfactory system has led to the general acceptance that *C. aura* relies to a great extent on this sense to locate carrion. There are, however, discrepancies between the observed response of Turkey Vultures to ethanethiol, as reported by Stager (1964), and the predictions of our model based on the apparent threshold levels of this odorant. Stager (1964) observed Turkey Vultures responding to ethanethiol at approximately 61 m altitude and 183 m downwind from the odorant source. Our model predicts (Table 1) that thresholds of roughly 1×10^{-12} to 1×10^{-13} M would be necessary before a Turkey Vulture could detect ethanethiol at this altitude, whereas our threshold data indicate that response levels to this odorant are considerably higher at approximately 1×10^{-6} M. In his experiment, Stager forced pure ethanethiol under pressure into the atmosphere. Under this experimental design, ethanethiol emission rates (Q) were likely to have been excessive, causing threshold-level concentrations to occur at greater distances both downwind and above the source than normally would be produced by a decaying carcass.

In the context of the odorant-dispersion model presented here, our analysis of olfactory sensitivity in the Turkey Vulture strongly suggests that the odorants used in our investigation are unlikely carrion cues and casts some doubt on the probable importance of this sense as a food-locating mechanism. Admittedly, the Gaussian model is simpler than the phenomena it describes. Nonetheless, odorant concentrations are in some manner dependent on emission rates. The absolute quantity and rate of odorant emission depends on the mass of the carcass and the rate at which decomposition occurs. Unlike other cathartids, Turkey Vultures appear to feed primarily on small-bodied prey such as rodents and snakes (Stager 1964). There is some evidence to suggest that they also prefer freshly killed carcasses over those that are putrified (Owre and Northington 1961). Both of these considerations suggest that Turkey Vultures prefer to feed on carrion that would be expected to yield relatively little odorant. Detection of odorants from freshly killed, small-bodied animals even at low foraging altitudes would not be expected unless threshold levels were also low.

The intent of this paper is not to categorically refute the generally accepted role of olfaction in *C. aura*. Rather, we have attempted to address problems associated with odorant dispersion and altitude as they pertain to olfactory cues, and to establish a theoretical framework by which future investigations might proceed. According to the model we present, olfactory sensitivity in Turkey Vultures should be comparable to that of mammals if olfactory cues are to be detected at foraging altitudes below 10 m (Table 1). While our data do not support this contention, we recognize that thresholds of this magnitude may exist for carrion-associated odorants other than those used in this study. Other compounds, such as putrescine, cadaverine, several alcohols, fatty acids, and thiols, are also by-products of carrion decomposition. Any of these chemicals, either singly or in combination, may be important as olfactory cues to Turkey Vultures.

Similarly, our approach to the Gaussian gas dispersion equation was far from exhaustive. Modifications of this equation are available for various substrate and atmospheric conditions (Strom 1976) that, if appropriately modified for threshold data, might increase the flexibility of the model. Although numerous field studies by micrometeorologists have confirmed the general utility of the Gaussian equation (see Pasquill 1974, Panofsky and Dutton 1984) other nonstatistical treatments (e.g. gradient-transfer theory) might better describe the concentration gradients of carrion odorants.

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