Odor Detection Thresholds in Tree Swallows and Cedar Waxwings

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Most Procellariiformes, cathartid vultures, pigeons, and kiwis use their sense of smell for orientation and foraging (Stager 1964, Wenzel 1968, Grubb 1974, Papi 1986, Waldvogel 1989, Lequette et al. 1989). Otherwise, little is known concerning the importance of olfaction to birds, although anatomical evidence suggests that many species should possess an acute sense of smell (Bang and Cobb 1968, Wenzel 1973, Bang and Wenzel 1986). Recently we began to collect behavioral and physiological data on the olfactory ability of passerines (Clark and Mason 1987, 1989; Mason et al. 1989; Clark and Smeraski 1990). Passerines are of special interest because the relative size of their olfactory bulb is among the smallest reported for birds and, conventionally, olfactory prowess is assumed to correlate positively with relative bulb size (Bang and Cobb 1968). The present study is designed to assess the sensitivity of passerines to a standard odorant. While by no means a complete assay of olfactory function, the results of experiments such as this one permit interspecific comparisons of sensitivity, and they serve as a relative index of olfactory ability. Such evaluations are prerequisite to speculations concerning whether or not a species uses olfaction in the wild.

Five adult Tree Swallows (*Tachycineta bicolor*) were trapped at nest boxes in May 1988 at Tinicum National Wildlife Refuge, Philadelphia, Pennsylvania, and transported to the Monell Center. In August 1989, five adult Cedar Waxwings (*Bombycilla cedrorum*) were obtained from USDA/APHIS personnel in Gainesville, Florida, and transported to the Monell Center in Philadelphia. In the laboratory, the birds were housed individually in cages in a room with a constant ambient temperature of 23°C, and a constant 14L: 10D cycle (0700–2100). Water, food (crickets, mealworms, and grapes for the Tree Swallows; banana mash, blueberries, and apples for the waxwings), and medicated shell grit were available *ad libitum*. The diet was supplemented daily by vitamin solution injected into the fruit. Four birds of each species remained in good health and maintained weight throughout the experiments.

I used cyclohexanone (CH) [$C_6H_{10}O$, mw 98.14, bp 155.6°C, d^{20}_4 0.9478] as the standard odorant. This substance was selected because its physicochemical properties and binding to receptor proteins were the subject of previous studies in our laboratory (Mason et al. 1984, 1987). Although CH is without any known biological significance to either species, vertebrate olfactory receptors are sensitive to a wide range of reagents that are not encountered naturally (Fazzalari 1978). This suggests that the functional design of such receptors is for the perception of volatile chemicals per se. Besides, the search for biologically relevant odorants for passerines seems premature in the absence of data that imply that olfactory sensitivity exists.

Tree Swallows and Cedar Waxwings were evaluated for their ability to detect odor using a cardiac conditioning paradigm (Michelsen 1959, Walker et al. 1986). Cardiac conditioning is a technique to train animals to associate electric shock with a strong odor cue. The cardiac acceleration that occurred in response to odor presentation, but prior to shock, was interpreted as a conditioned response.

Details on how subjects were prepared, signal processing, and the odor delivery system are published elsewhere (Clark and Mason 1989). Briefly, birds were restrained and placed within a darkened sound-attenuating chamber with their nares placed at the exit port of a dilution olfactometer. Heart rate was monitored with a Type II ECG lead configuration (Sturkie 1965) via a high impedance probe, amplifier, and oscilloscope. The frequency of heart beats was counted by processing the 'R' component of the amplified ECG signal to a TTL pulse via a Schmitt trigger circuit, and recording the timed pulses via custom software to a computer.

Birds were trained to attend to the reinforced stimulus (S^+) by presenting 10 s of CH at 5% vapor saturation (% VS) and following it immediately with electric shock (2.5 VDC for 2 s) applied across the legs of the subject through the recording electrodes. The ECG signal was lost at this point, so records were kept only during the 10 s before and 10 s during stimulus delivery. This concentration was selected because previous evidence suggested that 5% VS represents a strong olfactory cue, but not so strong as to elicit trigeminal responding (Walker et al. 1979). To control for possible attentiveness to cues associated with operation of the olfactometer, birds were presented with 10 s of a nonreinforced control (S_0; i.e. humidified, filtered air, matched to the vapor saturation of the S^+). The S^+ and S_0 were presented in paired trials with the sequence within pairs randomly selected. The intertrial intervals between all stimulus presentations were randomly selected (60–300 s) via the computer-automated dilution olfactometer. A cardiac acceleration of at least 10% of the prestimulus heart rate in response to stimuli was interpreted as positive. To avoid fatigue, birds were never given more than 100 trials per day. The minimum number of trials given any bird was 30. If the training criterion was not met (3:1 S^+:S_0 positive response over 20 consecutive trials), the bird was given a day's rest, and training was re-

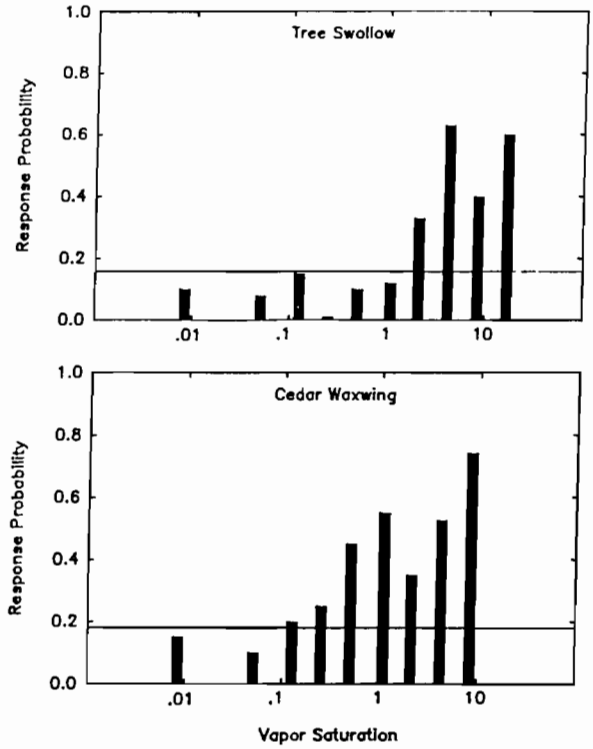

Fig. 1. The average detection threshold to different intensities of cyclohexanone. The horizontal line reflects the upper 95% confidence limit for responding to humidified air (the control). The detection threshold was defined as the concentration where response probability exceeded the baseline value.

sumed on the following day. Approximately half the birds reached criterion on the first training day; no bird took more than three training days. Cedar Waxwings trained to the criterion condition more quickly than Tree Swallows. After the training criterion was met, birds were tested for detection threshold to CH (nonreinforced presentation) in an ascending odor concentration series. Each concentration series was presented five times to each individual. At the end of each series, birds were presented with one blank (0% VS) and five reinforced presentations of 5% VS CH (S^+). This reinforcement guarded against extinction of the conditioned response during the course of testing.

The lowest detection thresholds were observed for Cedar Waxwings (Table 1) and are similar to the range of values reported for European Starlings (*Sturnus vulgaris*), Brown-headed Cowbirds (*Molothrus ater*), Rock Doves (*Columba livia*), and Northern Bobwhite (*Colinus virginianus*) (Stattelman et al. 1975, Clark and Mason 1989, Clark and Smeraski 1990). The detection threshold for CH in Tree Swallows was much higher (Fig. 1). Individual detection thresholds within each species ranged over one order of magnitude (Table 1). These individual differences are expected. In pigeons, the between-subject differences in detection for other

TABLE 1. Range of detection threshold to cyclohexanone for Cedar Waxwings, Tree Swallows, and humans. Because barometric pressure and room temperature varied, the actual number of molecules of odorant at the olfactometer port varied somewhat, even though odor dilutions were held constant throughout experiments (see Dravnieks 1975).

Bird	ppm	Molecules/ml	% vapor saturation
Cedar Waxwing			
Min	6.80	1.698×10^{14}	0.150
Max	86.46	2.137×10^{15}	1.300
Tree Swallow			
Min	73.42	1.813×10^{15}	1.300
Max	317.80	7.785×10^{15}	5.000
Human[a]	0.40	1.000×10^{13}	

[a] Stone et al. 1972 (Percept. Psychophys. 12: 501-504).

reagents can be as much as three orders of magnitude (Henton 1969, Henton et al. 1966, Walker 1983, Walker et al. 1986). The smaller variability reported here most likely reflects the homogeneous conditions extant in a single laboratory. Similar small variation for detection thresholds occurs for other vertebrates (Fazzalari 1978), including humans, where the between-subject differences in detection to an odorant also are approximately one order of magnitude (Murphy and Cain 1986).

The average detection thresholds differed in each species (Fig. 1). The number of responses to presentation of blanks (0% VS) was used to calculate the mean rate of false positives (0.12 for Tree Swallows and 0.15 for Cedar Waxwings). The upper 95% confidence limit was used to define the intrinsic rate of responding (0.158 for Tree Swallows and 0.182 for Cedar Waxwings). The concentration for which responding occurred above the intrinsic response rate was assumed to define the detection threshold. The average detection threshold to CH for swallows was 2.5% VS (133.6 ppm, 3.313×10^{15} molecules/ml at 23°C with 760 mm Hg), whereas the average detection threshold for waxwings was 0.3% VS (16.03 ppm, 3.976×10^{14} molecules/ml). For perspective, at one atmosphere and 23°C, a 1.3% VS dilution of CH presented to humans has a strong odor resembling peppermint and oil, but a dilution of 0.3% VS is not usually apparent. The humans' threshold to CH is slightly lower than the values reported for waxwings (Table 1).

Direct comparison to the sensitivity of other birds can be made only approximately because no single reagent has been used as a standard odorant. Nonetheless, the detection values reported here for Cedar Waxwings compare favorably with the lowest values reported for other birds, whereas those for Tree Swallows are among the highest reported (Clark and Mason 1989). Though they did not measure threshold

values, Wenzel and Sieck (1972) reported that detection capabilities of canaries, quail, ducks, Turkey Vulture, Manx Shearwater (*Puffinus puffinus*), and Black-footed Albatross (*Diomedea nigripes*) for a variety of reagents were in the 0.01–0.5 ppm range. These results suggest that nonpasserines have slightly better olfactory acuity.

Animals that consume fruit may attend to chemical, as well as visual, cues to assess ripeness. This is the case for frugivorous bats, which are attracted to volatiles emitted from ripening fruit (Reiger and Jakob 1988). Perhaps this accounts for the better sense of smell in the predominantly frugivorous waxwing than in the insectivorous swallow. Whether waxwings actually attend to volatiles emitted from ripe and unripe fruit remains to be determined. Based on preliminary data we suggest that passerines that are primarily insectivorous are characterized by a poor sense of smell, whereas birds that are predominately frugivorous, omnivorous, and granivorous are characterized by a good sense of smell (Clark and Mason 1989, Clark and Smeraski 1990, L. Clark unpubl.).

Birds were held under USFWS permit PRT-719909. Experimental procedures comply with NIH and USDA/APHIS guidelines on experimental use on animals and were approved by Monell's Institutional Animal Care and Use Committee. I thank J. R. Mason and C. A. Smeraski for reading an earlier draft of this paper. M. Avery kindly provided the Cedar Waxwings.

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