

## The Chemical Senses in Birds

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### I. CHEMOSENSORY SYSTEMS

The chemical senses are commonly thought to fall into three classes: (1) olfaction (smell), (2) gustation (taste), and (3) chemesthesis (the common chemical sense). In birds, as in most other vertebrates, olfaction is usually thought to be a telereceptor, capable of receiving airborne chemical stimuli in extreme dilution over relatively great distances. Olfactory receptors are located in the nasal conchae. Gustation, on the other hand, usually requires more intimate contact between the source(s) of chemical stimuli and receptors. Gustatory receptors are located in the taste buds of the oral cavity. Chemesthesis is usually reserved for nonspecific stimuli, which are often irritating or painful. Chemoreceptive fibers are concentrated in exterior mucous membranes, although they occur throughout the animal.

Traditional emphasis in describing responsiveness to chemical stimuli has been placed on taste and smell. This emphasis is misplaced. Trigeminal chemoreception (chemesthesis) also may be involved. The sensory afferents of the trigeminal and olfactory nerves are in close proximity in the nasal cavity, and the trigeminal and gustatory nerves are in close proximity in the oral cavity. Most chemicals can stimulate multiple sensory afferents, although circumstances may favor detection by one sensory system over others. Except in the case of electrophysiological studies in which specific nerve function in response to specific chemical stimulus can be docu-

mented, attributing specific sensory mediation of a chemostimulant is not possible.

## II. CHEMESTHESIS

Chemesthesia is the perception of chemically induced pain. A major component of the chemesthetic system is the trigeminal nerve (TN). The TN is the principal somatic sensory nerve of the head, and its primary function is the coding of mechanical and thermal stimuli. However, the trigeminal nerve also contains chemoreceptive fibers that mediate the detection of chemical irritants (Silver and Maruniak, 1980). The somatosensory system is the primary somatic sensory system of the rest of the body. Like the TN, the somatosensory system primarily codes for mechanical and thermal stimuli, but it does have sensory afferents that are chemosensitive (Kitchell and Erikson, 1983), though little is known about this system in birds. Sensitivity to chemical irritants is adaptive because animals can avoid noxious stimuli before actual physical damage occurs.

### A. Trigeminal Chemoreceptors

Chemosensitive fibers of the avian trigeminal and somatosensory systems are similar to mammalian sensory afferents. Most are unmyelinated C-type polymodal nociceptors with conduction velocities of 0.3–1 m/sec. However, some myelinated A-delta high-threshold mechanoreceptors with conduction velocities of 5–40 m/sec also respond to chemical stimuli. The discharge patterns and conduction velocities for the chicken (*Gallus gallus var domesticus*), duck (*Anas platyrhynchos*), and pigeon (*Columba livia*) are similar to those observed in mammals (Gentle, 1989; Necker, 1974).

The underlying physiological and biochemical processes of chemically induced pain appear to be similar for birds and mammals. Endogenous pain-promoting substances such as substance P, 5HT, histamine, bradykinin, and acetylcholine evoke pain-related behaviors in chickens, pigeons, and guinea pigs (Gentle and Hill, 1987; Gentle and Hunter, 1993; Szolcsanyi *et al.*, 1986). Prostaglandins that modulate the pain response in mammals also subserve this function in starlings (*Sturnus vulgaris*), and their effects can be abolished by prostaglandin biosynthesis inhibitors, such as aspirinlike analgesics (Clark, 1995a). However, there are profound differences in how birds and mammals respond to exogenous chemical stimuli. In mammals, chemicals such as capsaicin are potent trigeminal irritants. These irritants deplete substance P from afferent terminals

and the dorsal root ganglion, producing an initial sensitization followed by a desensitization to further chemical stimulation (Szolcsanyi, 1982). In contrast, birds are insensitive to capsaicin (Mason and Maruniak, 1983; Szolcsanyi *et al.*, 1986). Peripheral presentation of capsaicin to pigeons and chickens does not cause release of substance P in avian sensory afferents (Pierau *et al.*, 1986; Sann *et al.*, 1987; Szolcsanyi *et al.*, 1986).

### B. Innervation of Chemesthetic Receptors

The trigeminal nerve is the Vth cranial nerve in birds, arising from the rostralateral medulla near the caudal surface of the optic lobe (Getty, 1975; Schrader, 1970). The TN travels along with the trochlear nerve (IV), entering a fossa in the floor of the cranial cavity where the trigeminal ganglion (TG) is found. The TG is subdivided into a smaller medial ophthalmic region and a larger lateral maxillomandibular region from which the nerve splits into three branches. In the chicken, the ophthalmic branch of the TN innervates the frontal region, the eyeball, upper eyelid, conjunctiva, glands in the orbit, the rostradorsal part of the nasal cavity, and the tip of the upper jaw. The ophthalmic branch has a communicating ramus with the trochlear nerve which serves for motor control of the eye region. This aspect can provide for reflexive response to irritating stimuli to the ocular region. The larger medial ramus accompanies the olfactory nerve into the nasal fossa via the medial orbitonasal foramen. The maxillary branch of the TN provides sensory input from the integument of the crown, temporal region, rostral part of the external ear, upper and lower eyelids, the region between the nostrils and eye, conjunctival mucosa, the mucosal part of the palate, and the floor and medial wall of the nasal cavity. The mandibular branch of the TN provides sensory input from the skin and rhamphotheca of the lower jaw, intermandibular skin, wattles, oral mucosa of the rostral floor of the mouth, and the palate near the angle of the mouth.

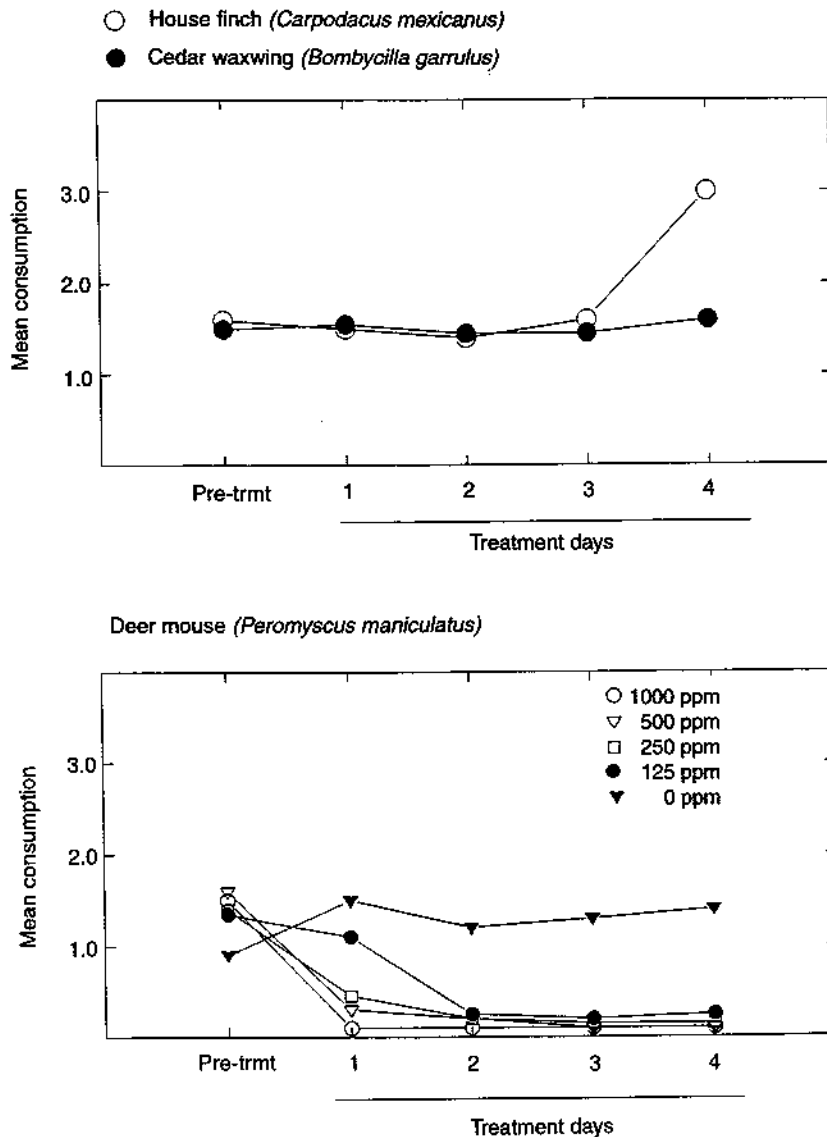
### C. Behavioral Responses to Chemical Stimuli

Although the morphological organization of the peripheral trigeminal system in birds is not very different from that found in mammals (Dubbeldam and Karten, 1978; Dubbeldam and Veenman, 1978), profound functional differences appear to exist (Mason *et al.*, 1989; Norman *et al.*, 1992; Mason and Otis, 1990; Mason *et al.*, 1991a,b). Birds rarely avoid mammalian irritants, even though the avian trigeminal system is responsive to chemical stimuli (Walker *et al.*, 1979; Mason and

Silver, 1983). For example, cedar waxwings (*Bombicilla cedrorum*; Norman *et al.*, 1992) are indifferent to  $\geq 1000$  ppm capsaicin, the pungent principle in *Capsicum* peppers, whereas mammals typically avoid much lower concentrations: 100 ppm capsaicin is typically avoided by rodents (Figure 1). Nevertheless, it is interesting to note that birds can be trained to avoid mammalian irritants (Mason and Clark, 1995a) and that some trigeminal input appears to mediate the response (Mason and Clark, 1995b).

Many aromatic structures are aversive to birds (Avery and Decker, 1991; Clark and Shah, 1991a,

1993; Crocker and Perry, 1990; Crocker *et al.*, 1993; Kare, 1961; Mason *et al.*, 1989). Several lines of evidence suggest that a variety of compounds have intrinsic properties that cause them to be aversive on a purely sensory basis. First, the aversive quality is unlearned; that is avoidance occurs upon initial contact (Clark and Shah, 1991b). Second, there is no evidence that consumption is altered by gastrointestinal feedback—intake of fluid treated with these sensory repellents is constant over time (Clark and Mason, 1993). Third, birds seem unable to associate the aversive quality of the stimulus with other chemosensory cues,



**FIGURE 1** Responses of house finches (*Carpodacus mexicanus*), cedar waxwings (*Bombicilla cedrorum*), and house mice (*Mus musculus*) to capsaicin adulterated chow. (Modified from Norman *et al.* (1992) with permission.)

suggesting that conditioned flavor avoidance learning does not occur (Clark, 1995b; Mason *et al.*, 1989). Fourth, birds do not habituate to the stimulus—avoidance persists in the absence of reinforcement (Clark and Shah, 1994; Mason *et al.*, 1989).

#### D. Structure–Activity Relationships for Aromatic Stimuli

The structure–activity relationships of aromatic avian repellents have been elucidated. An aromatic parent structure is critical for repellency. Factors that affect the delocalization of electrons around the aromatic structure contribute to modifying the repellent effect. Thus, acidic substituents to the benzene ring generally detract from repellency, and this is amplified if the acidic function is contained within the electron-withdrawing group. Electron donation to the benzene ring enhances repellency. Heteroatoms that distort the plane of the aromatic structure tend to lessen repellency (Clark and Shah, 1991a, 1994; Clark *et al.*, 1991; Mason *et al.*, 1991a; Shah *et al.*, 1991, 1992) (Figure 2).

#### E. Responses to Respiratory Stimuli

Changes in carbon dioxide concentration in the nasopharynx region can cause species-specific changes in reflexive breathing in birds (Hiestand and Randall,

1941). However, concentrations of carbon dioxide that are sufficiently high to be irritating to mammals have no effect on blood pressure, heart rate, tidal volume, breathing frequency, upper airway resistance or lower airway resistance in geese (*Anser anser* and *Cygnopsis cygnoid*; Callanan *et al.*, 1974). Similarly, geese respond differently than mammals to exposure to sulfur dioxide, but in a similar manner when exposed to ammonia and phenyl diguanide (Callanan *et al.*, 1974).

#### F. Nasal and Respiratory Irritation and Interaction of the Olfactory and Trigeminal Systems

The trigeminal nerve is important in the perception of odors (Keverne *et al.*, 1986; Silver and Maruniak, 1980; Tucker, 1971). Electrophysiological evidence shows that the trigeminal nerve is responsive to odors, albeit generally less sensitive than the olfactory nerve (Tucker, 1963). Behavioral assays yield similar results. Pigeons trained to respond to odors fail to respond after olfactory nerve transection. However, odor responding can be reinstated if the odor concentration is increased (Henton, 1969; Henton *et al.*, 1966; Michelsen, 1960). Walker *et al.* (1979, 1986) found that odor sensitivity of pigeons decreased by 2–4 log units (vapor saturation) after olfactory nerve transection.

Although olfaction can modulate responding to chemical irritants, it is relatively unimportant. Clark

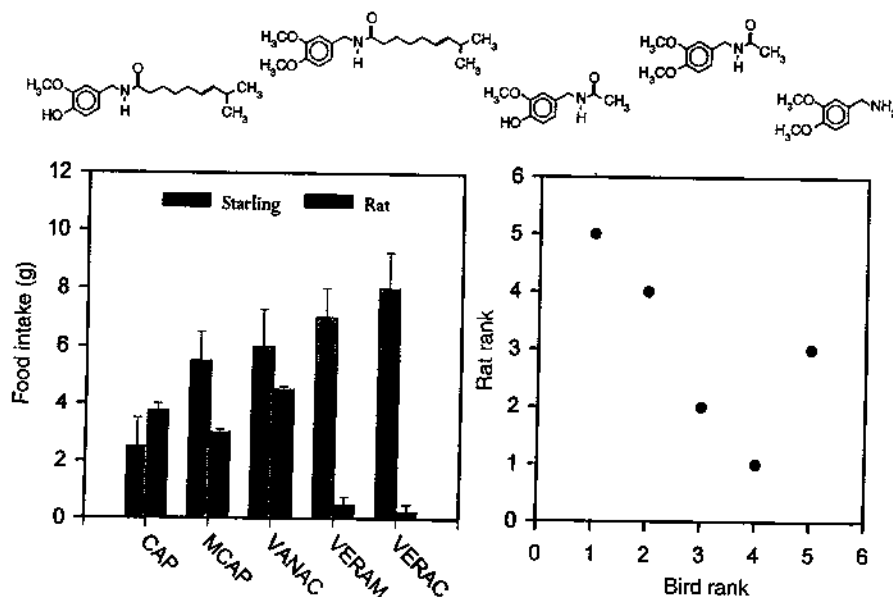


FIGURE 2 (Left) Consumption of food adulterated with capsaicin derivatives for rats and starlings. Codes are CAP, capsaicin; MCAP, methyl capsaicin; VANAC, vanillyl acetamide; VERAM, veratryl amine; VERAC, veratryl acetamide. Structures shown are in order presented in panel codes. (Right) The rank order of food intake for rats and starlings, demonstrating an inverse relationship between palatability.

(1995a) and Mason *et al.* (1989) showed that avoidance of repellent anthranilates was partially a consequence of olfactory cues. When the olfactory nerves of starlings were transected, avoidance of the anthranilate repellents was mildly suppressed. When the ophthalmic branches of the trigeminal nerve were cut, the starlings became insensitive to the repellent effects of the anthranilates (Mason *et al.*, 1989).

### G. Summary

The anatomical configuration and the physiological and biochemical processes of chemosensory afferents of the avian trigeminal and somatosensory systems are similar in birds and mammals. However, there are significant differences in sensitivity to exogenous chemical stimuli between these two taxa. Structure-activity studies suggest that these differences may reflect different receptor mechanisms in peripheral afferents. Confirmation using molecular and pharmacological techniques is needed to clarify this possibility.

## III. GUSTATION

### A. Taste Receptors

In comparison to other vertebrates, birds have few taste buds (Table 1). They are distributed throughout the oral mucosa, but most often in close association with salivary gland openings (Berkhoudt, 1985). The greatest numbers are on the caudal surface of the tongue and the pharyngeal floor (Kare, 1971; Gentle, 1975; Kare and Rogers, 1976). Ontogenetic changes in taste bud number occur (Duncan, 1960). Adult chickens have twice the number of taste buds of day-old chicks (Lindenmaier and Kare, 1959; Saito, 1966). However, within

TABLE 1 Absolute Number of Taste Buds in Various Animals<sup>a</sup>

Species	Number	Source
Chicken	24	Lindenmaier and Kare (1959)
Bullfinch	46	Duncan (1960)
Starling	200	Bath (1906)
Japanese quail	62	Warner <i>et al.</i> (1967)
Lizard	550	Schwenk (1985)
Kitten	473	Elliot (1937)
Bat	800	Moncrieff (1951)
Human	9,000	Cole (1941)
Pig	15,000	Moncrieff (1951)
Rabbit	17,000	Moncrieff (1951)
Catfish	100,000	Hyman (1942)

<sup>a</sup> Modified from Kare and Mason (1986).

adults, the number of taste buds declines with age (Botezat, 1910; Duncan, 1960; Lalonde and Eglitis, 1961).

Saliva is critical for the transport of taste stimuli to receptors (Belman and Kare, 1961). This is particularly true for birds, since avian taste buds do not open directly into the oral cavity via taste pores (Berkhoudt, 1985). Although the role of saliva on avian taste responding has not been extensively studied, there is evidence that changes in salivary flow rate affect taste related behaviors. Gentle and Dewar (1981) and Gentle *et al.* (1981) reported significant declines in taste avoidance by chicks that were vitamin A and zinc deficient. These deficiencies lower salivary flow rate.

### B. Innervation of Taste Receptors

The lingual branch of the glossopharyngeal nerve was once considered the only gustatory nerve in birds (Kitchell *et al.*, 1959; Duncan, 1960; Halpern, 1963; Kadono *et al.*, 1966; Landolt, 1970). However, more recent investigations show that the palatine branch of the facial nerve (Krol and Dubbeldam, 1979) and the chorda tympani (Berkhoudt, 1985; Gentle, 1979, 1983) also transmit gustatory information.

### C. Taste Behavior

Simple evaluations of ingestion are the most common laboratory method used to measure the sensitivity of birds to taste stimuli, although operant methods have been used (Mariotti and Fiore, 1980). Usually, the test stimuli are presented in aqueous solution, and animals choose between mixtures and distilled water. Chickens show a characteristic response to aversive oral stimulation typified by persistent tongue and beak movements and head-shaking and beak-wiping behaviors (Gentle 1973, 1976, 1978). No characteristic responses to presentations of neutral or appetitive oral stimuli have been observed (Gentle, 1978; Gentle and Harkin, 1979).

### D. Response to Sweet

Many species show modest preferences for natural sugars mixed with drinking water (Brindley, 1965; Brindley and Prior, 1968; Duncan, 1960; Engelmann, 1934, 1937, 1960; Gentle 1972, 1975; Gunthor and Wagner, 1971; Harriman and Milner, 1969; Rensch and Neunzig, 1925; Warren and Vince, 1963). Strong preferences are exhibited by parrots, budgerigars, hummingbirds, and other nectar-feeders (Bradley, 1971; Hainesworth and Wolf, 1976; Kare and Rogers, 1976; Stromberg and Johnsen, 1990).

A variety of granivores and some omnivores reject sugars, perhaps for physiological reasons. For example, red-winged blackbirds select pure water over sucrose (Rogers and Maller, 1973; Martinez del Rio *et al.*, 1988). Common grackles (*Quiscalus quiscula*), European starlings, cedar waxwings, and robins (*Turdus migratorius*), also reject sucrose, although other sugars (e.g., fructose, glucose) are preferred (Schuler, 1980, 1983). Brugger and Nelms (1991), Brugger (1992), and Brugger *et al.* (1992) have suggested that rejection occurs because these birds lack the enzyme sucrase. Ingestion of sucrose by sucrase-deficient birds causes sickness, due to malabsorption (Martinez del Rio, 1990; Martinez del Rio *et al.*, 1988; Martinez del Rio and Stevens, 1989; Brugger and Nelms, 1991).

Besides taste, osmotic pressure, viscosity, melting point, nutritive quality, digestibility, and toxicity are all involved in birds' response to tastes. Some have suggested that visual properties and surface texture sometimes take precedence over all other qualities in the birds' selection of food (Engelmann, 1957; Kare and Rogers, 1976; Morris, 1955; Kear, 1960; Mason and Reidinger, 1983a,b). Across species, no physical or chemical characteristic has been shown to reliably predict how a bird on an adequate diet will respond to the taste of a solution (Kare and Medway, 1959).

#### E. Response to Salt

Sodium chloride rejection thresholds for 58 species ranged from 0.35% in a parrot to 37.5% in the pine siskin (*Carduelis pinus*; Rensch and Neunzig, 1925). Salt-eating has been reported for a number of species (Reeks, 1920; Mousley, 1921, 1946; Pierce, 1921; McCabe, 1927; Gorsuch, 1934; Aldrich, 1939; Marshall, 1940; Peterson, 1942; Calhoun, 1945; Packard, 1946; Bleitz, 1958; Duncan, 1964; Cade, 1964; Dawson *et al.*, 1965; Mason and Espallat, 1990). Numerous finches of the family Carduelidae have notorious appetites for salt. Cross-bills can be caught in traps baited with salt alone (Welty, 1975; Willoughby, 1971). Cade (1964) suggests that finches, which have 0.001–0.03% sodium in their diets (Altmann and Dittmer, 1968), are chronically sodium deficient.

The presence of a nasal salt gland is associated with salt acceptance taste thresholds. Birds without such glands generally refuse concentrations of salt that are hypertonic to their body fluids (Bartholomew and Cade, 1958; Bartholomew and MacMillan, 1960). However, rejection thresholds in no-choice tests do not always predict responding in choice situations. When given a choice, gulls (*Larus spp.*) (with salt glands) select pure water over saline solution (Harriman, 1967; Harriman

and Kare, 1966). Similarly, penguins prefer fresh water after having been at sea for extended periods (Warham, 1971). Preference could reflect the toxic effects of chronic exposure to saline or salt waters. Mallards possess salt glands (Shoemaker, 1972), but hatching success and duckling survival is influenced by the salinity of drinking water in the natal marsh (Mitcham and Wobeser, 1988). The order of acceptability of ionic series by birds does not appear to fit into the lyotropic or sensitivity series reported for other animals.

#### F. Response to Sour

Birds are tolerant of acidic and alkaline solutions (Fuerst and Kare, 1962; Table 2), and some species exhibit preferences for acid over plain tapwater (Brindley and Prior, 1968). Not surprisingly, species differences exist. Rensch and Neunzig (1925) and Engelmann (1934) reported that pigeons were more sensitive than ducks or fowl. Engelmann (1950) also reported that chicks were more sensitive than adults. Berkhoudt (1985) reports that hooded crows (*Corvus corone*) are profoundly sensitive to hydrochloric acid and speculates that this sensitivity might be linked to the assessment of the quality of carrion as potential food. Although the ecological reason(s) for acid tolerance in some avian species remains unclear, one possibility is that it permits the exploitation of certain otherwise unpalatable food resources. For example, even though starlings prefer insect prey to fruit, juvenile starlings are less successful in capturing animal prey than are adults (Stevens, 1985). Accordingly, juveniles eat large amounts of fruit because it is readily available. Much of this fruit is unripe and sour.

#### G. Response to Bitter

Avian responsiveness to bitter is enigmatic. In some cases, compounds evoke similar responses in mammals and birds (e.g., quinine hydrochloride; Engelmann, 1934; Gentle, 1975). In others, compounds that are extremely bitter to humans (e.g., sucrose octaacetate) are readily accepted by birds (Halpern, 1963; Heinroth, 1938). This acceptance may reflect physiological insensitivity (Kitchell *et al.*, 1959; Landolt, 1970). There is evidence that acceptance may decrease as individuals age (Brindley, 1965; Cane and Vince, 1968).

The bitter phenolic compounds produced by some plants (Robinson, 1983) and utilized by various species of pharmacophagus insects (Nishida and Fukami, 1990) may serve as defenses against birds (e.g., Greig-Smith, 1988; Rodriguez and Levin, 1976). There is abundant evidence that the tannin content of fruits and grain is

TABLE 2 The Influence of pH on Fluid Preferences of the Chick<sup>a</sup>

Substance	pH1 <sup>b</sup>	pH2 <sup>c</sup>	Versus	Percentage intake <sup>d</sup>
Acetic acid	2.9	3.2	Water	16.1
Acetic acid	4.1	4.5	Water	53.3
Acetic acid	4.9	7.3	Water	50.0
Acetate buffer	4.0	4.1	Acetate buffer, pH 6	47.8
Acetate buffer	4.0	4.1	Acetate buffer, pH 5	38.0
Acetate buffer	4.0	4.1	Water	52.1
Acetate buffer	5.1	5.1	Water	57.6
Acetate buffer	5.1	5.1	Acetate buffer, pH 6	38.0
Acetate buffer	6.0	6.0	Water	54.6
Acetate buffer	6.0	6.1	Water	54.2
Acetate buffer	6.0	6.1	Phosphate buffer, pH 7	53.0
Acetate buffer	6.0	6.1	Phosphate buffer, pH 6	53.9
Acetate buffer	6.0	6.1	Veronal buffer, pH 7	52.4
Glycine buffer	2.3	2.3	Glycine stock	61.2
Glycine buffer	3.0	3.2	Glycine stock	52.8
Glycine stock	5.4	6.6	Water	50.7
Glycine buffer	7.2	7.0	Glycine stock	48.9
Glycine buffer	9.0	7.8	Glycine stock	49.2
Glycine buffer	10.0	8.7	Glycine stock	48.8
Glycine buffer	11.0	9.0	Glycine stock	49.8
Hydrochloric acid	1.1	1.1	Water	4.0
Hydrochloric acid	1.5	1.6	Water	18.6
Hydrochloric acid	2.1	2.1	Water	36.5
Hydrochloric acid	1.6	1.6	Glycine stock	24.7
Hydrochloric acid	1.7	1.7	Glycine stock	16.4
Hydrochloric acid	2.0	2.0	Glycine stock	16.4
Hydrochloric acid	2.1	2.1	Glycine stock	39.8
Hydrochloric acid	1.7	1.7	Water	14.8
Hydrochloric acid	2.0	2.0	Water	50.0
Hydrochloric acid	3.0	3.1	Sulfuric acid, pH 3	49.4
Hydrochloric acid	3.0	3.2	Water	59.1
Hydrochloric acid	3.1	3.1	Sodium hydroxide, pH 10.2	53.3
Hydrochloric acid	4.1	7.4	Water	48.8
Lactic acid	2.3	2.3	Water	14.6
Lactic acid	2.9	3.0	Water	60.6
Lactic acid	4.1	6.7	Water	50.2
Nitric acid	1.1	1.1	Water	8.1
Nitric acid	2.0	2.0	Water	62.0
Nitric acid	3.0	3.2	Water	52.5
Phosphate buffer	6.0	6.0	Water	52.3
Phosphate buffer	6.0	6.0	Phosphate buffer, pH 7	53.6
Phosphate buffer	6.0	6.0	Veronal buffer, pH 7	48.0
Phosphate buffer	7.0	7.2	Water	49.0
Potassium hydroxide	11.1	9.0	Water	48.3
Potassium hydroxide	11.1	10.1	Sodium hydroxide, pH 11	47.9
Potassium hydroxide	12.0	11.2	Water	36.4
Potassium hydroxide	13.0	12.1	Water	2.7
Sodium hydroxide	10.2	9.2	Water	45.0
Sodium hydroxide	11.1	9.5	Water	46.8
Sodium hydroxide	12.2	11.2	Water	33.3
Sodium hydroxide	13.0	12.4	Water	1.8
Sulfuric acid	1.2	1.3	Water	15.2
Sulfuric acid	1.5	1.5	Water	35.4
Sulfuric acid	1.9	1.9	Water	54.2
Sulfuric acid	2.0	2.0	Sulfuric acid, pH 3	45.7
Sulfuric acid	3.1	3.2	Water	55.7
Sulfuric acid	4.1	6.9	Water	51.2
Veronal buffer	7.0	7.0	Water	51.8

<sup>a</sup> From Fuerst and Kare (1962).

<sup>b</sup> pH1 = initial.

<sup>c</sup> pH2 = after 24 hr.

<sup>d</sup> Percentage intake = (volume of test fluid consumed/total consumption) × 100. Each intake percentage is the mean of 18 daily values.

associated with resistance to bird damage (Bullard *et al.*, 1981; Greig-Smith *et al.*, 1983; Mason *et al.*, 1984), and laboratory preference tests show that consumption is negatively correlated with tannin concentration (Mason and Espaillat, 1990). Other phenolic substances (e.g., phenylpropanoids, including coniferyl and cinnamyl derivatives; Crocker and Perry, 1990; Jakubas *et al.*, 1992) produce analogous effects. Jakubas and his colleagues (Jakubas *et al.*, 1992) suggest that it may be possible to genetically engineer crops to produce analogs of coniferyl alcohol as an inherent defense against pests and pathogens. The occurrence of coniferyl alcohol is widespread in higher plants because it is the primary precursor of lignin (Hahlbrock and Scheel, 1989; Lewis and Yamamoto, 1990). It may be possible to localize production of these compounds to specific plant tissues (Collins, 1986; Jakubas *et al.*, 1992; McCallum and Walker, 1990). By localizing the production of repellent phenylpropanoids to specific plant tissues, autotoxic effects could be minimized along with the impact of these compounds on the nutritional value and palatability of the grain.

#### H. Response to Other Tastes

Apart from responses to simple tastes, reactions to more complex substances and synthetic flavors have been reported (Kare *et al.*, 1957; Romoser *et al.*, 1958; Kare and Medway, 1959; Kare and Pick, 1960; Deyoe *et al.*, 1962). In general, birds are more sensitive to such stimuli in drinking than in feeding tests.

Very few experiments have dealt with natural taste compounds. However, there is evidence that several species of shorebirds can discriminate between clean sand and sand that had contained worms (Gerritsen *et al.*, 1984; van Heezik *et al.*, 1983). Conceivably, these birds were detecting amino acids in mucus secretions of the worms. Espaillat and Mason (1990) reported that both European starlings and red-winged blackbirds detect and show preferences toward diets adulterated with L-alanine (Figure 3). Whether or not L-alanine sensitivity reflects sensitivity to other free amino acids or to protein is unknown. However, L-alanine and similar substances (e.g., L-glutamine) occur as free amino acids in vegetable matter, fruits, and meat (Hac *et al.*, 1949; Maeda *et al.*, 1958; Baker and Baker 1983). These substances could aid in food search and selection. At least for starlings, assimilation efficiency increases as the overall protein content of the diet increases (Twedt, 1984).

There is also some evidence that taste sensitivity may assist in the rejection of potentially dangerous natural substances. Berkhoudt (1985) reports that a great-crested grebe (*Podiceps cristatus*) apparently used taste cues to reject minnows with slime infections of the epidermis.

#### I. Temperature and Taste

The domestic fowl is acutely sensitive to the temperature of water. Acceptability decreases as the temperature of the water increases above the ambient. Fowl can discriminate a temperature difference of only 5°F, and usually reject the higher temperature. Similar results have been reported for red-winged blackbirds (Mason and Maruniak, 1983). Chickens suffer from acute thirst rather than drink water 10°F above their body temperature. Because the response to temperature may take precedence over all chemical stimulants (Kare and Rogers, 1976), temperature should be eliminated as a variable in taste studies of the fowl. The ecological reason(s) underlying the interaction between taste and temperature remains obscure.

#### J. Summary

Kare and Beauchamp (1976), in discussing the comparative aspects of the sense of taste in birds and mammals, pointed out that most of the work on the basic mechanism of taste has been conducted with mammals. This mammalian work has suggested that the initial interaction of a taste stimulus and a receptor cell occurs on the microvilli of taste receptor cells. Although stimulus-receptor interactions in avian taste are probably similar to those described for mammals, this has not been demonstrated.

Birds have a sense of taste. However, no pattern, whether chemical, physical, nutritional, or physiologic, can be correlated consistently with the bird's taste behavior. The behavioral, ecologic, and chemical context of a taste stimulant can influence the birds' response. The observed response, particularly to sweet and bitter, indicates that the bird does not share human taste experiences. The supposition that there is a difference in degree between individual birds and an absolute difference between some species appears warranted.

### IV. OLFACTION

#### A. Morphology of Olfactory System

Olfactory receptors are located in the olfactory epithelium in the caudal conchae where each receptor cell is surrounded by a cluster of supporting cells. The receptor nerve dendrite passes through these cells to the lumen, ending in a knob bristling with 6–15 cilia. The length of the cilia vary with species. Black vultures have cilia of 40–50  $\mu\text{m}$ , while that of the domestic fowl is about 7–10  $\mu\text{m}$  (Shibuya and Tucker, 1967). To gain access to receptors, odor molecules must diffuse through a mucous membrane. The cilia of the sensory cells have no transport function. Rather, the secretions covering



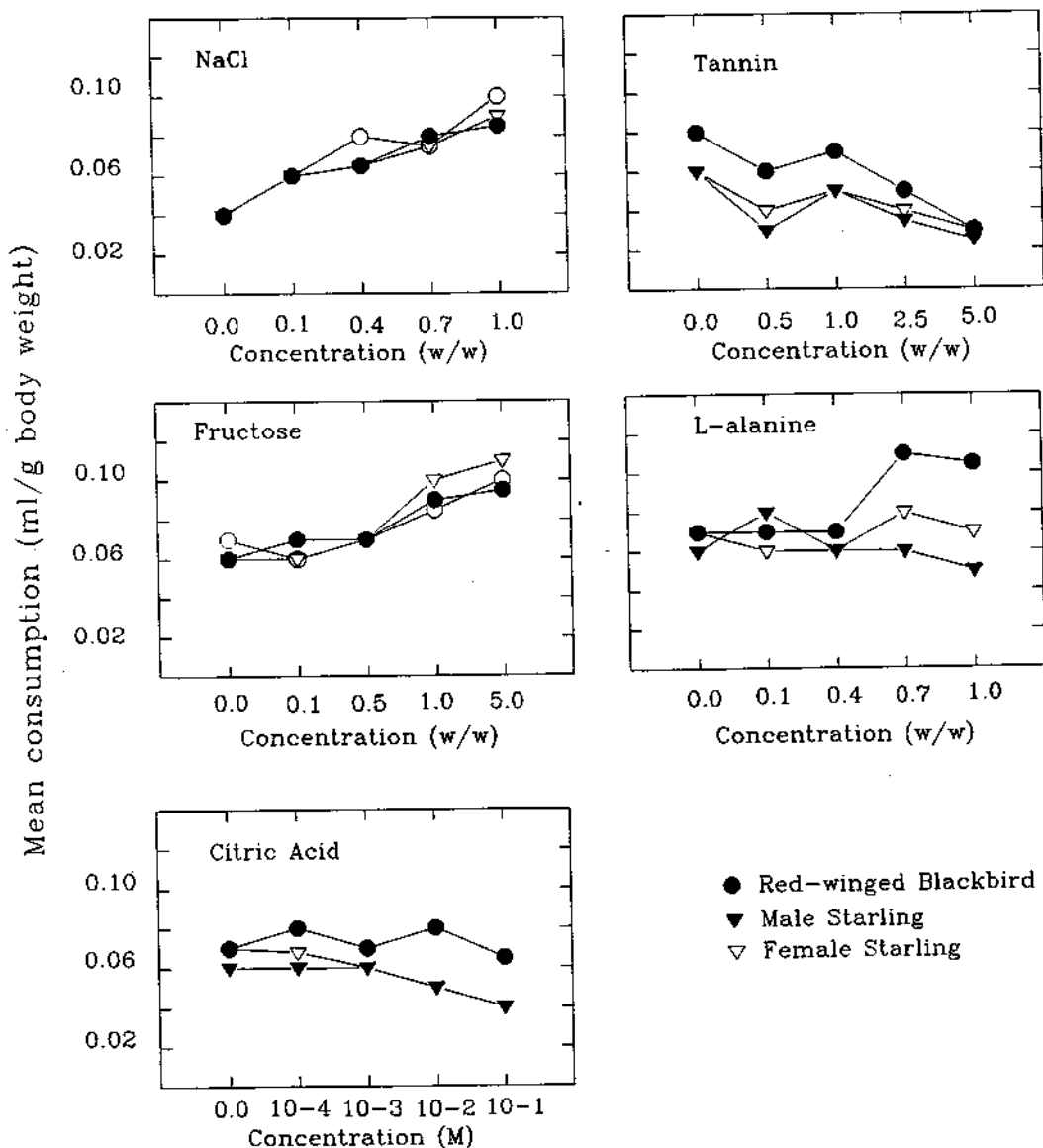


FIGURE 3 Mean consumption of sodium chloride, fructose, citric acid, tannin, and L-alanine per gram of body weight by male red-winged blackbirds (*Agelaius phoeniceus*) and male and female european starlings (*Sturnus vulgaris*). (From Espaillet and Mason (1990) with permission.)

the cilia provide rapid flow for transport of odor molecules and must constantly be replaced to avoid receptor habituation. Olfactory gland secretions are removed by traction of the surrounding respiratory cilia.

The nasal conchae are important structures that influence nasal air flow dynamics and direct odors to the olfactory epithelium (Bang, 1960, 1961, 1963, 1964, 1965, 1966; Bang and Cobb, 1968). The extent of scrolling of the caudal conchae is correlated with the relative size of the olfactory bulb (Bang and Wenzel, 1986). Furthermore, olfactory thresholds and relative size of the olfactory bulb are inversely related at the taxonomic ordinal level; that is, orders with high olfactory thresholds have

relatively small olfactory bulbs (Clark *et al.*, 1993; Table 3, Figure 4). These patterns suggest that the elaborated olfactory systems belong to species with demonstrated reliance on odor cues in the field (Stager, 1964; Hutchison and Wenzel, 1980).

### B. Innervation of Olfactory Receptors

Birds have a fully developed olfactory bulb, but lack an accessory olfactory system—the vomeronasal organ and accessory olfactory bulb (Rieke and Wenzel, 1975, 1978). However, the latter has been identified in the early embryonic development of some birds (Matthes,

TABLE 3 Summary of Mean Ratios of Ipsilateral Olfactory Bulb Diameter to Cerebral Hemisphere Diameter and Their Standard Errors (SE) for Several Orders of Birds<sup>a</sup>

Order	N	Ratio	SE	Order	N	Ratio	SE
Anseriformes	4	19.4	1.5	Psittaciformes	2	8.0	1.4
Apodiformes	8	12.3	1.9	Falconiformes	5	17.4	2.6
Apterygiformes	1	34.0	0.0	Charadriiformes	9	16.4	0.9
Caprimulgiformes	3	23.3	0.7	Galliformes	3	14.2	1.4
Ciconiiformes	2	20.9	0.6	Piciformes	5	11.4	1.3
Columbiformes	2	20.0	1.4	Passeriformes	25	13.3	0.7
Cuculiformes	4	19.5	0.6	Pelecaniformes	4	12.1	1.6
Gaviiformes	1	20.0	0.0	Coraciiformes	5	14.5	1.6
Gruiformes	14	22.2	0.9	Sphenisciformes	1	17.0	0.0
Podicipediformes	2	24.5	1.8	Strigiformes	2	18.5	0.4
Procellariiformes	10	29.1	1.4				

<sup>a</sup> Data adapted from Bang and Cobb (1968). Sample sizes are in terms of number of species (N).

1934). The olfactory bulb is composed of concentric structures, where the incoming olfactory nerve fibers constitute the outer layer. The branching terminals penetrate to the adjacent, glomerular layer, where they connect with dendrites of mitral and tufted cells in spherical arborizations called glomeruli. The perikarya of these cells are in the deeper mitral cell layer, where their axon leave to project to many areas of the fore-brain. There are many interneuronal connections in the layers between the mitral and glomerular regions. There are no direct connections between contralateral bulbs (Rieke and Wenzel, 1978).

### C. Olfactory Neuronal Response

Single and multiunit electrophysiological responses to odor stimuli are typically taken as definitive evidence of olfactory capacity. Electrophysiological recordings

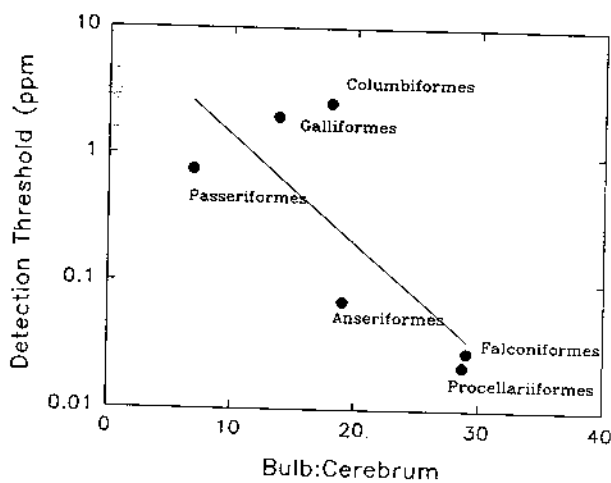


FIGURE 4 Relationship between detection olfactory threshold and relative size of the olfactory bulb for different orders of birds. (From Clark and Shah (1993) with permission.)

of units and nerve fibers from mammals, amphibians, reptiles, and birds respond to odor stimuli in a similar fashion, irrespective of the gross anatomical development of the species' olfactory apparatus (Tucker, 1965; Shibuya and Tonosaki, 1972). In black vultures, the electroolfactogram (EOG) appears during inspiration and less so at expiration. The EOG also coincides with peak spike activity (Shibuya and Tucker, 1967). The spike duration of 3–4 msec is similar to that observed for the tortoise and frog (Gesteland *et al.*, 1963; Shibuya and Shibuya, 1963). Because olfactory nerve fibers are unmyelinated, conduction velocities are slow, about 1.5 m/sec (Macadar *et al.*, 1980). As is the case for mammals, continuous presentation of the stimulus to the bird's receptor field will result in physiological adaptation of the nerve units. Recovery can be achieved within a few minutes of rest. In terms of nerve function, species with even the most vestigial olfactory anatomies compare favorably with those with more developed anatomies in terms of olfactory detection thresholds (Tucker, 1965).

Olfactory nerve sections have been used to verify that spontaneous and trained behaviors are based upon odor cues. Transected olfactory nerves grow back within 30 days of transection and recover full physiologic capacity to respond to odor stimuli (Tucker *et al.*, 1974). Healed nerves often were smaller, have neuromas, and are enmeshed in scar tissue. However, electrophysiological recordings and autonomic reflex responses to odorant did not differ between controls and nerves cut 6 months or more before (Tucker, 1971; Tucker *et al.*, 1974).

### D. Laboratory Detection and Discrimination Capabilities

Physiological responses (e.g., change in respiration or heart rate) to novel odor stimuli have been observed (Wenzel and Sieck, 1972). However, habitua-

tion to the stimulus under this paradigm is always a difficulty.

Various operant and classical conditioning paradigms have also been employed to determine olfactory ability (Michelsen, 1959; Henton *et al.*, 1966; Henton, 1969). Positive or negative reinforcement is used to make the olfactory stimulus a "biologically" relevant cue, irrespective of whether the odor cue is of natural relevance to a species. Overall, classical conditioning techniques have proven to be relatively poor assays for olfactory discrimination in birds (Calvin *et al.*, 1957), but conditioned suppression variants have proven to be quite reliable (Henton *et al.*, 1966; Clark and Mason, 1987). A generally successful assay for determining olfactory detection and discrimination thresholds is cardiac conditioning (Walker *et al.*, 1986; Clark and Mason, 1989; Clark and Smeraski, 1990; Clark, 1991a; Clark *et al.*, 1993). In this procedure, the odor (the conditional stimulus) is paired with an aversive experience; for example, shock (the unconditional stimulus). Heart rate is compared pre- and poststimulus presentation throughout training, when a criterion level of cardiac acceleration is achieved as a result of the stimulus-shock pairing, tests can proceed on detection or discrimination tasks. Most birds that have been tested have shown olfactory capabilities comparable to mammals (Davis, 1973), and even passerines, with the least developed olfactory system, demonstrate behavioral responsiveness to odors (Clark and Mason, 1987; Clark and Smeraski, 1990; Clark, 1991a; Clark *et al.*, 1993) (Table 4).

### E. Olfactory Performance in the Field

The use of olfactory cues for locating food has been documented for a number of species. Turkey vultures are attracted to ethyl mercaptan fumes (Stager, 1964, 1967) and can locate decomposed carcasses in the absence of visual cues (Houston, 1987). Procellariiformes can use odor cues as navigational aids in locating food from considerable distances (Table 5). Black-footed albatrosses (*Diomedea nigripes*) are attracted to bacon drippings from distances as great as 20 miles (Miller, 1942). Using cardiac conditioning techniques for estimating odor detection thresholds, field observations, and detailed atmospheric models of odor dispersion, Clark and Shah (1992) estimated that the Leach's storm petrel (*Oceanodroma leucorhoa*) is capable of detecting and homing in on an odor target for distances from 1 to 12 km.

Procellariiformes also appear to rely on olfactory cues to locate their burrows, showing differential return rates to their nest sites as a function of surgical manipu-

lation: control (C), sham surgery (SS), and olfactory nerve section (ONS). For Leach's storm petrel the return rates were C = 91%, SS = 74%, and ONS = 0% (Grubb, 1974). For the wedge-tailed shearwater the return rates were C = 90%, SS = 70%, and ONS = 25% (Shallenberger, 1975).

Pigeons can use odor cues for orientation and navigation (Papi, 1986; Wallraff, 1991; Waldvogel, 1989). However, reliance on odor cues for orientation is dependent upon the atmospheric predictability of the cues experienced during the bird's development and early training experience (Wiltschko *et al.*, 1987). Pigeons can obtain positional information when atmospheric odors are derived from boundary-layer free airspace in an open landscape. However, positional information is obscured when the atmosphere sample is derived from close to ground level (Wallraff *et al.*, 1993). When regional odor maps cannot be relied upon because of atmospheric instability, pigeons use a variety of alternative cues, such as visual, magnetic, and polarized light to orient themselves (Waldvogel, 1987).

A number of species have now been shown to be capable of using olfactory cues to locate food. Ravens (*C. corax*; Harriman and Berger, 1986), magpies (Buitron and Nuechterlein, 1985), jays, crows (Goodwin, 1955), chickadees (*Parus atricapillus*; Jarvi and Wiklund, 1984), hummingbirds (Goldsmith and Goldsmith, 1982; Ioale and Papi, 1989), honey guides (Archer and Glen, 1969), and kiwis (Wenzel, 1968) have all been shown to be capable of using olfactory cues to locate and discriminate between foods.

There are several intriguing studies suggesting that odor recognition is important in the reproductive behavior of birds. Male mallards decreased social displays and sexual behavior toward females when their olfactory nerves were sectioned (Balthazart and Schoffeniels, 1979). When unfamiliar fruit odors were applied to squabs of the ring dove (*Streptopelia risoria*), parents decreased parental care, resulting in higher mortality of scented squabs. Bilateral olfactory nerve cuts eliminated the differential feeding of the scented and control squabs (Cohen, 1981). Olfactory recognition of parents and/or home sites may be advantageous to young as well. Just as in mammals (Corey, 1978), domestic chicks show neophobia to familiar nests treated with novel odors (Jones, 1988) and demonstrate a preference for familiar nest odors (Jones and Faure, 1982; Wurdinger, 1982).

There is also evidence that starlings may use olfaction to select nest material used in the fumigation of ectoparasites and pathogens (Clark and Mason, 1985, 1987, 1988; Clark 1991b) or in the selection of material used in

TABLE 4 Summary of Behavioral Olfactory Threshold Data for Different Species of Birds

Species	Ratio <sup>a</sup>	Stimulus	Threshold (ppm)		Source <sup>b</sup>
			Min	Max	
Rock dove <i>Columba livia</i>	18.0	<i>n</i> -Amyl acetate	0.31	29.80	5,6,9,10
		Benzaldehyde		0.75	10
		Butanethiol	13,820		7
		Butanol	0.17	1.30	10
		<i>n</i> -Butyl acetate	0.11	2.59	5,10
		Butyric acid	2.59		5
		Ethanethiol	10,080		7
		Heptane	0.29	0.38	8
		Hexane	1.53	2.98	8
		Pentane	16.45	20.76	8
Chicken <i>Gallus gallus</i>	15.0	Heptane	0.31	0.57	8
		Hexane	0.64	1.00	8
		Pentane	1.58	2.22	8
Northern bobwhite <i>Colinus virginianus</i>	—	Heptane	2.14	3.49	8
		Hexane	3.15	4.02	8
		Pentane	7.18	10.92	8
Black-billed magpie <i>Pica pica</i>	—	Butanethiol	13,416		7
		Ethanethiol	8,400		7
European starling <i>Sturnus vulgaris</i>	9.7	Cyclohexanone	2.50		3
Cedar waxwing <i>Bombycilla cedrorum</i>	—	Cyclohexanone	6.80	86.46	1
Tree swallow <i>Tachycineta bicolor</i>	15.0	Cyclohexanone	73.42		1
Brown-headed cowbird <i>Molothrus ater</i>	7.0	Ethyl butyrate	0.76		2
Catbird <i>Dumetella carolinensis</i>	—	Cyclohexanone	35.14		4
Eastern phoebe <i>Sayornis phoebe</i>	—	Cyclohexanone	35.61		4
European goldfinch <i>Carduelis carduelis</i>	—	Cyclohexanone	13.05		4
Great tit <i>Parus major</i>	—	Cyclohexanone	34.10		4
Black-capped chickadee <i>Parus atricapillus</i>	3.0	Cyclohexanone	59.95		5

<sup>a</sup> The ratio of the longest axis of the olfactory bulb to that of the ipsilateral cerebral hemisphere.

<sup>b</sup> Sources: (1) Clark (1991a); (2) Clark and Mason (1989); (3) Clark and Smeraski (1990); (4) Clark *et al.* (1993). Reprinted by permission of the publisher from (Cedar thresholds in passerines, Clark *et al.*), *Comp. Biochem. Physiol.*, **104A**, 305–312. Copyright 1993 by Elsevier Science Inc.; (5) Henton (1969); (6) Henton *et al.* (1996); (7) Snyder and Peterson (1979); (8) Stattelman *et al.* (1975); (9) Walker *et al.* (1979); (10) Walker *et al.* (1986).

“anting” behavior, which is postulated to be a grooming response to rid the bird of ectoparasites (Clark *et al.*, 1990). Multiunit recordings from olfactory nerves indicate starlings respond to a number of natural plant odors and are capable of making discriminations between complex sets of odors (Clark and Mason, 1987). However, olfactory discrimination by starlings shows a strong correlation with breeding season (specifically nest-building), suggesting hormonal influence on detection

and discrimination ability in this species (Clark and Smeraski, 1990).

#### F. Summary

All evidence indicates that the extent of olfactory development in birds is on par with that found in mammals. Some species, such as passerines, have relatively poorly developed olfactory capacities, though nonethe-

TABLE 5 Summary of Olfactory Orientation toward a Prey-Odorized Target for Seabirds

Taxa	Percentages <sup>a</sup>		Source
	Sea water	Cod liver oil	
Albatrosses			
<i>Diomedea exulans</i>	12	0	Lequette <i>et al.</i> (1989)
<i>Phoebastria palpebrata</i>	0	14	Lequette <i>et al.</i> (1989)
Pelicanoididae			
<i>Pelecanoides</i> sp.	0	0	Lequette <i>et al.</i> (1989)
Procellariidae			
<i>Pagodroma nivea</i>	—	78	Jouventin and Robin (1984)
<i>Pachyptila</i> spp.	0	0	Lequette <i>et al.</i> (1989)
<i>Procellaria aequinoctialis</i>	3	58	Lequette <i>et al.</i> (1989)
<i>Macronectes</i> spp.	16	30	Lequette <i>et al.</i> (1989)
<i>Daption capense</i>	10	54	Lequette <i>et al.</i> (1989)
<i>Daption capense</i>	0	82	Jouventin and Robin (1984)
<i>Puffinus gravis</i>	5	95	Grubb (1972)
<i>Puffinus griseus</i>	67	33	Grubb (1972)
Oceanitidae			
<i>Oceanodroma leucorhoa</i>	0	100	Grubb (1972)
<i>Oceanites oceanicus</i>	24	76	Grubb (1972)
<i>Oceanites oceanicus</i>	13	77	Jouventin and Robin (1984)
<i>Oceanites oceanicus</i>	0	87	Lequette <i>et al.</i> (1989)
<i>Fregetta tropica</i>	0	95	Lequette <i>et al.</i> (1989)
Nonprocellariiformes			
<i>Larus dominicanus</i>	11	0	Lequette <i>et al.</i> (1989)
<i>Phalacrocorax atriceps</i>	0	0	Lequette <i>et al.</i> (1989)
<i>Sterna</i> spp.	9	0	Lequette <i>et al.</i> (1989)

<sup>a</sup> Values are the percentage of the birds observed that were attracted to the target (control or cod liver oil-soaked sponge).

less show some degree of olfactory acuity. Other species, such as procellariiformes, have olfactory systems acutely sensitive to odor cues. Relative to mammals, few systematic physiological and behavioral studies are available. This gap in knowledge is unfortunate because there is a well-developed anatomical database on the avian olfactory system.

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