Chapter 7

# The Chemical Senses in Birds

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## 7.1 CHEMICAL SENSES

The chemical senses generally fall into three categories: chemesthesis (irritation and pain), olfaction (smell), and gustation (taste). Traditionally, the emphasis in describing responsiveness to chemical stimuli has been placed on taste and smell. The reality is more complex. For example, the sensory afferents for chemesthetic perception are in close proximity with olfactory receptors in the nasal cavity and with gustatory receptors in the oral cavity. Because external chemical stimuli can be processed by multiple sensory systems, there has been a great deal of confusion in the literature on the importance of individual sensory modalities. Generally, the principal mediating sensory modality may be related to stimulus type, concentration, and presentation. However, when perception of external chemical stimuli occurs via the integrated perception across modalities, the combined perceptual quality is commonly referred to as flavor.

## 7.2 CHEMESTHESIS

Chemesthesis is the perception of chemically induced pain. The first neural mediator of noxious stimuli is the nociceptor (Woolf and Ma, 2007). These primary sensory neurons are the interface between the internal and external environments. Nociceptors have cell bodies located in the dorsal root ganglion, a peripheral axon that innervates tissues, and a central axon that enters the spinal cord to transfer information to the central nervous system. Nociceptors have three functions: (1) detection of potentially damaging external noxious stimuli, which is useful in warning an animal to the risk of injury; (2) detection of endogenous inflammatory stimuli, which is useful in initiating and promoting behaviors conducive to healing and repair; and (3) detection of neural damage and ectopic firing. This latter function is a pathological condition of chronic pain. Nociceptors have high thresholds for exogenous stimuli, presumably because it would be maladaptive to defensively respond to every external assault. Nociceptors have low thresholds for endogenous stimuli. This is an adaptive response to promote healing once damage has occurred (Patapoutian et al., 2009).

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 TN also contains chemoreceptive fibers that mediate the detection of chemical irritants (Silver and Maruniak, 1981). 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 chemosensory (Gentle, 2011; Necker, 2000; Wild, 1985).

### 7.2.1 Trigeminal and Somatosensory Nerves

The morphological organization of the peripheral TN in birds is not very different from that found in mammals (Dubbeldam and Karten, 1978; Dubbeldam and Veenman, 1978; Gottschaldt, 1985). The TN is the fifth cranial nerve in birds, arising from the rostrolateral medulla near the caudal surface of the optic lobe (Getty, 1975; Schrader, 1970).

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The TN travels along 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 (*Gallus gallus domesticus*) the ophthalmic branch innervates the frontal region, the eyeball, upper eyelid, conjunctiva, glands in the orbit, the rostrodorsal part of the nasal cavity, and the tip of the upper jaw. The ophthalmic branch as a communicating ramus with the trochlear nerve 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 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 of the medial wall of the nasal cavity. The mandibular branch provides sensory input from the skin and rhamphotheca of the lower jaw, intermandibular skin, wattles, oral mucosa of rostral floor of the mouth, and the palate near the angle of the mouth (Getty, 1975; Schrader, 1970).

### 7.2.2 Performance Characteristics of Nociceptors

Pain and irritation perception begin with activation of primary sensory nociceptors. In birds, chemosensitive fibers in the TN and somatosensory nerves are similar to mammalian afferents. Most are unmyelinated C-type polymodal nociceptors with conduction velocities of 0.3–1 m/s. However, some myelinated A-delta high-threshold mechanoreceptors with conduction velocities of 5–40 m/s also respond to chemical stimuli. The discharge patterns and conduction velocities for the chicken, mallard (*Anas platyrhyncos*), and pigeon (*Columba livia*) are similar to those observed in mammals (Gentle, 1989; Necker, 1974).

Although birds have slightly different neural architecture relative to mammals, the underlying functions of neural connections have been evolutionarily preserved (Butler and Cotterill, 2006; Dugas-Ford et al., 2012; Güntürkün, 2012). This also applies to the underlying physiological and biochemical processes of chemically induced pain. Generally, birds have the same classes of neuropeptides as mammals, but their structures are not totally homologous. Avian endogenous pain-promoting substances such as substance P, 5-HT, histamine, bradykinin, and acetylcholine evoke inflammation and pain-related behaviors in chickens, pigeons, rats, dogs, and guinea pigs (Szolcsanyi et al., 1986; Gentle and Hill, 1987; Gentle and Hunter, 1993; Koda et al., 1996; Hu et al., 2002; Ohta et al., 2006). Prostaglandins that modulate the pain response in mammals also serve this function in birds, and their effects can be abolished by prostaglandin biosynthase inhibitors such as aspirin-like analgesics (Clark, 1995).

Despite these physiologically mediated similarities, 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 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; Szolcsanyi et al., 1986; Sann et al., 1987). These taxon-specific responses to exogenous chemical stimuli underscore taxonomic differences in both endogenous neuropeptides and receptors, whose significance has been implicated in the evolutionary ecology of the taxa (Mason et al., 1991; Clark, 1998; Tewksbury and Nabhan, 2001).

### 7.2.3 Receptor Mechanisms

Nonselective transient receptor potential (TRP) cation channels are involved in sensory neuron activation events, neurotransmitter release, release of inflammatory mediators, and other aspects of pain transduction (Cortright et al., 2007; Figure 7.1). Most of what is known about TRP channels is derived from work done on mammals (Holzer, 2011). However, increasingly more comparative evolutionary similarities and differences are being characterized for other taxa (Saito and Shingai, 2006; Saito et al., 2011). TRPV1 (initially called VR1) was first cloned in mammals and found to respond to the exogenous vanilloid, capsaicin (Caterina et al., 1997), as well as endogenous agonists, anandamide, and 12-HPETE, which are structurally similar to capsaicin (Zygmunt et al., 1999; Hwang et al., 2000). TRPV1 is also activated by heat (>43 °C) and acid (pH ≤ 6). The sensation that TRPV1 activation evokes in humans via these polymodal nociceptors is one of tingling and burning, like the sensation produced by capsaicin found in chili peppers. Like its mammalian counterpart, the TRP receptor in birds (cTRPV1, chick dorsal root ganglion) responds to high temperatures (≥45 °C) and extracellular acid solution (pH ≤ 4). However, cTRPV1 is different, showing a 68% identity and 79% similarity to rat TRPV1. These differences in receptor composition manifest as a poor response to capsaicin (Jordt and Julius, 2002) and explain the behavioral differences in capsaicin sensitivity between birds and mammals; mammals are behaviorally sensitive to capsaicin and birds are not (Mason et al., 1991; Norman et al., 1992).

Currently, 28 TRP channels, grouped into six functional subfamilies, have been characterized. The subfamilies are

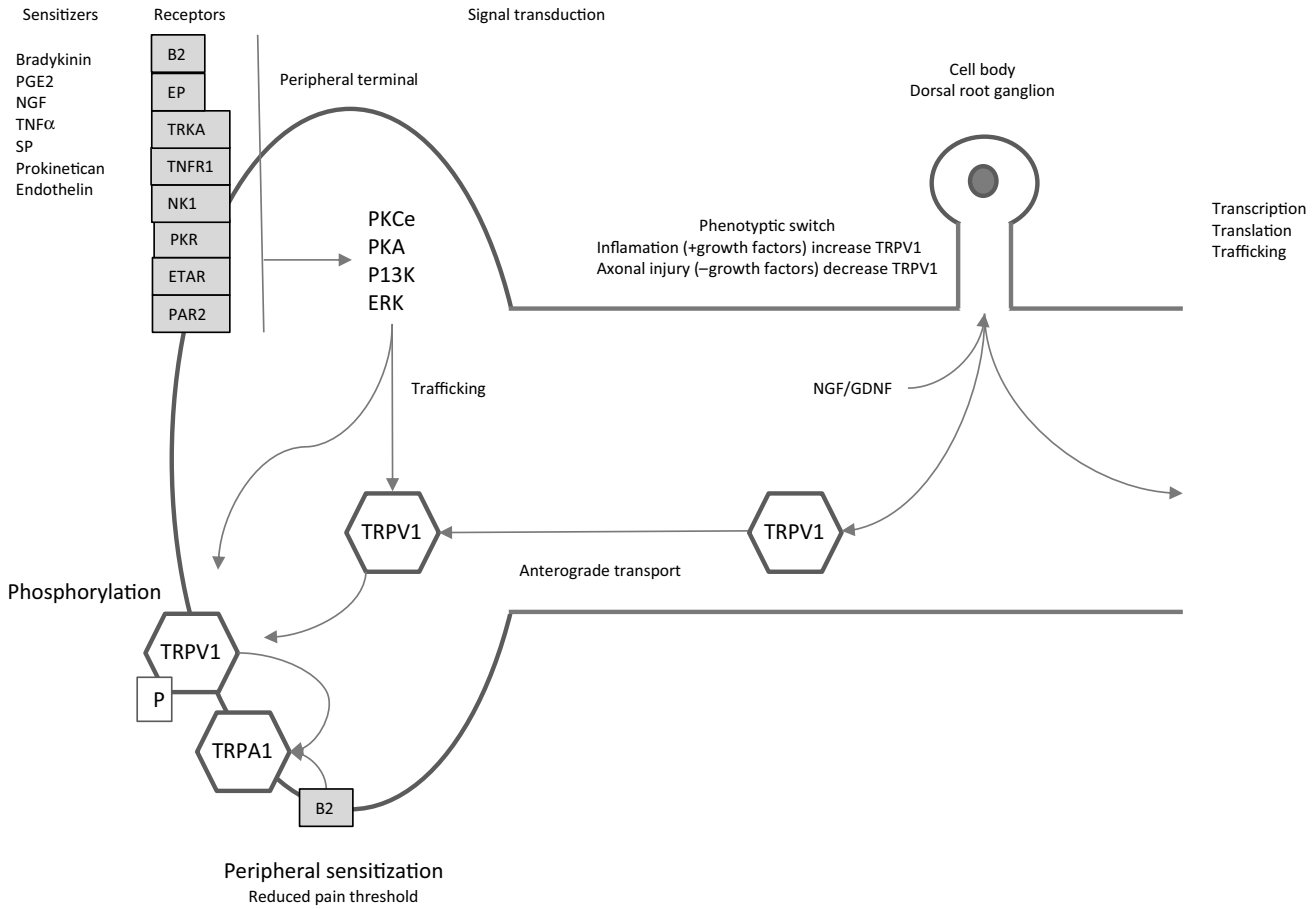


**FIGURE 7.1 Changes in transient receptor potential (TRP) channels produced by inflammation.** Endogenous sensitizers act on receptors expressed by nociceptors to activate intracellular signal transduction pathways. Pathways phosphorylate TRP channels, altering trafficking to the membrane, thresholds, and kinetics. Growth factors, such as nerve growth factor (NGF), are retrogradely transported to the cell body of the nociceptors. Through intracellular signaling pathways, expression of TRP channels is increased and they are transported to the peripheral terminal. Changes in transcription and translation of TRP channels and other proteins can switch the chemical phenotype of the neurons from their state in naive conditions to an altered state during inflammation. B2, bradykinin receptor; ERK, extracellular signal-regulated kinase; ETAR, endothelin receptor type A; GDNF, glial-cell-derived neurotrophic factor; NK1, neurokinin receptor 1; PAR2, protease-activated receptor 2; PGE2, prostaglandin E2; PI3K, phosphoinositide 3-kinase; PK, protein kinase; PKR, prokineticin receptor; TNFα, tumor necrosis factor α; TNFR1, TNF receptor 1; TRKA, tyrosine kinase receptor A. *Adapted from Patapoutian et al. (2009).*

responsive to exogenous compounds that code for qualitative perceptual similarities (e.g., the "hotness" of capsaicin, the "burn" of cinnamon oil, the "coolness" of menthol, the irritation of mustard oil; Holzer, 2011). Although the specific homologies for other TRP channels in birds are generally not known, based on behavioral responsiveness to a variety of mammalian irritants, it is anticipated that TRP channel receptor molecules in birds would be structurally similar and/or have similar expression in nociceptors to that found in mammals for cinnamon oil, allicin (garlic/onion), and menthol and divergent for mustard oil and anthranilate (grape) compounds (Clark, 1998; Stucky et al., 2009).

Digital fluorescence imaging of intracellular calcium $[Ca^{2+}]_I$ in vitro preparations of chicken and rat trigeminal dorsal root ganglia show that there are separate and overlapping populations of neurons that are sensitive to the well-described avian irritant, methyl anthranilate, and capsaicin (Kirifides et al., 2004). In the chicken, 48% of neurons responded to methyl anthranilate, whereas only 16% responded to capsaicin. Moreover, there was a greater change in $[Ca^{2+}]_I$ to equimolar concentrations of methyl anthranilate (78%) relative to capsaicin (43%). Increases in $[Ca^{2+}]_I$ were dependent upon extracellular calcium for both methyl anthranilate and capsaicin. However, responses to methyl anthranilate, but not capsaicin, were dependent on extracellular sodium. This suggests different transduction mechanisms for the two compounds. Together, these observations provide further rationale for the observed behavioral differences in birds to these two compounds. Starlings (*Sturnus vulgaris*) demonstrate congenital avoidance to methyl anthranilate but not capsaicin, although they could be trained to avoid capsaicin in conditioned

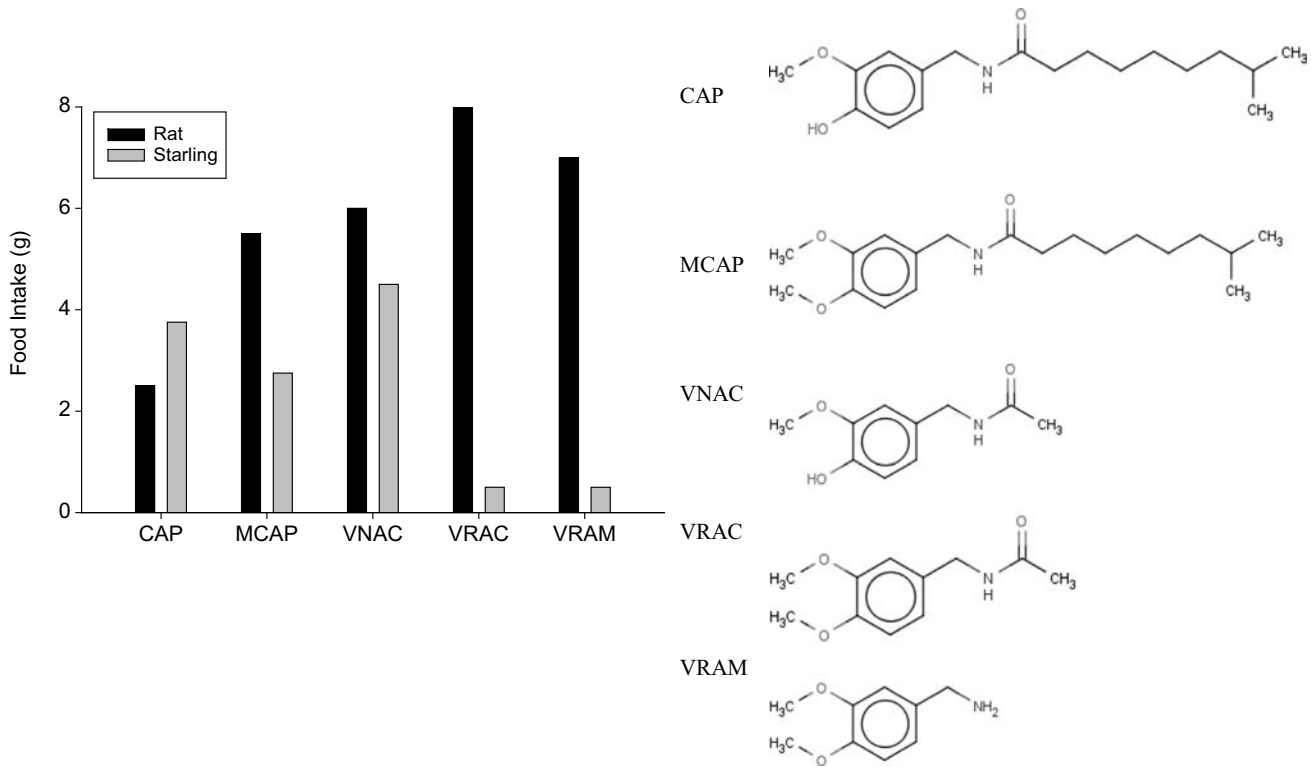


**FIGURE 7.2 Consumption of food treated with capsaicin (CAP), methyl capsaicin (MCAP), vanillyl acetamide (VNAC), veratryl acetamide (VRAC), and veratryl amine (VRAM) in rats and starlings.** Note the general inverse relationship of consumption as structure changes, suggesting functional receptor differences in the two taxa. Bird repellents are more basic and rigid (planar) than mammal aversive compounds. Concentration applied: 1000 ppm. Consumption of 4 g of untreated food is control baseline intake for both species. *Data adapted from Mason et al. (1991).*

avoidance paradigms, and that avoidance was contingent upon an intact ophthalmic branch of the TN (Mason and Clark, 1995). These observations also suggest that while birds can perceive capsaicin, although somewhat poorly, it is not coded as pain, highlighting the importance of central processing in the perceptual interpretation of peripheral signals.

### 7.2.4 Chemical Structure–Activity Relationships to Irritants

Despite the apparent insensitivity of birds to capsaicin, they can respond to other vanilloid compounds (Figure 7.2). Aromatic compounds that are considered aversive by birds are qualitatively characterized as having an aromatic heterocyclic core, high degree of basicity, high degree of lipophilicity, and a high degree of electronegativity (Figure 7.3). The core aromatic heterocycle of a repellent compound is enhanced by substitutions that affect electron donation: amino > methoxy > methyl > hydroxyl groups. Resonance of lone pairs of electrons enhances repellency as a function of substituent position: ortho > para > meta. Acidic substituents in the electron withdrawing group detract from aversive qualities of the compound. Steric effects and extreme delocalization of lone pairs of electrons, as might occur in meta isomers and aromatic structures with multiple substituted electron donating groups, tend to interfere with repellency (Mason et al., 1989; Clark, 1991a; Clark and Shah, 1991, 1994; Clark et al., 1991; Shah et al., 1991).

Quantitative structure–activity relationships of aromatic compounds and repellency are consistent with earlier qualitative studies. The aversive properties of 14 derivatives of cinnamic acid compounds are characterized by heat of formation (DH(f)), polarizability (XY and YY), and superdelocalizability (Sr). All of these descriptors are electronic (Watkins et al., 1999). These findings generally align with a reanalysis of the quantitative structure–activity relationships of the 117 compounds described above (Clark, 1997). Canonical analysis of the relationship of physicochemical, topological, and electrostatic descriptors and the response shape of the four-parameter fluid intake curve showed that 94% of variance in the response profile could be accounted for by five parameters: polarizability, ES2, ANC, KAPPA2, and CHI2. Polarizability is the relative susceptibility of the electron cloud of a molecule to be distorted by presence of an external electric field. Owing to distortion, an induced electric dipole moment appears. Temporary dipoles induce dipoles in other molecules, resulting in van der

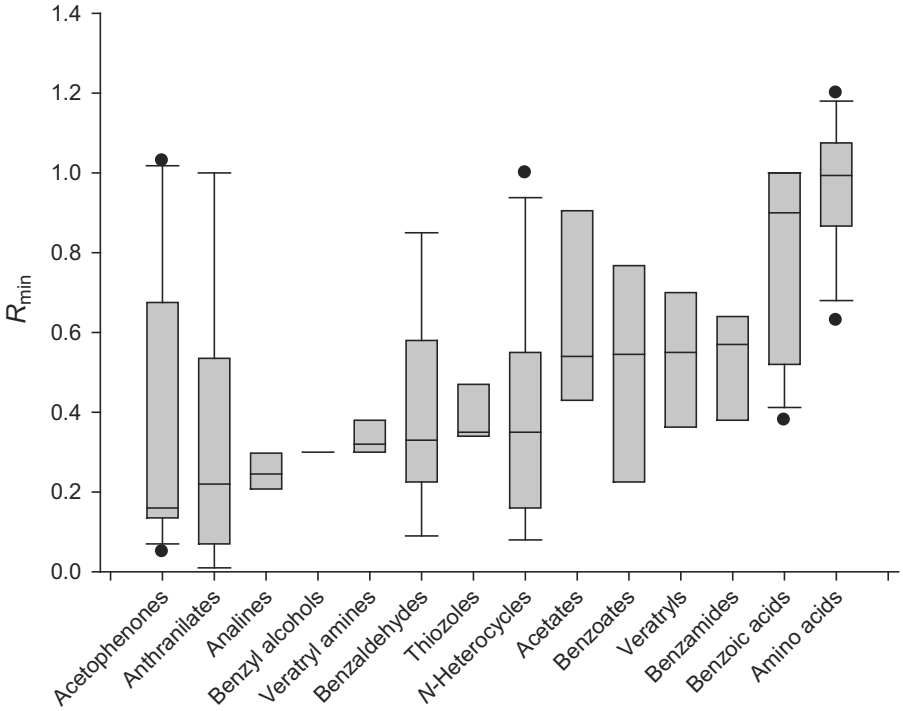


**FIGURE 7.3 The relative reduction of fluid intake for solutions as a function of chemical class, which assumes a benzene parent structure with the nomenclatural taxonomy defined by the principal electron withdrawing group.** Fluid intake is the asymptotic minimum intake in one-bottle 6-h drinking trials ($R_{min}$). Strongly aversive solutions (where $R_{min}$ is not statistically distinguishable from zero) have $R_{min} \leq 0.2$. Moderately aversive solutions have $0.2 < R_{min} \leq 0.4$, weakly aversive solutions have $0.4\ R_{min} \leq 0.6$, and solutions with $R_{min} > 0.6$ are not aversive at all (not statistically different from water controls). Median $R_{min}$ (solid bars), $R_{min}$ 25–75th percentile (shaded box), $R_{min}$ 5–95th percentile (capped line), and the range of $R_{min}$ (open symbols). *Adapted from Clark (1997).*

Waals intermolecular forces by orienting the temporary and induced dipoles with each other. ES2 is an electrotopological descriptor that describes electronic interactions between molecules. ANC is a partial negative electronic charge descriptor of electrostatic potential that influences molecular interactions. CHI2 and KAPP2 are valence connectivity and shape descriptors that may describe the rigidity of the molecule and accessibility of the molecule to receptor systems. The importance of electronic features of molecules is consistent with studies of TRPA1 channel modulation and activation of cysteine-reactive chemicals. TRP channel activation was found to be more dependent on chemical reactivity relative to molecular shape (Hinman et al., 2006; Macpherson et al., 2007). However, the importance of gaining access to proximity of the TRP channels owing to influences of molecular flexibility and shape still remains to be more fully explored.

### 7.2.5 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 chickens. Geese and chickens 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; McKeegan et al., 2005).

### 7.2.6 Nasal and Respiratory Irritation and Interaction of Olfaction and Chemesthesis

The TN is important in the perception of odors (Tucker, 1971; Silver and Maruniak, 1981; Keverne et al., 1986). Electrophysiological evidence shows that the TN responds to odors, although it is 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 transections. However, odor responding can be reinstated if the odor concentration is increased (Michelsen, 1959; Henton, 1969; Henton et al., 1966). Odor sensitivity of pigeons decreased by 2–4 log units (vapor saturation) after olfactory nerve transaction (Walker et al., 1979).

Although olfaction can modulate responding to chemical irritants, it is relatively unimportant (Clark, 1995). In European starlings, avoidance of anthranilate compounds

was partially a consequence of olfactory cues. When the olfactory nerves were transected, avoidance was only mildly diminished. When the ophthalmic branches of the TN were transected, the starlings became insensitive to the aversive properties of the anthranilates (Mason et al., 1989).

### 7.2.7 Behavioral Responses to Irritants

Many aromatic molecules are aversive to birds (Kare, 1961; Mason et al., 1989; Crocker and Perry, 1990; Clark and Shah, 1991, 1993; Crocker et al., 1993). 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, 1991). Second, there is no evidence that consumption is altered by gastrointestinal feedback; intake of fluid treated with those sensory stimuli is constant over time (Clark and Mason, 1993). Third, unlike mammals, birds seem unable to associate the aversive quality of the stimulus with other chemosensory cues, suggesting that conditioned flavor avoidance learning does not occur (Clark, 1996; Clark and Avery, 2013). Fourth, birds do not habituate to the stimulus; avoidance persists in the absence of reinforcement (Clark and Shah, 1994).

### 7.2.8 Applications

Current interest in chemesthetic function and properties in birds is largely focused in four areas: (1) the evolutionary phylogenetic relationships of receptor mediated perception of noxious stimuli and its consequence to the foraging ecology of birds (Clark, 1998; Tewksbury and Nabhan, 2001); (2) the applicability of using aversive compounds in modulating feeding behavior of birds to develop repellents for prevention of crop damage or otherwise mitigating against damage caused by birds (Mason and Clark, 1997; Clark and Avery, 2013); (3) efforts to gain a better understanding of pathologic pain caused by "debeaking" and promotion of animal welfare in domestic chicken production through better management methods or development of appropriate analgesics (Kuenzel, 2007; Gentle, 2011); and (4) discovery of better analgesics for management of pain in veterinary clinical settings.

## 7.3 OLFACTION

### 7.3.1 Morphology of Olfactory System

Air entering a bird's nasal cavity passes through a series of mucous-covered, invaginated chambers called nasal conchae. Nasal conchae influence air flow dynamics and direct odors to the caudal-most chamber, which contains the chemically sensitive olfactory epithelium (reviewed in Roper, 1999; see also: Bang, 1960, 1961, 1963, 1964, 1965, 1966; Bang and Cobb, 1968). The surface of the olfactory epithelium is composed of receptor cells, which detect odorous compounds and occur at the ends of olfactory nerve dendrites. Each receptor cell is surrounded by a cluster of supporting cells and ends in a knob bristling with 6–15 cilia that extend into the lumen. The length of cilia varies by species. Black vultures, for example, have cilia of 40–50 μm, whereas domestic fowl have cilia of 7–10 μm (Shibuya and Tucker, 1967). To gain access to the cilia of receptor cells, odor molecules must diffuse through a mucous membrane. Cilia themselves provide no transport function. Rather, secretions covering cilia provide rapid flow for odor molecules. Olfactory gland secretions must be removed and replaced to maintain diffusion and avoid receptor habituation to odorant molecules. Traction of nearby respiratory cilia facilitates removal of secretions.

The extent of scrolling of caudal conchae correlates with the surface area of olfactory epithelium and the relative size of the olfactory bulb, which is the region of the brain that processes odor input (Bang and Cobb, 1968; Bang, 1971; Bang and Wenzel, 1985; reviewed in Roper, 1999; Hagelin, 2007a). Avian orders with relatively larger olfactory bulbs have lower detection thresholds, indicating they are more sensitive to certain odorous compounds than those with relatively small olfactory bulbs (Clark et al., 1993; Table 7.1, Figure 7.4). Elaborated olfactory systems typically belong to species with demonstrated reliance on odor cues in the field (Stager, 1964; Hutchison and Wenzel, 1980; Hagelin, 2004) and, in some species, correlate positively with the number of olfactory receptor genes (Steiger et al., 2008). Fossil evidence also indicates olfactory bulb size was relatively large early in bird evolution, revealing a previously unrecognized emphasis on smell (Zelenitsky et al., 2011).

Although a larger olfactory bulb size or greater scrolling of receptor epithelium likely indicates greater functional capacity (e.g., more cells and neural circuits; Meisami, 1991), it is important not to dismiss avian species with relatively "unelaborate" olfactory systems (Hagelin, 2007b). Both field and laboratory tests indicate that several taxa with relatively small olfactory bulbs can discriminate between and/or adaptively employ certain odors, such as those related to breeding and nesting (e.g., crested auklets (*Aethia cristatella*) Hagelin et al., 2003; European starlings Clark and Mason, 1985; Gwinner and Berger, 2008; Corsican Blue Tit (*Parus caeruleus ogliastrae*) Petit et al., 2002).

### 7.3.2 Innervation of Olfactory Receptors

Olfactory receptor cells from each nasal cavity transmit information via the olfactory nerve to the olfactory bulb, located in the anterior region of each brain hemisphere. Each olfactory bulb is composed of concentric cell layers.

**TABLE 7.1 Summary of Mean Ratios of Ipsilateral Olfactory Bulb Diameter to Cerebral Hemisphere Diameter and Their Standard Errors (SE) for Several Orders of Birds**

| 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 |
| Columbiformes | 2 | 20.0 | 1.4 | Piciformes | 5 | 11.4 | 1.3 |
| Cuculiformes | 4 | 19.5 | 0.6 | Passeriformes | 25 | 13.3 | 0.7 |
| Gruiformes | 14 | 22.2 | 0.9 | Pelecaniformes | 4 | 12.1 | 1.6 |
| Gaviformes | 1 | 20.0 | 0.0 | Coraciiformes | 5 | 14.5 | 1.6 |
| Podicipediformes | 2 | 24.5 | 1.8 | Sphenisciformes | 1 | 17.0 | 0.0 |
| Procellariiformes | 10 | 29.1 | 1.4 | | | | |

Sample sizes indicate the number of species (*N*).
**Source:** Data adapted from Bang and Cobb (1968).

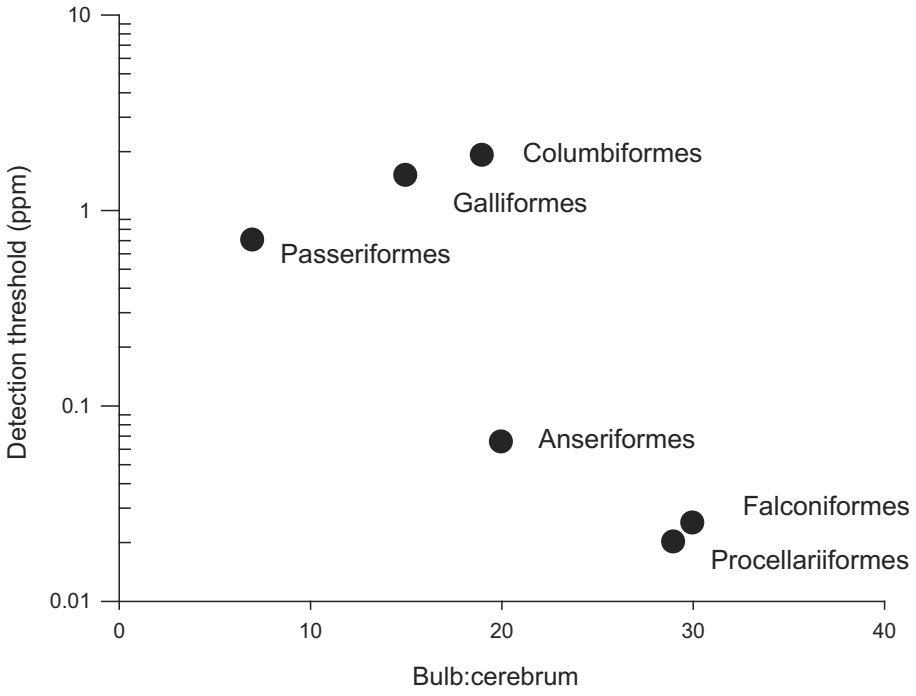


**FIGURE 7.4 Relationship between olfactory detection threshold and relative size of the olfactory bulb for different orders of birds.** *Adapted from Clark and Shah (1993).*

Incoming olfactory nerve fibers constitute the outer layer. Branching nerve terminals penetrate into 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 axons leave to project to many areas of the forebrain.

Like other vertebrates, the olfactory bulbs of birds are bilaterally symmetrical; each is associated with its own (ipsilateral) brain hemisphere. The layering of different cell types within avian olfactory bulbs is qualitatively similar to reptiles, in that well-defined cell layers (like those of mammals) are lacking (Allison, 1953; Andres, 1970). However, there are many interneuron connections in the cell layers

between the mitral and glomerular regions. There are no direct connections between the two (contralateral) olfactory bulbs (Rieke and Wenzel, 1978).

Although birds clearly have olfactory bulbs, they appear to lack an accessory olfactory system (Rieke and Wenzel, 1974, 1978). Both olfactory and accessory olfactory structures commonly occur in other vertebrates. The accessory olfactory system is frequently linked to conspecific scent stimuli that modulate social behavior (e.g., reproduction, aggression). However, there is good evidence for mammals that both the main olfactory and accessory olfactory systems can detect and process overlapping sets of odor stimuli (Keller et al., 2009). Accessory olfactory structures include the vomeronasal organ and accessory olfactory bulb. It is possible that accessory olfactory bulbs in birds occur during early embryonic development only, but are lost later on (Matthes, 1934). This idea, however, has received little scientific attention.

### 7.3.3 Olfactory Neuronal Response

Electrophysiological responses to odor stimuli are taken as definitive evidence of olfactory capacity. These can be recorded from a single "unit" (neuron) or multiunit nerve fibers. Recordings of black vultures indicate that the electro-olfactogram appears primarily during inspiration, which coincides with peak spike activity (Shibuya and Tucker, 1967). Electrophysiological recordings of mammals, amphibians, reptiles, and birds all show similar responses, irrespective of the size of a species' olfactory apparatus (Tucker, 1965; Shibuya and Tonosaki, 1972).

Single-unit responses from within the olfactory bulb of domestic chickens show widely variable rates of spontaneous firing (mean 4.9 spikes/s, range 0.1–32.4 spikes/s) prior to odor exposure (McKeegan, 2002). Odor stimulation modifies spontaneous firing via excitation or inhibition. Avian firing rates appear to fall in between rates reported for mammals and reptiles (McKeegan, 2002, 2009). Single units of chickens responded to two or more odors and revealed surprising sensitivity to biologically relevant scents associated with captivity (e.g., hydrogen sulfide). Responses to extremely low (<0.5 ppm) stepwise changes in concentration to hydrogen sulfide revealed a level of fine-tuning not previously reported for other vertebrates (McKeegan et al., 2002). Continuous presentation of a stimulus can result in physiological adaptation of both single-unit (McKeegan and Lippens, 2003) and nerve-unit recordings, like mammals. Recovery can be achieved within a few minutes of rest.

Olfactory nerve fibers are unmyelinated, which produces slow conduction velocities of about 1.5 mJ/s (Macadar et al., 1980). Interestingly, transected olfactory nerves (which experimentally inhibit olfaction) can repair and recover full physiological capacity within 30 days (Tucker et al., 1974). Although healed nerves are scarred and smaller, recordings and autonomic reflexes to odorants did not differ between controls and nerves that had been cut at least 6 months earlier (Tucker, 1971; Tucker et al., 1974).

Another means of quantifying olfactory neural responses involves calcium imaging (Restrepo et al., 1995). This method uses fluorescence to quantify changes in the flux of calcium ions associated with neural activation (i.e., signal transduction) of a single olfactory receptor neuron (ORN). Jung et al. (2005) tested responses of acutely dissociated ORNs from olfactory epithelium of embryonic domestic chicks. Avian ORNs were placed in Ringer's solution containing liquid solutions of odorants. The fluorescence patterns, which correspond to increases or decreases in $Ca^{2+}$ concentration, were remarkably similar to those of other vertebrates (mammals and fish) that had been tested with the same set of odorants (Jung et al., 2005).

### 7.3.4 Laboratory Detection Thresholds, Discrimination, and Seasonal Change

Physiological responses (e.g., change in respiration or heart rate) to novel odor stimuli have been observed (Wenzel and Sieck, 1972). Habituation to the stimulus under this paradigm, however, is problematic. Operant and classical conditioning paradigms that use positive or negative reinforcement (Michelsen, 1959; Henton et al., 1966; Henton, 1969) are usually poor at determining olfactory thresholds or discrimination (Calvin et al., 1957). However, two process learning paradigms, such as cardiac conditioning, have proven to be a successful technique for detection, discrimination, and threshold testing (Rescorla and Solomon, 1967; Walker et al., 1986; Clark and Mason, 1989; Clark and Smeraski, 1990; Clark, 1991a; Clark et al., 1993). During cardiac conditioning, an odor (the conditional stimulus) is paired with an aversive experience, such as a shock (the unconditional stimulus). Heart rate is compared before and after stimulus presentation during training until a level of cardiac acceleration is reliably achieved, indicating a bird has learned to associate the odor in anticipation of a shock. Thereafter, tests of detection or odor discrimination can proceed. Most birds tested with this paradigm have shown olfactory capabilities comparable to mammals (Davis, 1973). 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 7.2).

European starlings offer an interesting case study of olfactory structure, function, and seasonality. Male starlings incorporate green plants that are rich in aromatic volatiles into nests, some of which act as a fumigant against parasites and pathogens (Clark and Mason, 1985, 1987, 1988; Clark, 1991b; Gwinner, 1997; Gwinner et al., 2000; Gwinner and Berger, 2005). Starlings are most sensitive to, and can discriminate between, plant odors during spring only, rather than

**TABLE 7.2 Summary of Selected Behavioral Olfactory Threshold Data for Different Species of Birds**

| Species | Ratio[1] | Stimulus | Threshold (ppm) Min | Threshold (ppm) Max | Source |
|---|---|---|---|---|---|
| Rock dove (*Columba livia*) | 18.0 | *n*-Amyl acetate | 0.31 | 29.8 | Henton (1969), Henton et al. (1966), Walker et al. (1979), Walker et al. (1986) |
| | | Benzaldehyde | 0.47 | 00.75 | Walker et al. (1986) |
| | | Butanethiol | 13,820 | – | Snyder and Peterson (1979) |
| | | Butanol | 0.17 | – | Walker et al. (1986) |
| | | *n*-Butyl acetate | 0.11 | 2.59 | Henton (1969), Walker et al. (1986) |
| | | Butyric acid | 2.59 | – | Henton (1969) |
| | | Ethanethiol | 10,080 | – | Snyder and Peterson (1979) |
| | | Heptane | 0.29 | 0.38 | Stattelman et al. (1975) |
| | | Hexane | 1.53 | 2.98 | Stattelman et al. (1975) |
| | | Pentane | 16.45 | 20.76 | Stattelman et al. (1975) |
| Chicken (*Gallus gallus*) | 15.0 | Heptane | 0.31 | 0.57 | Stattelman et al. (1975) |
| | | Hexane | 0.64 | 1.00 | Stattelman et al. (1975) |
| | | Pentane | 1.58 | 2.22 | Stattelman et al. (1975) |
| Northern bobwhite (*Colinus virginianus*) | – | Heptane | 2.14 | 3.49 | Stattelman et al. (1975) |
| | | Hexane | 3.15 | 4.02 | Stattelman et al. (1975) |
| | | Pentane | 7.18 | 10.92 | Stattelman et al. (1975) |
| Black-billed magpie (*Pica pica*) | – | Butanethiol | 13,416 | – | Snyder and Peterson (1979) |
| | | Ethanethiol | 8400 | – | Snyder and Peterson (1979) |
| European starling (*Sturnus vulgaris*) | 9.7 | Cyclohexane | 2.50 | – | Clark and Smeraski (1990) |
| Cedar waxwing (*Bombycilla cedrorum*) | – | Cyclohexane | 6.80 | 86.46 | Clark (1991a) |
| Tree swallow (*Tachycineta bicolor*) | 15.0 | Cyclohexane | 73.42 | – | Clark (1991a) |
| Brown-headed cowbird (*Molothrus ater*) | 7.0 | Ethyl butyrate | 0.76 | – | Clark and Mason (1989) |
| Catbird (*Dumetella carolinensis*) | – | Cyclohexane | 35.14 | – | Clark et al. (1993) |
| Eastern phoebe (*Sayornis phoebe*) | – | Cyclohexane | 35.61 | – | Clark et al. (1993) |
| European goldfinch (*Carduelis carduelis*) | – | Cyclohexane | 13.05 | – | Clark et al. (1993) |
| Great tit (*Parus major*) | – | Cyclohexane | 34.10 | – | Clark et al. (1993) |
| Black-capped chickadee (*Parus atricapillus*) | 3.0 | Cyclohexane | 59.95 | – | Henton (1969) |

[1]*The ratio of the longest axis of the olfactory bulb to that of the ispsilateral cerebral hemisphere.*

in summer and fall. Spring is coincident with nest building and suggests a hormonal influence (Clark and Smeraski, 1990).

Birds treated with testosterone (T), a hormone that enlarges song-learning nuclei of the brain and alters behavior, exhibited enlarged olfactory bulbs year-round, indicating a proximate effect on bulb structure. However, perception of plant odor in T-implanted males was greatest during spring only, indicating that perception was independent of T-treatment and olfactory bulb volume. One hypothesized but untested mechanism is that an increase in receptor cell density in starling olfactory epithelium occurs in spring (DeGroof et al., 2010).

### 7.3.5 Development

Volatile compounds diffuse through avian eggshell (Rahn et al., 1979), providing an opportunity for odor exposure within the egg (Tolhurst and Vince, 1976; Sneddon et al., 1998). Many vertebrates, including birds, detect and learn chemical information as embryos (e.g., humans: Schaal et al., 2000; Mennella et al., 2001; other mammals: Hepper, 1988; Bilko et al., 1994; amphibians: Mathis et al., 2008; birds: Porter and Picard, 1998; Bertin et al., 2012). Early exposure can cause changes in neuroanatomy, which alters chemosensory perception in a way that can adaptively shape responses later in life (e.g., to food, mates, etc.) (Todrank et al., 2011).

Studies of domestic chickens, the avian model for development, indicate that odor detection can occur before or after young pierce the egg's air sac and begin breathing air (Tolhurst and Vince, 1976; Bertin et al., 2012; Hagelin et al., 2013). ORNs are functional 6 days prior to air-breathing (on embryonic developmental day 13; Lalloué et al., 2003), when nasal passages are full of amniotic fluid. Embryos at this stage swallow frequently, facilitating fluid movement, similar to mammals in utero (Sneddon et al., 1998). Airbreathing begins approximately 2 days prior to hatching, on embryonic developmental day 19 (Tolhurst and Vince, 1976).

The magnitude of embryonic response varies relative to stimulus concentration and timing of exposure (Bertin et al., 2010). Later developmental stages show relatively greater responses to odors (Gomez and Celli, 2008; Bertin et al., 2012). Detectable stimuli include artificial odors (Sneddon et al., 1998), as well as naturally occurring scents, such as nest materials (Gwinner and Berger, 2008), food-related odors (Burne and Rogers, 1999; Cunningham and Nevitt, 2011), and compounds found in plumage scent of at least one alcid species (Hagelin et al., 2013).

### 7.3.6 Field Studies and Behavioral Ecology

Like other vertebrates, birds detect and respond adaptively to odors (reviewed in Roper, 1999; Hagelin, 2007a; Balthazart and Taziaux, 2009; Caro and Balthazart, 2010). Hagelin (2007a) made a distinction between environmentally derived odors (e.g., food, predators) and those produced by birds themselves (e.g., body odors, fecal odor, preen gland secretions). The latter can have social and reproductive implications. This section considers examples of adaptive olfactory responses to environmental odors as well as bird-derived scents.

The use of olfactory cues for locating food has been documented for numerous species, such as procellariids, vultures, corvids, hummingbirds, honeyguides, parrots, and kiwis (Roper, 1999). Turkey vultures (*Cathartes aura*), for example, are attracted to ethyl-mercaptan, a volatile associated with decomposed carcasses (Stager, 1964, 1967), and locate food without visual cues (Houston, 1986). Procellariiforms also forage over considerable distances. Black-footed albatrosses (*Diomedea nigripes*) respond to bacon grease over 31 km away (20 miles; Miller, 1942), whereas Leach's storm petrel (*Oceanodroma leucorhoa*) home to scent targets at a distance of 1–12 km (Clark and Shah, 1992). Some procellariiformes also respond to a compound that is correlated with prey called dimethyl-sulfide (DMS) (Nevitt et al., 1995). DMS smells like rotten seaweed and results from the breakdown of metabolic products of marine algae (phytoplankton). Petrels, however, do not feed on phytoplankton. Rather, DMS concentrates in locations where a bird's prey (zooplankton, such as krill) is actively grazing on phytoplankton. Grazing by zooplankton lyses phytoplankton cells and thereby creates a DMS odor plume, which some birds follow to locate food (Nevitt, 2011).

With regard to predators, the scent of urine and/or feces has an aversive effect on some avian species (blue tits (*Cyanistes caeruleus*), Amo et al., 2008; house finches (*Carpodacus mexicanus*), Roth et al., 2008; red junglefowl (*Gallus gallus*), Zidar and Løvlie, 2012), but not all (eastern blue birds (*Sialia sialis*), Godard et al., 2007; house wren (*Troglodytes aedon*), Johnson et al., 2011). Application of predator odor can also deter breeding ducks and songbirds (Eicholz et al., 2012; Forsman et al., 2013). Responses appear to be innate rather than learned (Amo et al., 2011b), although sleeping birds are unreactive (Amo et al., 2011a).

Odors are also germane to avian orientation and navigation (reviewed in Wallraff, 2005; Gagliardo, 2013). Homing pigeons, for example, exhibit larger olfactory bulbs than nonhoming breeds (Rehkämper et al., 1988, 2008). Investigators have also altered pigeon homing behavior via experimental disruption of the olfactory system. Manipulations include olfactory nerve transection (Papi et al., 1971; Gagliardo et al., 2006, 2009), anesthesia of olfactory mucosa (Wallraff, 1988), ablating the central piriform cortex of the brain (Papi and Casini, 1990), and nostril plugging. The last of these manipulations indicates that pigeons rely more on their right nostril for olfactory information (Gagliardo et al., 2007, 2011). *ZENK*, an

immediate early gene expressed in olfactory neurons, also implicates the use of olfaction during the process of homing (Patzke et al., 2010).

Emerging evidence for passerine species further supports olfaction during migration. For example, adult gray catbirds (*Dumetella carolinensis*) rendered temporarily anosmic (by washing the olfactory tissues with zinc sulfate) oriented differently from adult controls but similarly to juvenile birds, which were migrating for the first time and therefore unable to navigate (Holland et al., 2009). With regard to cellular mechanisms, black-headed buntings (*Emberiza melanocephala*) increase activation of olfactory tissues (as measured by c-fos immunoreactivity) during migration. These birds exhibit a seasonally enhanced emphasis on olfaction while migrating, compared to visual systems (Rastogi et al., 2011).

Many birds produce a variety of odorous compounds (Table 7.3; reviewed in Campagna et al., 2011). For example, a seabird colony, with its dense numbers of birds, burrows, and feces, makes for a potent chemosensory experience. Pioneering work by Grubb (1974) on Leach's storm petrel showed differential return rates to nest sites after surgical manipulation, indicative of olfactory-based homing: 91% for controls, 74% for sham surgery, and 0% for olfactory nerve section. Several petrel species have since been shown to discriminate between the odor of their own nest and conspecific burrows (Mínguez, 1997; De León et al., 2003; Bonadonna et al., 2003a,b). Attraction to home nest odor is also reported for passerines (Caspers and Krause, 2010; Krause and Caspers, 2012).

**TABLE 7.3 Some Avian Orders Considered To Be Very Odorous by Ornithologists**

| Order | Common Name | Number of Species[1] |
|---|---|---|
| Procellariiformes | Petrels, shearwaters, diving petrels | 16 |
| Ciconiiformes | Herons, storks, new world vultures | 12 |
| Anseriformes | Ducks, geese, swans, screamers | 49 |
| Charadriiformes | Sandpipers, gulls, auks | 23 |
| Psittaciformes | Parrots | 14 |
| Cuculiformes | Cuckoos | 16 |
| Coraciiformes | Kingfishers, rollers, hoopoes, woodhoopoes | 14 |
| Piciformes | Woodpeckers, barbets, tucans | 33 |
| Passeriformes | Grackles, starlings, ravens, finches, honeycreepers | 46 |

[1]*Data compiled from Weldon and Rappole, 1997.*

Avian chemical substances are linked with a variety of social contexts (reviewed in Hagelin, 2007a; Hagelin and Jones, 2007; Balthazart and Taziaux, 2009; Caro and Balthazart, 2010). Uropygial gland secretions, for example, show some level of hormonal control and exhibit individual, sex, and age-specific patterns (e.g., Procellariiformes: Mardon et al., 2010, 2011; Anseriformes: Kolattukudy et al., 1987; Galliformes: Karlsson et al., 2010; passerines: Whittaker et al., 2010; Whelan et al., 2010; Shaw et al., 2011; Amo et al., 2012a). Pioneering work by Balthazart and Schoffeniels (1979) indicated male mallards decreased social displays and sexual behavior toward females when their olfactory nerves were sectioned, suggesting that intact olfactory system is critical to courtship and mating. Crested auklets produce a seasonally elevated scent associated with a stereotyped behavior that focuses on the scented region of the body (the nape). Auklets are attracted to natural feather odor, a chemical cocktail of odor compounds, and scented decoys, which suggests odor has a social function (Hagelin et al., 2003; Jones et al., 2004; Hagelin, 2007a). Odorous compounds of crested auklets can also negatively impact ectoparasites in experimental tests (Douglas, 2008, 2013).

Procellariiform seabirds show a surprising level of body odor discrimination, in that they are attracted to mate odors and avoid self-odor (Antarctic petrel (*Pachyptila desolata*) Bonadonna and Nevitt, 2004; blue petrels (*Halobaena caerulea*), Mardon and Bonadonna, 2009). Furthermore, preference for the odor of unrelated individuals over those of kin was recently discovered (European storm petrel (*Hydrobates pelagicus*), Bonadonna and Sanz-Aguilar, 2012). Such results suggest that body odors could provide a mechanism for inbreeding avoidance, known as self-referent phenotype matching (Mateo and Johnston, 2000). This may be particularly important in petrels which are a long-lived philopatric species that mates for life. Petrels are also likely to encounter kin on their natal breeding grounds that they have never met before (Bonadonna and Nevitt, 2004; Bonadonna and Sanz-Aguilar, 2012). Recent evidence for passerines suggests that conspecific odor may provide relevant social information. Bird responses to scent correlated with social rank (house finch, Amo et al., 2012b), sex (European starling, Amo et al., 2012a), and body size (dark-eyed junco (*Junco hyemalis*), Whittaker et al., 2011).

### 7.3.7 Summary

Every bird tested has exhibited a functional sense of smell (Bang and Wenzel, 1985). The extent of olfactory development also is on par with that found in mammals. However, ornithologists have largely overlooked the role of olfaction in avian biology. Many birds adaptively employ

environmental odors; they also produce and respond to conspecific scents. Although passerines have a relatively poorly developed olfactory anatomy, they nonetheless show some degree of olfactory acuity. Other species, such as procellariiformes, have olfactory systems that are acutely sensitive to odor cues and capable of a surprisingly detailed level of conspecific odor discrimination. Given the broad range of contexts that implicate avian olfaction, future interdisciplinary research that compares olfactory mechanisms in birds to better-known vertebrate systems, such as mammals and fish, holds exciting promise.

## 7.4 GUSTATION

### 7.4.1 Taste Receptors

Relative to other vertebrates, birds have fewer taste receptors and taste receptor genes (Berkhoudt, 1985; Shi and Zhang, 2005) (Table 7.4). Notwithstanding these observations, birds have a well-developed system for gustation with functional significance for their behavior, ecology, and evolution. Taste receptors are located in taste buds throughout the oral cavity. The greatest concentration of avian taste receptors is found around salivary glands in the soft epithelium of the palate, the posterior tongue, and the oropharynx (Bath, 1906; Lindenmaier and Kare, 1959; Saito, 1966; Ganchrow and Ganchrow, 1985). Afferent taste signals in birds are carried in the glossopharyngeal nerve (cranial nerve IX; Duncan, 1960). The glossopharyngeal nerve innervates the posterior buccal and pharyngeal areas (Kare and Mason, 1986). Unlike mammals, the facial nerve (VII) does not innervate the avian tongue (Wenzel, 1973). Rather, glossopharyngeal afferents in birds enter the medulla and join fibers from the facial (including chorda tympani) and vagus nerves (X) to form a well-developed *fasciculus solitarius* (Lindenmaier and Kare, 1959). The chorda tympani innervates taste buds adjacent to the anterior mandibular salivary glands, situated in the buccal epithelium of the lower jaw (Kare and Mason, 1986).

**TABLE 7.4 Abundance of Taste Buds among Vertebrate Species[1]**

| Species | Taste Buds | Source |
|---|---|---|
| Domestic chick (day-old) | 5–12 | Lindenmaier and Kare (1959) |
| Domestic chicken (3 months) | 24 | Lindenmaier and Kare (1959) |
| Blue tit | 24 | Gentle (1975) |
| Bullfinch | 41–42 | Duncan (1960) |
| Pigeon | 59 | Moore and Elliot (1946) |
| Japanese quail | 62 | Warner et al. (1967) |
| European starling | 200 | Bath (1906) |
| Parrot | 300–400 | Bath (1906) |
| Domestic cat (juvenile) | 473 | Elliot (1937) |
| Lizard | 550 | Schwenk (1985) |
| Bat | 800 | Moncrieff (1946) |
| Domestic cat (adult) | 2755 | Robinson and Winkles (1990) |
| Human | 6974 | Miller and Reedy (1990) |
| Rabbit | 17,000 | Moncrieff (1946) |
| Pig | 19,904 | Chamorro et al. (1993) |
| Ox | 35,000 | Moncrieff (1946) |
| Catfish | 100,000 | Hyman (1942) |

[1]*Modified from Kare and Mason (1986) and Mason and Clark (2000).*

### 7.4.2 Response to Sweet

Birds have a well-developed sense of taste that generally corresponds to their feeding habits. Frugivorous and omnivorous birds tend to perceive and prefer sweet more so than species in other foraging guilds. For example, European starlings prefer 0.5–5% D-fructose solutions (w/v) to distilled water (Espaillat and Mason, 1990). Sugar detection thresholds of cockatiels (*Nymphicus hollandicus*) is 0.36 M sucrose, 0.40 M fructose and 0.16 M glucose (Matson et al., 2000, 2001). The sugar detection thresholds of broad-billed hummingbirds (*Cynanthus latirostris*) is between 1.31 and 1.54 mM sucrose, 0.87–1.31 mM fructose, 1.54–1.75 mM glucose and 1.75–3.5 mM of a 1:1 mixture of fructose and glucose (Medina-Tapia et al., 2012). Interestingly, the sweet taste receptor gene Tas1r2 is absent in all bird genomes sequenced thus far, irrespective of their diet (Zhao and Zhang, 2012), suggesting that additional avian receptors may exist for sweet.

The order of preference among nectivorous passerines is sucrose = glucose + fructose = fructose > glucose > xylose (Lotz and Nicolson, 1996). Lesser double-collared sunbirds (*Nectarinia chalybea*) and Cape sugarbirds (*Promerops cafer*) absorb sucrose, glucose, and fructose from ingested food at nearly 100% efficiency, but xylose was excreted (Lotz and Nicolson, 1996; Jackson et al., 1998a,b). Although nectar composition and concentration are often considered independently, these characteristics may have a synergistic effect on the sugar preferences of nectar-feeding birds (Schondube and Martinez del Rio, 2003).

Sugar preferences among nectarivorous and frugivorous birds are concentration-dependent. Although nectarivorous birds in Africa prefer sucrose when offered a choice of 0.25 M solutions of glucose, fructose, and sucrose, no preference among these sugars was observed when their concentration was increased to 0.73 M; the dietary choices in these species indicate the birds had either reached a limit where they had sufficient energy intake or they were affected by

postingestion constraints (Downs and Perrin, 1996; Downs, 1997). House finches demonstrated no preference for equicaloric, 2% solutions of hexoses (1:1 mixture of fructose and glucose) and sucrose, and strong preference manifest for hexoses but not sucrose at 4, 6, and 10% concentrations; energetics, rather than sucrase deficiency, may determine finches' sugar preferences (Avery et al., 1999).

Studies of unrelated, nectarivorous birds (including a generalist, nonpasserine nectarivore) have demonstrated a distinct switch from hexose preference at low concentrations to sucrose preference at higher concentrations (Lotz and Schondube, 2006; Fleming et al., 2008; Brown et al., 2010a,c). Sucrose preference at higher concentrations may possibly be explained by taste perception due to differences in solution osmolality or a degree of imprinting due to experience with natural nectar compositions. Village weavers (i.e., generalist passerine nectarivores; *Ploceus cucullatus*) preferred hexose solutions at 5% and 10% sucrose equivalents (SE), yet no sugar preference was observed at 15, 20, and 25% SE (Odendaal et al., 2010). In contrast, dark-capped bulbuls (*Pycnonotus tricolor*), an opportunistic nectarivore, significantly preferred hexose solutions, irrespective of concentration (5–25%), when given a choice between equicaloric hexose and sucrose solutions (Brown et al., 2010b). Interestingly, malachite sunbirds (*Nectarinia famosa*) demonstrated either sucrose preference, no preference, or hexose preference when offered equimolar, equiweight, or equicaloric paired solutions of sucrose and hexose, respectively (Brown et al., 2008).

The bananaquit (*Coereba flaveola*) strongly prefers the most concentrated sucrose solution when the lowest concentration ranged from 276 to 522 mM. From 522 to 1120 mM sucrose concentrations, bananaquits adjust their volumetric food intake to maintain constant energy intake. At a sucrose concentration of 276 mM, however, bananaquits did not maintain their rate of energy intake by increasing food consumption (Mata and Bosque, 2004). Although nectarivorous birds generally prefer concentrated over dilute sugar solutions, the concentration difference that they can discriminate is smaller at low concentrations relative to high concentrations; this pattern may be a consequence of the functional form of intake responses that often results in decelerating sugar intakes with increasing sugar concentration (Martinez del Rio et al. 2001; Leseigneur and Nicolson, 2009). With regard to gender-specific food intake among nectarivorous birds, males take longer to digest than females when fed on sucrose-rich nectars as opposed to hexose-rich nectars; therefore, they can allow themselves a relatively lower digestive capacity (Markman et al., 2006). The digestive transit rates of Cape white-eyes (*Zosterops virens*) fed artificial fruit were faster for glucose- than sucrose-based diets, irrespective of concentration; increased food intake with decreasing glucose concentration and no significant differences in food intake with differing sucrose concentrations were observed (Wellmann and Downs, 2009). Indeed, nectar ingestion rate is determined by viscosity, and total food intake is primarily modulated by sugar concentration (Köhler et al., 2010).

Sugar preference and selection among nectarivorous and frugivorous birds are likely to have coevolutionary effects on flowering and fruit-bearing plants. Among 58 wild fruits studied in Hong Kong, all fruit species contained glucose, all but one contained fructose, and only 11 species contained sucrose; birds are known to eat 29 of these species without detectable sucrose and four with sucrose (Ko, 1996). From a comparative analysis of glucose, fructose, and sucrose in the nectar and fruit juice of 525 tropical and subtropical plant species, passerine nectars and fruits had low sucrose and high hexose content, respectively; the nectar of hummingbird flowers had very high sucrose content; microchiroptera nectars showed hexose richness and microchiropteran fruits had a sucrose content similar to passerine fruits; and megachiroptera nectars and fruits were sucrose-rich (Baker et al., 1998). The dichotomy between sucrose-rich nectars in hummingbird-pollinated plants and predominantly hexose-rich nectars in sunbird-pollinated plants appears to have little to do with bird physiology and may rather reflect patterns of nectar secretion or plant physiology and opportunist nectar feeders (Nicolson and Fleming, 2003; Fleming et al., 2004).

The hummingbird-passerine dichotomy was strongly emphasized until the discovery of South African plants with sucrose-dominant nectars, which are pollinated by passerines that demonstrate sucrose digestion and preference (Lotz and Schondube, 2006). Flowers adapted for specialized passerine nectarivores have nectar similar to that of hummingbird flowers in terms of volume (approx. 10–30 mL), concentration (15–25% w/w) and sucrose content (40–60% of total sugar). In contrast, flowers adapted to generalized bird pollinators are characterized by large volumes (approximately 40–100 mL) of extremely dilute (8–12%) nectar with minimal sucrose (0–5%; Johnson and Nicolson, 2008).

Rufous hummingbirds (*Selasphorus rufus*) preferred 50% sucrose to higher and lower concentrations, and they could distinguish solutions differing by only 1% sucrose (Blem et al., 2000). Sucrase activity is 10 times higher in hummingbirds than in passerines (Schondube and Martinez del Rio, 2004). Neither sex nor temperature affected sugar preferences among green-backed firecrown hummingbirds (*Sephanoides sephaniodes*; Chalcoff et al., 2008). Patterns of hummingbird sugar preference can be affected by different mechanisms, both pre- and postingestive. At low concentrations, gustatory thresholds may play an important role in sugar selection. At intermediate and high concentrations, however, sugar selection can be explained by sugar assimilation rates and velocity of food processing generated by osmotic constraints (Medina-Tapia et al., 2012).

Species belonging to the Sturnidae–Muscicapidae lineage do not express intestinal sucrase, despite having generalist diets comprising fruits with sugars of diverse kinds (Gatica et al., 2006). Members of the Sturnidae-Muscicapidae lineage are intolerant of solutions or fruit above 11–15% sucrose (Brown et al., 2012). Considering the phylogenetic constraint hypothesis for sucrose digestion in the Muscicapoidea superfamily, the lack of sucrase activity is a shared, derived character only for the Cinclidae–Sturnidae–Turdinae lineage (Gatica et al., 2006).

Within an experimental meal with varying sucrose concentration, captive whitebellied sunbirds (*Cinnyris talatala*) demonstrated a measurable increase in feeding frequency and food intake within 10 min after a decrease in sucrose concentration (Köhler et al., 2008). Similarly, Knysna turacos (*Tauraco corythaix*) preferred an artificial sucrose diet to an equicaloric glucose diet at low concentrations, whereas purple-crested turacos (*Gallirex porphyreolophus*) showed no preference for either diet. Both turacos species preferred a sucrose diet to an equimolar glucose diet at low concentrations. At high concentrations, neither species showed a preference for either equicaloric or equimolar diets; thus, energy requirements influence food preferences more than sugar type and birds will select fruit that is higher in energy irrespective of sugar type (Wilson and Downs, 2011).

### 7.4.3 Response to Salt

A comparison of the sodium chloride rejection thresholds among 58 bird species illustrated rejection thresholds ranging from 0.35% NaCl in a parrot to 37.5% NaCl in the pine siskin (*Carduelis pinus*; Rensch and Neunzig, 1925). Red-winged blackbirds (*Agelaius phoeniceus*) and European starlings preferred 0.1–1% NaCl solutions (w/v) to distilled water (Espaillat and Mason, 1990). The salt detection threshold of cockatiels is 0.16 M NaCl (Matson et al., 2000) and 0.16 M potassium chloride (Matson et al., 2001). With regard to the mechanism of salt perception, sodium in the oral cavity can cross the taste sensory cell membrane through the epithelial $Na^+$ channel (ENaC), thus triggering an action potential (Roura et al., 2012). Pigeons (*C. livia domestica*) learned to discriminate a safe 0.06 M NaCl solution and a toxic equimolar LiCl solution. Because the pigeons avoided the LiCl solution within a short presentation period of 5 minutes, it is unlikely that the birds were using an interoceptive stimulus of faint, postingestive malaise as a conditioned cue; thus, the pigeons' discrimination performance between the two chloride solutions was attributed to gustation (Nakajima and Onimaru, 2006).

### 7.4.4 Response to Sour

Sourness is related to the acidity of food, which is often caused by bacterial fermentation and typically evokes a rejection response. With regard to the mechanism of sour perception, the receptors for sour taste are thought to be transmembrane channels that are selective for hydrogen ions (Roura et al., 2012). Red-winged blackbirds and female starlings preferred distilled water to 0.01–0.1 M citric acid solutions (Espaillat and Mason, 1990). For the purpose of investigating sour detection thresholds, Matson et al. (2000) defined sourness as a pH, and they achieved sourness by varying the pH of a 0.05 M citrate buffer system. The sour detection threshold of cockatiels is pH 5.5 citric acid.

### 7.4.5 Response to Bitter

Bitter taste perception likely evolved as a protective mechanism against the ingestion of harmful compounds in food (Davis et al., 2010). Red-winged blackbirds and European starlings preferred distilled water to 0.5–5% tannic acid solutions (w/v; Espaillat and Mason, 1990). The bitter detection thresholds of cockatiels is 100 μM quinine, 1000 μM gramine, 500 μM hydrolysable tannin and 10,000 μM condensed tannin (Matson et al., 2004). Compared with pigs, chickens showed a lower sensitivity to glucosinolates (i.e., bitter plant metabolites); compared to ruminants, however, chickens showed a higher aversion to glucosinolates (Roura et al., 2012).

Bitter detection thresholds indicate that a birds' rejection of quinine occurs at lower concentrations than phytophagic mammals (Matson et al., 2004). White Leghorn and Rhode Island Red chickens were able to detect 2.0 mM quinine hydrochloride; broiler chickens detected 0.5 mM quinine hydrochloride (Kudo et al., 2010). Domestic chicks (14 days old) can discriminate between an untreated diet and a diet treated with 0.2% quinine hydrochloride (Ueda and Kainou, 2005).

Johnson et al. (2006) explored the functional significance of the phenolic compounds that impart a dark brown color to the nectar of the South African succulent shrub, *Aloe vryheidensis*. Dark-capped bulbuls were more likely to probe model flowers containing dark nectar than those containing clear nectar, suggesting a potential signaling function of dark nectar. The main effect of the phenolics, however, appears to be repellency of ''unwanted'' nectarivores that find their bitter taste unpalatable. Nectar-feeding honey bees and sunbirds are morphologically mismatched for pollinating *A. vryheidensis* flowers and strongly reject its nectar. Thus, the dark phenolic component of the nectar appears to function as a floral filter by attracting some animals visually and deterring others by its taste (Johnson et al., 2006).

The taste receptor type 2 (Tas2r) gene family encodes the chemoreceptors that are directly responsible for the detection of bitter compounds. The Tas2r cluster encodes up to 18 functional bitter taste receptors in the white-throated sparrow (*Zonotrichia albicollis*; Davis et al., 2010). Although

the tens to hundreds of taste buds observed among birds pales in comparison to the hundreds to thousands of taste buds found in other vertebrates (Table 7.4), this relative deficit does not preclude birds from detecting bitter compounds as effectively as those species with more taste buds. Future biochemical and genetic studies will be needed to identify the natural ligands for avian Tas2r gene clusters, and the intra- and inter-specific differences in these genes with variation in bitter taste perception (Davis et al., 2010).

### 7.4.6 Response to Umami

Male starlings preferred 0.7–1% L-alanine solutions to distilled water (Espaillat and Mason, 1990). The T1R1 umami receptor gene and the T1R3 sweet/umami receptor gene have been identified in chickens (Shi and Zhang, 2005). Moreover, the expression of T1R1 has been reported in hypothalamus, liver, and abdominal fat (Byerly et al., 2010). Thus, avian taste receptors and umami receptor genes may be involved in the orchestration of postingestive and metabolic events (Roura et al., 2012). Further research is needed to comparatively investigate avian feeding responses to umami tastants.

### 7.4.7 Response to Calcium

Calcium-deprived chickens preferred calcium-rich diets when offered a choice (Wood-Gush and Kare, 1966; Hughes and Wood-Gush, 1971). Similarly, consumption of supplementary calcium was inversely related to chicken's dietary calcium content (Taher et al., 1984). Further research is needed to distinguish the behavioral responses of birds to calcium as a tastant (i.e., sensory cue) versus the pre- and postingestive attributes of calcium-rich supplements. Although it is clear that animals can detect calcium in micromolar or low millimolar concentrations, it is less clear what they detect or how they detect it (Tordoff, 2001). The notion that calcium is a distinct taste quality is an anathema to many psychophysicists, who argue that there are very few basic taste qualities (sweet, sour, salty, bitter, and umami). To them, calcium taste is a complex of basic tastes, such as bitterness, sourness, and saltiness (Tordoff, 2001).

Calcium taste varies with both the form and the concentration of salt tested, but it nearly always includes sour and bitter components (Tordoff, 2001). The extracellular calcium-sensing receptor (CaR) is a multimodal sensor for several key nutrients, notably $Ca^{2+}$ and L-amino acids, and is expressed abundantly throughout the gastrointestinal tract in humans (Conigrave and Brown, 2006). Although the T1r3 receptor gene in mice (Tordoff et al., 2008) and the CaR have been identified as calcium sensors, it is yet uncertain if they mediate calcium appetite or taste (Roura et al., 2012) in birds.

### 7.4.8 Taste Behavior and Applications

Deterrents based merely on offensive flavors are not likely to be effective in the absence of aversive postingestive effects (Provenza, 1995). In this context, flavor is the perceptual integration of chemesthetic, olfactory, and gustatory stimuli. Red-winged blackbirds conditioned with sodium chloride paired with an intraperitoneal injection of a gastrointestinal toxin (lithium chloride) or a free choice of a postingestive, cathartic purgative (anthraquinone) or a postingestive, cholinesterase inhibitor (methiocarb) subsequently avoided the flavor (NaCl; Figure 7.5) and color of food experienced during conditioning. In contrast, blackbirds conditioned with sodium chloride paired with an intraperitoneal injection of an opioid antagonist (i.e., chemesthetic; naloxone hydrochloride) or a free choice of a preingestive, trigeminal irritant (methyl anthranilate) subsequently avoided only the color (not flavor; Figure 7.5) of food experienced during conditioning. Thus, red-winged blackbirds reliably integrate gustatory (and visual) experience with postingestive consequences to procure nutrients and avoid toxins (Werner and Provenza, 2011).

Avian taste behavior has been investigated in context of agricultural production, chemical defenses of insects and plants, coevolution in predator-prey and pollination systems, chemical ecology, conservation biology, and comparative physiology and taxonomy. For example, although avian feeding responses to secondary metabolites are species-specific (Saxton et al., 2011; Rios et al., 2012), increased sugar concentrations (not decreasing acid concentrations) are a functional cue for the onset of bird damage to ripening grapes (Saxton et al., 2009). Although increased sucrose content may deter sucrase-deficient birds from damaging commercial fruit (Brugger and Nelms, 1991), increased sucrose may also lead to increased crop damage by other species obligated to consume more of the less-digestible fruit to meet their energy requirements (Lane, 1997). This compensatory feeding hypothesis notwithstanding, McWhorter and Martinez del Rio (2000) observed a physiological constraint on sugar consumption among nectarivorous hummingbirds; the rate of intestinal sucrose hydrolysis can limit sugar assimilation and reduce sucrose preference. Indeed, the intake responses of nectar-feeding birds manifest from the integration of a behavioral response with the physiological processes that shape it (Martinez del Rio et al., 2001).

Several tastants have been used to condition aversions among birds associated with agricultural production. The risk of accidental poisoning of birds may be reduced by adding an aversive tastant (e.g., D-pulegone, quinine hydrochloride) to granular pesticides (Mastrota and Mench, 1995; Clapperton et al., 2012). Garlic oil was identified as an effective chemical repellent for European starlings (Hile et al., 2004) and quinine sulfate (bitterant) was used to

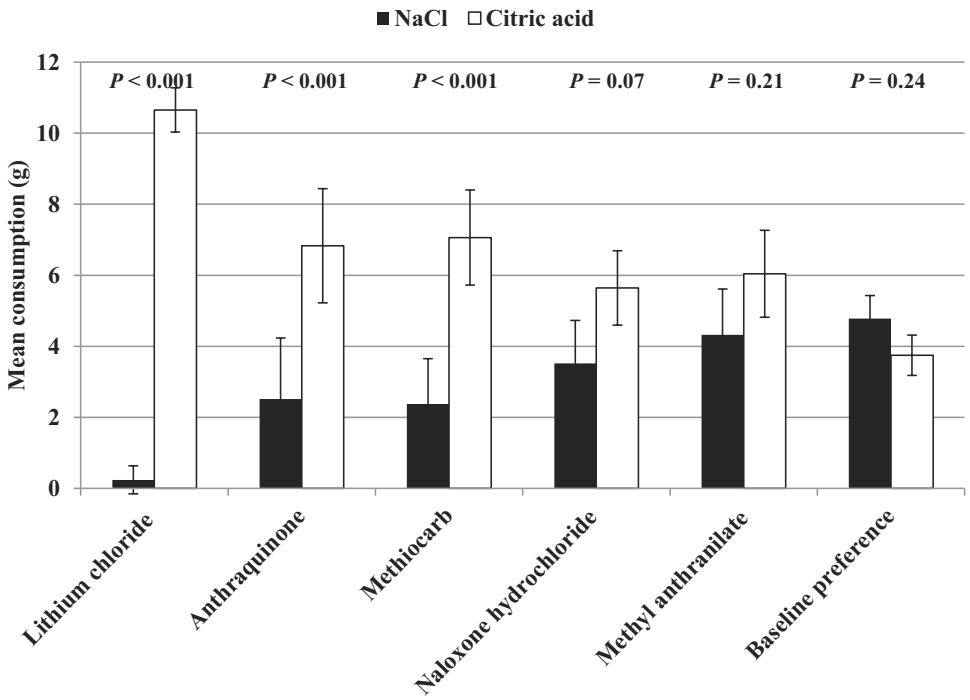


**FIGURE 7.5** Mean consumption (±2 SEM) of sodium chloride and citric acid subsequent to NaCl conditioning with: an intraperitoneal injection of a gastrointestinal toxin (lithium chloride), or a free-choice of a postingestive, cathartic purgative (anthraquinone) or a postingestive, cholinesterase inhibitor (methiocarb); or an intraperitoneal injection of an opioid antagonist (naloxone hydrochloride) or a free-choice of a pre-ingestive, trigeminal irritant (methyl anthranilate) in red-winged blackbirds (*Agelaius phoeniceus*). *From Werner and Provenza (2011), baseline preference data from Werner et al. (2008); with permission.*

condition taste aversions and thus reduce destructive feather pecking among laying hens (Harlander-Matauschek et al., 2009, 2010).

Relative preference for specific tastants has been used to enhance feeding for poultry production. The preference of chickens for oily diets (i.e., long-chain versus medium-chain triacylglycerol) is mediated by gustation (Furuse et al., 1996; Mabayo et al., 1996), not satiety (Vermaut et al., 1997). In contrast, the avoidance of a saponin-rich diet is not mediated by taste in domestic chicks (Ueda and Shigemizu, 2001); rather, crop distension causes decreased feed intake associated with tea saponin (Ueda et al., 2002).

Domestic chicks can use unpalatable taste (e.g., quinine) to adapt their visual foraging decisions (Rowe and Skelhorn, 2005; Skelhorn et al., 2008). Moreover, European starlings and domestic chicks can learn to use bitter taste cues to regulate consumption of toxic prey (Skelhorn and Rowe, 2010; Barnett et al., 2011). Similarly, red-winged blackbirds use affective processes (flavor-feedback relationships) to shift preference for both novel and familiar flavors (Werner et al., 2008).

### 7.4.9 Summary

The conventional notion regarding the "limited ability of birds to taste" (Kassarov, 2001) was shaped by a historic paradigm of taste research (i.e., elementary structure and function). Avian taste perception is currently investigated in context of ontogenetic and phylogenetic relationships within ever-changing environments. Birds use taste cues to select nutrients and avoid toxins; thereby, they affect the distribution, diversity, and coevolution of their prey. Thus, taste cues and postingestive consequences have behavioral, ecological, and evolutionary implications for domestic and wild birds. Future avian gustation research will develop our understanding of comparative biochemistry, molecular biology, and ethology—from an emphasis on anatomical structure to the physiological bases of behavior and performance.

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