

these are exemplified by the extremely rapid frequency changes within a time frame that is too rapid for human discrimination. Pumphrey (1961) notes that a small bird accomplishes this 10 times better than humans. Furthermore, Greenewalt (1968) points out that the syrinx of song birds enables them to produce two notes or phrases simultaneously and that "these sounds can be modulated, in either frequency, or in amplitude, or more usually in both, with extraordinary rapidity; so rapidly in fact that human ears cannot perceive the modulations as such, receiving instead an impression of notes of varying quality or timbre."

Quite fascinating is the recent disclosure that low-frequency sounds, termed *infrasounds*, can be detected as low as 0.05 Hz by homing pigeons in a sound-isolated chamber (Kreithen and Quine, 1979). Such sounds have been recorded in thunderstorms, earthquakes, auroras, ocean waves, and even mountain ranges, and are believed to be an important source of navigational and meteorological information during migration (Kreithen, 1979). At this level, pigeons are at least 50 dB more sensitive than humans (Kreithen and Quine, 1979). In addition, a few birds, e.g., oil-birds (*Steatornis caripensis*) (Griffin, 1953) and swiftlets (*Collocalia brevirostra unicolor*) (Novick, 1959), have successfully developed the ability to use their own sound (short clicks between 4 and 7 Hz) for *echolocation* as bats do, for acoustic orientation and navigation in the dark when pursuing prey and avoiding obstacles.

## The Chemical Senses in Birds

M.R. KARE AND J.R. MASON

The chemical senses are commonly thought to fall into three classes: (1) olfaction (smell), (2) gustation (taste), and (3) the common chemical sense. In birds, as in most other vertebrates, olfaction is usually thought to be a teloreceptor, capable of receiving airborne chemical stimuli in extreme dilution over relatively great distances. Gustation, on the other hand, usually requires more intimate contact of higher concentrations of the chemical stimuli with the taste receptors. Gustatory receptors are most often located in the taste buds of the oral cavity, although functional taste buds are found outside the oral cavity and on the body surface of some fish (i.e., the channel catfish, *Ictalurus punctatus*) (Pfaffmann, 1978). The common chemical sense is usually reserved for nonspecific stimuli, which are often irritating.

### Common Chemical Sense

"Parker (1922) suggests that the common chemical sense is relatively primitive and that taste and olfaction are later differentiations. The prevalence of the com-

mon chemical sense among vertebrates, and the diverse, relatively unspecialized nature of the receptors (i.e., free nerve endings), support this interpretation. In higher vertebrates, a major component of the common chemical sense is the trigeminal system. An extensive review of this system with special emphasis on trigeminal chemoreception in the nasal and oral cavities has been provided by Silver and Maruniak (1980).

Irritants such as ammonia and acids stimulate the free nerve endings of numerous surfaces, including those in the nasal chambers, mouth, and eyelids of vertebrates. The organization of the trigeminal system in birds does not appear to be essentially different from that found in mammals (Dubbledam and Karten, 1978), although its extent is exaggerated in some aquatic forms, such as ducks and flamingos (Welty, 1975). The well-developed nature of the trigeminal system in aquatic species may serve in the initiation of diving reflexes, or in the detection of tactile properties of foods. That latter possibility is consistent with evidence that pigeons use oral trigeminal cues for this purpose (Ziegler, 1977).

The pigeon and gray partridge are indifferent to strong ammonia solutions that stimulate trigeminal receptors in mammals (Soudek, 1929). Likewise, parrots consume *Capsicum* peppers that are rejected by mammals (Mason and Reidinger, 1983a), and red-winged blackbirds are relatively insensitive to capsaicin, the pungent principle in *Capsicum* peppers (Mason and Maruniak, 1983). From such results, one might conclude that the avian trigeminal system is relatively insensitive to chemical stimuli, although capsaicin and ammonia are probably not characteristic of irritants that birds are likely to encounter. Perhaps the use of ecologically and evolutionarily more relevant irritants (e.g., saponins in plants) would lead to different conclusions. Also, the avian trigeminal system may serve purposes different from those of the mammalian system. Pigeons may home using trigeminal cues, when other sensory inputs are blocked (Wallraff, 1980), and the European starling readily avoids nonirritating concentrations of phenethyl alcohol on the basis of trigeminally mediated information (Mason and Silver, 1983). These data suggest that some birds may be able to make qualitative discriminations between odors using only the trigeminal system, but this possibility remains controversial. Walker et al. (1979), using conditioned suppression, found that after bilateral section of the olfactory nerves pigeons could detect but no longer discriminate between the chemically similar compounds butyl and pentyl acetate. More systematic work is needed to elucidate the function(s) of the common chemical sense in birds.

### Smell

The question of whether or not birds possess olfactory capabilities was a controversial one for many years.

Nineteenth-century naturalists (e.g., Audubon, 1826) carried out experiments designed to test the olfactory ability of vultures. Both positive and negative results were obtained, and the reports of these early investigators were followed by others whose conclusions regarding the sense of smell in birds were as contradictory as they were numerous. Anatomic investigations carried out over the last two decades have indicated that birds possess olfactory systems whose complexity and development vary widely among species. Neural events, presumably the result of stimulus-receptor interaction, have been studied electrophysiologically in birds, and some species have been reported to regulate their behavior on the basis of olfactory information (Archer and Glen, 1969; Wenzel, 1973, 1980).

**The Olfactory Organ.** Bang (1971) has summarized the functional anatomy of the olfactory system of birds representing 23 orders. Birds possess several nasal conchae and lack a vomeronasal (Jacobsen's) organ, although the latter has been identified in the very early embryonic life of some birds (Matthes, 1934). Typically, the avian olfactory system consists of external nares (nostrils), nasal chambers (conchae), internal nares (choane), and olfactory nerves, the peripheral terminals of which lie in the olfactory epithelium, and the olfactory bulbs of the brain. There are three nasal chambers, but reportedly only the turbinates of the third (posteriosuperior) chamber possess olfactory epithelium (Bang, 1971). The first two chambers serve to moisten, warm, and cleanse inspired air. Other possible functions of these chambers are suggested by studies of "dynamic gliders," such as albatrosses, petrels, and fulmars (Welty, 1975). Dissections of the nasal chambers of these birds reveal a pair of small forward-opening pockets of the middle chamber, which may act as organs for detecting variable pressures produced by differing external airstream velocities (see Figure 2-14).

In pelicans and their allies, the external nares are small or closed and there is a reduction in size of other parts of the olfactory system, but the choane between the third chamber and the mouth are relatively large.

These openings may be adapted to provide retranasal access for volatile materials held in the mouth (Welty, 1975). The comparative anatomy of the nose and nasal airstreams is discussed by Bang and Bang (1959) (see Figures 2-15 and 2-16). Much general information on olfactory receptor cells, nerves, and central projections is found in Biedler (1971). (See Chapter 1 for further details on olfactory neural pathways.)

Numerous negative reports on olfaction in birds have probably discouraged the use of this animal class in olfactory research, and this may explain why so little work on the mechanism of olfaction deals with avian species. Yet olfaction is important for some birds (Wenzel, 1980), and intriguing evolutionary questions remain to be addressed. For example, there is as yet no explanation for the observation that diving petrels and auks, well-known examples of convergent evolution, differ sharply in respect to olfactory system. Very likely, olfactory development (or the lack of it) among avian species reflects the importance of this sense in locating food or in homing.

**Methods of Detecting Olfaction.** Two general laboratory methods have been used to detect olfactory perception in birds. The neurophysiological methods have involved recording from the olfactory nerve (Tucker, 1965) or directly from the olfactory bulb (Wenzel and Sieck, 1972) during odorant stimulus presentation in an olfactometer. Behavioral study of olfaction in birds involves two techniques. In the first, birds are required to discriminate between air and an odor that previous training has made relevant to the test (Shumake et al., 1970; Walker et al., 1979). The second technique involves continuous monitoring of heart rate and/or respiration during intermittent presentation of odorous stimuli (Wenzel, 1968). Which of these latter techniques is the more accurate depends in part on the species under investigation (Shallenberger, 1973, 1975).

**Olfactory Development in Various Species.** The olfactory system is well developed in kiwi, vulture, albatross, and petrels; moderately developed in the fowl, pigeon, and most birds of prey; and poorly developed

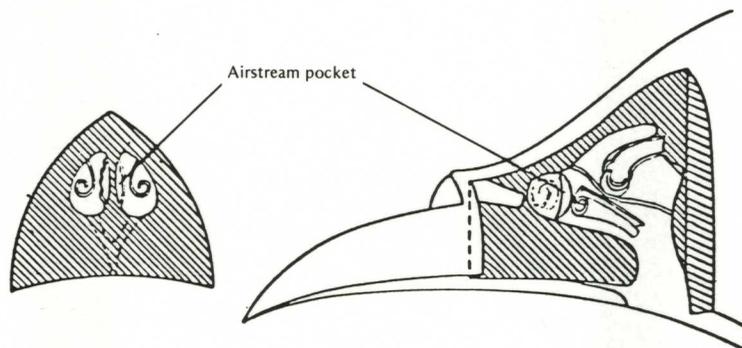


FIGURE 2-14. Cross and longitudinal sections of the nasal chambers of a fulmar, showing the location of the valvelike pockets that may serve sea birds as airvelocity sense organs to aid them in exploiting winds of varying speeds during dynamic gliding. (After Mangold, 1946.)

FIGURE section of the nasal chamber by diagram and lines. In head of extent of nasal land. (From E

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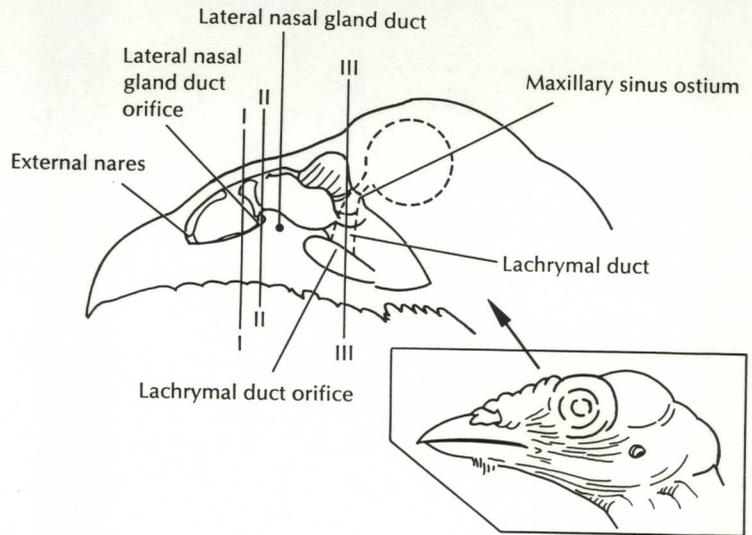
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FIGURE 2-15. Diagrammatic sagittal section of right medial surface of the nasal chambers of a chicken. Olfactory sensory area indicated by diagonal shading; position of eye and lachrymal duct, by broken lines. Inserts of partially dissected head of chicken gives an idea of extent of fossa in relation to external landmarks. Not drawn to scale. (From Bang and Bang, 1959.)



in songbirds. It is very possible that development (or the lack of it) is related to the foods and other resources exploited by various species.

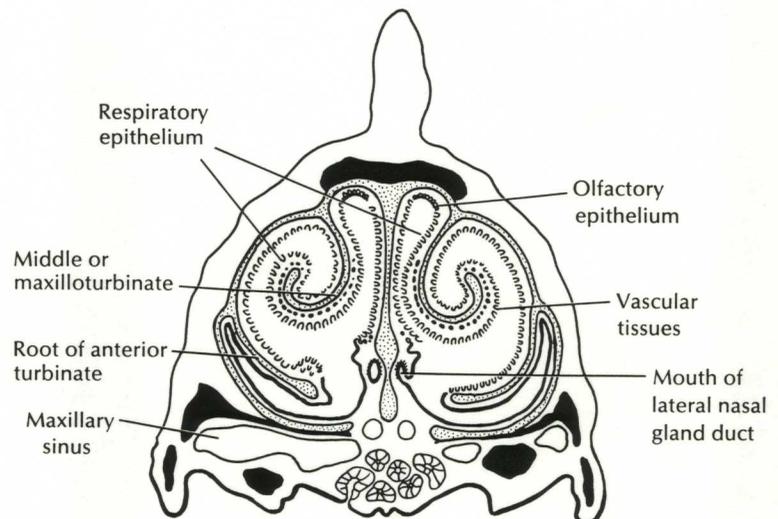
Vultures are carrion eaters, and their conspicuous circling behavior in the area of a carcass led to much early speculation that they locate sources of food by olfaction. This has been confirmed for the turkey vulture, and strongly suggested for the king vulture by Stager (1967). By careful release of ethyl mercaptan fumes in the path of migrating turkey vultures, Stager was able to demonstrate that vultures are led to the general area of food by olfaction. Once in the general area, these birds seem to rely more heavily on vision to lead them to the exact location of a food source. Conversely, ravens rely on visual cues to identify foraging locations, but sometimes then use subtle odor cues

to locate buried food stuffs (Synder and Peterson, 1979).

Several species of the Procellariiformes may use olfaction in navigation and nest location (Grubb, 1972). The most compelling evidence is for Leach's storm petrel, which usually return to their island nesting locations at night by flying upwind (Grubb, 1974). Severing the olfactory nerves or plugging the nares in these birds interferes with their ability to return to the nest. Nesting material effectively serves as a lure for the birds in total darkness, and these birds consistently chose the arm of a Y-maze that contains their own nesting material. An excellent review of seabird olfaction has been provided by Wenzel (1980).

The flightless kiwi is nocturnal and feeds largely on earthworms and other hidden food. Its vision is poor;

FIGURE 2-16. Diagram or map of sections through the anterior part of the respiratory portion of the nasal fossa of a chicken. Cartilage is stippled; bone is solid black; cornified squamous epithelium is solid black line. (From Bang and Bang, 1959.)



it is the only bird with nostrils at the tip of the beak, and it sniffs while foraging. It can detect food hidden or in the dark (Wenzel, 1968).

Stager (1967) suggested that African honeyguides locate beehives by means of olfaction and are attracted by burning beeswax candles. Honeyguides can locate abandoned hives presumably by smell, when other cues (e.g., vision, audition) are no longer available (Archer and Glen, 1969).

Operant conditioning techniques have been used to demonstrate that pigeons use olfactory cues to perform key-pecking and other tasks (e.g., Shumake et al., 1970). For example, homing pigeons with bilaterally sectioned olfactory nerves or nares plugged with cotton display an impaired ability to return to the home loft (Papi et al., 1973; Benvenuti et al., 1973). These and other experiments indicate that olfaction may play a role in the initial orientation of homing pigeons (Wallraff, 1979). Recent evidence suggests that olfactory cues are especially important for navigation by pigeons over long distances (e.g., 500 km). Like vultures, however, such cues appear relatively less important at short distances (e.g., 10 km), contrary to reports of homing by storm petrels (Grubb, 1974).

Gallinaceous birds have been the subjects of little olfactory research. Tucker (1965) presented electrophysiologic evidence that the bobwhite quail can perceive some odors. Stattleman et al. (1975) have determined that chickens are most sensitive to pentane and hexane, while pigeons are most sensitive to heptane. As in work with other species, it is unclear whether reagent-grade chemicals have any biological relevance to gallinaceous birds, and whether different results would obtain if biologically relevant stimuli were used.

The olfactory system in a number of aquatic species, e.g., penguins, geese, and terns, is well developed (Bang, 1971). Neuhaus (1963) reported that greylag geese respond to skatol, and odors of plants on which adult greylag geese will not feed (e.g., violet, lavender) are also aversive to goslings (Wurdinger, 1979).

The reports of olfactory behavior in many songbirds are predominantly negative, but the olfactory systems in such birds may be important for other purposes. Robnson et al. (1979) reported that the surgical removal of olfactory bulbs in male red-wing blackbirds caused hyperphagia, weight gains, increased thyroid follicular activity, and increased testicular development, suggesting that the olfactory bulbs in red-wings may be involved in the photoperiodic regulation of activity of the gonads and thyroids.

**Summary.** The evidence available on the sense of smell in birds does not permit many generalizations. The failure of birds to react to odors as they are presented in the laboratory does not necessarily reflect a deficit in acuity, but that the odor may not have reached olfactory receptors. The lack of sniffing behavior in

all birds but the kiwi may indicate that moving air is required to effect contact between the odor stimuli and receptors. On the other hand, the perfumes and reagent-grade chemicals that are most often used in the laboratory may not be biologically relevant to birds (Wurdinger, 1979) and/or may not be presented at levels that correspond to the birds' spectrum of chemical sensitivity.

### Taste

The function of taste is to encourage the ingestion of nutrients, to discriminate among foods that are available, and possibly to avoid those that are toxic. The taste system in a particular species can be expected to complement digestion, metabolism, and the dietary requirements of that species. While relationships, if any exist, have yet to be clearly defined between number of taste buds and taste behavior, the relatively poor taste acuity of avian species may be related to the relatively small number of sensory cells (Table 2-4).

**Taste Receptors (Buds).** Receptors are largely found at the base of the tongue and the floor of the pharynx, commonly in close association with the salivary glands (Gentle, 1971; Wenzel, 1973; Dmitrieva, 1981). However, taste buds can be found in other areas (Saito, 1966; Warner et al., 1967; Berkhoudt, 1977), and the number of buds and their distribution may change over time (Duncan, 1960). Whether or not such changes have any ecological importance to these animals is not clear.

Little use has been made of birds in neuroanatomic research on taste, although both the chorda tympani (Gentle, 1983) and the glossopharyngeal nerve (Berkhoudt, 1983) carry taste information. The chorda tympani innervates taste buds adjacent to the anterior mandibular salivary glands, situated in the buccal epithelium of the lower jaw. The glossopharyngeal nerve innervates the posterior buccal and pharyngeal areas. Cutaneous (as well as taste) information is carried by both nerves. The details of their distribution at the level of the first relay and at all higher points in the brain are unclear (Wenzel, 1980). The reader is referred to Berkhoudt (1983) for a review of the structure and function of avian taste receptors. Beidler (1971) also provides a discussion, based largely on mammalian research, of current knowledge and theories concerning central functions and peripheral mechanisms in taste.

**Methods of Study.** Early studies of taste in birds involved observation of individuals as they consumed foods or fluids. Preference testing is now the most common laboratory method used to measure the sensitivity of birds to taste stimuli. Usually the material to be tested is placed in aqueous solution, and the animal is given a choice between the mixture and distilled

TABLE 2-4. Numbers of taste buds in birds and various other vertebrates

Species	<i>n</i>	Reference
Blue tit	24	Gentle (1975)
Pigeon	37-75	Moore and Elliott (1946) Van Kan (1979)
Bullfinch	46	Duncan (1960)
Barbary dove	54	Gentle (1975)
Japanese quail	62	Warner et al. (1967)
Starling	200	Bath (1906)
Chicken	250-350	Van Prooije (1978) Saito (1966)
Duck	375	Berkhoudt (1977)
Parrot	300-400	Bath (1906)
Snake	0	Payne (1945)
Kitten	473	Elliott (1937)
Bat	800	Moncrieff (1951)
Human	9,000	Cole (1941)
Pig and goat	15,000	Moncrieff (1951)
Rabbit	17,000	Moncrieff (1951)
Catfish	100,000	Hyman (1942)

water, the two being presented simultaneously. However, single-stimulus methods, in which choices are presented singly at different times, and three-choice methods, in which a tastant and two control solutions are offered simultaneously, have been used to eliminate confounding by position bias. Cafeteria-type tests in which more than three taste stimuli are presented simultaneously seem to overwhelm the chicken's discriminatory ability.

Chickens show a characteristic response to aversive oral stimulation, as produced by quinine hydrochloride, typified by persistent tongue and beak movements, and headshaking and beak-wiping behavior. No characteristic responses to presentations of neutral or appetitive oral stimuli such as sucrose have been observed (Gentle, 1978; Gentle and Harkin, 1979).

Neurophysiologic studies of taste in birds have been few and have involved chickens or pigeons as experimental animals (Halpern, 1963; Landolt, 1970). Such studies usually involve the application of substances to the tongue of the subject and measurement of multi-unit or single-fiber activity in the glossopharyngeal nerve. Using these techniques, Kitchell et al. (1959) demonstrated the water taste phenomenon in birds. That is, water has been shown not to be a neutral carrier of taste stimuli, but to act as a taste stimulus itself under certain conditions. For example, adaptation to NaCl in humans will cause water to have a bitter or bitter-sour taste. Adaptation to the concentration of NaCl present in saliva is sufficient to produce this effect (McBurney, 1978). Electrophysiologically, water taste might be reflected in the response of sour- or bitter-sensitive neurons to water following adaptation. However, such results merely indicate whether a chemical can evoke a peripheral neural response. They do not indicate whether the chemical has an appealing

or offensive taste to the animal, and while there are examples of positive correlations between behavioral and electrophysiological response, there are also contradictions (Halpern, 1963). Operant techniques, which often have been used successfully in studies on vision or olfaction (see above), are not often used in taste research with birds.

Research on taste in birds has been handicapped by the general assumption that they live in the human sensory world. The taste sensations experienced by man cannot be assumed to be the same as for birds. For example, dimethyl anthranilate, a flavoring used in human foods, has been used to reduce food intake in growing chicks and turkey poults, and has been suggested as a bird repellent livestock-feed additive. This compound is offensive to starlings, Japanese quail, pigeons, red-wing blackbirds, jungle fowl, herring gulls, and finches at dilutions as low as 1 part in 10,000 in two-choice tests (Kare and Pick, 1960; Mason et al., 1985). Nevertheless, in order to compare results obtained from birds with results from other species, the classical categories of sweet, sour, bitter, and salty are frequently used.

**Ability to Taste.** *Sweet.* Many avian species evidence little or no interest in the common sugars, although parrots, budgerigars, hummingbirds, and other nectar feeders actively select sugar solutions. Kare and Medway (1959) observed that fowl on an *ad libitum* diet failed to perceive, or were indifferent to, dextrose and sucrose in food when tested at concentrations ranging from 2.5 to 25%. The findings are different, however, when tastants are presented in aqueous solution. Gentle (1972) reported that chickens exhibit rejection of 30% sucrose, fructose, or glucose solutions, and that glucose is rejected at concentrations as low as 5%. Several

investigators observed modest preferences for sugar solutions over water. Jacobs and Scott (1957) showed that chickens preferred a 12% sucrose solution to water. Japanese and bobwhite quail prefer some concentrations of sucrose and glucose (Brindley, 1965), but red-wing blackbirds select pure water over sucrose (Rogers and Maller, 1973). There is unanimity in the literature that birds reject such synthetic sweeteners as saccharin or dulcin. Curiously, even though chickens reject saccharin in behavioral tests, electrophysiologic techniques have failed to uncover neural activity when taste buds are rinsed with the substance (Welty, 1975). Collectively, the data suggest that nectar- or fruit-eating species are more likely to respond positively to sugars than are insectivorous or granivorous birds, which respond negatively or not at all.

The discovery that three tropical fruits contain intensely sweet proteins (Cagan, 1973) led to speculation on the role (if any) of the sweet principles in the plant. It is possible (though not demonstrated) that the sweet taste-active proteins may aid in seed dispersal by some frugivorous birds or other animals (Davison, 1962). No avian species have yet been tested with any of the sweet proteins.

A number of factors other than taste may be involved, individually or collectively, in the response of a bird to a sugar solution, e.g., osmotic pressure, viscosity, melting point, nutritive value, toxicity, and optical characteristics. Some have suggested that visual properties and surface texture sometimes take precedence over all other qualities in the birds' selection of food (Mason and Reidinger, 1983b). Across species, no physical or chemical characteristic can be used to reliably predict how a bird on an adequate diet will respond to the taste of a solution (Kare and Medway, 1959).

**Salt.** Birds kept on a salt-free diet will eagerly consume pure salt when it is made available to them. Numerous finches of the family Carduelidae have notorious appetites for salt, and cross-bills, for example, may be caught in traps baited with salt alone (Welty, 1975; Willoughby, 1971). Also, the domestic fowl maintained on a diet very low in sodium or calcium will exhibit a specific appetite and select, in a choice situation, the diet or solution that corrects its deficiency. However, the domestic chick delays drinking for extended periods to avoid consuming a sodium chloride solution whose concentration exceeds that which the chick's kidneys can handle (Kare and Biely, 1948). In fact, where no alternative is available, many chicks die of thirst rather than consume a toxic 2% salt solution. They accept sodium chloride solutions only up to about 0.9% (0.15 M). Various other birds without nasal salt glands that have been studied have similar taste-tolerance thresholds (Bartholomew and Cade, 1958).

Mourning doves freely drink any solution that is hypotonic to their body fluids (Bartholomew and MacMillian, 1960).

Rensch and Neunzig (1925) investigated sodium chloride thresholds (i.e., the lowest concentration at which solutions are rejected) for 58 species, and found that the thresholds ranged from 0.35% in a parrot to 37.5% in the siskin. Unlike the rat, which avidly selects some hypotonic concentrations of sodium chloride, many birds are indifferent up to the concentration at which they reject the salt solution.

The common tern, which has a nasal salt gland, has a high threshold for salt that has been associated with the intake of brackish water with its food. However, when given a choice, the herring or laughing gull (with salt glands) selects pure water over saline solution (Harriman, 1967; Harriman and Kare, 1966). Similarly, penguins are said to prefer fresh water after having been at sea for extended periods (Warham, 1971). The role of the nasal salt gland in the handling of salt is discussed elsewhere in this volume.

The order of acceptability of ionic series by birds does not appear to fit into the lyotropic or sensitivity series reported for other animals. No physical or chemical theory has been offered to explain the responses to sodium salts and chlorides presented in Table 2-5.

**Sour.** Birds have a wide range of tolerance for acidity and alkalinity in their drinking water (Figure 2-17 and Table 2-6). Fuerst and Kare (1962) reported that over an 18-day period, chicks will tolerate strong mineral acid solutions, i.e., pH 2 (Table 2-6). Organic acids are less acceptable, and the tolerance for the hydrogen ion is not equivalent to that for the hydroxyl ion. The starling and the herring gull also readily accept hydrochloric acid solutions. The chick's aversion to acid (sour) solutions is reduced by the addition of glucose (Gentle, 1972). Brindley and Prior (1968) reported that bobwhites prefer 0.05% HCl to water.

**Bitter.** Many tastants are offensive at low concentrations. These include compounds that are bitter to man but quite acceptable to birds, some that are offensive to both man and birds, and a third category of those quite acceptable to man but rejected by some birds.

Sucrose octacetate at a concentration bitter to man is readily accepted by the herring gull and the chicken. Bobwhite quail, which do not respond to sucrose octacetate as very young birds, gradually develop the ability to discriminate this compound (Cane and Vince, 1968). Quinine hydrochloride or sulfate, both of which are used extensively as standard bitter stimuli for man and rats, are also rejected by some species of birds, although bread mixed with quinine is readily eaten by some parrots, and grain dipped in picric acid is readily consumed by seed eaters and titmice (Heinroth, 1938). Among those birds that reject quinine however,

TABLE 2-5. Preference for sodium and chloride metallic solutions at various concentrations over distilled water (chicks)<sup>a</sup>

Solution	Concentration (g/100 ml)				
	0.1	0.2	0.4	0.8	1.0
Na acetate	55 <sup>a</sup>	52	56	52	51
Na sulfate	54	52	52	53	50
Na phosphate (monobasic)	52	53	52	52	54
Na succinate	49	52	54	50	56
Na citric	54	52	54	47	35
Na phosphate (diabasic)	51	49	47	44	14
Na tungstate	50	46	48	—	—
Na bicarbonate	52	43	38	20	14
Na benzoate	49	41	23	15	10
Na bisulfate	38	23	35	17	23
Na pyrophosphate	46	37	20	3	4
Na perborate	42	29	10	9	4
Na carbonate	42	30	10	4	2
Na phosphate (tribasic)	46	20	4	1	2
Na cholate	4	20	3	—	3
Sodium Cl	50 <sup>a</sup>	50	55	50	45
Magnesium Cl	49	51	51	53	45
Choline Cl	51	48	49	50	51
Manganese Cl	49	51	46	16	—
Strontium Cl	50	38	44	18	9
Ammonium Cl	49	46	35	12	6
Barium Cl	36	48	41	—	15
Calcium Cl	43	45	27	15	5
Zinc Cl	33	24	10	2	2
Cobalt Cl	26	12	6	5	6
Tin Cl	30	7	1	1	2
Copper Cl	6	11	3	8	4
Iron Cl	2	4	2	3	4

<sup>a</sup> Preference = (salt solution consumed × 100)/total fluid intake.

TABLE 2-6. Percent intake in chickens of acids and bases at different pH levels<sup>a</sup>

pH	1.0	2.0	3.0	4.0
<i>Acids</i>				
HCl	4 19	50	59	
H <sub>2</sub> SO <sub>4</sub>	15 35	54	56	
HNO <sub>3</sub>	8	62	52	
Acetic			16	53
Lactic		15 61		
<i>Bases</i>				
NaOH	45	47	33	2
KOH		48	36	3

<sup>a</sup> Tabled values are the mean of replicate lots. The percent intake = (volume of tested fluid/total fluid intake) × 100 (18 daily values were averaged). The position of the numbers is an indication of the pH of the test solution. For example, at pH 1.5 the average daily consumption of HCl was 19% of the total fluid intake. Distilled water was the alternative in every instance.

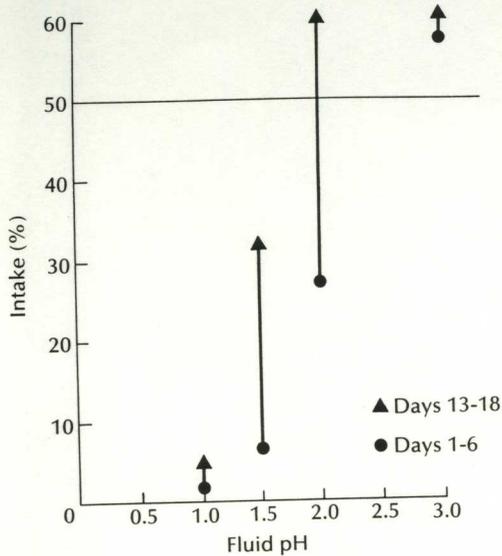


FIGURE 2-17. Daily consumption of HCl solutions for days 1-6 (●) compared with daily consumption for days 13-18 (▲), expressed as percent of total fluid intake at four pH levels. (From Fuerst and Kare, 1962.)

responding is influenced by deprivation, and as in the rat (Johnson and Fisher, 1973), there is increasing acceptance with increasing deprivation (Gentle, 1975). Both quinine and sucrose octaacetate evoke strong neural responses in the chicken.

The offensive secretions of some insects serve as a protective device against avian predators. Some of these have a caustic action on the eyes and possess offensive and possibly bitter tastes (Yang and Kare, 1968). Taste may serve as an important cue to adverse effects that may occur subsequent to ingestion of certain prey (Rozin and Kalat, 1971). For example, Wilcoxon *et al.* (1971) found that bobwhites could learn to associate adverse postingestional effects with particular tastes, but they were more responsive to visual cues. Similar results have been obtained for red-wing blackbirds (Mason and Reidinger, 1983b). Little is known about the chemistry of offensive tastes in relation to the human senses.

**Nutrition and Taste.** The function of taste in nutrition is an enigma. In some instances, the birds' preference compliments its nutritional needs. For example, when caloric intake is restricted, a chick selects a sucrose solution to which it is normally indifferent and increases its fluid intake to make up the deficiency (Kare and Ficken, 1963). However, a similarly correct nutritional choice is not made when the sugar is replaced with an isocaloric solution of fat or protein. In a comparison of the responsiveness of domestic and wild jungle fowl to chemical stimuli in caloric regula-

tion, Kare and Maller (1967) found that the wild strain was much more sensitive than the domestic. As such, the preference behavior of laboratory animals may not be a reliable guide to the nutritional adequacy of a diet (Kare and Scott, 1962). Presumably, this is a result of domestication, insofar as important traits may have been bred out of the population. Feed consumption is also discussed elsewhere in this volume.

**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, rejecting the higher temperature. Chickens suffer from acute thirst rather than drink water 10°F above their body temperature.

At the other extreme, the chicken readily accepts water down to freezing temperatures. This pattern of sensitivity to temperature has also been observed in electrophysiologic studies. A sizable minority of chickens lacks this sensitivity, however. Because the response to temperature may take precedence over all chemical stimulants, temperature should be eliminated as a variable in taste studies of the fowl.

**Saliva and Taste.** Saliva is involved in the normal phenomena of taste. Birds have been described as having a limited salivary flow. Using a technique that permitted continuous collection, Belman and Kare (1961) observed that the flow of saliva in the chicken was greater than that of man in terms of body weight but less in terms of food consumed.

**Individual Variation in Taste.** Japanese quail and domestic chickens have been tested to measure their reactions to a variety of chemicals, including ferric ammonium and calcium chloride. Individuals show markedly different thresholds. The distribution of thresholds is continuous, with reactions among birds to a single concentration of one chemical varying from preference to rejection. Chemical specificity is involved, because an individual that can taste one chloride at either unusually low or only very high concentrations is likely to respond in an average manner to the others. It has been possible to select and breed for taste sensitivity to a specific chemical. This individual variation is not limited to birds (Kare, 1961).

That birds differ in their taste preference as individuals, strains, or species has obvious ecologic advantages. For example, it may permit a population composed of different species to utilize more of the potential food in an environment than would be possible if all were to compete for a limited group of foods, and it contributes to an adaptive plasticity of food habits, making the invasion of new habitats and utilization of new foods possible.

Variation in response to taste is made more complex by seasonal changes in sensitivity. It is interesting to

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consider whether taste directs or follows the abrupt changes in feeding pattern of birds that are insectivorous for part of the year and granivorous for the rest. A possible role for taste in the intensive feeding prior to migration is therefore to be considered.

**Summary.** Kare and Beauchamp (1984), 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 stimulation has been conducted with mammals. This mammalian work has suggested that the initial interaction of a taste stimulus and a receptor cell may occur on the microvilli of the taste receptor cells, but this has not been demonstrated in Aves.

Birds have a sense of taste. However, no pattern, whether chemical, physical, nutrition, 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 bird's response. The observed response, particularly to sweet and bitter, indicates that the bird does not share human taste experiences. However, the supposition that there is a difference in degree between individual birds and an absolute difference between some species appears warranted.

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