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DIFFERENCES IN TASTE PREFERENCE BETWEEN RED-WINGED BLACKBIRDS AND EUROPEAN STARLINGS

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ABSTRACT.—Consumption of biologically relevant taste stimuli (NaCl, D-fructose, citric acid, tannic acid, L-alanine) by male and female European Starlings (*Sturnus vulgaris*) and male Red-winged Blackbirds (*Agelaius phoeniceus*) were examined in one-bottle tests. Male starlings showed greater avidity for fructose than females, and both males and females exhibited greater avidity for fructose than male Red-winged Blackbirds. In addition, male starlings consumed more citric acid than either female starlings or male Red-winged Blackbirds. For both species, high consumption of NaCl (relative to consumption of other tastes) and low consumption of tannic acid were consistent with data reported for other birds. High consumption of L-alanine by both species (with highest consumption exhibited by male Starlings) suggests sensitivity to and preference for free amino acids. We speculate that one mechanism for inter- and intra-specific differences in food selection under field conditions may be differences in taste sensitivity. *Received 17 July 1989, accepted 20 Sept. 1989.*

Interspecific differences in diet composition among avian species may reflect differences in food preference. In turn, differences in food preference could reflect several factors. For example, there may be interspecific differences in nutritional requirements or metabolic rate. Alternatively, there could be differences in the ability to locate and acquire different food types (Joern 1988). Finally, interspecific differences in taste sensitivity and/or taste preference could influence food selection. The present experiment was designed to assess the latter possibility with Red-winged Blackbirds (*Agelaius phoeniceus*) and European Starlings (*Sturnus vulgaris*). Sex differences in taste preference among starlings was also examined, because this species has been reported to exhibit sexual differences in foraging behavior (Feare 1984).

Red-winged Blackbirds and starlings were chosen for investigation because these species have similar overall feeding strategies. Both consume invertebrates during spring and summer and grains and fruits during fall and winter (Beal 1900, Taitt 1973, Wilson 1978, Feare 1984, Nero 1984). However, there are interspecific differences in overall diet composition. Red-winged Blackbirds are more granivorous than starlings (Harriman 1968, Martinez del Rio et al. 1988). Conversely, starlings consume more

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insects (Bruns and Haberkorn 1960, Martinez del Rio et al. 1988) and more fruit (Harriman 1968, Stevens 1985). If these differences in diet composition are reflected in taste sensitivity, then one might expect starlings to exhibit greater avidity for fructose, citric acid, or free amino acids than Red-winged Blackbirds. Red-winged Blackbirds might show greater tolerance (consumption) of phenolic substances such as tannic acid than starlings.

METHODS

Twenty-five adult male Red-winged Blackbirds and 50 adult starlings (25 males, 25 females) were decoy-trapped in Bowling Green, Kentucky, during October 1986 and shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. Upon arrival, each bird was caged individually (39 × 34 × 61 cm) and visually isolated with pieces of cardboard. Birds were maintained on a 10:14 h light:dark cycle, and water was provided from calibrated 200-ml drinking tubes attached to the center of the front of each cage. Dry food (Purina Flight Bird Conditioner) mixed with oyster shell grit was available ad libitum in food cups on either side of the drinking tubes. After 14 days of adaptation to the laboratory, all birds were placed on a mild water-deprivation schedule that continued for the remainder of the experiment. Deprivation involved removal of the drinking tube during the 14 h dark period of each light cycle. Testing began four days following onset of the water deprivation regime.

Five tastes, each at four different concentrations in aqueous solution, were used: NaCl (0.1%, 0.4%, 0.7%, and 1.0% w/v), D-fructose (0.1%, 0.5%, 1.0%, and 5.0% w/v), citric acid (0.1 mM, 1.0 mM, 0.01 M, 0.1 M), tannic acid (0.5%, 1.0%, 2.5%, and 5.0% w/v), and L-alanine (0.1%, 0.4%, 0.7%, and 1.0% w/v). Also, distilled water was presented as a control. All solutions (except the 5.0% tannic acid solution) were colored brown using McCormick's food coloring (one drop green and four drops red per 300 ml) to match the brown color of the 5.0% tannic acid solution.

Taste stimuli were chosen on the basis of possible biological relevance: all are found in foods consumed by passerines (Goldstein and Swain 1963, Greig-Smith et al. 1983, Wilson and Blunden 1983). Also, tastes were chosen to represent what we presumed to be different taste sensation categories (i.e., salty, sweet, sour, bitter/ astringent, umami [protein taste]). Taste concentrations were selected in part to approximate concentrations present in foods (e.g., concentrations of fructose [0.33 M; Schuler 1983] or citric acid [pH 3.3–4.3; Stevens and deBont 1980] in cherries, concentrations of tannic acid in ash seeds [15–30 mg/g; Greig-Smith 1988]), in part on the basis of work by others (e.g., citric acid, Harriman 1968), and in part on the basis of pilot experiments performed in our laboratory (Espaillat, unpubl. data). These pilot experiments were designed to determine the lowest concentration of tastes that produced reliable differences in consumption relative to consumption of distilled water.

Five Red-winged Blackbirds and 10 starlings (5 males and 5 females) were assigned randomly to each of five groups. Different groups were presented with different taste stimuli (one taste/group) in calibrated 200-ml drinking tubes attached to the center of the front of each cage. Although these one-bottle tests are less sensitive than two-bottle tests in measuring detection, we used the former technique to: (1) eliminate position preferences (Duncan 1960) and (2) assure measurable consumption of unpalatable tastes (e.g., tannic acid). While drinking behavior does not necessarily reflect feeding behavior, we used drinking tests rather than feeding tests to maximize the potential for taste detection. Daily sessions began 1 h after light onset and continued for 2 h on each of 20 successive test days. Measurements of consumption were made at 30-min intervals. The relatively short daily test durations were chosen to maximize the role of taste (rather than post-ingestional factors) in drinking behavior. No measurements of spillage were made, as we assumed that spillage would be proportional to consumption. Only one stimulus at one concentration was presented daily to each bird. Each concentration (including distilled water as 0.0% taste) of every taste was randomly presented to the birds in the appropriate group four times during the course of testing.

At the end of each test session, stimulus solutions were removed, and birds were permitted free access to distilled water for the remainder of the light period.

Because starlings weigh more than Red-winged Blackbirds, the data were expressed as fluid consumption per g of body mass. Means for the first 30 min of consumption were calculated for the four presentations of each stimulus concentration to each bird and these means were assessed in five two-way analyses of variance (ANOVA, one analysis per taste). The factors in the analyses were sex/species (i.e., male Red-winged Blackbirds, male starlings, female starlings) and concentration (a repeated measures factor). Measurement intervals were not considered as a factor in the analyses because most consumption occurred within the first 30 min of each test session and because patterns in consumption at 60 and 90 min merely reflected those established after 30 min. Tukey Honestly Significant Difference (HSD) tests were used to isolate significant differences among means ($P < 0.05$).

RESULTS

NaCl.—There were no sex/species differences ($P > 0.10$) in consumption of NaCl solutions. However, there were differences in consumption among concentrations ($F = 12.6$; df = 4,48; $P < 0.00001$). Any NaCl solution was preferred to distilled water, and higher NaCl concentrations were preferred to lower concentrations (Fig. 1).

Fructose.—There were significant sex/species differences ($F = 5.1$; df = 2,12; $P < 0.02$). Overall, Red-winged Blackbirds drank less fructose (per gram of body weight) than did starlings, and female starlings drank less fructose did than males. Moreover, post-hoc examination of a significant interaction between sex/species and concentration ($F = 2.6$; df = 8,48; $P < 0.02$) showed that while consumption of fructose by Red-winged Blackbirds did not vary as concentration increased (and at no concentration differed from consumption of distilled water), consumption by starlings did increase (relative to consumption of distilled water) at concentrations $\geq 0.5\%$. Male starlings showed greater consumption of the highest fructose concentration (5.0%) than did females (Fig. 1).

Citric acid.—There were significant sex/species differences ($F = 6.3$; df = 2,12; $P < 0.02$). As for fructose, male starlings consumed more citric acid overall than did either female starlings or male Red-winged Blackbirds. Also, there were significant differences among concentrations ($F = 4.8$; df = 4,48; $P < 0.002$). Post-hoc examination of this effect revealed that cosumption of concentrations ≥ 0.01 M were significantly less than consumption of distilled water (Fig. 1).

Tannin.—There were significant sex/species differences ($F = 7.3$; df = 2,12; $P < 0.01$) and significant differences among concentrations ($F =$

26.5; df = 4,48; $P < 0.00001$). Red-winged Blackbirds consumed more tannin than starlings, but for both species, consumption decreased as tannin concentration increased. Consumption of all tannin concentrations was less than that of distilled water (Fig. 1).

L-alanine.—There were significant differences among concentrations ($F = 6.5$; df = 4,48; $P < 0.0005$). As for NaCl and fructose, consumption increased with concentration (i.e., consumption significantly exceeded that of distilled water at concentrations ≥0.7%). In addition, post-hoc examination of a significant interaction between sex/species and concentration ($F = 4.5$; df = 8,48; $P < 0.01$) showed that both Red-winged Blackbirds and starlings showed increasing consumption with increasing concentration, but male starlings exhibited greater consumption than male Red-winged Blackbirds, and male Red-winged Blackbirds exhibited greater consumption than female starlings (Fig. 1).

DISCUSSION

Both Red-winged Blackbirds and starlings were sensitive to NaCl, fructose, citric acid, tannin and L-alanine. In addition, for fructose, citric acid, and L-alanine, there appeared to be species and sex differences in consumption. While these laboratory results do not necessarily reflect the importance of taste in free-ranging birds, they do provide substance for speculation.

The preference for (i.e., greater consumption of) increasing NaCl concentrations suggests that consumption of salt by free-ranging birds may be mediated by taste (as opposed to post-ingestional feedback). If true, then we speculate that the salt-eating behavior exhibited by a variety of other passerine species (see Coleman et al. 1985 for review) may be taste mediated. Although wild birds rarely show symptoms of sodium deficiency when kept on a low sodium diet (Cade 1964, Dawson et al. 1965), dietary sodium levels of 0.09 to 0.15% are required for maximum growth and egg production (Skadhauge 1981).

The present NaCl results conflict with those reported by Rogers and Maller (1973). Those authors found that Red-winged Blackbirds are indifferent to 0.2% NaCl (relative to water) in 2-bottle tests, yet we observed that 0.1% NaCl was preferred to water in 1-bottle tests. While this discrepancy is probably a function of different experimental designs, a clear explanation is not easily provided. Two-bottle tests are usually more sensitive than 1-bottle tests for evaluation of taste detection (Duncan 1960).

The positive association between fructose consumption and concentration in combination with the negative relationship between citric acid consumption and concentration are consistent with earlier reports (Har-

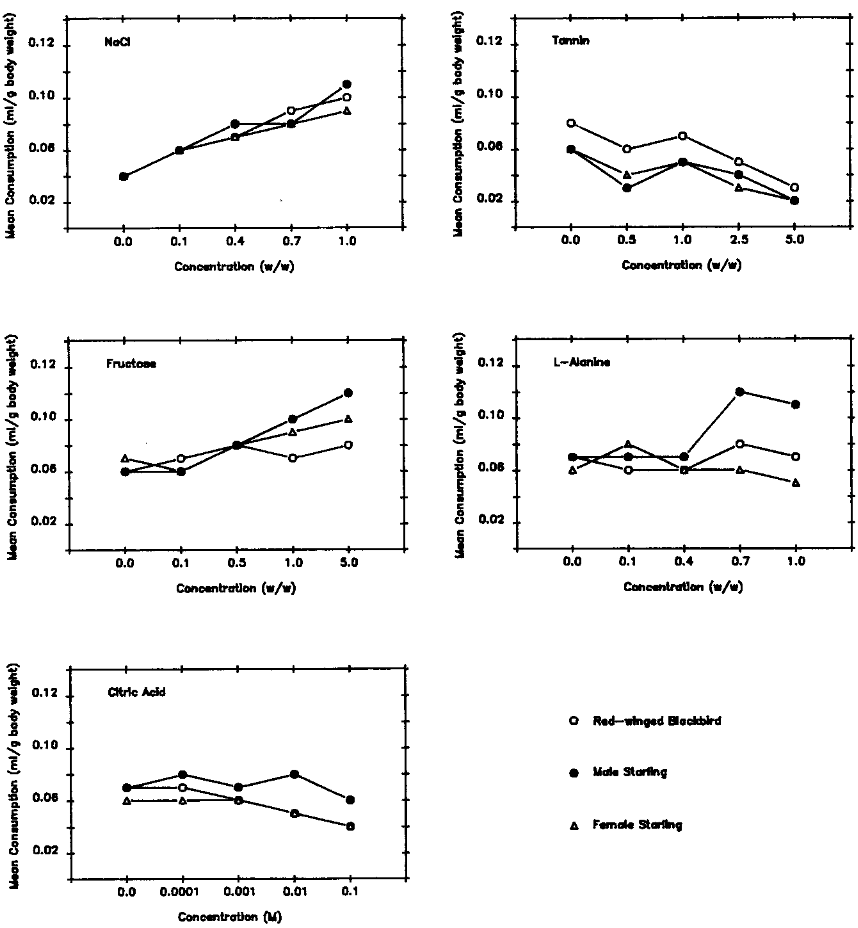

FIG. 1. Mean consumption of NaCl, fructose, citric acid, tannin, and L-alanine per gram of body weight by Red-winged Blackbirds, male starlings, and female starlings.

riman 1968, Martinez del Rio et al. 1988, Martinez del Rio and Stevens 1989). Because the pulp of many fruits is rich in both substances, it is reasonable to speculate that preference for fructose and preference for or tolerance of citric acid represent sensory adaptations to frugivory. The fact that starlings consumed more fructose and citric acid than Red-winged Blackbirds is consistent with this view, insofar as the former species eats relatively more fruit (e.g., Harriman 1968).

Tannic acid concentrations tested in the present experiment are equivalent to those found in various fruits (Goldstein and Swain 1963) and grain (Bullard et al. 1981). The finding that consumption decreased with increasing concentration for both species is consistent with data which show that the tannin content of fruits and grain is positively correlated with bird resistance (e.g., Bullard et al. 1981, Greig-Smith et al. 1983, Mason et al. 1984). That Red-winged Blackbirds were more tolerant than starlings of low (0.5–1.0%) tannin concentrations may reflect their granivorous feeding habits (i.e., Red-winged Blackbirds may be more likely to utilize tannin-containing foods).

We cannot explain our observation that both male starlings and Red-winged Blackbirds show greater consumption of L-alanine than female starlings. However, the more general finding that both species are sensitive to and prefer this amino acid at concentrations ≥0.7% is intriguing. Whether or not L-alanine sensitivity reflects sensitivity to other free amino acids or to protein is unknown. However, L-alanine and similar substances (e.g., L-glutamine) occur as free amino acids in both vegetable matter, fruit, and meats (Hac et al. 1949, Maeda et al. 1958, Baker and Baker 1983). Perhaps amino acid sensitivity aids in the identification of high protein foods. At least for starlings, assimilation efficiency increases as the protein content of a diet increases (Twedt 1984).

Overall, the present findings implicate chemosensory cues as one of the factors involved in foraging decisions. This possibility stands in contrast to models of foraging (e.g., Wunderlee and Cotto-Navarro 1988) that mainly or only consider energy (i.e., long-term physiological feedback) as a proximal determinant. Taste cues may provide an immediate sensory signal concerning the quality of a potential food item, thereby maximizing foraging efficiency.

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