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Thresholds for Sweet, Salt, and Sour Taste Stimuli in Cockatiels (*Nymphicus hollandicus*)

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Little is known about avian taste perception and how taste affects food choice. We designed a study to determine the concentrations of aqueous solutions of common chemical taste stimuli that result in altered consumption patterns. Using two-choice taste-preference tests, we studied the taste thresholds of caged cockatiels (*Nymphicus hollandicus*) for aqueous solutions of potassium chloride, a phosphate buffer (to test pH), fructose, and glucose. First, the preferred and nonpreferred bottle locations were determined for each bird. Then, depending on the compound, the test solutions were placed in bottles in either the preferred or the nonpreferred locations and water was placed in the opposite bottle. Four parameters were measured at the end of 3-day test periods (total consumption, consumption from water side, consumption from test solution side, and proportion of nonpreferred side consumption to total consumption). Experiments were repeated with increasing concentrations of test flavors until intake variables were significantly affected ($P < 0.05$). Cockatiels distinguished ($P < 0.05$) between purified water and 0.16 mol L^{-1} potassium chloride, 0.40 mol L^{-1} fructose, or 0.16 mol L^{-1} glucose. The test birds did not distinguish between water and 0.05 mol L^{-1} mono- and dibasic sodium phosphate buffer solution at any tested pH within the range of 4.9–7.7. When these findings are compared to previous experiments with the same birds, it becomes clear that the gustatory reactions of cockatiels for two different stimuli (e.g., NaCl and KCl) from the same general taste category (salt, sweet, sour) can vary widely. This variation in the responses to related stimuli could be the result of a number of factors including anion effects (for salts and acids) as well as nongustatory physiological processes (e.g., as renal control of blood osmolarity). Zoo Biol 20:1–13, 2001. © 2001 Wiley-Liss, Inc.

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INTRODUCTION

Despite the fact that birds have relatively few taste buds, many studies have demonstrated that flavors can affect avian food choice as well as the quantity of food

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or liquid consumed [Bartholomew and Cade, 1958; Cummings et al., 1994; Hainsworth and Wolf, 1976; Harriman and Milner, 1969; Harriman and Fry, 1990; Harriman and Kare, 1966; Kare et al., 1957; Kare and Pick, 1960; Matson et al., 2000]. The degree to which flavors affect these behaviors can be widely variable. At similar concentrations, a compound that reduces consumption in one species may increase consumption in another. Sucrose solutions have been demonstrated to be accepted or preferred in some species [Harriman and Milner, 1969; Kare et al., 1957] and rejected in others [Harriman and Fry, 1990; Matson et al., 2000]. Also, the behavioral responses of some birds may vary when presented with different taste stimuli, even those from the same taste category (e.g., sweet, sour, salt, and bitter). For example, Fuerst and Kare [1962] reported that the response of Barred Plymouth Rock-Rhode Island Red crossbred chicks to acidity (sourness) varied depending on whether the acid was organic or inorganic. The authors suggested that "at the same pH level organic acids will produce a stronger or a different stimulus than inorganic acids." In addition, many compounds have been found to vary from preferred to rejected depending only on concentration. Studying the sense of taste gives insight to factors that control food choice and specific appetites.

Many psittacine species are endangered because of poaching and habitat loss. Aviculturalists have worked to develop a set of husbandry conditions for captive propagation of psittacines [Millam, 1999]. However, little is known about the dietary needs of parrots and the role played by taste in the birds' food choices. The role of taste as a factor controlling food choice is an important consideration for diet development. Cockatiels (*Nymphicus hollandicus*), our study organism, are small granivorous psittacines native to Australia and are found throughout most of the country, particularly in the hot, arid central region [Jones, 1987].

We previously developed the methodology to test the taste thresholds of cockatiels for sodium chloride (NaCl), pH (citric acid buffer), and sucrose [Matson et al., 2000]. This was done by giving birds a choice between two bottles— one with water and one with a flavored test solution. The concentration at which the birds significantly altered their intake was defined as the taste threshold. Further, we compared the statistical power of testing these compounds on the preferred drinking side versus the nonpreferred drinking side of each bird when presented with the option to drink from both sides. In the present experiments, we used this methodology to determine the taste thresholds for potassium chloride, pH (phosphate buffer), fructose, and glucose of captive cockatiels.

MATERIALS AND METHODS

Cockatiels used in these experiments were part of the research and breeding flock of the Department of Animal Science at the University of California, Davis. Cockatiels were housed individually in cages (30 cm × 30 cm × 60 cm) located in a room that was maintained at 23°C. Light schedules were kept constant during each experimental series (either 9L:15D or 15L:9D, depending on the season). The birds were provided with a pelleted diet (Maintenance Crumbles, Roudybush, Cameron Park, CA) and water for ad libitum consumption. During the taste-preference trials, each cage was fitted with two 100-ml-capacity water bottles with drinking surfaces 1.5 cm in diameter and graduated in 1-ml increments (Bio-Serve, Frenchtown, NJ). The bottles were placed in cage locations (sides) so that the drinking surfaces were 25 cm apart. The water used throughout all experiments was distilled water that had been purified through a Milli-Q Water System (a carbon filter, two ion-exchange columns, an endotoxin filter, and a 0.20-µm ultrafilter; Millipore, Boston, MA). Compounds used for taste stimulus were potassium chloride (KCl, Sigma Chemical Company, St. Louis, MO, catalog #P-3911), fructose ($C_6H_{12}O_6$, Sigma, #F-0127), glucose ($C_6H_{12}O_6$, Sigma, #G-8270), and a buffer made of mono- and dibasic sodium phosphate (NaH_2PO_4, Sigma, #S-0751 and Na_2HPO_4, Sigma, #S-0876). All research was approved by the Animal Care and Use Committee at the University of California at Davis.

An equilibrium period was used to determine the total amount and preferred side of water consumption. During this period, the birds were provided with water on both sides of the cages for 3 days. The amount of water consumed during this equilibrium period was determined from the difference in the initial and final amounts of water in the bottles. Because of substantial variation between individual birds in the total amount and side-preference of water consumption, the birds were ranked according to the strength of their preference, as determined by the proportion of consumption from each side. Excessive water consumption during the equilibrium period (>80 ml from one side and/or >100 ml from both sides) was grounds for removing a bird from the experiment. If birds were added or removed from the test flock, it was done at the completion of an experimental period.

An experimental period followed the equilibrium period. The effects of preexisting side-preferences were minimized by assigning the birds to one of three experimental groups (n = 6–8 per group) in a manner that equally distributed the side-preference strengths among the groups. The three groups included: a control group receiving water on both sides of the cage; a treatment group with a low concentration of the test solution on one side and water on the other; and a treatment group with a high concentration of the test solution on one side and water on the other.

Previous results demonstrated that experiments have the highest probability of significance when the taste solution is placed on a particular side. Therefore, the test solutions in the present experiments were placed on the side of the cage that provided the greatest statistical power for that category of taste (sweet, sour, or salt), as reported by Matson et al. [2000]. Thus, we placed glucose and fructose on the nonpreferred side and KCl and the phosphate buffer on the preferred side. An experimental series with progressively increasing concentrations of the test compound was conducted for each compound. This was done by increasing the concentration of the test compounds through sequential experimental periods. An equilibrium period of 3 days, during which purified water was offered on both sides separated each experimental period. These equilibrium periods were used to measure side preference and reassign the birds to treatment groups as previously described.

The birds were first given concentrations of the test compound thought to be below their threshold. Consumption from each of the sides during the three-day experimental period was determined and the results were expressed as four consumption parameters. These parameters were: consumption from the test solution side; consumption from the water side; total consumption; and the proportion of consumption on the nonpreferred side (fructose or glucose solutions in the case of the sugars, water in the case of KCl and the phosphate buffer) relative to total consumption (Proportion).

A significant shift ($P < 0.05$) in one or more of the consumption measures (other than, or in addition to, the total consumption) of a test group, as compared to the same measure of the control (water-only) group, indicated that the birds perceived the taste of the test solution and altered their drinking behavior. At this point, the experimental series was discontinued. If only the total consumption parameter was significantly different between a test and control group, the experimental series was continued until a significant shift in an additional parameter was found. A shift only in total consumption could indicate a physiological response (e.g., increased urine production or change in thirst), rather than a response to taste. The concentration at which the control and test group parameters differed significantly was defined as the taste threshold.

Data Analysis

In order to compare the effects of different solution concentrations within the experimental series, the treatment means were standardized. The standardization was done by expressing the consumption parameter means of treatment birds as a percentage of the mean of the same parameter of the control birds.

Data for the four consumption parameters from each experimental period were analyzed by one-way analysis of variance (ANOVA). When an ANOVA was significant ($P < 0.05$), differences between individual treatment means were determined by least significant difference (LSD).

In several cases, there was a significant ANOVA ($P < 0.05$), but the LSD did not indicate that a treatment mean was significantly different from the control mean. In these cases (0.16 mol L^{-1} and 0.18 mol L^{-1} KCl and 0.16 mol L^{-1} and 0.20 mol L^{-1} glucose), the trials were repeated with the same test solution concentrations. Data from replicate experiments were analyzed using a general linear model (GLM) for treatment, repetition, and the treatment by repetition interaction. If neither repetition nor interaction were significant ($P>0.20$) as with glucose, then the data were pooled and analyzed by one-way ANOVA and LSD means comparisons. If repetition or interaction accounted for sufficient variation ($P < 0.20$), it was left in the model. This was the case with KCl.

RESULTS

Experiment 1: KCl

The sensitivity of cockatiels to a salt was tested by placing a potassium chloride solution on the preferred side, and purified water on the nonpreferred side. In this experimental series, six solutions of KCl were tested with concentrations ranging from 0.10 to 0.25 mol L^{-1} (Fig. 1). At 0.13 mol L^{-1}, none of the consumption parameters of the treatment groups differed significantly from the same parameters of the control group. At 0.16 mol L^{-1} and above, one or more of the consumption parameters of the treatment groups varied significantly from the same parameter in the control group. At 0.16 mol L^{-1}, the treatment Proportion was significantly greater than the control Proportion ($P < 0.031$). At 0.18 mol L^{-1}, both the consumption from the water side and the total consumption of the treatment group were significantly greater than those of the control group ($P < 0.016$ and $P = 0.004$, respectively). At the concentrations of 0.20 mol L^{-1} and 0.25 mol L^{-1}, consumption from the water side by the treatment group was significantly greater than the consumption by the control group from the

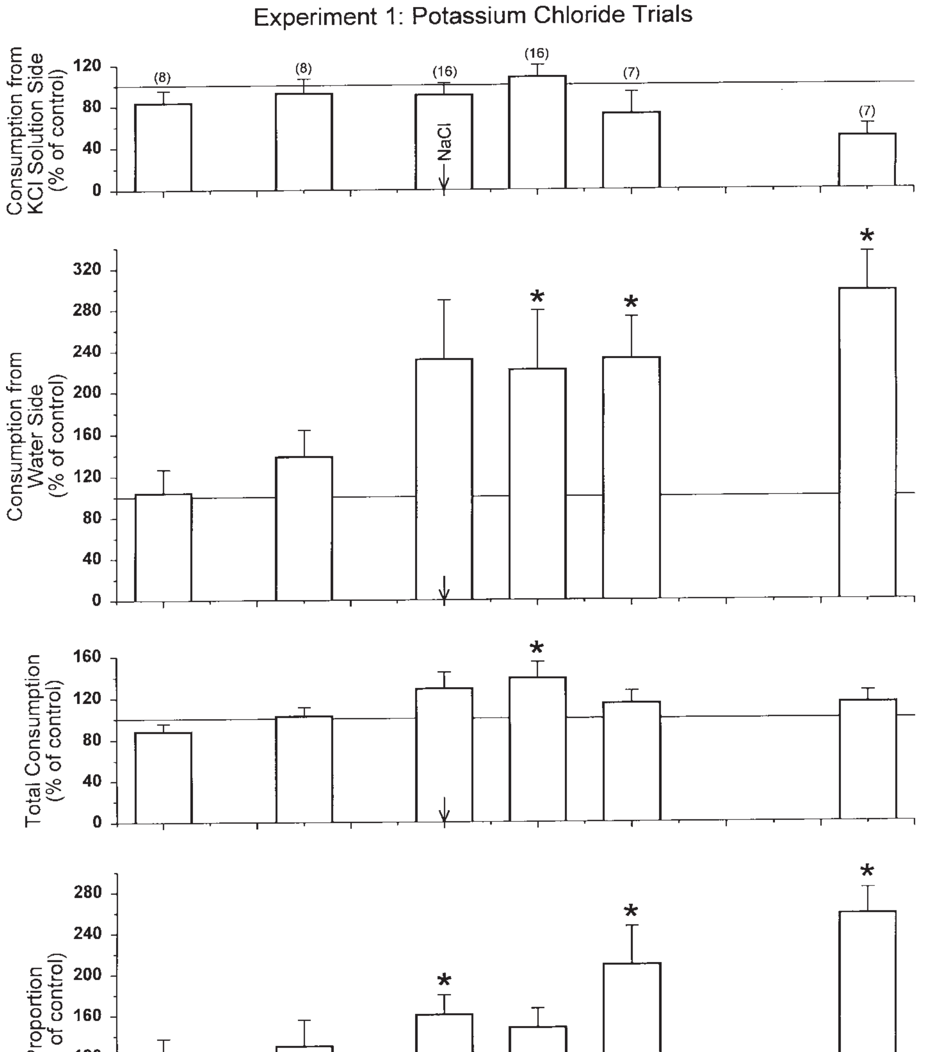

Fig. 1. Comparison of the effects of different concentrations of potassium chloride placed on each bird's previously established preferred side. The consumption parameters of control birds that were provided water on both sides were normalized to 100% and are indicated by the horizontal line at this value. Open bars indicate consumption by treatment groups (±SEM) expressed as a percentage of the control group. Stars (*) represent significant (*P* = 0.05) changes from the control. The numbers in parentheses indicate the sample size. Arrows represent the previously determined threshold level for sodium chloride solution [Matson et al., 2000].

same side ($P = 0.001$). In addition, at both of 0.20 mol L^{-1} and 0.25 mol L^{-1}, the treatment Proportion was also significantly greater than control Proportion ($P = 0.002$).

Experiment 2: Phosphate Buffer

The sensitivity of cockatiels to pH was determined using a 0.05 mol L^{-1} buffered solution of mono- and dibasic sodium phosphate using in ratios indicated by Gomori [1955]. The buffered solutions were offered to the birds on their preferred side. No significant differences were found between any of the treatment groups and the corresponding control groups for any of the parameters measured (Fig. 2). We were compelled to limit our observations on pH to the range of 4.9 and 7.7 because of the functional buffering range of this buffer system.

Experiment 3: Fructose

Fructose was the first of two comparison sugars used to test the threshold to sweetness. Fructose solutions were offered on the nonpreferred side. Six concentrations ranging from 0.16 mol L^{-1} to 0.49 mol L^{-1} were tested (Fig. 3). At 0.16 mol L^{-1} and 0.20 mol L^{-1}, the two lowest concentrations tested, the total consumption of the treatment group was significantly less than the total consumption of the control group ($P = 0.004$). However, both parameters contributing to total consumption by the treatment birds (consumption from water side and consumption from fructose solution side) were less than the same parameters of the control birds. Thus, it was unlikely that the decrease observed in total consumption was due solely to the taste of the sugar solution, and higher concentrations were tested.

No significant differences were found for 0.25 mol L^{-1} and 0.31 mol L^{-1} treatment groups. However, at the 0.39 mol L^{-1} level, consumption from the fructose solution side was significantly less than consumption from the corresponding side of the control group ($P = 0.013$). In addition, the total consumption parameters for 0.39 mol L^{-1} and 0.49 mol L^{-1} fructose solutions were significantly less than the total consumption of the corresponding control group ($P = 0.018$).

Experiment 4: Glucose

Glucose was the second sugar used to determine the threshold to sweetness (Fig. 4). As with fructose, glucose was tested on the nonpreferred side. Because the threshold was determined during the first experimental period, only two concentrations were tested, 0.16 mol L^{-1} and 0.20 mol L^{-1}. At the first level of 0.16 mol L^{-1}, the treatment birds consumed significantly less from the glucose solution side than the control birds did from same side ($P < 0.042$). At 0.20 mol L^{-1}, three parameters differed significantly from the same parameters of the control. First, the consumption from the treatment water side was significantly greater than the corresponding side of the control group birds ($P = < 0.037$). Second, the consumption from the treatment glucose solution side was significantly less than consumption from the equivalent control side ($P = < 0.001$). Third, the treatment Proportion was significantly less than the control Proportion ($P = < 0.001$).

DISCUSSION

When offered KCl, cockatiels first changed their consumption patterns at a concentration of 0.16 mol L^{-1}. Therefore, the taste threshold for KCl is 0.16 mol L^{-1}

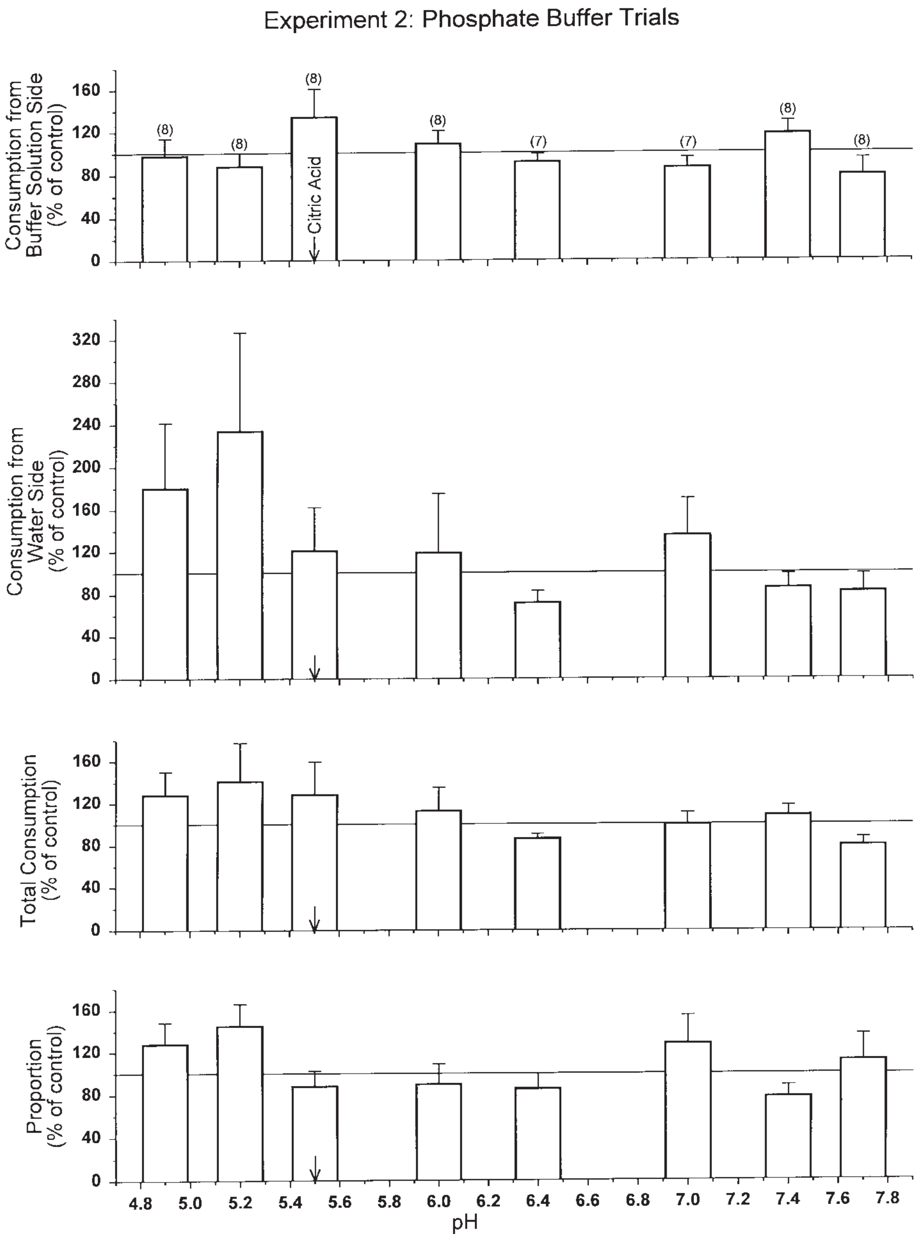

Fig. 2. Comparison of the effects of different pH values of 0.05 mol L^{-1} mono- and dibasic sodium phosphate buffer placed on each bird's previously established preferred side. The consumption parameters of control birds that were provided water on both sides were normalized to 100% and are indicated by the horizontal line at this value. Open bars indicate consumption by treatment groups (±SEM) expressed as a percentage of the control group. The numbers in parentheses indicate the sample size. Arrows represent the previously determined threshold level for citric acid buffer solution [Matson et al., 2000].

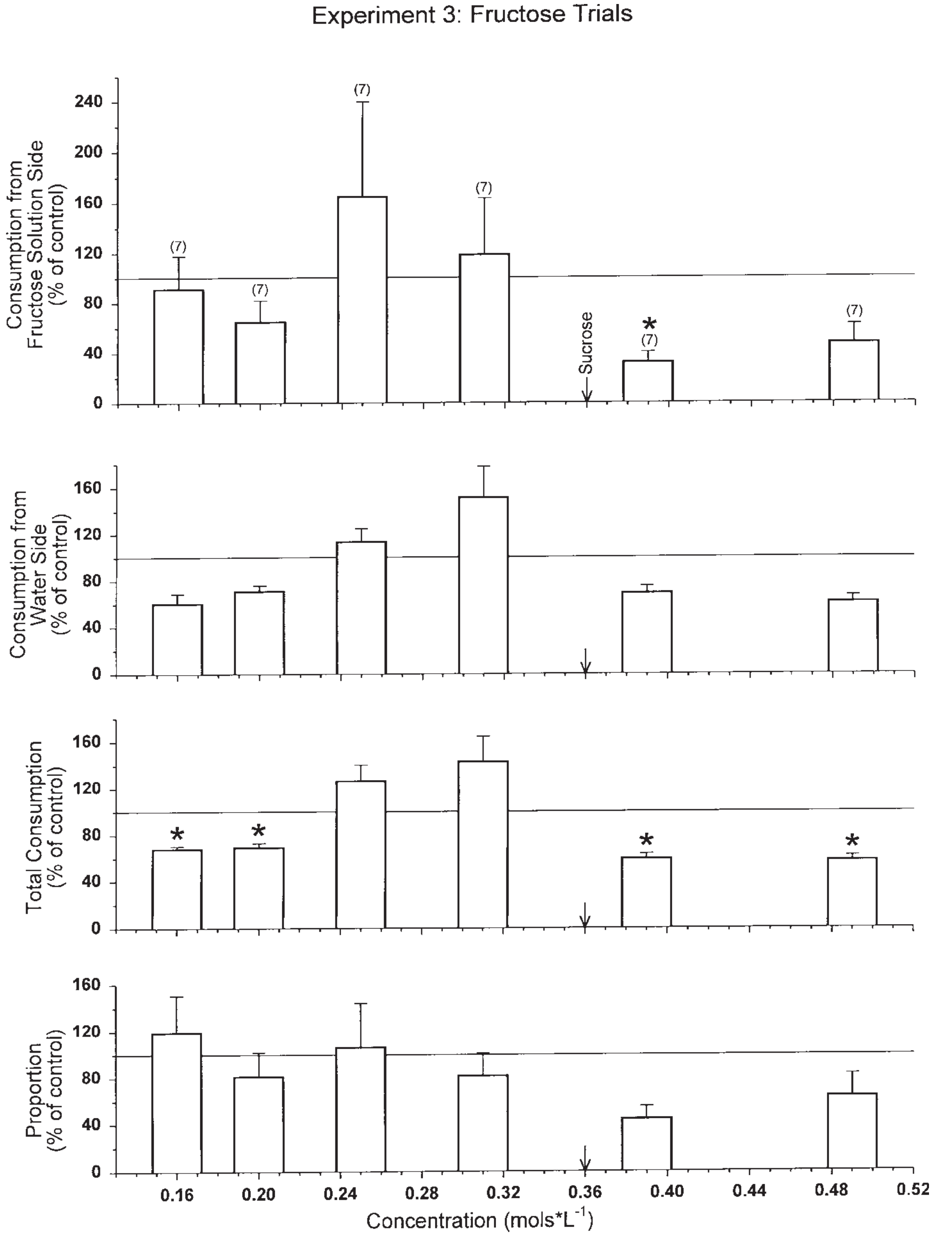

Fig. 3. Comparison of the effects of different concentrations of fructose placed on each bird's previously established nonpreferred side. The consumption parameters of control birds that were provided water on both sides were normalized to 100% and are indicated by the horizontal line at this value. Open bars indicate consumption by treatment groups (±SEM) expressed as a percentage of the control group. Stars (*) represent significant (P = 0.05) changes from the control. The numbers in parentheses indicate the sample size. Arrows represent the previously determined threshold level for sucrose [Matson et al., 2000].

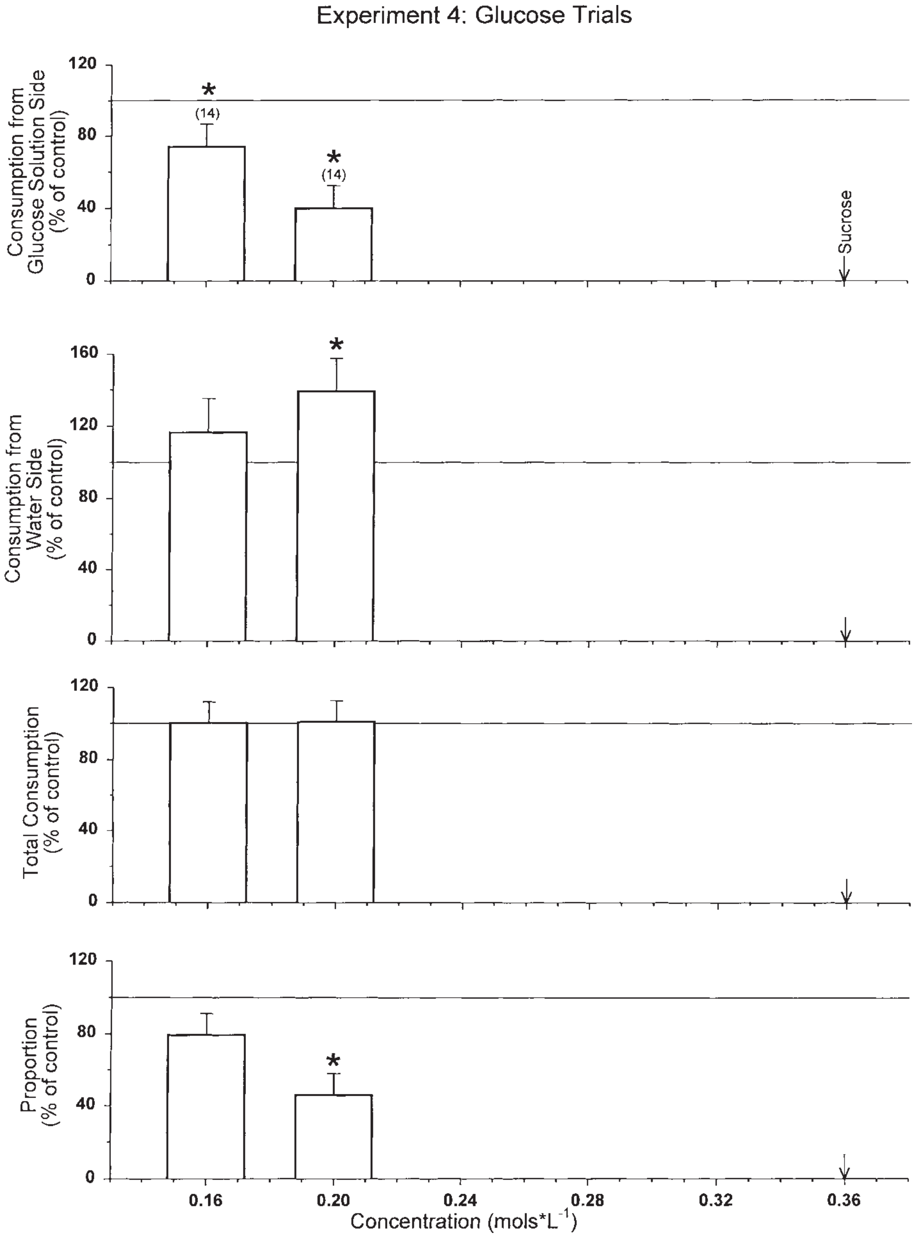

Fig. 4. Comparison of the effects of different concentrations of glucose placed on each bird's previously established nonpreferred side. The consumption parameters of control birds that were provided water on both sides were normalized to 100% and are indicated by the horizontal line at this value. Open bars indicate consumption by treatment groups (±SEM) expressed as a percentage of the control group. Stars (*) represent significant (P = 0.05) changes from the control. The numbers in parentheses indicate the sample size. Arrows represent the previously determined threshold level for sucrose [Matson et al., 2000].

which is identical to their threshold for NaCl [Matson et al., 2000]. At concentrations of ≥0.16 mol L^{-1} of either KCl or NaCl, birds shifted to consume more water, without necessarily decreasing their consumption of the salt solution. Gentle [1972] reports that Brown Leghorn chickens (*Gallus domesticus* L.) show a rejection of both salts, but KCl appeared to elicit a stronger negative response than NaCl. In addition, feral pigeons (*Columba livia* var Gmelin) also avoid the two chloride salts at high concentrations [Duncan, 1960]. However, the pigeons appear to be more sensitive to NaCl. At lower concentrations, pigeons show a preference for each of the salt solutions [Duncan, 1960].

The reported responses of cockatiels, chickens, and pigeons to NaCl and KCl could be related to the Na^+ and K^+ cations or to the Cl^- anions. In cockatiels, similar responses to NaCl and KCl could be attributable to their taste perception of Cl^- anion, whereas the differences in the aversiveness to NaCl and KCl in pigeons and chickens could stem from the effects of the different cations. Ye et al. [1991] suggest that it is, indeed, the anion that is responsible for much of the salty taste perceived when NaCl is consumed. In rats, Cl^- anions act by permeating the tight junctions between taste receptor cells, and anions counteract the electropositive field potential generated by the influx of Na^+ cations. Chloride permeates the tight junctions most effectively of the anions tested (chloride < acetate < gluconate), and leads to the greatest gustatory response [Ye et al., 1991]. In addition, electrophysiological data demonstrate differences in the ability of the tested salts to stimulate taste receptors. For some mammals, such as rats, NaCl is more stimulatory than KCl, while in others (rabbits, cats), the reverse is true [Pfaffmann, 1955]. These differences could be related to taste receptor physiology. Studies demonstrate that one mechanism for sodium transduction is the amiloride-sensitive sodium channels. These channels allow sodium, lithium, and protons to pass through, but are impermeable to potassium [Herness and Gilbertson, 1999].

Of all taste stimuli, acids have the widest range of stimulatory effects [Herness and Gilbertson, 1999]. This effectiveness results from the facts that protons, the most basic and common unit of sour taste stimulation, can permeate through tight junctions and can trigger most classes of ion channels [Settle et al., 1986; Herness and Gilbertson, 1999]. Despite this, when 0.05 mol L^{-1} mono- and dibasic sodium phosphate buffer solutions of various pH values (range: 4.9–7.7) were offered to cockatiels, no consumption parameters changed significantly. However, Matson et al. [2000] found that cockatiels consume significantly less of a citric acid solution at pH 5.0 (0.05 mol L^{-1}) than they do water. In addition, we reported that the Proportion of the pH 5.5 and 5.0 groups was significantly greater than the Proportion of the control group. Together, the results of these studies support the findings of other studies that indicate birds are more sensitive to pH changes of organic acids than to inorganic acids. Consumption behavior of cockatiels effectively mirrors the results of electrophysiological studies on rats and chickens, which demonstrate a stronger neural response to organic acids than to inorganic acids of the same pH [Fuerst and Kare, 1962].

It is important to note that at pH 5.0, the citric acid buffer system was very close to the middle of its effective buffering range (3.0–6.2). At the same pH, the phosphate buffer system used in this study is close to the acidic limit of its buffering range (4.8–7.7). In fact, regardless of buffering range, at all equivalent pH values, the citric acid buffer has a much higher buffering capacity than the phosphate buffer.

Our results, therefore, could be mediated as much by buffer capacity as by organic versus inorganic properties.

As with the other test compounds, sugar and sweetness preference varies between species and compounds. It has been hypothesized that nectarivorous and frugivorous birds should respond positively to sugars, and insectivorous and granivorous birds, neutrally or negatively [El Boushy et al., 1989, Kare and Mason, 1986]. Hummingbirds prefer sucrose, and passerines typically prefer glucose and fructose [Martínez del Rio et al., 1992]. However, some southern African nectarivorous passerines prefer sucrose, the dominant sugar in southern African food plants [Downs and Perrin, 1996; Jackson et al., 1998]. Sugar preference appears to be directly linked to the type of sugars in the nectar or fruit available.

Sugar preference and rejection trends in non-nectarivorous birds are less clear. Parrots and budgerigars reportedly prefer sugar solutions [Kare and Mason, 1986], but the only significant consumption change we observed in cockatiels was rejection of the sugar solutions. Matson et al. [2000] previously reported that a significant rejection of sucrose was first seen at 0.36 mol L^{-1}. The threshold for rejection of fructose was 0.39 mol L^{-1} and glucose was rejected at concentrations of 0.16 and 0.20 mol L^{-1}, the lowest two levels tested. While the threshold for glucose could be even lower than 0.16 mol L^{-1}, it was clear that the threshold for glucose was considerably lower than that of sucrose or fructose.

In common crows (*Corvus corax*), Harriman and Fry [1990] note a “moderate preference” for 0.10 mol L^{-1} glucose, but show a nonpreferential acceptance or a rejection of all other concentrations of glucose and all test concentrations of fructose and sucrose (concentrations of 0.05–1.00 mol L^{-1}). For glucose solutions ranging from 0 to 1.0 mol L^{-1}, pigeons show very little change in consumption patterns for the glucose solutions compared with pure water [Duncan, 1960]. For sucrose solutions ranging from 0 to 0.82 mol L^{-1}, pigeons increase their consumption of the sucrose solutions relative to water consumption up to a concentration of 0.41 mol L^{-1}, and then begin decrease their consumption. As with pigeons and crows, chickens have mixed reactions when offered the three sugars within a range of concentrations. Brown Leghorns significantly reject glucose and fructose at 0.28 mol L^{-1} and significantly prefer sucrose at 0.15 mol L^{-1}. Chickens significantly reject all three sugars at fructose or glucose concentrations of 1.66 mol L^{-1} or sucrose concentrations of 0.88 mol L^{-1} [Gentle, 1972].

We found it surprising that all the taste compounds tested were rejected by the cockatiels used in our study. At the time that these studies were initiated, we expected that at least some of the sugars and salts would be preferred by cockatiels. These expectations were based on anecdotes from psittacine owners who commonly report that their birds are attracted to sweet or salty food items. One of our goals in this study was to identify flavors that are appealing to cockatiels and find the levels required for improvement of palatability. These levels of preferred flavors could then be used to improve the acceptability of diets formulated using readily available ingredients that have low palatability. Clearly the experimental protocol used in this study did not yield information on preferred flavors that could be applied to diet formulation. However, we did show that any adulteration of the water supply, even with sugars, decreased consumption. Apparently the introduction of a novel taste to water is repulsive even though the same flavor might improve the palatability of food. These results suggest that water consumption should be monitored closely whenever water is used to deliver flavored compounds, such as drugs, vitamins or other dietary supplements.

CONCLUSIONS

1. The taste threshold of cockatiels to KCl was the same as the previously determined threshold to NaCl (0.16 mol L^{-1}).

2. Taste thresholds to a phosphate buffer (this experiment) and citric acid buffer (previous experiment) of the same concentrations differed with the birds being more sensitive to pH change in the citric acid buffer system.

3. While all sugars were rejected by the cockatiels, different thresholds exist for different sugars. Glucose was rejected at a much lower concentration than fructose (both determined in this experiment) or sucrose (determined in a previous experiment).

4. The one common feature of all tested compounds is that they resulted in decreased consumption of the test solution, increased consumption of pure water, or both. No test compound was preferred by the cockatiels. This observation is contrary to the findings of other studies which, using a variety of birds, have identified preferences for some of the same test compounds used in our experiments.

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