

Flavor Preferences in Cats (*Felis catus* and *Panthera* sp.)

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Four experiments examined flavor preference in cats. In the first experiment domestic cats exhibited no preference (both in 24-hr and 1-hr two-choice preference tests) for any of a variety of carbohydrate or artificial sweeteners regardless of whether a water or saline diluent was employed. A preference for sucrose or lactose dissolved in dilute milk compared with dilute milk alone was observed. This preference may have been based on textural rather than flavor characteristics of the milk-sugar solution. In the second experiment a similar lack of preference for carbohydrate sweeteners was found when using 5-min two-choice preference tests with wild cats (genus *Panthera*). In light of this lack of sweet preference among cats, Experiments 3 and 4 examined responses to solutions of hydrolyzed protein and individual amino acids and to emulsified fat mixtures. Solutions of hydrolyzed soy, lactalbumin, and casein; L-alanine and L-proline solutions; and butterfat mixtures were all preferred to the diluent. It is suggested that a pattern of responses characterized by an avidity for protein and fat products and no avidity for carbohydrate sweeteners may be typical of strict carnivores like cats.

An avidity for a variety of sweetening agents by animals from a relatively limited phylogenetic range has been experimentally demonstrated. These observations have led several investigators to assert that the preference for sweet is ubiq-

uitous (Bartoshuk, Harned, & Parks, 1971; Bartoshuk, Jacobs, Nichols, Hoff, & Ryckman, 1975; Frings, 1951; Pfaffmann, 1964). Many species including *Homo sapiens* show strong preferences for sucrose (e.g., Cagan & Maller, 1974; Desor, Maller, & Turner, 1973). However, there have been reports of several exceptions to this generalization (Kare & Ficken, 1963; Maller & Kare, 1967). The domestic cat was reported not to prefer sucrose or the synthetic sweetener sodium saccharin to water (Carpenter, 1956). Several studies dispute this observation (Bartoshuk et al., 1971; Bartoshuk et al., 1975; Frings, 1951; Wyrwicka & Clemente, 1970). A number of electrophysiological studies of the taste system of the cat indicate that neural fibers sensitive to sucrose are difficult to find. When such fibers are observed, they

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respond only when extremely high concentrations of solutions of sucrose are applied to the tongue (Boudreau, Bradley, Bierer, Kruger, & Tsuchitani, 1971; Cohen, Hagiwara, & Zotterman, 1955; Pfaffmann, 1955).

In view of the conflicting observations concerning the cat's response to sweeteners, we report here a series of studies wherein we examined the behavioral responses of felines to a variety of sweet substances in addition to sucrose and saccharin. Using several testing procedures and both domestic and wild cats, we observed no avidity for sweet carbohydrates or synthetic sweeteners. This unusual response of the cat to sweets prompted us to consider what classes of gustatory stimuli elicit ingestion in this animal. Although there have been a number of comparative studies on flavor preferences, the carnivores as a group have been neglected (Kare & Ficken, 1963). White and Boudreau (1975) recently reported that mixtures of saline and the amino acids *L*-proline, *L*-lysine and *L*-histidine at concentrations of 50 mM are preferred to saline alone. Mugford (1977) reported that the ingestion of solid food could be increased in satiated cats by suffusing the food with odors from meats. Thus, a second series of studies designed to examine the flavor preferences of cats was conducted. Short-term two-choice tests used water soluble compounds, which, a priori, we expected would be important to a carnivore's nutrition.

Experiment 1

To examine the ingestive responses of domestic cats to sweet substances, we compared long-term (24-hr) and short-term (1-hr) preference tests. By using a large sample of animals, several species of felids, and several behavioral testing methods, we hoped to clarify the behavioral responses to sweeteners.

Method

Subjects. Twenty-eight adult cats, ranging in weight from 2.6 to 5.3 kg, were tested: 8 males, 4 of which had been castrated for at least 1 yr, and 20

females, 15 of which had been ovariectomized for at least 1 yr. The animals were divided into four equivalent groups of seven animals each on the basis of body weight and sexual condition (male or female, and intact or castrated). The cats were housed individually in cages measuring .88 × .72 × .72 m. Each cage contained two identical glass bottles with stainless steel (AtCo Mfg. Co.) spouts, which the animals licked to obtain their fluids. The bottles were mounted on the center of the cage door, with the drinking spouts separated from each other by approximately 100 cm. Deionized water was available ad lib. The cats were maintained throughout the testing on a single feeding of a commercial, dry diet, which contained no less than 30% protein and no less than 12% moisture (Purina Cat Chow). The single feeding was given approximately 30 min before testing with fluids or before changing the positions of the bottles (for the second day of the 24-hr tests). This regimen was adopted to ensure sufficient fluid intake at testing and to prevent the excessive weight gain that occurs under ad lib feedings.

Procedure. In the first series, ten 24-hr two-choice taste tests were conducted. For each test each of the four groups of cats was given a choice between a single (different) concentration of a sapid solution (which was alternated from the left to right side every 24 hr) and deionized water for two consecutive days. The bottles were labeled and weighed before and after each 24 hr to the nearest gram. The difference in weight between the initial and final weighing was used as a measure of consumption. After the 24-hr tests were concluded, a second series consisting of 28 one-hr tests was conducted. Here, the same procedures were followed except that only two concentrations and two groups of cats were used in each test.

All solutions were prepared with reagent-grade chemicals. All solutions were refrigerated after preparation; they were allowed to return to room temperature for several hours before presentation. Each test, comprising two consecutive 24-hr presentations of fluids, was followed by at least 1 day during which only deionized water was available in order to reduce the likelihood of carry-over effects of one flavor upon another.

The 24-hr tests were conducted with the following: sucrose, *D*-fructose, *D*-mannose, *D*-glucose, *D*-galactose (.075-.60 M), and sodium and calcium saccharin (1.55-12.4 mM). In addition to the studies with single sweet stimuli, the same concentrations of sucrose or fructose were offered in solutions containing 30 mM of NaCl. In these studies the sugar-NaCl solutions were offered as a choice with 30 mM NaCl. These sugar-saline solutions were tested because Bartoshuk et al. (1971) reported that the cat avidly consumes sucrose in saline solutions of this concentration but does not prefer it when it is dissolved in deionized water.

The responses to *D*-glucose, sucrose, *D*-fructose, maltose (all at .30 and .60 M), lactose (.15 and .30 M), sodium and calcium saccharin, and sodium and calcium cyclamate (.0062 and .0124 M) were examined in 1-hr tests (see Table 1). The carbohydrates

were tested both with a water diluent and with a saline (30 mM) diluent. Finally, the cats were tested with sugar (.5 M sucrose or lactose) solutions, with dilute (20%) milk as a diluent since Frings (1951) and Bartoshuk et al. (1975) reported that this mixture is preferred to plain dilute milk.

Results and Discussion

In none of the 10 long-term tests did the cats demonstrate a preference for any of the sweeteners. They avoided the highest concentrations of saccharin. Figure 1 shows the proportion of sugar solution consumed. Analyses of variance (stimulus \times concentration) of these proportions indicated that no sugar was preferred to water.

In 18 of the 20 one-hr tests with sugars, no significant preference was found (Table 1). In neither of the experiments in which there was a statistically significant preference for sugar in water (glucose and sucrose) over water was this difference evident upon repeating the same experiment. Sodium and calcium saccharin were avoided, whereas cats were indifferent to sodium and calcium cyclamate. At the concentrations used here the responses to nonnutritive sweeteners were similar to those reported by Bartoshuk et al. (1975). These data with short-term tests corroborate the findings for the 24-hr tests: Do-

mestic cats evidence no preference for any of these sweet substances.

Frings' (1951) observation that cats prefer sucrose (.5 M) in dilute milk (1 part whole milk to 4 parts water), but not in water, was evaluated in the final series of experiments with domestic cats and sweeteners. Cats preferred whole milk to dilute milk (Figure 2). They also preferred either .5 M lactose or .5 M sucrose (Figure 2) in dilute milk to dilute milk, the latter as reported by Frings. Thus, in these tests, the animals consistently preferred the mixtures with greater density and higher caloric content.

At isomolar concentrations, sucrose is judged by human adults as tasting sweeter than lactose (e.g., Moskowitz, 1974) and is preferred to lactose by rats, calves, and rhesus monkeys (Kare & Ficken, 1963; Maller, 1973; Richter & Campbell, 1940). When cats were offered a direct choice between solutions of .5 M lactose in dilute milk and .5 M sucrose in dilute milk, however, the mixtures were accepted equally (Figure 2). That is to say, when the mixtures were of equal density and caloric content, there was no preference for either one, even though they differed in sweetness to man and in acceptability to other species.

Thus, we suggest that the preferential

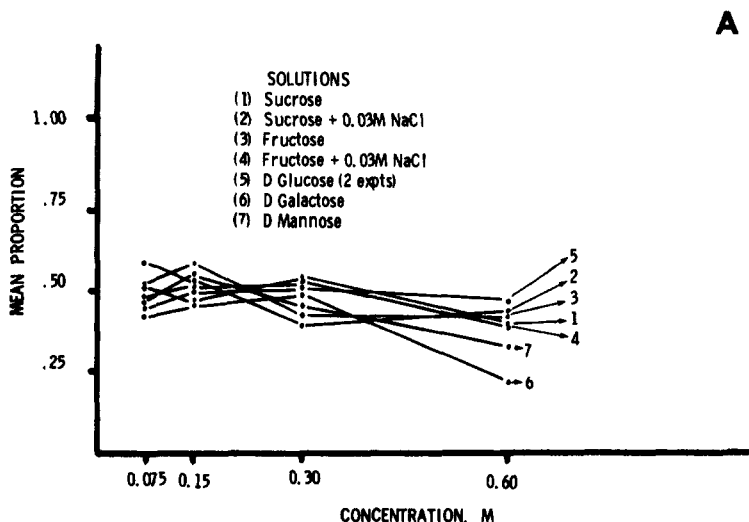


Figure 1. Mean proportion of sugars consumed from the total fluid by domestic cats. (Each point represents data from seven cats for 24-hr tests.)

Table 1
Number of 1-Hr Preference Tests in Which Cats Prefer Sweetener to Diluent or Diluent to Sweetener or Were Indifferent

Substance	Diluent	No. of tests	Preference ^a		
			Sweetener	Diluent	Indifferent
Glucose	H ₂ O	2	1	0	1
	.03 M NaCl	2	0	0	2
Sucrose	H ₂ O	3	1	0	2
	.03 M NaCl	2	0	0	2
Fructose	H ₂ O	3	0	0	3
	.03 M NaCl	2	0	0	2
Lactose	H ₂ O	2	0	0	2
	.03 M NaCl	2	0	0	2
Maltose	H ₂ O	1	0	0	1
	.03 M NaCl	1	0	0	1
Sodium saccharin	H ₂ O	1	0	1	0
Calcium saccharin	H ₂ O	1	0	1	0
Sodium cyclamate	H ₂ O	1	0	0	1
Calcium cyclamate	H ₂ O	1	0	0	1

Note. Concentrations of all sugars except lactose were .30 and .60 M; lactose, .15 and .30 M. Artificial sweeteners were .0062 and .0124 M. Each $n = 7$ at each concentration.

^a Significance level (difference between sweetener and diluent) $p < .05$ by analysis of variance. There were no significant concentration effects or interactions.

ingestion of the dilute milk-sugar mixture compared with dilute milk was more likely made on the basis of sensory cues other than sweetness (e.g., textural qualities associated with the greater density). Further experiments are required, however, to directly test this hypothesis.

Experiment 2

The previous experiments strongly suggest that domestic cats do not preferen-

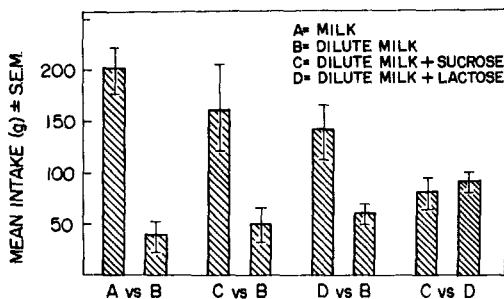


Figure 2. Mean intake of solutions in four 1-hr choice tests. (The $n = 28$ for the first test, 7 for Tests 2 and 3, and 14 for Test 4. A significant preference [$p < .05$, t test] for one solution over the other occurred in Tests 1, 2, and 3. There was no significant preference in Test 4. The term "milk" means whole, homogenized, vitamin D fortified milk as purchased commercially; the term "dilute milk" means 1 part whole milk plus 4 parts deionized water.)

tially ingest sweet carbohydrates. These results are in agreement with the observations of Carpenter (1956). However, our findings are in disagreement with those of Bartoshuk et al. (1971) in that in our experiments the use of 30 mM NaCl as the diluent for sucrose (or for any other sweetener) did not result in an avidity for this mixture. The difference between our findings and those of Bartoshuk et al. could be due to differences in the sample of felids and/or to the different testing procedures employed. To further assess these possibilities, we next tested 12 members in four species of the genus *Panthera* for their responses to sucrose solutions. In these tests, the possibility that post-ingestional factors might play a role was reduced further than it was in the preceding experiments by providing a very brief (5 min) stimulus presentation (Cagan & Maller, 1974).

Method

Subjects. Three lions (*Panthera leo*; 2 female, 1 male), 3 tigers (*P. tigris*; 1 female, 2 male), 3 leopards (*P. pardus*; 2 female, 1 male), and 3 jaguars (*P. onca*; 2 female, 1 male) were used in this experiment. Each animal was housed alone during testing in a cage (approximately 4 × 4 m) at the Philadelphia Zoological Gardens. All subjects were healthy adults and were gonadally intact (except for the male lion).

Procedure. The wild cats were offered brief two-choice tests between sucrose (.3 M or .6 M) and water or sucrose in 30 mM NaCl and 30 mM NaCl. Each of the solutions (approximately 500 ml) to be compared was placed in one of two galvanized iron pans (22.9 × 35.6 × 5.1 cm) with a handle 1-m long (the reason for this is obvious!). The two pans were placed simultaneously (5 cm apart) into the cat's home cage. Each cat was allowed 5 min from the time it took the first lap, to sample the solutions. The number of laps made to each sample was counted. The interobserver agreement on the number of laps was determined to be highly reliable ($r = .89$, $p < .01$). If a cat tasted neither sample within 10 min, the test was stopped and "no sample" was recorded. Each pair of samples (tastant and diluent) was tested on 2 days, with the position of the tastant alternated from day to day.

Results and Discussion

Difference scores (sugar solution minus diluent) were analyzed with a three-factor (sucrose concentration [2] × diluent [2] × species [4]) analysis of variance with repeated measures. Since there were no significant main effects or interactions, the data were collapsed, and a single analysis was conducted for comparison of sucrose and diluent alone. There was no difference between laps elicited by sucrose and laps elicited by the diluent (sucrose: $M = 76.5 \pm 22.5$; diluent: $M = 59.6 \pm 21.0$).

These data, in conjunction with those of the previous experiment, further support Carpenter's (1956) original conclusion that cats do not exhibit an avidity for sucrose solutions. Using testing periods of various lengths (24 hr, 1 hr, and 5 min) and several species of felids, we did not observe a preference for sucrose dissolved in water or in 30 mM NaCl. We thus suggest that the weight of evidence now favors the view that felids do not prefer to ingest substances with a taste described by man as sweet. Since at least some sweet substances are preferred by the vast majority of animals so far examined, the cat stands as a graphic exception to the generalization that sweet substances are preferred substances among mammals.

Experiment 3

If sweeteners do not stimulate ingestion in the cat, what simple substances then

are likely to do so? The sense of taste of strict carnivores has not been extensively evaluated, but it seems likely that substances characteristic of the cats' normal diet would be selected. In the following two experiments, this hypothesis was evaluated by testing ingestive responses to (a) protein mixtures, (b) fat mixture, and (c) amino acid solutions.

Method

Subjects. The subjects were the same sample of domestic cats used in Experiment 1.

Procedure. The 1-hr, two-choice preference test procedure employed in Experiment 1 was used here.

1. Protein mixtures. Cats were offered choices of four concentrations (3.0%, 1.5%, .75%, and .375% w/v) of solutions of casein hydrolysate (enzymatic), lactalbumin hydrolysate (enzymatic), and soy hydrolysate (all purchased from ICN Pharmaceuticals) with deionized water. In a subsequent test, two groups ($n = 14$) of cats were given a direct choice between solutions of 1.5% soy hydrolysate and 1.5% casein hydrolysate.

2. Fat mixtures. Cats were tested next with four concentrations (3%, 1.5%, .75%, and .375% w/v) of two fats. Butterfat and pure corn oil were purchased commercially. To prepare the butterfat emulsion, we melted butter and added 2.5 g of an emulsifier (Tween-80) and then 1 l of water. The mixture was then gently warmed and mixed for 10–15 min. Except for melting, since it was liquid at room temperature, corn oil mixtures were prepared in the same way. The butterfat and corn oil emulsions were offered as choices with deionized water with Tween-80 dissolved in it. Immediately before the mixtures were poured into the test bottles and before the bottles were put up for the 1-hr tests, the fat mixtures were gently agitated. Finally, a 1.5% butterfat mixture was offered as a choice with 1.5% corn oil mixture to two groups ($n = 14$) of cats.

3. Amino acid solutions. Solutions of amino acids—glycine (.02, .04, .08, and .16 M) and L-glutamic acid and L-alanine (.01, .02, .04, and .08 M)—were offered in choices with water. The amino acids were purchased from the Ajinomoto Company.

Results and Discussion

Solutions of casein, lactalbumin, and soy hydrolysate were preferred to water (Figure 3): (flavor vs. water) casein, $F(1, 24) = 13.6$, $p < .01$; lactalbumin, $F(1, 24) = 20.3$, $p < .01$; soy, $F(1, 23) = 11.3$, $p < .01$. (One animal spilled its water and thus its data were eliminated. This occurred several times during these experiments). For casein and lactalbumin, there

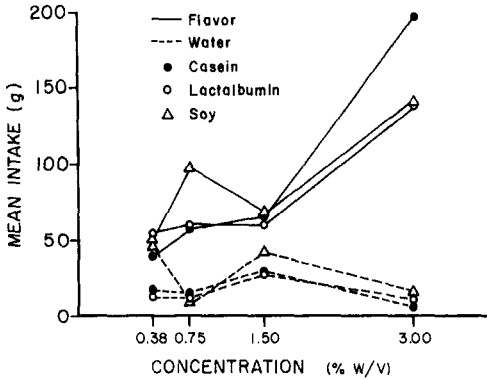


Figure 3. Mean intake of hydrolyzed protein solutions (flavor) and water diluent in two-bottle choice tests with domestic cats. (There were seven animals tested at each concentration.)

were significant concentration effects, $F(3, 74) = 3.8$ and $4.8, p < .05$. An analysis of variance (two-way, with repeated measures) directly comparing responses to all three substances by using difference scores (flavor-water) revealed no significant differences among them. However, when 1.5% solutions of casein hydrolysate and soy hydrolysate were presented to the animals simultaneously in a choice test, they preferred the former (casein: $M = 133.3 \pm 20.5$ g; soy: $M = 55.0 \pm 11.8$ g), related $t(13) = 3.42, p < .01$.

For the fats, both the emulsions of butterfat, $F(1, 24) = 41.0, p < .01$, and of corn oil, $F(1, 23) = 13.0, p < .01$, were preferred to water-Tween-80 solution (Figure 4). For the butterfat there was a significant concentration effect, $F(3, 24) = 3.5, p < .05$, and no interaction. There were no other significant effects with the corn oil. Comparison of the two fats (two-way analysis of variance with repeated measures) by using difference scores indicated that the butterfat was preferred to corn oil, $F(1, 23) = 27.2, p < .01$. Similarly, when the animals were given a direct choice, 1.5% butterfat was preferred to 1.5% corn oil (butterfat: $M = 81.6 \pm 3.4$ g), $t(13) = 2.70, p < .05$.

Finally, tests with amino acids indicated that (Table 2) cats were indifferent to glycine at the concentrations offered and avoided L-glutamic acid. On the first test with L-alanine this amino acid was

preferred to water. When the same test was repeated, the preference for L-alanine was not significant (Table 2). There were no significant concentration effects or interactions in any of these tests.

In summary, these data indicate that domestic cats prefer solutions of protein and fat mixtures to water. The components in these mixtures that stimulate ingestion are not known. The results of Mugford (1977) on the efficacy of odors in stimulating ingestion suggest that substances having olfactory properties may be of greatest importance. However, taste responses to amino acids cannot be discounted.

Our experiments suggest that L-alanine may be preferred to water. Further, White and Boudreau (1975), in experiments reported after the conclusion of these tests, showed that several other amino acids stimulate ingestion when compared with water. Thus, these studies clearly demonstrate that salient components (derived from proteins and fats) of foods naturally eaten by cats stimulate ingestion whereas sweeteners do not.

The portion of this study involving fat preference warrants one further comment. The possibility that the cats were avoiding the water-Tween-80 solutions, rather than preferring the fat, was not eliminated. However, the large volume intake for the 3% concentration and the concentration ef-

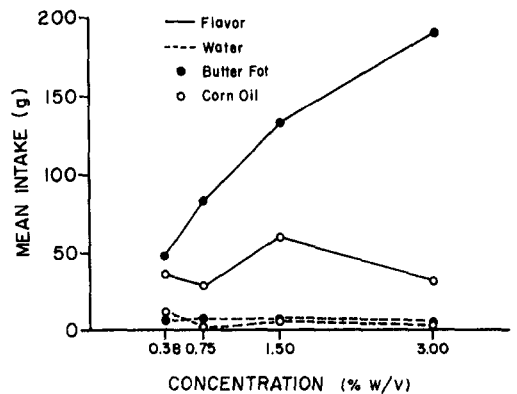


Figure 4. Mean intake of emulsified fat mixtures (flavor) and water-Tween 80 diluent (water) in two-bottle choice tests with domestic cats. (There were seven animals tested at each concentration.)

Table 2
 Mean (\pm SE) Flavor and Water Ingested by All Cats in Four Tests with Amino Acids

Test substance	Consumption (in g)		F	p
	Flavor	Water		
Glycine	37.0 \pm 4.6	38.8 \pm 4.9	1.6	ns
L-Glutamic acid	4.1 \pm .8	29.5 \pm 3.9	55.2	<.01
L-Alanine (1)	51.4 \pm 5.1	29.6 \pm 3.2	13.1	<.01
L-Alanine (2)	43.8 \pm 5.2	30.8 \pm 3.7	3.2	ns

Note. As there were no concentration effects, concentrations are collapsed, and means represent average data over all four concentrations. The $N = 28$. The F values are for flavor versus diluent from two-factor analysis of variance with repeated measures; $df = 1, 24$.

fects strongly indicate that aversion to the Tween-80 cannot explain the butterfat results. Further work on vegetable fat is indicated.

Both the individual tests and the direct comparison clearly demonstrate that fat from an animal source is preferred to that from vegetable sources. For protein sources, only the direct comparison indicated a significant preference for substances derived from the animal source. Taken together, these data suggest that animal-derived substances are more potent ingestive stimuli than are substances of a similar class derived from plant sources.

Experiment 4

In an effort to extend the observations reported in Experiment 3, we conducted a final study with the wild cats. Using the brief 5-min tests, we examined responses to solutions of protein products.

Method

Subjects. The same 12 wild cats used in Experiment 2 were the subjects.

Procedure. The 5-min choice test described in Experiment 2 was used again. These animals were tested with solutions of 3% casein hydrolysate, 3% soy hydrolysate, and .05 M proline.

Results and Discussion

Two-factor repeated-measures analyses of variance (four species and two flavors) were conducted for each flavor. Since there were only three subjects/species (and only two for one species for each substance tested since one animal failed to sample

the substances on both days), the practical significance of species differences is very questionable. Thus, we concentrate on flavor differences and restrict any generalizations to the genus *Panthera*.

Casein (3%) was preferred to water (179 laps vs. 10 laps), $F(3, 7) = 20.59$, $p < .01$, as was 3% soy (57 laps vs. 16 laps), $F(3, 7) = 10.76$, $p < .05$. When difference scores (flavor-water) for casein and soy were compared, casein was preferred to soy, $F(3, 7) = 9.85$, $p < .05$. Finally, proline also was preferred to water (39 laps vs. 13 laps), $F(3, 7) = 19.83$, $p < .01$.

These data show that in brief tests, protein products are preferred by members of the genus *Panthera*. For casein hydrolysate and soy hydrolysate, the responses of these wild cats were similar to the domestic animals in that the animal-derived substance was preferred to that from the vegetable source. Our tests with a single amino acid, proline, were conducted because White and Boudreau (1975) had reported that this amino acid was the most potent one tested at stimulating ingestion in domestic cats. Our data, from the brief-exposure method with a water rather than a saline diluent, indicate that proline is also a preferred amino acid among wild cats, which thus extends the White and Boudreau observation.

General Discussion

The data presented here provide the strongest evidence available to support the conclusion that felines do not have an avidity for carbohydrate sweeteners and thus constitute a major exception to the ubiquity of this preference among mam-

mals. Although our results are consonant with most electrophysiological studies and support the conclusions of Carpenter (1956), they are in disagreement with those of Bartoshuk et al. (1971) concerning the ability of a 30 mM saline diluent to induce a preference for sucrose. Several possible explanations for the differences between the work of Bartoshuk et al. (1971) and our studies can be eliminated. First, since we used a large number of domestic cats as well as wild cats, it seems unlikely that our samples were aberrant. Second, we conducted many tests with a variety of sweetening agents and found no evidence for the efficacy of the 30 mM saline diluent, thus eliminating the possibility that our data were produced by restricted testing. Third, use of three testing paradigms (24 hr, 1 hr, and 5 min) reduces the likelihood that our testing procedures would miss a dramatic result such as that described by Bartoshuk et al. (1971). Finally, the possibility that the lack of preferences may be due to conditioned aversions is unlikely. Intake of large amounts of sucrose (and other sugars) has been reported to make cats sick (e.g., Carpenter, 1956). However, the sugars in dilute milk experiments, in which there was a significant preference for the sugar-milk mixture compared with diluted milk alone, were done after all other testing. If conditioned aversions had been formed and the response was to the sweetness of the dilute milk-sucrose solutions, one would have expected an avoidance of the mixture instead of the preference we observed. Further, if conditioned taste aversions were formed, one would expect the solutions of sugar in saline to be avoided; instead, cats ingested them indifferently compared with diluent.

A remaining methodological difference between our testing procedures and those of Bartoshuk et al. (1971) was that for each experiment with each sweetener tested, we used only one group of animals at each concentration. Bartoshuk et al., however, repeatedly tested the same nine cats with increasing concentrations, first, of sucrose versus water and, second, with sucrose-saline solutions versus saline. For

each concentration of sugar tested by these investigators, cats were allowed access for 6 hr each day for four consecutive days. Rest days separated testing at each concentration. Although it is not readily apparent how this discrepancy could account for our different results, perhaps some form of sensitization resulted from the repeated testing paradigm with step-wise increasing concentrations. A related hypothesis, that neophobic responses to carbohydrates by cats in our experiments could explain the differences, is unlikely, since this would predict that the sweeteners would be rejected, compared with the diluent, rather than ingested indifferently, as we found to be the case. Although we cannot reject the possibility that methodological differences could explain our differential findings, we conclude that our more extensive tests strongly indicate that the saline diluent is not *generally* effective at inducing cats to exhibit preferences for carbohydrates.

The concentrations of sweeteners used in this study were well within the range that elicits preferential ingestion in most mammalian species previously studied (e.g., Cagan & Maller, 1974; Carpenter, 1956; Desor, Maller, & Turner, 1973; Kare & Ficken, 1963; Maller, 1973; Richter & Campbell, 1940). On the basis of the failure of these cats to exhibit a preference for or a rejection of the carbohydrate sweeteners, we have no direct evidence that the cats could distinguish between the tastant and the diluent. For a more definitive answer to the question of whether the cats could *detect* (as distinguished from *prefer*) the taste of the sugar solutions compared with the diluent, a further series of studies with a conditioning paradigm controlling for viscosity is required.

One question that remains unanswered is the nature of the sensory stimuli that results in a preferential intake of .5 M sucrose or .5 M lactose in dilute milk compared with dilute milk alone. We suggest that some correlate of differential density, rather than differences in sweet taste, accounts for this response. One possibility is that the animals prefer a more

viscous solution. Direct tests of this hypotheses, with various thickening agents, are required, however, before it can be accepted.

Although sweet carbohydrates and synthetic sweeteners do not stimulate ingestion, substances associated with the carnivorous cat's natural foods do. Domestic cats have a relatively high dietary requirement for protein (Scott, 1957), and this requirement is complemented by the demonstrated preference for solutions of hydrolyzed proteins and individual amino acids. Our data, especially those involving wild cats when tests were only 5 min long, strongly suggest that the preferential intake is based on sensory rather than post-ingestional cues.

Which sensory system(s) is involved has not been determined. Mugford (1977) showed that meat odors are sufficient to stimulate ingestion. The protein solutions had definite odors to humans, and the animals (especially the *Panthera*) often sniffed these solutions before taking them into their mouths. Thus it seems likely that olfaction plays at least some role in the sampling and/or acceptance of the solutions. For the pure amino acids, the role of olfaction is less clear. White and Boudreau (1975) stated that the amino acids they used were odorless to them, which suggests taste played the major sensory role. However, human inability to smell a substance does not prove that the animal also lacks that ability.

Supporting the possible role of taste in guiding ingestion of amino acid and perhaps of hydrolyzed protein solutions is the work of Boudreau (1974). He demonstrated that amino acids are sufficient to stimulate taste fibers. Further, White and Boudreau found that they could predict, on the basis of electrophysiological activity in the taste system, which amino acids would be preferred. It may very well be that both olfaction and taste play a role in controlling ingestion. Further experiments with cats having specific olfactory impairments are required to resolve this question.

In conclusion, we found that hydrolyzed protein, emulsified fats, and amino acid

solutions strongly stimulate ingestion but carbohydrates do not. That these ingestive responses are based mainly on sensory cues is evident from the brief exposure (5 min for *Panthera*) of the preference tests. Since felidae are strict carnivores (Ewer, 1973), this pattern of sensory response to food substances is not unexpected. The ontogeny of this flavor preference pattern and the extent to which it can be influenced by previous intake experience remain to be investigated. In addition, only through further studies with other strict carnivorous species (e.g., mink, sea lions, carnivorous fish, and insects) will we be able to determine the extent to which this lack of responsiveness to carbohydrates, coupled with a strong response to animal-product substances, is the common pattern.

References

- Bartoshuk, L. M., Harned, M. A., & Parks, L. H. Taste of water in the cat: Effects on sucrose preference. *Science*, 1971, 171, 699-701.
- Bartoshuk, L. M., Jacobs, H. L., Nichols, T. L., Hoff, L. A., & Ryckman, J. J. Taste rejection of nonnutritive sweeteners. *Journal of Comparative and Physiological Psychology*, 1975, 89, 971-975.
- Boudreau, J. C. Neural coding in cat geniculate ganglion tongue units. *Chemical Senses and Flavor*, 1974, 1, 41-51.
- Boudreau, J. C., Bradley, B. E., Bierer, P. R., Kruger, S., & Tsuchitani, C. Single unit recordings from the geniculate ganglion of the facial nerve of the cat. *Experimental Brain Research*, 1971, 13, 461-488.
- Cagan, R. H., & Maller, O. Taste of sugars: Brief exposure single-stimulus method. *Journal of Comparative and Physiological Psychology*, 1974, 87, 47-55.
- Carpenter, J. A. Species differences in taste preferences. *Journal of Comparative and Physiological Psychology*, 1956, 49, 139-144.
- Cohen, M. J., Hagiwara, S., & Zotterman, Y. The response spectrum of taste fibres in the cat: A single fibre analysis. *Acta Physiologica Scandinavica*, 1955, 33, 316-332.
- Desor, J. A., Maller, O., & Turner, R. E. Taste in acceptance of sugars in human infants. *Journal of Comparative and Physiological Psychology*, 1973, 84, 496-501.
- Ewer, R. F. *The carnivores*. Ithaca, N. Y.: Cornell University Press, 1973.
- Frings, H. Sweet taste in the cat and the taste-spectrum. *Experientia*, 1951, 7, 424-426.
- Kare, M. R., & Ficken, M. S. Comparative studies on the sense of taste. In Y. Zotterman (Ed.),

- Olfaction and taste*. Oxford: Pergamon Press, 1963.
- Maller, O. Quality and intensity of sugar solutions as determinants of ingestion by the rhesus monkey (*Macaca mulatta*). *Folia Primatologica*, 1973, 20, 72-77.
- Maller, O., & Kare, M. R. Observations on the sense of taste in the armadillo (*Dasypus novemcinctus*). *Animal Behaviour*, 1967, 15, 8-10.
- Moskowitz, H. The psychology of sweetness. In H. Sipple & K. McNutt (Eds.), *Sugars in nutrition*. New York: Academic Press, 1974.
- Mugford, R. A. External influences upon the feeding of carnivores. In M. K. Kare & O. Maller (Eds.), *The chemical senses in nutrition II*. New York: Academic Press, 1977.
- Pfaffmann, C. Gustatory nerve impulses in rat, cat and rabbit. *Journal of Neurophysiology*, 1955, 18, 429-440.
- Pfaffmann, C. Taste, its sensory and motivating properties. *American Scientist*, 1964, 52, 187-206.
- Richter, C. P., & Campbell, K. H. Taste thresholds and taste preferences of rats for five common sugars. *Journal of Nutrition*, 1940, 20, 31-46.
- Scott, P. P. Problems encountered in studying the nutrition of the cat. *Proceedings of the Nutrition Society*, 1957, 16, 77-83.
- White, T. D., & Boudreau, J. C. Taste preferences of the cat for neurophysiologically active compounds. *Physiological Psychology* 1975, 3, 405-410.
- Wyrwicka, W., & Clemente, C. D. Effect of electrical stimulation in VPM on saccharin preference and water intake in cats. *Experientia*, 1970, 26, 617-619.

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