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Gustatory Responsiveness of Black-and-White Ruffed Lemurs (*Varecia variegata variegata*) to Food-Associated Sugars

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Abstract Nonhuman primates differ widely in various aspects of their ecology and are thus particularly suitable for studying the mechanisms underlying interspecies differences in taste perception. Therefore, we assessed taste preference thresholds as well as relative preferences for five food-associated sugars in three adult black-and-white ruffed lemurs (*Varecia variegata variegata*) using two-bottle choice tests of brief duration (1 min). We found that the subjects significantly preferred concentrations as low as 25 mM sucrose and fructose, and 50 mM glucose, maltose, and lactose over tap water. When given a choice between all binary combinations of the same five saccharides presented at equimolar concentrations of 50, 100, and 200 mM, respectively, the subjects displayed marked preferences for individual sugars in the following order: sucrose > fructose > glucose ≥ maltose ≥ lactose. The sensitivity of the black-and-white ruffed lemurs to the five saccharides falls into the same range as that reported in other primates. The pattern of relative preferences for food-associated sugars was found to be largely similar to that reported in platyrrhine primates and in human subjects, but differed from that reported in a catarrhine primate. Taken together, the results of the present study support the notions that the taste sensitivity in primates for food-associated sugars may correlate with phylogenetic relatedness, with body mass, and with lactose content in milk. Further, the results support the notion that relative preferences for food-associated sugars in primates, but not necessarily their sweet-taste sensitivity, may correlate with dietary specialization.

Keywords Black-and-white ruffed lemurs · Food-associated sugars · Gustatory responsiveness · Relative sweetness · Taste preference thresholds · *Varecia variegata*

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Introduction

Both genetic and psychophysical studies on the sense of taste in primates reported marked differences among species, both in the ability to perceive a given taste substance and in threshold concentrations with a given taste substance (Glaser 1986; Laska *et al.* 2001; Li *et al.* 2011; Liman 2006; Simmen and Hladik 1998). Several hypotheses have been proposed to explain the observed interspecies differences, for example, in the perception of and sensitivity for taste substances described as sweet by humans: phylogenetic relatedness has been found to account for the ability, or inability, of primates to perceive certain sweet-tasting substances (Glaser *et al.* 1995; Nofre *et al.* 1996); the degree of frugivory has been found to correlate positively with taste sensitivity for food-associated sugars in platyrrhine primates (Laska *et al.* 1996); and body mass has been found to correlate negatively with taste thresholds for sucrose and fructose when strepsirrhines, platyrrhines, and catarrhines are considered together (Simmen and Hladik 1998). However, all of these hypothetical explanations, which are not mutually exclusive, are based on a rather limited set of data and therefore it is clearly important to include more primate species to corroborate or reject them.

The black-and-white ruffed lemur (*Varecia variegata variegata*) is commonly considered as the most frugivorous of all Malagasy lemurs (Britt 2000; Junge *et al.* 2009; Ratsimbazafy 2006). At the same time, it is the largest of all extant members of the family Lemuridae, with an average body mass of 3.5 kg in both males and females (Smith and Jungers 1997). So far, the black-and-white ruffed lemur has been assessed for taste responsiveness only to artificial sweeteners such as monellin, thaumatin, aspartame, alitame, cyanosuosan, magapame, sucrononate, and cyclamate (Glaser *et al.* 1978, 1992, 1995; Nofre *et al.* 1996), but not to naturally occurring food-associated carbohydrates. Fruits, the main food of black-and-white ruffed lemurs (Ratsimbazafy 2006; Schmidt *et al.* 2010), contain a variety of soluble carbohydrates (Kinghorn and Soejarto 1986) although sucrose and its monosaccharide components fructose and glucose are usually quantitatively predominant and may account for >90% of total sugar content (Nagy and Shaw 1980). Milk, as the first diet in the life of mammals, contains considerable amounts of lactose, ranging from 6 to 9 g/100 ml in primates (Hinde and Milligan 2011). Maltose is only rarely present in plant material in free form but originates in considerable amounts from enzymatic degradation of starch during mastication and thus contributes to the taste sensation while an individual is feeding on starch-containing plants (Beck and Ziegler 1989).

It was therefore the aim of the present study to assess the taste responsiveness of black-and-white ruffed lemurs to these five food-associated sugars. More specifically, we 1) determined taste preference thresholds for sucrose, fructose, glucose, maltose, and lactose in *Varecia variegata variegata*; and 2) assessed relative preferences of black-and-white ruffed lemurs for these five saccharides when presented at equimolar concentrations. To this end, we employed a two-bottle preference test of short duration (Richter and Campbell 1940). This method allows a researcher to measure directly absolute and relative preferences for different taste substances and largely rules out the influence of postingestive factors on the individuals' ingestive behavior.

Methods

Subjects

We determined taste preference thresholds for and assessed the relative sweetness of five saccharides in three adult male black-and-white ruffed lemurs (*Varecia variegata variegata*). The individuals were 12, 13, and 18 yr old at the start of the study. This all-male and captive-bred group was housed at Kolmården Wildlife Park, Sweden, in a 205 m^3 indoor exhibit with access to a 160 m^2 outdoor island with natural vegetation. We performed the tests in a smaller room adjacent to the indoor exhibit, with two entrances connecting the two rooms. The smaller holding room held three compartments in which the subjects were tested separately to avoid competition and distraction. All three individuals were trained to enter the test compartments voluntarily and were completely accustomed to the procedure followed. The lemurs were fed fresh fruits and vegetables, e.g. apples, bananas, grapes, melons, mangoes, figs, tomatoes, cucumber, carrots, broccoli, avocado, with seasonal variations, once per day at approximately 08:00 h. Commercial primate chow pellets (Trio Munch for Old World and New World primates, Dietex International Ltd., Witham, UK) and water were provided *ad libitum*. The amount of fresh food offered daily to the subjects was such that leftovers were still present on the floor the next morning. Thus, it was unlikely that ravenous appetite affected the lemurs' ingestive behavior.

Taste Stimuli

We used the following five saccharides: sucrose (CAS# 57-50-1), fructose (CAS# 57-48-7), glucose (CAS# 50-99-7), maltose (CAS# 6363-53-7), and lactose (CAS# 63-42-3). All substances were obtained from Sigma-Aldrich (St. Louis, MO) and were of the highest available purity (≥99.5%).

Procedure

We used a two-bottle preference test of short duration (Richter and Campbell 1940). The lemurs were allowed to drink for 1 min from a pair of simultaneously presented graduated cylinders of 100 ml with metal drinking spouts. We performed four such 1-min trials per day and subject, two of them in the morning (*ca.* 1 h before feeding) and two in the afternoon (*ca.* 7 h after feeding).

Determination of Taste Preference Thresholds

To determine taste preference thresholds, the lemurs were given the choice between tap water and defined concentrations of a saccharide dissolved in tap water. With all five saccharides, testing started at a concentration of 200 mM and proceeded in the following steps (100, 50, 20, 10 mM, etc.) until an individual failed to show a significant preference. To maintain the lemurs' motivation and willingness to cooperate, testing of the different concentrations did not follow a strict order but was pseudo-randomized. This was true both within a given session (morning or afternoon) or between sessions. The order in which the five saccharides were tested was the same

for all three individuals: (1) sucrose, (2) fructose, (3) glucose, (4) maltose, and (5) lactose.

Assessment of Relative Sweetness

To assess the relative sweetness of the five saccharides, the lemurs were given the choice between two saccharide solutions presented at equimolar concentrations. All 10 possible binary stimulus combinations were tested. To assess whether relative preferences were stable at different concentrations, three series of tests were performed at 50, 100, and 200 mM, respectively. Here, too, testing of the different stimulus combinations did not follow a strict order but was pseudo-randomized.

In both experiments, we presented each pair of stimuli 10 times per individual, and the position of the stimuli was pseudo-randomized to counterbalance possible position preferences. Care was taken that an individual sampled both stimuli at least once during each trial.

Data Analysis

For each individual, we recorded the amount of liquid consumed from each bottle, summed it for the 10 trials with a given stimulus combination, converted it to percentages (relative to the total amount of liquid consumed from both bottles), and took 66.7% (i.e., two thirds of the total amount of liquid consumed) as the criterion of preference. We chose this rather conservative criterion for reasons of comparability of data, as the same criterion had been used in previous studies on sweet-taste responsiveness with other primate species (Laska 1996, 1997, 2000; Laska *et al.* 1996, 1998, 1999), and to avoid misinterpretation due to a too liberal criterion. In addition, we performed binomial tests and regarded an individual as significantly preferring one of the two stimuli if it reached the criterion of 66.7% and consumed more from the bottle containing the preferred stimulus in at least 8 out of 10 trials (binomial test, $P < 0.05$).

Thus, we defined taste preference threshold as the lowest concentration at which the subjects met both aforementioned criteria. Preliminary analyses of the data indicated that there were no systematic differences in choice behavior and liquid consumption between the first and the second presentation of a session, or between the morning and the afternoon session, respectively. Intraindividual variability of the amount of liquid consumed across the 10 trials with a given stimulus combination was low and averaged <20%. Thus, a theoretically possible bias in the overall preference score due to excessive drinking in aberrant trials did not occur.

We performed comparisons of published data on taste performance between primate taxa using the Mann–Whitney *U*-test for independent samples. We performed correlational analyses using the Spearman rank-correlation test. All data are reported as mean values ± SD.

Ethical Note

The experiments reported here complied with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health Publication no. 86-23, revised 1996) and also with current Swedish laws.

Results

Taste Preference Thresholds

Taste preference thresholds of the three black-and-white ruffed lemurs were found to be 25 mM for sucrose and fructose and 50 mM for glucose, maltose, and lactose, respectively (Fig. 1). All subjects failed to show a significant preference for the lowest concentrations presented, suggesting that the preference for higher concentrations was indeed based on the chemical nature of the stimuli. In most cases, interindividual variability of scores was low for both sub- and suprathreshold concentrations tested (see Fig. 1) and with only few exceptions all three individuals either reached the criterion of preference (>66.7% of total consumption, plus binomial test, $P < 0.05$) with a given stimulus combination or all three failed to do so.

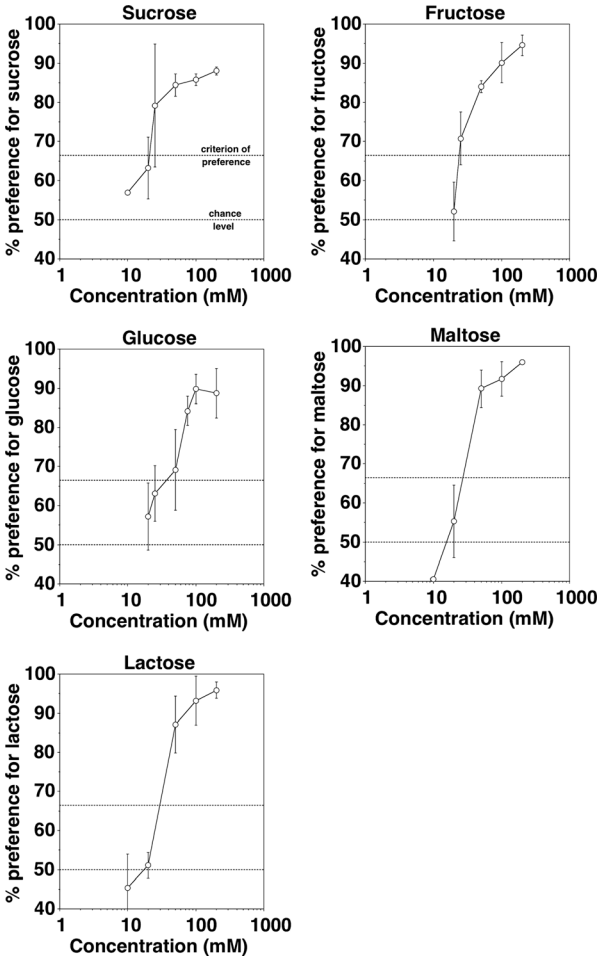

Fig. 1 Mean taste responses (± SD) of three black-and-white ruffed lemurs to aqueous solutions of sucrose, fructose, glucose, maltose, and lactose tested against tap water. Each data point represents the mean value of 10 trials of 1 min per individual. The dotted horizontal lines at 66.7% and at 50% indicate the criterion of preference and the chance level, respectively.

Relative Sweetness

When given the choice between two aqueous saccharide solutions presented at equimolar concentrations of 50, 100, and 200 mM, respectively, the black-and-white ruffed lemurs significantly preferred sucrose over all other saccharides and fructose over glucose, maltose, and lactose (Fig. 2). Further, at the two highest concentrations tested (100 mM and 200 mM) the lemurs significantly preferred glucose over lactose and maltose over lactose. Interindividual variability was remarkably low, as can be inferred from the small SDs and with only one exception (maltose vs. lactose at 50 mM) all three individuals either reached the criterion of preference (>66.7% of total consumption, plus binomial test, $P < 0.05$) with a given stimulus combination or all three failed to do so.

Discussion

The results of the present study can be regarded as a first and preliminary approximation of the gustatory responsiveness of the black-and-white ruffed lemur to the food-associated sugars tested. The concentrations of sucrose, fructose, and glucose present in the majority of ripe tropical fruits in general (Nagy and Shaw 1980) as well as of Malagasy fruits consumed by lemurs (Curtis 2004; Schmidt *et al.* 2010; Yamashita 2008) have been found to be considerably higher than the taste preference thresholds determined here and thus they should contribute substantially to the taste sensation in black-and-white ruffed lemurs while feeding on fruits. Hinde and Milligan (2011) reported the lactose content of the milk of black-and-white ruffed lemurs to be 7.7 g/100 ml, corresponding to a concentration of 225 mM, which according to the findings of the present study is also well above the preference threshold of 50 mM and thus readily perceptible for black-and-white ruffed lemurs. The sensitivity of the black-and-white ruffed lemur for maltose found here suggests that this carbohydrate is also very likely to add to the taste sensation while feeding on starch-containing plants.

The taste sensitivity of *Varecia variegata* for all five saccharides tested here falls into the range reported in other nonhuman primates tested with the same or a similar method (two-bottle preference tests of short duration) and with detection threshold values

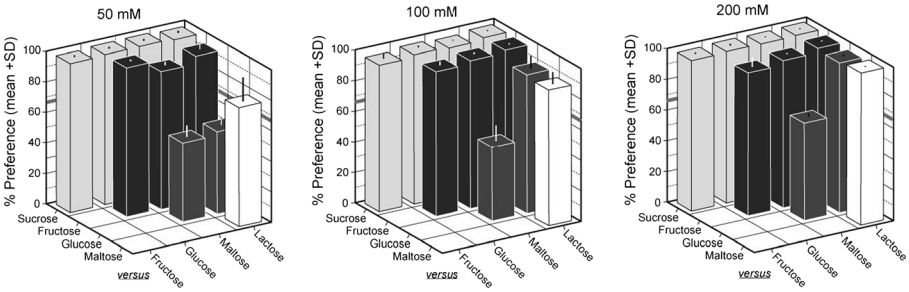

Fig. 2 Relative taste preferences of three black-and-white ruffed lemurs when given the choice between two aqueous saccharide solutions presented at equimolar concentrations of 50, 100, and 200 mM, respectively. Each bar represents the mean preference (± SD) from 10 trials of 1 min per individual for the saccharide on the left side. The horizontal line at 66.7% indicates the criterion of preference.

obtained in humans, using signal detection procedures (Table I). However, the pattern of sweet-taste sensitivity displayed by the black-and-white ruffed lemur is rather unusual: whereas most primate species tested so far are more sensitive to sucrose than to fructose, *Varecia variegata* was equally sensitive with both saccharides. Similarly, the black-and-white ruffed lemur was equally sensitive with glucose, maltose, and lactose whereas most other primate species tested so far differ in their threshold values with these saccharides. In agreement with most other primates, however, the black-and-white ruffed lemur was more sensitive to sucrose and fructose compared to the other three saccharides (see Table I). *Varecia variegata* displayed lower threshold values, that is, a higher sensitivity for fructose, glucose, and lactose compared to human subjects. This is remarkable considering that the sophisticated psychophysical signal detection procedures employed with human subjects are considered to be more sensitive and thus yield lower threshold values than the simple two-bottle preference test used with nonhuman primates (Spector 2003).

Relationship with Phylogenetic Relatedness

Previous studies have shown that only catarrhine primates, but not strepsirrhine and platyrrhine primates are able to detect the artificial sweeteners aspartame and cyclamate (Glaser *et al.* 1995; Nofre *et al.* 1996). In contrast, the sweet-tasting dipeptide derivatives L-aspartyl-(*R*)-α-methylphenethylamine and L-aspartyl-L-(*O-tert*-butyl)serine methyl ester have been reported to be detectable only for strespirrhines and catarrhines, but not for platyrrhines (Glaser *et al.* 1996). These differences in the ability, or inability, to perceive certain sweet-tasting substances between primate taxa are thought to be based on adaptive changes in the recognition sites of the sweet-taste receptor during primate evolution, which, in turn, may be the result of adaptive changes in diet (Liman 2006). With regard to differences between major primate taxa in sensitivity for sweet-tasting substances we found that strepsirrhines (including the black-and-white ruffed lemur tested here) are significantly less sensitive for sucrose compared to catarrhines (Mann–Whitney *U*-test, $Z = -2.77$, $P = 0.0056$) but as not less sensitive than platyrrhines (Mann–Whitney *U*-test, $Z = -1.70$, $P = 0.0883$). Within the strepsirrhine, members of the family Lemuridae (including the black-and-white ruffed lemur tested here) are significantly more sensitive for sucrose compared to members of other strepsirrhine families (Mann–Whitney *U*-test, $Z = -2.20$, $P = 0.0276$). These findings support the notion that phylogentic relatedness may not only account for the ability, or inability, of primates to perceive certain sweet-tasting substances, but may also correlate with taste sensitivity for food-associated sugars.

Correlation with Degree of Frugivory

Several lines of evidence support the hypothesis that a species' dietary specialization affects its taste perception. Recent genetic studies, for example, have shown that carnivorous mammals such as cats lost the ability to detect sweet-tasting substances due to pseudogenization of the *Tas1r2* gene which codes for one of the two proteins that form the mammalian sweet-taste receptor (Jiang *et al.* 2012). Psychophysical studies have shown that the degree of frugivory correlates positively with taste sensitivity for food-associated sugars in

Table I Taste preference thresholds (in mM) for food-associated sugars in primates

Species	Sucrose	Fructose	Glucose	Maltose	Lactose	Reference
Strepsirrhine primates						
Varecia variegata variegata	**25**	**25**	**50**	**50**	**50**	1
Eulemur coronatus		21				2
Eulemur fulvus	9	22.5				2
Eulemur macaco	8	14				2
Eulemur mongoz	125	110				3
Hapalemur simus	17.5	18.5				2
Hapalemur griseus		16.5				2
Phaner furcifer	65					2
Microcebus murinus	167	47.5				3, 4
Microcebus coquereli	90					2
Cheirogaleus major	50					2
Cheirogaleus medius	143					3
Propithecus verreauxi	52.5					2
Loris tardigradus	50					3
Nycticebus coucang	330					3
Galago senegalensis	66					3
Platyrrhine primates						
Ateles geoffroyi	3	15	20	20	10	5
Saimiri sciureus	10	40	90	90	100	6
Saguinus midas niger	66	66	330		250	3
Saguinus fuscicollis	50					3
Saguinus oedipus	125	16				2, 3
Cebuella pygmaea	33	50	100		125	3
Callithrix jacchus	25	29.5				3, 7
Callithrix geoffroyi		41				2
Callithrix argentata		19.5				2
Leontopithecus rosalia		19.5				2
Leontopithecus chrysomelas		21.5				2
Callimico goeldii		31				2
Cebus apella	8					2
Aotus trivirgatus	17					3
Catarrhine primates						
Macaca nemestrina	10	20	20	10	30	8
Macaca mulatta	6					3
Macaca radiata	10			10		9
Papio hamadryas anubis	10	20	25	20	20	10
Cercopithecus pygerythrus	11					3
Cercopithecus nictitans	11					3
Pongo pygmaeus		15				11
Pan troglodytes		45				11

Table I (continued)

Species	Sucrose	Fructose	Glucose	Maltose	Lactose	Reference
Gorilla gorilla		75				11
Homo sapiens	10	40	80	31	72	12

[1] Present study; [2] Simmen and Hladik (1998); [3] Glaser (1986); [4] Simmen *et al.* (1999); [5] Laska *et al.* (1996); [6] Laska (1996); [7] Simmen (1994); [8] Laska (2000); [9] Sunderland and Sclafani (1988); [10] Laska *et al.* (1999); [11] Simmen and Charlot (2003); [12] van Gemert (2011).

platyrrhine primates (Laska *et al.* 1996). Whereas qualitative data on the diet of strepsirrhine primates are abundant, quantitative data that would allow for correlational analyses with sweet-taste sensitivity are, unfortunately, sparse in this taxon. Among the strepsirrhines for which taste threshold data are available (see Table I), quantitative data on their degree of frugivory are available only for four species: Britt (2000) and Hladik (1979) reported that the diet of *Varecia variegata* (the species studied here), *Propithecus verreauxi*, *Eulemur fulvus*, and *Galago senegalensis* comprises 92%, 65%, 34%, and 19% of fruit, respectively. These data on the degree of frugivory do not correlate significantly with the sucrose sensitivity reported in these species (Spearman, $r_s = -0.40$, $P = 0.4884$). This finding does not support the notion that the degree of frugivory correlates with sweet-taste sensitivity in strepsirrhines. However, more species need to be included into such analyses to draw valid conclusions as to a possible correlation between dietary specialization and sweet-taste sensitivity in strepsirrhines.

Correlation with Body Mass

It is well established that body mass in primates positively correlates with basal metabolic rate, which in turn reflects an animal's energy requirements (Smith and Jungers 1997; White and Seymour 2003). As the sense of taste is critical for primates to meet their metabolic needs, taste sensitivity for energy-rich soluble carbohydrates might therefore correlate with body mass. Body mass correlates negatively with taste thresholds for sucrose and fructose when data from strepsirrhines, platyrrhines, and catarrhines are considered (Simmen and Hladik 1998). The results of the present study corroborate this finding and extend it to strepsirrhines considered separately: Figure 3 illustrates that taste preference thresholds for sucrose and fructose in strepsirrhine primates (including those of *Varecia variegata*, the species studied here) correlate negatively with body mass. In the case of sucrose, this correlation is statistically significant (Spearman, $r_s = -0.56$, $P = 0.0431$), in the case of fructose it is not (Spearman, $r_s = -0.26$, $P = 0.4884$), perhaps due to the limited number of species for which fructose thresholds are available. However, with both food-associated sugars the values for the black-and-white ruffed lemur fit closely to the regression line (see Fig. 3). Thus, the findings of the present study support the notion that body mass may correlate with sweet-taste sensitivity in strepsirrhine primates.

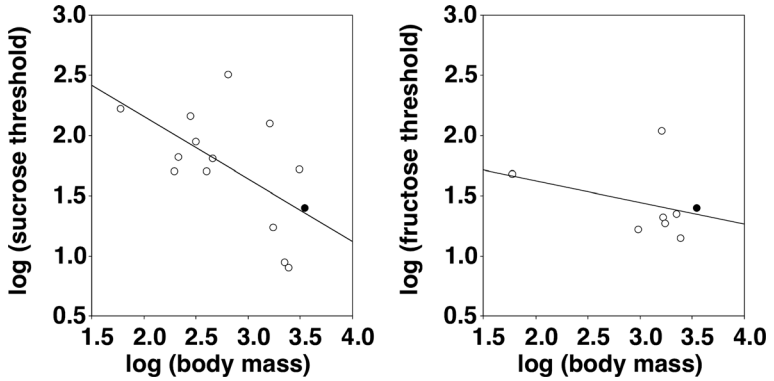

Fig. 3 Taste preference thresholds for sucrose (left) and fructose (right) in strepsirrhine primates as a function of body mass. Each data point represents the value for a given species, and the black data points represent the values for *Varecia variegata variegata*. The solid lines indicate the regression with the best goodness-of-fit according to linear regression analysis (sucrose: $R^2 = 0.35$, equation for line of best fit: $y = 3.19 - 0.52x$; fructose: $R^2 = 0.12$, equation for line of best fit: $y = 1.99 - 0.18x$). Body mass values taken from Smith and Jungers (1997).

Correlation with Lactose Content in Milk

The evolutionary origin of the preference that primates and many other, but not all, mammals display toward sweet-tasting substances remains controversial. One hypothesis to explain the widespread preference for food-associated sugars among mammals states that it arises from an animal's experience with the sweet taste of lactose in milk, the first diet in the life of every mammal (Ramirez 1990). If that was the case, then one might expect that sweet-taste sensitivity should correlate with lactose content in milk. Strepsirrhine primates indeed display a strong negative correlation between taste preference thresholds for sucrose and the lactose content of their milk (Spearman, $r_s = -0.84$, $P = 0.0601$). This correlation is not statistically significant, probably owing to the limited number of species for which both measures are available.

As taste preference threshold values for lactose in strepsirrhines have so far been determined only in *Varecia variegata*, we use threshold values for sucrose as a proxy of sweet-taste sensitivity. Thus, the findings of the present study support the notion that lactose content in milk may correlate with sweet-taste sensitivity in strepsirrhine primates.

Relative Sweetness

Psychophysical studies have shown that sucrose, fructose, glucose, maltose, and lactose are qualitatively indiscriminable for humans when their relative concentrations are suitably adjusted (Breslin *et al.* 1996). Similarly, electrophysiological studies in nonhuman primates have shown that these five food-associated sugars elicit indiscriminable patterns of neural activity in the taste cortex, suggesting that they evoke the same taste quality of sweetness (Plata-Salaman *et al.* 1993). However, sugars have also been shown to differ in their stimulating efficiency, that is, certain sugars (e.g., sucrose) are perceived by humans as "sweeter" than other sugars (e.g., fructose) when presented at equimolar concentrations (Pfaffmann *et al.* 1971). In nonhuman

primates, these differences in stimulating efficiency between sugars are reflected in differences in their attractiveness when presented at equimolar concentrations. Thus, relative preferences as determined in the second experiment of the present study can be regarded as a proxy for relative sweetness as perceived by the lemurs.

The pattern of relative preferences found here in the black-and-white ruffed lemur is identical or at least largely similar to that found in squirrel monkeys and spider monkeys, both tested with the same or a similar method (two-bottle preference tests of short duration), and to the pattern of relative sweetness as reported by human subjects (Table II). All four species clearly prefer sucrose over the other saccharides tested. However, pigtail macaques differ markedly in their relative preferences for food-associated sugars: unlike the other primates tested so far, but similar to rats, *Macaca nemestrina* clearly prefers maltose over sucrose. One possible explanation proposed to underlie this interspecies difference in relative preferences for food-associated sugars is that rodents such as rats (and possibly also macaques) have an additional taste receptor for starch-derived polysaccharides that also responds to maltose but not to sucrose (Sclafani 2004). The evolution of such an additional taste receptor is thought to be the result of a starch-rich diet as is typical for rodents such as rats. The fact that the diet of pigtail macaques in the wild contains high amounts of starch whereas the diet of *Varecia variegata* does not, but contains high amounts of soluble carbohydrates instead, is in line with this notion. Thus, the findings of the present study support the idea that relative preferences for food-associated sugars may correlate with dietary specialization in primates.

Conclusions

Taken together, the results of the present study support the notions that the taste sensitivity in primates for food-associated sugars may correlate with phylogenetic relatedness, with body mass, and with lactose content in milk. Further, the results support the notion that relative preferences for food-associated sugars in primates, but not necessarily sweet-taste sensitivity, may correlate with dietary specialization.

Table II Relative taste preferences for food-associated sugars in primates and the rat

Species	Relative taste preference	Reference
Varecia v. variegata	**Sucrose > fructose > glucose ≥ maltose ≥ lactose**	1
Saimiri sciureus	Sucrose > fructose > glucose ≥ maltose ≥ lactose	2
Ateles geoffroyi	Sucrose > fructose > glucose ≥ lactose ≥ maltose	3
Homo sapiens	Sucrose > fructose > maltose ≥ glucose ≥ lactose	4
Macaca nemestrina	Maltose > sucrose > glucose ≥ fructose ≥ lactose	5
Rattus norvegicus	Maltose > sucrose = glucose > lactose	6
Rattus norvegicus	Maltose > sucrose > glucose = fructose	7

[1] Present study; [2] Laska (1997); [3] Laska *et al.* (1998); [4] Pfaffmann *et al.* (1971); [5] Laska (2000); [6] Richter and Campbell (1940); [7] Sclafani and Mann (1987).

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