Food preferences and nutrient composition in zoo-housed ring-tailed lemurs, *Lemur catta*

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**ABSTRACT**

The aim of the present study was to assess the occurrence of spontaneous food preferences in zoo-housed ring-tailed lemurs and to analyze whether these preferences correlate with nutrient composition. Using a two-alternative choice test three female and one male *Lemur catta* were repeatedly presented with all possible binary combinations of 12 types of food which are part of their diet in captivity and found to display the following rank order of preference: apple > sweet potato > melon > beetroot > carrot > egg > eggplant > pumpkin > cucumber > tomato > cabbage > mealworm. Correlational analyses revealed a highly significant positive correlation between this food preference ranking and the total carbohydrate and sucrose contents of the foods (p < 0.01, respectively). No other significant correlations with any other macro- or micronutrient were found. These results suggest that zoo-housed ring-tailed lemurs are not opportunistic, but selective feeders with regard to maximizing their net gain of energy as only the content of carbohydrates, but not the contents of total energy, proteins or lipids significantly correlated with the displayed food preferences. Further, we found that ring-tailed lemurs that were raised on a vegetable-based diet did not significantly differ in their food preferences, and in particular in their predilection for food items high in carbohydrates, from animals that had previously been fed a fruit-based diet. This suggests that the lemurs’ preference for carbohydrate-rich food items may be innate and not affected by experience with different diets.

**1. Introduction**

The diet of most primate species includes a wide variety of plant foods [1]. Nevertheless, most primates are highly selective feeders and display marked preferences for certain types of plants or plant parts [2, 3]. Field studies on both primates and other herbivores suggest that their food choices can be attributed to two main factors: the nutritional and/or toxic content of the plant part in question [4, 5] and its relative spatial and temporal distribution [6]. Additional factors such as body size or gut morphology are thought to also affect food selection in primates but are commonly regarded as evolutionary adaptations to the two main factors mentioned above [7]. Numerous studies have found negative correlations between food selection of primates and the content of plant secondary compounds such as alkaloids, phenolics or tannins that are toxic or inhibit the digestion of proteins and polysaccharides [e.g. 8–10]. In contrast, only few studies so far reported positive correlations between the food preferences displayed by primates and the nutrient content of plants [11, 12]. However, according to optimal foraging theory, natural selection should favor individuals which succeed in maximizing their net intake of energy and other critical nutrients and, accordingly, this should be reflected in their food selection patterns and food preferences [13, 14]. One possible explanation for the paucity of data on positive correlations between food preferences of primates and the content of certain nutrients is the highly complex chemical composition of plant foods. Herbivorous species have to permanently make trade-offs between the need to meet their nutrient and energy requirements and the need to avoid ingestion of too high amounts of toxic compounds that plants use to defend themselves against predation [15]. This, in turn, makes it difficult to identify those nutrients that herbivorous animals may actively seek.

One approach to overcome this difficulty and to obtain information on which nutrients may affect primate food selection in a positive manner is to present animals with food items that contain only small and thus presumably negligible amounts of plant secondary compounds and to assess if their choice behavior correlates positively with any nutrient. Cultivated fruits and vegetables conform with this idea as they...
are low in plant secondary compounds and are well-characterized with regard to their nutrient and energy content [16]. Using this approach, previous studies found that pig-tailed macaques (*Macaca nemestrina*) and white-handed gibbons (*Hylobates lar*) are selective feeders with regard to maximizing their net gain of energy by preferring foods that are high in carbohydrates [17, 18]. Squirrel monkeys (*Saimiri sciureus*) and spider monkeys (*Ateles geoffroyi*), in contrast, were found to display food preferences which significantly correlated positively with total energy content, irrespective of the source of energy [17, 19]. Thus, there are different strategies with regard to food choices that catarhchinine and platyrhynine primates can adopt to meet their energy requirements. So far, no strepsirrhine primate species has been assessed for possible positive correlations between preferences for certain cultivated fruits and vegetables and their nutrient composition. The present study therefore aimed to fill this gap.

Ring-tailed lemurs (*Lemur catta*) are known to consume a wide variety of food items of both plant and animal origin [20–22]. Nevertheless, they are considered as opportunistic frugivores/folivores and are highly adaptive to seasonal changes in their diet [23]. Free-ranging *Lemur catta* have been reported to select foods containing high levels of carbohydrates when those are seasonally available [24]. They have also been observed to spend a considerable proportion of their feeding time foraging on arthropods such as cicadas and caterpillars, and thus on protein-rich foods of animal origin [25]. Additionally, *Lemur catta* in the wild have been reported to regularly drink water from open sources such as streams or springs [26]. Finally, ring-tailed lemurs have also been observed to consume salt, presumably to meet their sodium requirements [27].

It was therefore the aim of the present study to assess food preferences in a group of zoo-housed ring-tailed lemurs for a variety of cultivated fruits and vegetables as well as foods of animal origin, and to analyse whether these preferences correlate with the abundance of macro- or micronutrients. We hypothesized that ring-tailed lemurs 1. should show marked preferences for specific foods and that these preferences are based on their nutrient composition, 2. should prefer food items high in carbohydrate content, 3. should prefer food items high in protein content, 4. should be indifferent to differences in water content of food items, and 5. should prefer food items high in sodium content.

The opportunity to include both animals that grew up on a vegetable-based diet and animals that switched from a fruit-based to a vegetable-based diet two years prior to the present study allowed us to additionally assess possible effects of experience with a given diet (or lack thereof) on food preferences. Here, we hypothesized that ring-tailed lemurs 6. should differ in their food preferences based on experience with their captive diet.

2. Materials and methods

2.1. Animals

Four ring-tailed lemurs (*Lemur catta*), maintained at Furuviksparken (Sweden), participated in the study. They comprised two adult females of 13 (Ester) and 17 (Bi) years of age and two infant siblings of one year (Lily) and three months (Vide) of age, respectively. All lemurs except the oldest female were born at Furuviksparken. The lemurs were housed in an indoor enclosure of 200 m², with access to a 5,000 m² outdoor enclosure. A small corridor connected the indoor and outdoor enclosure. The lemurs were fed a variety of vegetables and two kinds of commercial primate pellets (*Zoo primate high fiber pellets and leaf-Eating primate pellets*, from Granovit, Kaiseraugust, Switzerland) twice per day. Fresh leaves, grass and other plant material as well as arthropods were available from the natural vegetation outdoors. Water was always available ad libitum. Due to problems with obesity and reproduction the lemurs had been switched from a diet based on a high proportion of fruits to a diet based on vegetables which now includes only small amounts of fruit as rewards during behavioral training. The switch of diet occurred 2 years prior to the start of the study.

2.2. Procedures

Food preferences were assessed using a two-alternative choice test. The animals were presented with pairs of equally-sized food items, and their choice behavior, i.e. which of the two food items was consumed first, was recorded. Animals were tested singly in order to avoid competition or distraction affecting a lemur's choice behavior. Testing took place in the morning, between 07:30 and 08:30, before the lemurs were fed their first meal of the day.

During the sessions two of the lemurs approached a wooden shelf mounted on the outside of the mesh of a connecting tunnel, chose one of a pair of simultaneously presented food items and then retreated, so that the rejected food item could be removed. The other two lemurs approached a metal tray held by the experimenter instead of the wooden shelf. In order to prevent an animal from taking both food items at the same time, the food items were placed 20 cm apart. All foods were cut into cubes of approximately 1 cm³ to avoid choice behavior being affected by size differences. (In the case of mealworms, an amount approximating a volume of 1 cm³ was presented.) Each session consisted of eight pairwise presentations and the position of the food items (e.g. cucumber presented left and carrot presented right) was pseudorandomized in order to counterbalance possible side preferences. Each pair of food items was presented to an animal for a total of 10 times and care was taken to never present a food item that had been part of the previous pair.

The following 12 types of food were employed: apple (*Malus pumila*), beetroot (*Beta vulgaris*), carrot (*Daucus carota*, subsp. *sativus*), cucumber (*Cucumis sativus*), eggplant (*Solanum melongena*), sweet potato (*Ipomoea batatas*), butternut pumpkin (*Cucurbita moschata*), napa cabbage (*Brassica rapa* subsp. *pekinesis*), honey melon (*Cucumis melo*), tomato (*Solanum lycopersicum*), mealworm (*larva of Tenebrio molitor*) and hardboiled egg (egg from *Gallus gallus domesticus*). The rationale for choosing these types of food was a) that all of them were part of the animals' diet in the zoo and thus familiar to the lemurs, b) that data for the contents of macro- and micronutrients in these types of food are available, allowing us to assess possible correlations between food preferences and nutrient contents [16, 28], and c) that they differ markedly in their contents of macronutrients. With regard to the latter point it should be mentioned that the contents of total energy, carbohydrates, lipids, protein, dietary fiber, and water differed by up to a factor of 22, 21, 219, 45, 24, and 1.6, respectively, between the types of food used here. The exact values of the contents of the macro- and micronutrients of all twelve food items are summarized in Supplementary Table 1.

In an attempt to minimize the inevitable intraspecific variation in nutrient composition, care was taken to always present food items of a given type with the same degree of ripeness.

2.3. Data analysis

A total of 2640 choices (66 binary combinations x 10 presentations per animal x 4 animals) were recorded, and food preference rankings were established using the following criteria:

Criterion 1 (individual level): The sum total of choices for each of the 12 types of food across all binary combinations was built for each individual animal. The theoretical maximum score for any type of food with this criterion is 110 (11 combinations x 10 presentations per animal x 1 animal). In cases when a lemur failed to make a choice between two food items within 10 seconds, each of the two items were assigned 0.5 points.

Criterion 2 (group level): This criterion adopts the same procedure of building the sum total of choices as for criterion 1, although, here, the data for all four animals were collapsed. Thus, the theoretical
maximum score for any type of food with this criterion is 440 (11 combinations x 10 presentations per animal x 4 animals).

Additionally, two-tailed binomial tests using the sum total of choices for each member of a given binary combination were performed to assess significant preferences both at the individual level and at the group level (p < 0.05). Correlations between the food preference rankings and the contents of nutrients were evaluated by calculating Spearman rank-order correlation coefficients r_s which were tested for significance by computing z-scores. The same test was also used to assess whether the food preference rankings of the four lemurs correlated with each other.

3. Results

3.1. Food preferences

Table 1 summarizes the choice behavior of the lemurs in the food preference tests, i.e. the number of choices made by the lemurs in favour of each member of a given pair of food items. With 46 of the 66 binary combinations, the lemurs displayed a statistically significant preference for one of the options (two-tailed binomial test, p < 0.05). Apple was clearly the most attractive food and, accordingly, was significantly preferred over all 11 other food items (p < 0.05). The high attractiveness of apple is further illustrated by the fact that 93.6% of all possible choices were in favour of this food item (Table 2). Sweet potato, beetroot, carrot, and egg were significantly preferred over any other food item. Mealworm was the least preferred food and, accordingly, only 23.1% of all choices, and thus the lowest percentage of all options, were in favour of mealworm.

3.2. Rankings derived from the food preferences

The food preference rankings derived from the lemurs’ choice behavior are summarized in Table 2. All four lemurs displayed similar rankings of preference for the 12 food items. Accordingly, their rankings all significantly correlated with each other (Spearman r_s ≥ 0.62, p < 0.05, with all six comparisons). Similarly, the food preference rankings of the two animals that had previously been fed a fruit-based diet and of the two animals that had been raised on a vegetable-based diet, respectively, significantly correlated with each other (Spearman r_s ≥ 0.84, p < 0.01), suggesting that experience with a different diet (or a lack thereof) did not have a significant effect on the lemurs’ food choices.

3.3. Food preference rankings and nutritional content

The Spearman rank-order correlation statistics between the food preference ranking and the nutritional content of the food items are summarized in Table 3. The food preference rankings displayed by the lemurs correlated highly significantly with total carbohydrate content and with the content of sucrose (Spearman, p < 0.01). This was true both when the four lemurs were considered separately and when they were considered as a group. However, the lemurs’ food preference rankings did not significantly correlate with total energy content (Spearman, p > 0.05). Similarly, the food preference rankings did not correlate significantly with any other macro- or micronutrient (Spearman, p > 0.05). Here, too, this was true both for the individual lemurs and for the group.

4. Discussion

The results of the present study demonstrate that zoo-housed ring-tailed lemurs display marked food preferences in a two-alternative choice test using cultivated fruits and vegetables as well as foods of animal origin. Further, the results show that these preferences significantly correlated positively with the contents of total carbohydrates and sucrose of the food items used, but not with total energy content. These findings are consistent with our first two hypotheses. Interestingly, the lemurs did not prefer food items that are high in protein content, which is in contrast with our third hypothesis. Taken together, these findings suggest that ring-tailed lemurs are not opportunistic feeders with regard to energy gain but rather seek to meet their

Table 1
Choice behavior of the ring-tailed lemurs in the food preference tests

|          | Apple | S.potato | Melon | Beetroot | Carrot | Egg | Eggplant | Pumpkin | Cucumber | Tomato | Cabbage | Mealworm |
|----------|-------|----------|-------|----------|--------|-----|----------|---------|----------|--------|---------|----------|
| Apple    | X     | ← ←      | ← ←   | ← ←      | ← ←   | ← ← | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Sweet potato | 11:29 | X        | \    | \        | \     | ← ← | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Melon    | 3:37  | 14:26    | X     | ← ←      | ← ←   | ← ← | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Beetroot | 9:31  | 15:25    | 1:25  | X        | ← ←   | ← ← | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Carrot   | 2:38  | 6:34     | 6:34  | 12:5:27.5| X     | ← ← | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Egg      | 2:38  | 6:34     | 7:33  | 11:29    | 16:24 | X   | ← ←      | ← ←    | ← ←      | ← ←   | ← ←    | ← ←    |
| Eggplant | 1:39  | 0:40     | 0:5:39.5| 2:5:37.5| 2:5:37.5| 7.5:32.5| X        | \      | \        | \     | \      | \      |
| Pumpkin  | 0:40  | 0:40     | 0:5:39.5| 3:5:36:5 | 2:5:37.5| 9:31 | 19:21    | X       | ← ←      | ← ←   | ← ←    | ← ←    |
| Cucumber | 0:40  | 0:40     | 1:39  | 4:36     | 2:38  | 6:34 | 17:23    | 20:20   | X        | ← ←   | ← ←    | ← ←    |
| Tomato   | 0:40  | 0:40     | 0:40  | 5:35     | 1:39  | 8:5:31:5| 16:24    | 18:22   | 19:5:20:5| X     | ← ←    | ← ←    |
| Cabbage  | 0:40  | 1:39     | 0:40  | 4:36     | 3:37  | 8:5:31:5| 17:23    | 19:21   | 18:5:21:5| 18:5:21:5| X | ← ← |
| Mealworm | 0:40  | 0:40     | 0:40  | 3:37     | 0:40  | 6:34  | 16:5:23:5| 17:23   | 20:5:19:5| 18:5:21:5| 20:20 | X |

The table indicates the number of choices (from n = 4 animals) for each member of a given pair of food items. The first value applies to the food item to the left and the second to the food item on the top.

← indicates a significant preference for the food item to the left (p < 0.01).
\ indicates a lack of significant preference for either member of a pair (p > 0.05).

Table 2
Food items and their corresponding rank order of preference

| Criterion 1 | Viola | Lily | Bi | Ester | Criterion 2 | ∑Viola + Lily + Bi + Ester |
|-------------|-------|------|----|-------|-------------|---------------------------|
| Apple       | 101   | 101  | 101 | 106   | Apple       | 412 (93.6)                |
| Sweet potato| 88    | 85   | 94  | 102   | Sweet potato| 369 (83.9)                |
| Melon       | 88.5  | 96   | 77  | 85.5  | Melon       | 347 (78.9)                |
| Beetroot    | 89.5  | 89.5 | 49.5 | Beetroot| 313.5      | (71.3)                   |
| Carrot      | 75    | 61   | 67  | 76.5  | Carrot      | 279.5 (63.5)              |
| Egg         | 25    | 69   | 78.5 | 64    | Egg         | 256.5 (53.8)              |
| Eggplant    | 36.5  | 37   | 24.5 | 28.5  | Eggplant    | 126.5 (28.8)              |
| Pumpkin     | 39.5  | 25.5 | 26.5 | 31    | Pumpkin     | 122.5 (27.8)              |
| Cucumber    | 30.5  | 27.5 | 25.5 | 28    | Cucumber    | 111.5 (25.3)              |
| Tomato      | 34    | 21.5 | 25.5 | 30    | Tomato      | 111 (25.3)                |
| Cabbage     | 25    | 27   | 26  | 31.5  | Cabbage     | 109.5 (24.9)              |
| Mealworm    | 25.5  | 23.5 | 25  | 27.5  | Mealworm    | 101.5 (23.1)              |

Numbers in parentheses indicate the percentage of choices in favour of a given type of food (relative to the theoretical maximum of 440 choices / type of food).
requirements of metabolic energy by preferring foods that are high in soluble carbohydrates. This is remarkable considering that in the natural habitat of primates the availability of fruits that are high in carbohydrates is usually more variable and dependent on the season of the year than the availability of arthropods that are high in protein [29]. However, ring-tailed lemurs may be an exception from this rule as their native habitat of Madagascar provides at least two plant species (Melia azedarach and Ficus spp.) which produce carbohydrate-rich fruits year-round and are heavily exploited by Lemur catta [21]. Further, field studies suggest that, although ring-tailed lemurs are considered as opportunistic frugivores/folivores that are highly flexible in their diet [23], they spend a markedly higher proportion of time feeding on fruit (31%, [24]) compared to feeding on arthropods (15.7%, [25]). As soluble carbohydrates and proteins provide the same amount of energy (4 calories) per gram, it is plausible that the expenditure of time and energy that ring-tailed lemurs have to invest to procure equal amounts of calories from these two macronutrients favors foraging for fruits over foraging for arthropods.

In order to assess whether the marked preferences of the ring-tailed lemurs for food items high in soluble carbohydrates are based on the carbohydrates’ taste property of sweetness or on their physiological property of being an easily metabolizable source of energy, studies determining taste preference thresholds as well as on relative taste preferences would be needed. Whereas a variety of nonhuman primate species have been studied in this respect [30, 31], corresponding data for Lemur catta are so far largely lacking.

Our finding that ring-tailed lemurs display a marked preference for foods that are high in soluble carbohydrates is in line with studies in pig-tailed macaques (Macaca nemestrina) and white-handed gibbons (Hylobates lar) which employed the same method as the present study [17, 18]. However, the food preferences of squirrel monkeys (Saimiri sciureus) and spider monkeys (Ateles geoffroyi), which were also tested using the same method as in the present study, significantly correlated positively with total energy content, irrespective of the source of energy [17, 19]. Thus, there are clearly different strategies with regard to food choices that primates can adopt to meet their energy requirements. Several possible explanations for these between-species differences in food preferences with regard to macronutrients have been put forward and include differences in the degree of frugivory [17], the degree of food competition with sympatric species [32], and the abundance of certain plant species that serve as staple foods [33]. As these possible explanations are not mutually exclusive, further studies including additional primate species are needed to draw reliable conclusions regarding the causes underlying the food selection strategies of non-human primates to maximize the net gain of metabolic energy.

In contrast to our third hypothesis, the lemurs of the present study did not prefer food items high in protein content. This finding deserves some discussion as the protein leverage hypothesis states that human subjects will prioritize the consumption of protein in food over other macronutrients and will eat until their protein needs have been met, regardless of total energy content [e.g. 34–36]. Studies in free-ranging nonhuman primates lend some support to the notion of a pivotal role of protein in food selection [37, 38]. However, it should be mentioned that no study on food preferences in captive nonhuman primates ever reported a positive correlation with protein content [e.g. 17–19]. This might be explained by the fact that the diets fed to primates in human care provide a sufficient amount of protein, possibly due to the pellets that often form part of their daily provisioning, so that the animals can meet their protein requirements without the need to display significant preferences for food items containing high amounts of this macronutrient. Studies on captive primates kept on a protein-deficient, but otherwise nutritionally complete diet would be needed to test whether the protein leverage hypothesis may contribute to the food preferences observed in e.g. zoo settings.

Our finding that the ring-tailed lemurs did not base their food preferences on water content of the food items is consistent with our fourth hypothesis. This finding is not trivial considering that squirrel monkeys [17], spider monkeys [19], and also pacas (Agouti paca), a highly frugivorous rodent [39], have been found to display significant correlations between their food preferences and the water content of the tested food items. A plausible explanation for our result is that ring-tailed lemurs, unlike the aforementioned species, are known to regularly drink water from open sources such as streams or springs [26] and thus do not depend on juicy fruits to meet their water requirements.

In contrast to our fifth hypothesis, the ring-tailed lemurs did not prefer food items high in sodium content. Certain minerals such as sodium have frequently been reported to be in short supply in the natural diet of primates. Accordingly, several studies reported that e.g. ring-tailed and brown lemurs (Lemur catta and Lemur fulvus; [27]), black-and-white colobus monkeys (Colobus guereza; [40]), cotton-top tamarins (Saguinus oedipus; [41]), red howler monkeys and white-bellied spider monkeys (Alouatta seniculus and Ateles belzebuth; [42]), and chimpanzees (Pan troglodytes; [43]) display marked predilections for edible material such as soil or wood which are high in those minerals that are otherwise lacking in their diet.

Table 3

| Macronutrients | Spearman Rank-Order Correlation (rs) | p-value |
|----------------|-------------------------------------|---------|
| Carbohydrates | 0.73                                | 0.00763 |
| Saturated fatty acids | -0.32                             | 0.30    |
| Poly-unsaturated fatty acids | -0.37                             | 0.23    |
| Monounsaturated fatty acids | -0.29                             | 0.36    |
| Monounsaturated fatty acids | -0.12                             | 0.22    |
| Carbohydrates | -0.34                               | 0.29    |
| Protein | -0.32                               | 0.36    |
| Total nitrogen | -0.43                             | 0.17    |
| Vitamin A | 0.11                                | 0.74    |
| Vitamin B1 | -0.38                               | 0.22    |
| Vitamin B2 | -0.12                               | 0.24    |
| Vitamin B3 | -0.29                               | 0.35    |
| Ascorbic acid | 0.19                               | 0.59    |
| Vitamin D | -0.29                               | 0.36    |
| Vitamin E | -0.20                               | 0.53    |
| Folate | -0.15                               | 0.65    |
| Pantothenate | -0.35                             | 0.26    |
| Biotin | -0.21                               | 0.50    |
| Niacin | -0.43                               | 0.16    |
| Magnesium (Mg) | 0.00                               | 1.00    |
| Phosphorous (P) | -0.34                             | 0.29    |
| Calcium (Ca) | -0.34                               | 0.29    |
| Magnesium (Mg) | -0.10                               | 0.76    |
| Iodine (I) | -0.33                               | 0.30    |

Values for the statistical measure rs may range from +1 (perfect positive correlation) to -1 (perfect negative correlation). Statistically significant correlations are shown in bold typeface.
Our finding that the ring-tailed lemurs showed neither significantly positive nor significantly negative correlations between their food preferences and any of the micronutrients (i.e., minerals and vitamins) tested is not self-evident as studies in captive squirrel monkeys [17], spider monkeys [19], and white-handed gibbons [18] – all tested using the same method as in the present study – showed significant positive correlations between food preferences and the contents of copper (in Saimiri sciureus), copper, magnesium and manganese (in Ateles geoffroyi), and selenium (in Hylobates lar), respectively. This suggests that not only diets of primates in the wild, but also diets of zoo-housed primates may lack important micronutrients such as certain minerals that the animals in question may therefore actively seek to consume. This notion is consistent with the well-established phenomenon of animals displaying a craving for specific types of food as a result of prolonged specific nutrient deficiencies [44]. Our findings can therefore be interpreted as indicating that the diet fed to the zoo-housed ring-tailed lemurs of the present study does not lack any micronutrients, at least not to a degree so as to induce corresponding food preferences.

In this context, it is also important to note that the diet of zoo-housed primates usually differs markedly in its nutritional composition from that of their conspecifics in the wild. Cultivated fruits, for example, which often form the basis of the diet of primates in human care, have been selectively bred to appeal to human tastes [45]. Accordingly, cultivated fruits are generally higher in soluble carbohydrates, and lower in fiber and plant secondary compounds compared to the non-cultivated fruits that primates co-evolved with and feed on in the wild [46]. Since primates in human care are often kept on a diet based on cultivated fruits, health issues such as obesity, diabetes, and problems with reproduction are a frequent consequence [47, 48]. Therefore, a balanced diet for zoo-housed primates needs to avoid presenting the animals with a too high abundance of certain macro- or micronutrients. This is particularly true for captive lemurs which have repeatedly been reported to be vulnerable to hepatic iron storage disease [49, 50]. The development of this disease which is characterized by accumulation of iron in the liver and which can be fatal in lemurs is fostered by a fruit-based diet as cultivated fruits are low in iron-binding polyphenols [51].

As the commercial varieties of vegetables have been found to be more similar in their nutrient composition to the wild fruits consumed by free-ranging primates than cultivated fruits are, zoos increasingly replace the fruit-based diets fed to their primates with vegetable-based diets [52, 53]. This has also been the case with the lemurs of the present study two years prior to the start of our food preference tests. In contrast to our sixth hypothesis, we found that ring-tailed lemurs that grew up on a vegetable-based diet did not significantly differ in their food preferences, and in particular in their predilection for food items high in carbohydrates, from animals that had previously been fed on a fruit-based diet. This finding suggests that the switch of diet two years prior to the present study had little, if any effect on the animals’ food preferences, and that the preference for foods high in carbohydrates may be innate and is not affected by a diet aiming at a limited access to sweet-tasting carbohydrates. The latter notion is in line with the well-established “sweet tooth” that primates display [54] as all primate species tested so far vividly prefer e.g. sweet-tasting solutions in two-alternative choice tests [e.g. 30, 31]. Thus, the switch from a fruit-based to a vegetable-based diet, although in most cases clearly beneficial for zoo-housed primates [52, 53], needs to take into consideration that nonhuman primates are likely to keep their predilection for sweet-tasting food items. This, in turn, may cause problems with the process of familiarization with and acceptance of novel and more healthy food items.

Our finding that the two infant lemurs included in the present study did not significantly differ in their food preferences from the adults may seem counter-intuitive considering that infant mammals usually differ in their nutritional needs from those of adult conspecifics [51]. These differences in the nutritional needs of infant and adult animals may, although not necessarily, be accompanied by differences in the food preferences they display. However, it is also well-established that food preferences observed in infant mammals are strongly affected by their mothers’ diet [55]. As the mother of both infant lemurs of the present study has been fed the same vegetable-based diet during pregnancy that the infants were provided with after weaning, this might at least partially explain our finding of similar food preferences in both infant and adult ring-tailed lemurs.

Taken together, the results of the present study suggest that zoo-housed ring-tailed lemurs are not opportunistic, but selective feeders with regard to maximizing their net gain of energy as only the content of carbohydrates, but not the contents of total energy, proteins or lipids significantly correlated with the displayed food preferences. The lack of significant correlations between food preferences and the content of any of the micronutrients suggests that the diet fed to our lemurs was balanced. Further, we found that ring-tailed lemurs that grew up on a vegetable-based diet did not significantly differ in their food preferences, and in particular in their predilection for food items high in carbohydrates, from animals that had previously been fed a fruit-based diet. This suggests that the lemurs’ preference for carbohydrate-rich food items may be innate and not affected by experience with different diets.

Ethical note
The experiments reported here comply with the American Society of Primatologists’ Principles for the Ethical Treatment of Primates, with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU), and also with current Swedish animal welfare laws.

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Declarations of Competing Interest
None.

Supplementary materials
Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.physbeh.2020.113125.

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