Fuel for the brain: investigating the relationship between age and sweetness preference in different non-human primate species

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Citation

Jong Pen, W. de. (2025). *Fuel for the brain: investigating the relationship between age and sweetness preference in different non-human primate species*.

Universiteit Leiden

Psychologie
Faculteit der Sociale Wetenschappen

Fuel for the brain: investigating the relationship between age and sweetness preference in different non-human primate species

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Word count: 12025
Cognitive Psychology
Thesis Msci Applied Cognitive Psychology

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Abstract

As obesity and overweight are increasing globally among children, many dietary programs focus on limiting sugar intake in this group. However, some researchers are concerned that such reduction strategies may have harmful consequences in young children. It is thought that children are naturally drawn to sweet foods due to the vital role sugars play in brain development. To learn more about the potential evolutionary origins behind this preference, studying our nearest evolutionary relatives can provide valuable insights. This study therefore examined the effect of age on sweetness preference across four non-human primate species. In addition, the roles of brain growth and taxonomic distance were also taken into consideration. Sweetness preference was studied in zoo-housed gorillas *(Gorilla gorilla gorilla)*, mandrills *(Mandrillus sphinx)*, white-faced sakis *(Pithecia pithecia)*, and Goeldi's monkeys *(Callimico goeldii)* using (1) a self-designed two-choice task and (2) by observing normal dietary intake. A self-designed method was also used to estimate the extent of completed brain growth in the studied species. The results showed no significant effects of age, brain growth, or taxonomic distance on sweetness preference. It was found, however, that sex predicted sweetness preference in some of my models. It can thus be concluded that none of the proposed hypotheses were supported. Although this study has some conceptual and methodological shortcomings, it can nevertheless provide new insights into the debate on the origins of the preference for sweetness in human children. Recommendations for future research on sweetness preference and brain-size measurement in non-human primates are provided.

Keywords: sweetness preference, non-human primates, brain development, evolutionary psychology, feeding behavior

Summary for the General Public (Layman's Abstract)

Around the world, more and more children are becoming overweight or obese. Parents are therefore often advised to reduce their children's sugar intake. Some researchers, however, are concerned that following these recommendations may be dangerous for children's brain development. It is thought that sugars play an important role in brain growth, which may explain the exaggerated preference for sweetness in human children. To learn more about the evolutionary origin behind this preference in human children, I studied some of our closest animal relatives: gorillas, mandrills, white-faced sakis and Goeldi's monkeys. Together with my research team, I studied whether age, brain growth, and evolutionary closeness influenced sweetness preference in these primate species. We did this by observing the animals' choices between sweet and non-sweet food, alongside their overall diet preferences. Contrary to my expectations, no effects of age, brain growth, or evolutionary closeness on the preference for sweetness were found. I did find, however, that in some cases female primates were more likely to prefer sweet food than males. Although this study had some limitations, it indicates that young non-human primates may not have the same exaggerated preference for sweetness that exists in human children. Future research could further explore if this preference is unique to humans and whether it has a biological or cultural origin.

Fuel for the brain: investigating the relationship between age and sweetness preference in different non-human primate species

According to recent numbers of the WHO (2024), obesity and overweight are increasing globally at an alarming rate. Children are one of the demographical groups being affected, with estimations suggesting that 1 of every 5 children or adolescents is overweight and 8.5% of them obese (Zhang et al., 2024). To combat these raising numbers, more attention has been paid to lifestyle factors associated with weight gain, particularly diet. Carbohydrates, and more specifically sugars, are a major cause of overweight and obesity (Della Torre et al., 2015). Many dietary programs focused on preventing and reducing overweight therefore often target sugar intake (Lanigan, 2018). However, some researchers are worried about these dietary programs (Archer, 2018). They state that sugars play an essential role in childhood development and that reduction of sugar intake can cause physical harm to young children.

Although it is widely known that too much sugar can be harmful to the body, sugar intake is at the same time essential for physical growth in children (Kalhan & Kiliç, 1999). Children need substantial amounts of energy, and this is particularly due to the high speed in which the brain develops in the first years of life (Georgieff et al., 2018). It has therefore been suggested by evolutionary theories that children have an inborn preference for food that is high in energy (Ventura & Mennella, 2011). More specifically, it is thought that the taste of sweetness may signal the presence of energy sources. Literature suggests thus that the preference for sweet tastes in children may have a biological origin. On the other hand, other researchers think that taste preferences are influenced and determined by cultural characteristics (Venditti et al., 2020). For instance, the preference for sweetness seems to be more pronounced in modern lifestyles compared to traditional styles. Research therefore provides contrasting perspectives on the preference for sweetness in children.

To learn more about the evolutionary origin of the preference for sweetness in human children, studying our nearest evolutionary relatives can provide valuable information. More specifically, overlapping age-related taste preferences between humans and non-human primates can tell us more about the biological need for sweet food in human children. However, to date, no research on age-related taste preferences has been performed in non-human primates. Therefore, the current study can provide valuable information on the preference for sweetness in both non-human primates and humans. In addition, conclusions drawn from this study can have practical relevance in providing information that can be implemented in dietary recommendations for human children.

Sugar and the brain

In the first years of life, the human brain develops rapidly (Gilmore et al., 2018). Children are born with a postnatal brain size that is only 27% of its adult size, which grows substantially in the following years to 90% at the age of six (Robson & Wood, 2008; Stiles & Jernigan, 2010). Because substantial brain development takes place in these earliest years, large amounts of energy are required. Glucose, in particular, is an essential energy source. This can be found in carbohydrates, and more specifically, sugars and starches (Slavin & Carlson, 2014). The main food sources of carbohydrates include vegetables, fruits, and milk products. After these nutrients are broken down into glucose, energy is provided to the central nervous system. Because of its dependence on glucose, sufficient glucose intake is therefore essential for brain development in childhood. In line with this, research shows that children have heightened levels of glucose metabolism (Kuzawa et al., 2014). Specifically, glucose comprises 66% of the body's resting metabolism and 43% of its daily requirements in children. Glucose uptake in the cerebral cortex during childhood is moreover twice as high compared to adulthood (Chugani et al., 1987). It can therefore be concluded that sufficient glucose intake is crucial for brain development in young children. This is illustrated by cases of hypoglycemia, or low blood glucose. In hypoglycemia, low glucose levels can lead to harmful consequences in the central nervous system, including neuronal damage (Cacciatore et al., 2022). The effects of low blood glucose are thought to be especially damaging and long-lasting during infancy and childhood (Duvanel et al., 1999). Through its direct effects on brain growth, hypoglycemia can cause significant cognitive impairments in these age groups. For example, a study by Roeper et al. (2024) found that children between 7 and 11 years old with a history of hypoglycemia had an IQ score that was averagely 4.8 points lower than that of their peers.

As glucose plays an important role in childhood development, and particularly brain growth (Duvanel et al., 1999), natural attraction to carbohydrates can be thought to be biologically advantageous in children. According to evolutionary theories, the taste of sweetness may perform this function and make children attracted to food containing carbohydrates (Ventura & Mennella, 2011). In other words, sweet tastes may act as a signal for food sources that are rich in energy and contribute to physical growth. The taste of sweetness can therefore motivate feeding behavior in children. This is supported by research, which shows that brain regions important for motivation and experiencing reward (i.e., ventral striatum and medial orbitofrontal cortex) are also involved in food processing (Rolls & McCabe, 2007). In line with this, literature provides evidence that humans are able to detect sweetness prenatally and that this ability interacts with affective systems (Ventura & Mennella, 2011). This was illustrated by Tazter et al. (1985), who found that the suckling response of premature babies was stronger and more frequent when they were exposed to water that was sweetened with glucose compared to neutral water. It can therefore be suggested that children have an innate response to the taste of sweetness.

When comparing sweetness to other tastes, experimental studies show that human children have a stronger preference for sweetness (Kostecka et al., 2021; Mennella & Bobowski, 2015). Moreover, the preference for sweet tastes is stronger in young children compared to adults and adolescents, with the latter having a stronger preference than the former (Venditti et al., 2020). For instance, in the study by Mennella et al. (2014) taste preferences of children between 5 and 10 years old were compared to those of their mothers by manipulating sucrose concentrations in glasses of water. The results showed that children had a stronger preference for water with high sucrose concentrations than their mothers. Similarly, according to a longitudinal study by Desor and Beauchamp (1987), the preferred levels of sucrose decline with age. When participants were presented with four cups containing different sucrose solutions, half of them chose the highest sucrose concentrations when they were adolescents, whereas preferences were evenly distributed among the four cups when the participants reached adulthood. In addition, Coldwell et al. (2009) studied the relationship between bone growth and sweetness preference. The results from the study showed that adolescents with lower bone growth had a less pronounced preference for sweetness than adolescents who were still having growth spurts. Therefore, the authors concluded that the preference for sweet tastes is related to physical growth. Finally, a similar preference for sweetness in children has been found across various countries and cultures, including Europe, North America, and South America (Ventura & Mennella, 2011). It is therefore thought that the preference for sweetness among infants and children may be universal.

Primates

When comparing human brains to those of non-human primates, the difference in size is substantial (Sherwood et al., 2008). The human brain, weighing approximately 1400g, is three times larger than that of extant non-human great apes. The prefrontal cortex, in particular, shows a considerable larger relative size in humans (Donahue et al., 2018). However, despite these differences, the human brain might be less extraordinary than formerly thought and shares many similarities with other primates (Herculano-Houzel, 2012). For example, Desilva and Lesnik (2006) found that the average chimpanzee brain size at birth is around 39% of its adult size. In the first years of life, the brain develops rapidly, reaching its adult size between 5 and 7 years of age (Herndon et al., 1999; Leigh, 2004). Similarly, gorillas are born with a brain size of a little more than 40% of its adult size, reaching adult size by 3 or 4 years of age (Mcfarlin et al., 2012). Despite the initial size differences between human newborns and other species, brain growth trajectories are similar to those of humans, showing a rapid increase in size during the first years of life (Gilmore et al., 2018). Young non-human primates may therefore have similar energy demands as human children. In addition, considerable overlaps exist in brain circuits related to rewards and motivation between humans and other primates (Neubert et al., 2015). Because these neural decision processes are largely overlapping, tastes may have a similar motivational value for non-human primates. This corresponds with research on associative learning in non-human primates, showing that dopamine neuron firing and dopamine release in response to food functions in the same way as in humans (McCutcheon, 2015).

However, brain development between non-human primate species differs widely. Non-human haplorrhine primates are traditionally taxonomized into the following categories: great apes, Old World monkeys, and New World monkeys (Goodman et al., 1998). Whereas great apes are the nearest human evolutionary relatives, New World monkeys are the furthest away of the three non-human haplorrhine primate categories. Humans diverged 7–8 million years ago from the nearest related great apes, 31 million years ago from Old World monkeys, and 57.5 million years ago from New World monkeys (Langergraber et al., 2012; Takahata & Satta, 1997). When comparing the earlier described brain development of great apes to that of Old World monkeys, research shows that the latter are born with a larger brain size that develops more slowly over the postnatal period (Leigh, 2004). For example, rhesus macaques are born with a postnatal brain size of about 54% of their adult size (Scott et al., 2015). Moreover, the decline in brain growth after infancy appears to be less steep in Old World monkeys compared to other primates. Brain development in New World monkeys appears to be more rapid compared to Old World monkeys, but growth trajectories differ widely between species (Leigh, 2004). For instance, whereas the brain of the squirrel monkey reaches it adult brain size before six months of age, brain development in other New World monkeys takes considerably longer. Generally, it is common for New World monkeys to be born with a brain that is over 50% of its adult size.

Although there are considerable differences between non-human primate diets, most species include substantial amounts of sweet foods in their diet (Remis, 2002). Great apes, including gorillas and chimpanzees, tend to include food in their diet, such as fruit that is high in non-starch sugars and sugars-to-fibers ratios. Research suggests that there is a link between diet and brain size (Jones & MacLarnon, 2004). More specifically, frugivorous animals have considerably larger brain sizes than animals that are folivores. For instance, when comparing frugivores to folivores bats, Jones and MacLarnon (2004) found that the former have a significantly larger brain than the latter. Likewise, brain size may also be predicted by diet in primates (DeCasien et al., 2017). For example, the frugivorous western gorilla has a relatively larger brain and longer life history compared to the folivorous mountain gorilla (Breuer et al., 2008).

Experimental studies suggest that non-human primates are sensitive to sweetness and prefer sweet tastes over neutral ones (Hurtado et al., 2023; Laska et al., 1999; Norlén et al., 2018). For example, Laska et al. (1999) found that baboons preferred water containing sugars over neutral water. More specifically, minimum concentrations of only 10 mM sucrose, 20 mM fructose, lactose, and maltose, and 25 mM glucose were preferred over tap water. Based on these findings the authors concluded that baboons may base their food choices on the extent of sweetness. Studies on other primates, including white-faced sakis and chimpanzees found similar results on sweetness sensitivity (Hurtado et al., 2023; Norlén et al., 2018). Both the white-faced sakis and chimpanzees had a lowest preference threshold for sucrose (10mM and 20mM, respectively) and preferred sucrose over other sugars. Moreover, in the study by Hurtado et al. (2023), subjects were more willing to participate in the high sugar concentration trials. Thus, the same preference for sweetness seems to be present among great apes, Old World monkeys, and New World monkeys. The low preference thresholds suggest that sugar consumption has evolutionary value to primates and reflects their sensitivity to certain nutrients. This corresponds with the idea that threshold preferences are adapted to the animals' diet. For example, research shows that carnivorous mammals lack a functioning sweet-taste receptor (Jiang et al., 2012).

Although its hypothesized relation with brain growth raises the expectation that young non-human primates would benefit more from a stronger sweetness preference than adults, it has remained unknown whether age has an influence on the preference for sweetness in these species. To learn more about the relation between age and sweetness preference in non-human primates, the following four species were included in this study: western lowland gorilla *(Gorilla gorilla gorilla)*, mandrill *(Mandrillus sphinx)*, white-faced saki *(Pithecia pithecia)*, and Goeldi's monkey *(Callimico goeldii)*.

Western lowland gorilla (Gorilla gorilla gorilla)

Western lowland gorillas are taxonomized as great apes (Goodman et al., 1998). They are born with an average postnatal brain size of 217g, growing to an adult brain mass of 522.7g (DeSilva & Lesnik, 2008). In other words, western lowland gorillas are born with a brain of more than 40% of their adult size. Although information on growth trajectories is lacking in this species, the closely related mountain gorilla *(Gorilla beringei beringei)* shows rapid brain growth in the first years of life and reaches adult size at the age of 3 or 4 (Mcfarlin et al., 2012). However, compared to mountain gorillas, growth trajectories are considerably slower in western lowland gorillas and they reach a larger adult brain size (Breuer et al., 2008). While females reach adulthood around the age of ten, males can grow on till eighteen years when they become a silverback. The diet of the western lowland gorilla is relatively frugivorous, consisting chiefly of fruit, herbs, and leaves (Lodwick & Salmi, 2019).

Mandrill (Mandrillus sphinx)

Mandrills belong to the taxonomy of Old World monkeys (Goodman et al., 1998). Although research shows that the average mandrill brain size in adulthood is 123g (DeFelipe, 2011), the postnatal brain size of this species is unknown. Research on other Old World monkeys indicates that primates belonging to this taxonomy are born with a prenatal brain size that is between 50 and 60% of its adult size (DeSilva & Lesnik, 2008). Compared to great apes, brain development in Old World monkeys is thought to take place over a longer period. Although brain growth trajectories have not been studied within mandrills, it is known that female mandrills reach their adult body size at the age of 7, while males often continue to grow until 9 or 10 years of age (Setchell et al., 2001). Mandrills are known to consume considerable amounts of fruits during fruit-rich seasons, whereas their diet is largely comprised of seeds and woody tissues when fruit availability is low (Hongo et al., 2017).

White-faced saki (Pithecia pithecia)

Similar to the Goeldi's monkey, white-faced sakis belong to the taxonomy of New World monkeys (Goodman et al., 1998). They have an average adult brain size of 31.7g, but to my knowledge, no information on the postnatal brain size of this species is available (Harvey & Clutton-Brock, 1985). However, other closely related New World monkey species (including *Alouatta palliatta* and *Ateles geofrroyi*) are born with postnatal brain sizes ranging from 50 to 60% of their adult size. This suggests that the white-faced saki postnatal brain size lies somewhere in this range. The diet of white-faced sakis mainly consists of fruits, leaves and, insects, but fruit is their dominant nutritional source (Norconk & Conklin-Brittain, 2004).

However, compared to other frugivores their lipid consumption is considerable due to high intake of young seeds and other plants high in lipids.

Goeldi's monkey (Callimico goeldii)

Goeldi's monkeys are taxonomized as New World monkeys (Goodman et al., 1998). They are born with a postnatal brain size of 5.8g, which grows to an adult size of 10.8g (Harvey & Clutton-Brock, 1985). Thus, Goeldi's monkeys are born with a brain of more than 50% of its adult size. While it is unknown at what age the Goeldi's monkey reaches adult brain size, most increase in body weight takes place in the first 24 months of life (Ross et al., 2010). The Goeldi's monkey diet consists primarily of fungi, fruits, arthropods, and exudates (Porter et al., 2007).

This study

The aim of this study was to determine the relationship between age and preference for sweetness in non-human primates. More specifically, my research team and I compared the preference for sweet foods in subjects belonging to different species and varying in age. In addition, we studied whether this relationship is mediated by remaining brain growth to adult stage. This was based on the assumption that human children have a stronger preference for sweetness due to their considerable remaining brain growth. As non-human primates are evolutionary and genetically close to humans (Takahata & Satta, 1997), studying the former could tell us more about the biological causes of human behavior. In other words, assessing the relationship between age and brain growth and sweetness preference in non-human primates can help us learn more about the biological origins underlying the exaggerated preference for sweet food in human children. Additionally, the current study can provide a different perspective on the sweetness preference compared to other studies which suggest that the preference for sweet tastes in humans is culturally determined (Sorokowska et al., 2017). The current study can therefore provide new insights into the debate on whether the sweetness preference is biologically or culturally determined. Based on these research goals, this study can provide various practical implications. For instance, conclusions drawn from this study can be helpful in designing appropriate diet guidelines for young children. Although it is important that diet professionals should take the negative effects of excessive sugar intake into account, its potential significance to brain and body growth should not be forgotten. The current study can therefore provide information that is valuable to science and society.

Hypotheses

Firstly, it was expected that in all included subjects, age would be negatively related to the preference for sweetness. In other words, younger subjects would exhibit a stronger sweetness preference than older subjects. This resulted in the following hypothesis:

- H1: There is a negative relation between age and sweetness preference in non-human primates.

This hypothesis was based on human research, showing that young children have a stronger preference for sweetness than juveniles and adults, with the former having a stronger preference than the latter (Venditti et al., 2020). Similarities between humans and non-human primates are expected due to overlap in brain development (Mcfarlin et al., 2012).

Secondly, I hypothesized that the preference for sweetness is dependent on the extent of completed brain growth. Additionally, it was expected that the relationship between completed brain growth and sweetness preference is stronger than the relationship between age and sweetness preference. This resulted in the following hypotheses:

- H2a: There is a negative relationship between completed brain growth and sweetness preference in non-human primates.
- H2b: The relationship between completed brain growth and sweetness preference is stronger than the relationship between age and sweetness preference.

These hypotheses are supported by literature suggesting that the preference for sweetness in human children is linked to nutritional needs for the support of brain growth and not body growth in general (Ventura & Mennella, 2011).

Finally, I predicted that the effect of age on sweetness preference interacts with subjects' evolutionary relatedness to humans. This resulted in the following hypothesis:

- H3: The negative effect of age on sweetness preference in non-human primates is moderated by evolutionary relatedness to humans, with the effect being strongest in great apes, then Old World monkeys, and weakest in New World monkeys.

This hypothesis was based on research showing that great apes are evolutionary closest to humans, followed by Old World monkeys and New World monkeys, respectively, and therefore are likely to have a brain structure that is more similar to humans (Takahata & Satta, 1997).

Methods

Study subjects

Data was collected at ARTIS Amsterdam Royal Zoo between 17-03-2025 and 16-05-2025. The following four species were included in this study: western lowland gorilla, mandrill, white-faced saki, and Goeldi’s monkey. The studied species belong to the following taxonomic groups: great apes (western lowland gorilla), old world monkeys (mandrill), and new world monkeys (white-faced saki and Goeldi’s monkey). The western lowland gorilla group consisted of nine individuals aged between 76 months (6 years) and 459 months (38 years), including six males and three females (see Table A1 in Appendix A). Their diet included primarily vegetables and pellets, making it relatively low in sugar. However, depending on the day food such as honey or seeds were added to the diet. The mandrill group consisted of ten individuals aged between 58 months (4 years) and 288 months (23 years), including three males and seven females (see Table B1 in Appendix B). Their diet was primarily comprised of vegetable and fruits. In addition, depending on the day they also received food such as pellets, seeds, and honey. The white-faced saki group consisted of four individuals aged between 23 months (1 year) and 423 months (35 years), including three males and one female (see Table C1 in Appendix C). Their diet contained various fruits and vegetables and other food such as eggs, pellets, and nuts. The sugar levels in this diet were considerably higher compared to the western lowland gorilla and mandrill group. Finally, the Goeldi’s monkey group consisted of five individuals aged between 4 months and 123 months (9 years), including four males and one female (see Table D1 in Appendix D). Their diet was similar to that of the white-faced saki group. More detailed information on all diets is available in the appendix (see Table A2, Table B2, Table C2, and Table D2).

This study was part of an enrichment program of ARTIS Amsterdam Royal Zoo by providing a novel food source and choice. The research activities of this study were completely integrated into the daily routine of all the studied subjects and participation was voluntary. None of the animals were manipulated, nor were they deprived of water or food at any time during the study. As the current study was non-invasive, it does not fall under the definition of an animal experiment according to Article 1 of the Dutch Experiments on Animals Act. Complying with Dutch law, the study adhered to all institutional guidelines for animal research. The study was conducted with the approval of ARTIS Amsterdam Royal Zoo.

Tasks

Two-Choice Task

The preference for sweetness in non-human primates was studied using a task designed by my research team and me, taking inspiration from previous preference tests that have been conducted at ARTIS Zoo, alongside normal diet intake during feeding time. In the self-designed task, subjects were presented with courgette pieces that were either sweet or non-sweet. Piles of courgettes were spread around the enclosure, each containing both sweet and non-sweet courgette pieces. As non-human primates share strong similarities in vision with humans (Jacobs, 2008), it was assumed that courgette pieces could be distinguished based on color (i.e., dark green or light green). Through this task, sweetness preference was determined by measurement of the following variables: the first courgette piece that was consumed (see Table F1 in Appendix F for definition) by the subject, the proportion of sweet courgette pieces consumed by the subject, and the proportion of non-sweet courgette pieces that were rejected by the subject. Based on these variables, it could be determined whether the subjects preferred one courgette type over the other. More information on each variable is provided in the statistical analysis section. Additionally, availability of both courgette types was taken into account to know what options were left to the subject. In order to give all subjects the possibility to pick one or more courgette pieces, the number of piles was brought into proportion to the number of studied subjects in the enclosure. Subjects' engagement with the courgette pieces was measured for a total time of 45 minutes per observation. Because the self-designed task was not based on earlier research, extensive pre-testing was performed in all included subjects. In this phase, attention was paid to subjects' engagement with courgette pieces, location of the courgette pieces, and the influence of social dynamics.

Normal Diet Task

In addition, the preference for sweetness in all included subjects was assessed based on their normal diet intake. This was determined by using the following variables: (1) the relative sugar concentration of the first normal diet item that was consumed by the subject and (2) the order of the first twenty consumed food items. More information on these variables is also included in the analysis section. Food items such as pellets and seeds were not included in the data collection due to incomparability in terms of quantity and effort to other food items. Measurement of normal diet intake was therefore focused exclusively on the provided vegetables and fruits. The following exclusion criteria were used during data collection: food that was stolen, less than two bites taken, and the subject being out of sight. In addition, in the self-designed task courgette leftovers (i.e., peels) were excluded from the data collection.

Procedure

Measuring Sweetness Preference

Data on sweetness preference was collected by observing feeding behavior in the included subjects using continuous sampling. During each session, every observer in my research team studied one subject for a total time of forty-five minutes. Two types of courgettes were used that differed slightly in color: *cucurbita pepo* (dark green) and *cucurbita pepo magda (F1)* (light green). This helped subjects and my research team to distinguish the courgette based on physical characteristics. During the first half of the study, the light green cucurbita pepo magda (F1) courgette slices were sweetened, while the dark green courgette cucurbita pepo slices were sweetened during the second half of the study. This was done to account for the potential effects of color on food choice. For a more detailed description of the courgette preparation process, see Appendix E. After being soaked in sweetened water, 149 mM of sucrose was absorbed in the courgette slices. Both the non-sweet dark green and light green courgettes slices, on the other hand, contained 74mM of sucrose. These sucrose levels were sufficiently above the taste thresholds of non-human primates, as literature shows that New World monkeys, Old World monkeys, and great apes are all able to detect sucrose levels as low as 20mM (Hurtado et al., 2023; Laska et al., 1999; Norlén et al., 2018). Moreover, since most primate diets are relatively low in sugar content in ARTIS Zoo, it can be expected that their sensitivity to sucrose was heightened. The sucrose levels in the current study were discussed with the zoo vet and permission for using them was gained.

After the courgette slices were soaked in either neutral water or sweetened water, they were cut into smaller pieces proportionally to the size of the studied species. While the western lowland gorilla group received courgette slices that were cut in half, the mandrill, white-faced saki, and Goeldi’s monkey group received slices that were cut in four. Courgette pieces were presented to the subjects alongside their normal diet during feeding time. Placement of the courgette pieces, however, differed between species and was dependent on their enclosure and feeding behavior. Sufficient courgette pieces were placed in the enclosure by the caretakers to ensure availability for all individuals and avoid competition. In the western lowland gorilla group, nine piles consisting of eight courgette pieces (four sweet and four non-sweet) were spread around the enclosure and located somewhat separately from the normal diet food. In the mandrill group, ten pieces of an equal amount of courgette pieces were spread around the enclosure in a similar manner. Contrary to the two previous groups, in the white-faced saki group courgette pieces were placed in feeding troughs. Four feeding troughs were spread around the enclosure, each one containing eight courgette pieces (four sweet and four non-sweet). In the Goeldi's monkey group, courgette pieces were also placed in feeding troughs. The enclosure included three feeding troughs, resulting in 14 courgette pieces (7 sweet and 7 non-sweet) per trough. After all pieces were placed in the enclosure, the observation started. As focal continuous sampling was used in the current study, each observer focused on one subject during the observation and measured its feeding and social behavior. Observing non-adult and adult individuals simultaneously ruled out other confounding variables, such as hunger and satiation levels. Measurements were based on behavior descriptions included in an ethogram made in advance of the data collection (see Table F1 in Appendix F). A randomized schedule was followed for the data collection in which all subjects were evenly rotated.

Measuring Brain Size

To measure the extent of completed brain growth for each individual included in this study, brain surface areas estimated based on photographs of lateral head views. Inspiration for this method was taken from the study by (Breuer et al., 2007), where photogrammetry was used to measure body length and head size. In advance of taking pictures, we measured the length of several objects within the relevant enclosures to serve as reference points for scale. These objects included, for example, a barrel, a low wall, and a feeding trough. In the gorilla and mandrill groups, photographs were taken using a camera placed on a fixed stand in front of the enclosure. This resulted in a consistent view and angle on the reference objects. For the white-faced saki and Goeldi's monkey groups, pictures were taken manually by another observer and me due to height differences between the camera stand and the enclosures. Individuals were photographed when they moved into a lateral view. We aimed to capture the individuals in this position as it enabled us to calculate a complete surface area of one side of the brain. Although not used in the current study, back and forepaw length were assessed for all individuals as a measure of body length. After properly positioned pictures were made of all individuals ImageJ (version 1.54p; National Institutes of Health, Bethesda, MD, USA) image analysis software was used for analyzing and estimating brain size.

For each image, we drew three reference lines to assess brain surface area: (1) a vertical line from posterior to the eye down to the jawline, (2) a parallel line going over the ear, and (3) a horizontal line extending from the jawline to the neck (see Figure G1 and Figure G2 in

Appendix G). These lines were drawn based on our earlier studies of skull sizes of primates included in this study. The exact length of each line could be calculated in centimeters using ImageJ by comparing the number of pixels to the known length of a relevant reference object also visible in the picture. Based on the anatomical lines that were drawn, three separate surface areas were calculated. Adding these separate surface areas resulted in a total brain surface area for an individual. Consequently, to estimate the extent of completed brain growth, brain surface area of the individuals below or around the sexual maturation age were compared to the average brain surface area of adult individuals within the same group. Due to sex differences in brain size, individuals were compared to adults of their own sex. Dividing the brain surface area to that of the corresponding adult resulted in an exact percentage of completed brain growth for that individual (see Table A1, Table B1, Table C1, and Table D1 for more information in appendix). In the mandrill group, however, it was decided to compare the brain surface area of two young males to that of the average of both sexes as discrepancies with the adult male were surprisingly large.

Design

This study used a mixed factorial design with between subject factors. The studied dependent variable was sweetness preference, which has a ratio level of measurement. Sweetness preference was measured in multiple ways, as explained in the statistical analysis section. The following independent variables were included in this study: age and completed brain growth. Whereas age was measured in months, completed remaining brain growth was measured in percentages. Both variables had a ratio level of measurement. In addition, the current study controlled for the following moderating variables: random individual effects, species, sex, diet sugar content, colored courgette, trial number, and hierarchical order. Species and sex were included as covariates as individual differences in sweetness preference may have been caused by species-dependent diets in ARTIS Zoo and differences in nutritional intake between sexes. Diet sugar content was included to control for the day-dependent diet in the gorilla and mandrill groups, meaning the sugar concentration of the diet differed per day, potentially making individuals more likely to prefer sweetness on low-sugar days. As primates are known to prefer some colors over others (Hernández et al., 2021; Wells et al., 2008), courgette color was also controlled for. Trial number was included as covariate, as sweetness preference in later stages of the study may have been either stronger due to learning effects or weaker due to a loss of novelty. Finally, hierarchical order was controlled for by creating a hierarchical ranking based on extensive observations (see Figure A2 in Appendix A and Figure B2 in Appendix B). Although it was attempted to make all food options accessible for each individual, it could not be ruled out that higher-ranking individuals monopolized certain (high-sugar) food items or exerted other forms social influence over lower-ranking individuals. All included subjects were observed multiple times over a range of approximately two months, hence the random effect of individual was included in the statistical model.

Apparatus

Hardware equipment used during the data collection included voice recorders and binoculars. Microsoft Office Excel software was used for integration of data. ImageJ (version 1.54p; National Institutes of Health, Bethesda, MD, USA) image analysis software was used for brain size measurement.

Observations

Data collection in the current study was performed by four university students with an academic education. Interrater variability was controlled for by performing an interobserver test and calculating a subsequent Spearman's rank correlation coefficient (r_s). The following behaviors were included in the interobserver test: eating behavior, rejections, and displacements (see Table F1 in Appendix F for definitions). For eating behavior, r_s ranged from 0.70 to 0.89; for rejections, r_s ranged from 0.60 to 1.00; and for displacements, r_s ranged from 0.65 to 0.90. Although correlation coefficients should be at least 0.70 according to Bateson and Martin (2021), minimal values were not lower than 0.60, making the relationships fairly substantial. For more information on the interobserver test, see Table H1, Table H2, and Table H3 in Appendix H.

Statistical Analyses

In the first analysis, the hypothesis that there is a negative relation between age and sweetness preference (H1) was tested using a binomial generalized linear mixed model (first choice courgette), two beta generalized linear mixed models (proportion sweetness and rejected unsweet courgette), and two linear mixed-effects models (first choice normal diet and food order normal diet), with sweetness preference as the response variable and age in months as the fixed effect. The predictor age in months was always log-transformed to take the non-linear relationship between age and sweetness preference into account and standardized to control for inter-species differences. As this hypothesis examined the overall effect of age on sweetness preference across all species, no interaction between age and species was included here. This interaction effect was therefore examined later in the analysis.

In the second analysis, the hypothesis that there is a negative relation between completed brain growth and sweetness preference (H2a) was likewise tested using (1) a binomial generalized linear mixed model, (2) two beta generalized linear mixed models, and (3) two linear mixed-effects models, with sweetness preference as the response variable and completed brain growth as fixed effect in all models. Before conducting the main analysis, a multicollinearity check was performed using variance inflation factor (VIF) values. As the results suggested considerable levels of multicollinearity between age and completed brain growth, it was decided to test the effect of the two predictors in separate models. Additionally, the hypothesis that the effect of remaining brain growth on sweetness preference is stronger than the effect of age on sweetness preference (H2b) was tested by comparing the AIC values of the two models.

Finally, the hypothesis that the effect of age on sweetness preference is moderated by evolutionary relatedness (H3) was tested by conducting pairwise comparisons of the estimated marginal slopes of the previously performed models, with sweetness preference as the response variable and the interaction between age in months and species as the fixed effect. Separate analyses were conducted for the full species sample and for a subset including only individuals from the gorilla and mandrill groups. In the all-species subset, the following covariates were included: species, sex, and colored courgette. The same covariates were included in the gorilla-mandrill subset, alongside diet sugar content and normalized David's Score. Individual was added as the random intercept in all analyses. The covariate trial number was removed from all models due to considerable levels of multicollinearity with the covariate colored courgette. Data was described as missing when subjects were out of observer sight for a certain amount of time. All data was screened for the presence of potential outliers before performing the statistical analyses. The remainder of this section will be used to explain the sweetness preference variables and provide information on their operationalization.

Courgette First Choice Model

It was measured during the data collection whether the first courgette consumed by the subject was sweet or non-sweet. This was operationalized in the data sheet by the assignment of binary values to both options (non-sweet courgette = 0 and sweet courgette = 1). However, if the subject had no choice option due to lack of availability of one type, that data point was not included in the model.

Proportion Sweet Courgette Model

In this model, the number of consumed sweet courgettes was compared to the total number of courgettes that were consumed by the subject during the total observation time. The following equation was therefore used to calculate this proportion: $\frac{\text{total number of consumed sweet courgette}}{\text{total number of consumed courgettes}}$. If the subject had no choice option due to lack of availability of one type, the data point was not included in the model.

Proportion Rejected (Non-Sweet) Courgette Model

Rejection occurred when the subject did not consume a piece of food after tasting, sniffing, or holding it earlier (see Table F1 in Appendix F for definitions). In this model, a proportion of non-sweet courgette rejection was calculated using the following equation: $\frac{\text{total number of rejected non-sweet courgette}}{\text{total number of rejected courgette}}$.

Normal Diet First Choice Model

Similar to the courgette first choice model, this model measured the first consumed food by the subject that is part of the normal diet. This variable was operationalized by dividing the sugar concentration of the first consumed food item by the average sugar concentration of the normal diet, resulting in a standardized value. Courgettes were not included in the model.

Food Order Correlation Model

Finally, to test whether individuals had the tendency to consume high-sugar food items earlier and low-sugar food items later in the food order, a Spearman's rank correlation was computed by running a test on the sugar concentrations of the first twenty food items that were consumed by the subject using R (version 4.4.2.). This resulted in a value ranging from -1.00 to 1.00, with negative values suggesting that food items early in the food order are higher in sugar content. However, for the sake of consistent interpretation, correlation values where inverted so that higher values represented a stronger tendency to choose food items high in sugar earlier in the consumption order. Courgettes were not included in the model.

All hypotheses were tested at alpha level .05. The statistical analysis was performed using R (version 4.4.2).

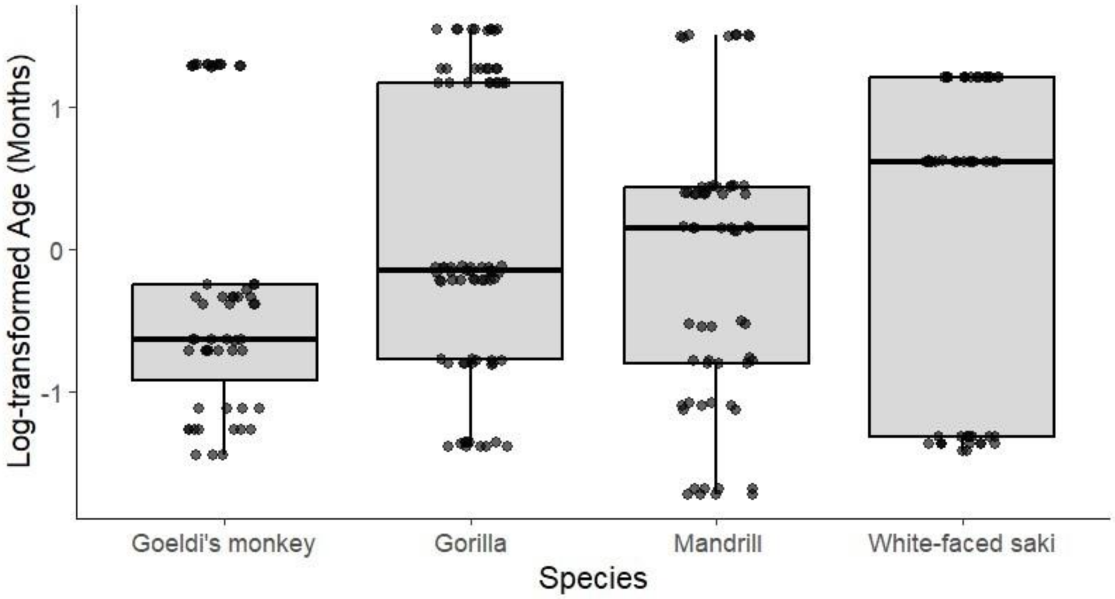
Results

Individuals were excluded from analyses for a given model if they did not have at least five recorded observations of the preference measure (e.g., courgette first choice model). Four individuals were removed altogether from the data analysis because they had fewer than five observations in any of the models. Additionally, one pregnant individual belonging to the Goeldi's monkey group was excluded from further analyses as the pregnancy may have influenced feeding behavior during data collection. The number of observations ranged from 24 to 142 in the all-species models and from 55 to 79 in the gorilla-mandrill subset.

The species included in this study differed in their mean age. Individuals belonging to the Goeldi's monkey group had the lowest mean age, while this was highest in the white-faced saki group (Figure 1).

Figure 1

Boxplot Showing the Log-Transformed Age Distribution for All Species and Across All Models

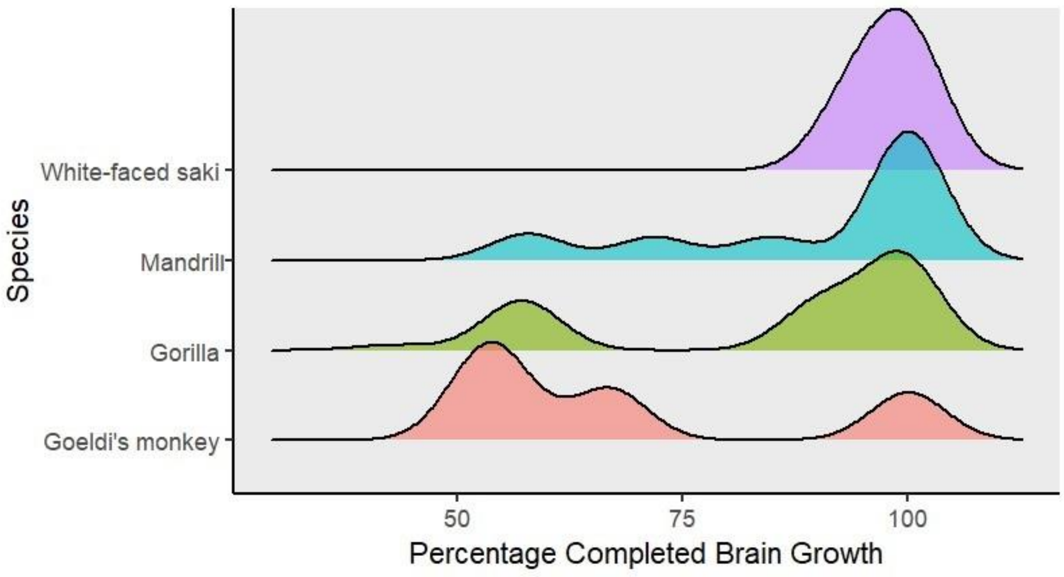


Note: log-transformed age was standardized to account for inter-species differences.

Completed brain growth showed a similar distribution to that of age (Figure 2). Levels of completed brain growth were relatively low in the Goeldi's monkey group, whereas individuals in the white-faced saki group had little or no brain growth remaining. Although brain growth was completed in most individuals belonging to the gorilla and mandrill groups, each group had a number of individuals with considerable brain growth remaining.

Figure 2

Density Plot Showing the Distribution of Percentage Completed Brain Growth for All Species and Across All Models



The pooled mean proportions of the first choice courgette, proportion sweet, and rejected unsweet courgettes models are all above 0.5 (Table 1). The mean of the continuous first choice normal diet is higher than 1. Finally, the mean correlation for the food order normal diet is positive and greater than 0.

Table 1

Descriptive Statistics for the All-Species Sweetness Preference Models

Terms	Mean	SD	N
First Choice Courgette	0.57	0.39	142
Proportion Sweet	0.65	0.41	142
Rejected Unsweet Courgette	0.79	0.36	24
First Choice Normal Diet	1.08	0.56	129
Food Order Normal Diet	0.23	0.56	98

Note: means of the first choice courgette and proportion sweet models represent proportions, with higher values indicating a greater likelihood of choosing the sweet courgette. The mean of the rejected unsweet courgette model also represents a proportion, with higher values indicating a greater likelihood to rejection of the sweet courgette. The mean of the first choice normal diet model represents a continuous variable, with values > 1 indicating a greater likelihood of choosing a high-sugar food item first. The mean of the food order normal diet model represents a Spearman's rank correlation, with positive values indicating a greater likelihood of choosing high-sugar food items earlier in the food order.

It is important to note that three of the performed models (i.e., first choice courgette, first choice normal diet, and food order normal diet) gave boundary (singular) fit warnings. It was nevertheless decided to run these models, but results should be interpreted with caution. Additionally, individuals belonging to the white-faced saki group were not included in the first choice normal diet and food order normal diet models due to a lack of observations. The linear mixed-effects models were checked for the assumptions of normality of residuals and normality of random effects. Both assumptions were met (see Appendix I).

H1: Effect of Age on Sweetness Preference

Five all-species models were performed to study the effect of age on sweetness preference: a binomial generalized linear mixed model (first choice courgette), two beta generalized linear mixed models (proportion sweetness and rejected unsweet courgette), and two Gaussian linear mixed-effects models (first choice normal diet and food order normal diet). Each model included age as the fixed effect, alongside the following covariates: species, sex, and colored courgette. Individual was included as a random intercept. Finally, to account for the limited number of recorded observations in the rejected unsweet courgette model, colored courgette was in this model removed as covariate. No interactions were tested for this hypothesis.

None of the performed models found a significant effect of age (Table 2). However, sex had a significant effect on first choice courgette (β = -1.064, *SE* = 0.418, *p* = 0.011) and proportion sweetness (β = -0.619, *SE* = 0.257, *p* = 0.016), with male individuals being less likely to choose the sweet courgette option than females. Additionally, it was found that individuals belonging to the gorilla (β = 0.401, *SE* = 0.097, *t*(129) = 4.133, *p* < 0.001) and mandrill (β = 0.326, *SE* = 0.139, t(129) = 2.335, *p* = 0.020) groups had significantly higher values in first choice normal diet model than individuals in the Goeldi's monkey group. This means that the first consumed normal diet food item in the gorilla and mandrill groups was higher in sugar content relative to the overall diet compared to the Goeldi's monkey group. Lastly, there was a significant effect of the courgette color in the food order normal diet model (β = -0.518, *SE*= 0.229, *t*(85) = -2.768, *p* < 0.007), indicating that items high in sugar content appeared later in the food order when the light green courgette was sweetened compared to when the dark green was sweetened.

Table 2

Results of the Performed Models in the All-Species Sample: Fixed Effects of Log-Transformed Age and Likelihood Ratio Tests for Full Models.

Terms	Estimate	SE	z/t-value	p-value	χ^2 (full model)	p-value (full-null model)
First Choice Courgette	-0.019	0.191	-0.101	0.920	13.669	0.034
Proportion Sweetness	0.001	0.122	0.007	0.994	10.505	0.105
Rejected Unsweet Courgette	-0.019	9.860	-0.002	0.998	3.301	0.509
First Choice Normal Diet	-0.014	0.043	-0.322	0.748	15.062	0.010
Food Order Normal Diet	-0.116	0.095	-1.223	0.225	10.864	0.054

The same models were performed to study the effect of age on sweetness preference in the gorilla-mandrill subset. Alongside the fixed effect of age, the following covariates were now included: species, colored courgette, normalized David's Score, and diet sugar content. The covariate sex was excluded from all models in the gorilla-mandrill subset due to considerable levels of multicollinearity with species. Individual was again included as random intercept. No interactions were tested for this hypothesis.

Again, there was no effect of age in any of the performed models (Table 3). However, individuals belonging to the mandrill group differed significantly from the Gorilla group in the first choice courgette (β = 2.275, *SE* = 0.921, *p* = 0.014) and proportion sweetness (β = 1.060, *SE* = 0.454, *p* = 0.020) models, suggesting a stronger preference for the sweet courgette option in mandrills compared to gorillas. In the food order normal diet model, significant effects of courgette color (β = -0.776, *SE* = 0.240, *t*(55) = -3.232, *p* = 0.002) and diet sugar content (β = -0.156, *SE* = 0.072, *t*(55) = =2.155, *p* = 0.036) were found.

Table 3

Results of the Performed models in the Gorilla-Mandrill Subset: Fixed Effects of Log-Transformed Age and Likelihood Ratio Tests for Full Models.

Terms	Estimate	SE	z/t-value	p-value	χ^2 (full model)	p-value (full-null model)
First Choice Courgette	0.234	0.287	0.810	0.418	8.866	0.115
Proportion Sweetness	0.092	0.174	0.529	0.597	8.868	0.115
First Choice Normal Diet	-0.008	0.057	-0.143	0.886	4.189	0.523
Food Order Normal Diet	-0.078	0.122	-0.636	0.528	12.910	0.024

H2a: Effect of Completed Brain Growth on Sweetness Preference

To study the effects of brain growth on sweetness preference, the five models were performed again, with completed brain growth replacing age as the fixed effect. Species, sex, and courgette color were included as covariates and individual as the random intercept.

All models revealed that that there was no significant effect of completed brain growth (Table 4). Sex did have a significant effect on first choice courgette (β = -1.154, *SE* = 0.439, *p* = 0.009) and proportion sweetness (β = -0.667, *SE* = 0.270, *p* = 0.014), suggesting again that male individuals were less likely to choose the sweet courgette option than females. It was also found again that individuals belonging to the gorilla (β = 0.410, *SE* = 0.102, *t*(129) = 4.025, p < 0.001) and mandrill (β = 0.340, *SE* = 0.146, *t*(129) = 2.339, p < 0.021) groups had significantly higher values in first choice normal diet model than individuals in the Goeldi’s monkey group.

Table 4

Results of the Performed Models in the All-Species Sample: Fixed Effects of Percentage Completed Brain Growth and Likelihood Ratio Tests for Full Models.

Terms	Estimate	SE	z/t-value	p-value	χ^2 (full model)	p-value (full-null

						model)
First Choice Courgette	-0.008	0.011	-0.678	0.498	14.122	0.028
Proportion Sweetness	0.004	0.007	-0.501	0.616	10.755	0.100
Rejected Unsweet Courgette	-0.032	0.030	-1.063	0.288	3.301	0.348
First Choice Normal Diet	-0.001	0.002	-0.370	0.712	15.095	0.001
Food Order Normal Diet	-0.004	0.005	-0.814	0.418	10.041	0.074

H2b: Stronger Predictive Value of Brain Growth Compared to Age

To examine whether completed brain growth predicted sweetness preference better than age, the AIC values of the previously performed all-species models were compared. As is shown in Table, the ΔAIC of each model was ≤ 2. Following the thumb rule by Burnham and Anderson (2002), it can therefore be concluded that completed brain growth and age had equal predictive value.

Table 5

AIC Comparison Between Percentage Completed Brain Growth and Log-Transformed Age Models

Terms	**AIC Percentage Completed Brain Growth**	**AIC Log-transformed Age**	**Δ AIC**
First Choice Courgette	192.267	192.720	0.453
Proportion Sweetness	-706.168	-705.916	0.252
Rejected Unsweet Courgette	-153.767	-151.767	2.000

First Choice Normal Diet	197.220	197.253	0.033
Food Order Normal Diet	221.516	220.693	0.823

H3: Interaction Between Age and Species

Finally, to test for an interaction effect between age and species, all models were performed once more. The model included *age x species* as the interaction term, alongside sex and colored courgette as covariates and individual as the random intercept. For each model, pairwise comparisons of the estimated marginal slopes were conducted. Only the rejected unsweet courgette model was excluded from the analysis due to an insufficient number of included individuals.

All estimated marginal slopes are presented in Table 6. No significant pairwise differences between species were found in any of the models ($p > 0.05$ for all pairwise comparisons).

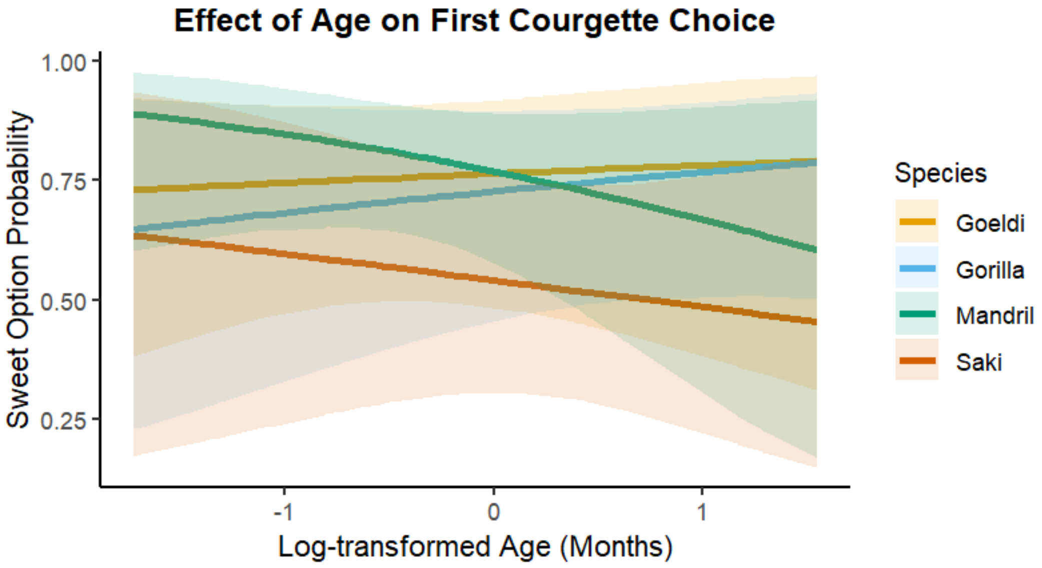
Table 6

Estimated Marginal Slopes for the Interactive Effect Between Age and Species and Likelihood Ratio Tests for Full Models.

Terms	**β Goeldi’s monkey**	**β Gorilla**	**β Mandrill**	**β White-faced saki**	**χ^2 (full model)**	**p-value (full-null model)**
First Choice Courgette	0.100 (SE = 0.429)	0.213 (SE = 0.330)	-0.504 (SE = 0.507)	-0.224 (SE = 0.487)	15.772	0.072
Proportion Sweet	0.271 (SE = 0.282)	-0.035 (SE = 0.209)	-0.281 (SE = 0.295)	0.021 (SE = 0.313)	12.120	0.207
First Choice Normal Diet	-0.050 (SE = 0.084)	0.047 (SE = 0.069)	-0.092 (SE = 0.106)		16.919	0.018
Food Order Normal Diet	-0.267 (SE = 0.185)	-0.032 (SE = 0.127)	-2.060 (SE= 2.160)		12.881	0.075

Figure 3

Graph Depicting the Effect of Age on First Choice Courgette for Each Species



Note: no significant effect of age on first choice courgette was found for any species.

Discussion

The current study was performed with the aim of examining the relationship between age and sweetness preference in non-human primates. As brain development is thought to be a key factor underlying the preference for sweetness in human children (Duvanel et al., 1999), additional attention was paid to the effect of brain growth. This study therefore not only provides new insights into the relation between age and sweetness preference in non-human primates, but can also give us a better understanding of the possible evolutionary origins of taste preferences in humans.

First of all, I hypothesized that a negative relationship between age and sweetness preference in human primates would exist. This was based on scientific evidence showing that human children have a stronger preference for sweetness compared to adults, and findings suggesting that brain structure and development is largely overlapping between humans and non-human primates (Neubert et al., 2015; Mcfarlin et al., 2012; Venditti et al., 2020). However, the results of the current study did not find a significant relation between age and sweetness preference in non-human primates. I did therefore not find support for the first hypothesis. Although this finding suggests that the theory proposed in this paper may have no empirical support, several methodological factors may have been of influence. Firstly, it should be noted that sweetness preference was studied in a different way compared to previous research in non-human primates. In the earlier mentioned studies by Hurtado et al. (2023), Laska et al. (1999), and Norlen et al. (2018), preference for sweet tastes was examined using the so-called two-bottle preference test. During this test, subjects were offered a choice between drinking tap water and water including sugar concentrations (i.e., sucrose, glucose, fructose, maltose, and lactose of high purity) ranging from 10mM to 200mM. Sweetness preference was determined based on the choice between the two options. Similarly, sweetness preference in humans has also been studied by manipulating sugar concentrations in neutral substances, such as water, broth, and jelly (Mennella et al., 2014). The current study, however, examined sweetness preference by adding a fixed concentration of sucrose to a non-neutral food item (courgette) and by observing feeding behavior in relation to the non-manipulated normal diet. As sweetness interacted with flavor and nutrients inherent to courgettes and food items belonging to the normal diet, these factors may have affected subjects' sweetness preference. This did not occur in studies using sugared water, for example, because water has a neutral taste and contains no macronutrients. Although the current study deviated in some aspects from earlier studies on taste preferences in non-human primates, it is important to note that those earlier studies did not investigate the effect of age in non-human primate sweetness preference.

Another aspect of the current study worth discussing is the relatively low-sugar diet of individuals within the gorilla and mandrill groups. While the overall gorilla diet ranged from food items with sugar concentrations from 0 to 5 percent and in the mandrill group even up to 16%, both groups often only received food relatively low in sugars during the observations. For example, individuals belonging to the gorilla group on most days received chicory (2.4% sugar content) alongside another food item relatively low in sugar, such as celery (1%) or bok choy (1.6%). The sweetened courgette was therefore often the sweetest available option for the gorilla and mandrill groups. Individuals belonging to the Goeldi's monkey and white-faced saki groups, on the other hand, received food items relatively high in sugar concentration such as bell pepper (4.3%), carrot (5%) and papaya (7.8%) on a daily basis. As primates have the tendency to prefer higher sugar concentrations over lower sugar concentrations (Hurtado et al., 2023; Laska et al., 1999; Norlén et al., 2018), it may have been the case that both adult and non-adult individuals within the gorilla and mandrill groups had an exaggerated preference for the sweetened courgette, which was often the food item with the highest sugar concentration in their diet. Although I did control for daily differences in sugar content in the gorilla and mandrill groups, the effect of age may nevertheless have been masked as the sweetened courgette was the sweetest option in most cases.

The second hypothesis of this study proposed that there would be a negative relation between the extent of completed brain growth (in percentages) and sweetness preference (H2a), and that the effect size of completed brain growth is stronger than that of age (H2b). This was based on literature suggesting that the preference for sweetness is linked to the nutritional needs for the support of brain growth (Ventura & Mennella, 2011). As I did not find any significant effects, both hypotheses were not supported. Although the method for measuring brain size performed in this study was used by Breuer et al. (2007) to measure body size in wild gorillas, it has not been used to assess brain size before. As it was not possible for us to compare our brain size estimates to the actual brain sizes of the individuals included in this study, the level of accuracy of this novel approach is uncertain. The reliability of completed brain growth of the younger study subjects as predictor is therefore unknown.

Finally, I hypothesized that the negative effect of age on sweetness preference would be moderated by evolutionary relatedness to humans. More specifically, the effect of age was expected to be largest in gorillas, followed by mandrills, and then white-faced sakis and Goeldi’s monkeys. As no significant differences between species were found, the third hypothesis was also rejected.

While this study did not find evidence for a relationship between age or brain growth and sweetness preference, the results did show that sex significantly predicted this preference in the first choice courgette and proportion sweetness models. Female individuals were more likely to choose the sweet courgette option as their first choice and consumed a higher proportion of sweetened courgettes overall compared to males. While not much information is available on the relation between sex and taste preferences in non-human primates and studies on sex differences in humans provide mixed findings (Sena-Esteves et al., 2017; Yamazawa et al., 2007), both early and recent research has showed evidence for a similar pattern in rats and mice (Valenstein et al., 1967; Pan et al., 2024). It has been suggested that the preference for sweetness in female animals may be related to increased taste sensitivity as a result of hormonal fluctuations during the estrous cycle and pregnancy (Clarke & Ossenkopp, 1998). This corresponds with the observation in the current study that the pregnant individual excluded from the data analysis showed the most pronounced preference for sweet courgette pieces.

Significance

As the effect of age on sweetness preference has not previously been tested in non-human primates, this study provides new insights into animal taste preferences and the evolutionary origins of human behavior. Contrary to the stated hypotheses, I did not find a significant effect of age or the extent of remaining brain growth on sweetness preference. The results do therefore not support the idea that the exaggerated preference for sweetness in human children has an evolutionary origin. However, it remains possible that this preference emerged in a later evolutionary phase or is related to human-specific characteristics. It can therefore not be ruled out that an effect of age on sweetness preference may exist in more closely related species, such as chimpanzees and bonobos. Thus, it is important to keep the discussion on the origin of the preference for sweetness in human children open and consider both the evolutionary and cultural perspectives. In addition to increased theoretical understanding, new methods on measuring taste preference and brain size were developed in the current study and can be built upon by future studies. Both methods did not impose demands on the studied individuals, such as forced choice or sedation, and could be performed within the animals' regular enclosures. The methods thereby fully took account of the wellbeing of all studied subjects and correspond with the ethical guidelines for animal research. Compared to earlier animal research, the methods used in this study offer significant improvements. In a time of changing ethical standards, zoos can therefore provide an ethically responsible environment for conducting animal research.

Based on the conclusions of this study, it is recommended that developers of dietary guidelines adopt a nuanced perspective that takes both possible evolutionary and matri-cultural factors influencing sweetness preference into account (Venditti et al., 2020). However, it remains fixed that human children have a biological need for food containing carbohydrates, including sugar (Duvanel et al., 1999). It is essential that children on the one hand consume sufficient sugar levels to meet their biological needs, while at the same time ensuring that these levels do not exceed healthy intake and thereby increase the risk of overweight and obesity. Instead of targeting natural sugars, such as found in fruits, diet experts should focus on reducing the intake of processed sugars in children, which have been consumed increasingly in younger age groups over the past decades (Lara-Castor et al., 2024).

Limitations

Although I aimed to answer the stated hypotheses in a thorough and reliable manner, some limitations are faced. Firstly, the measurements to assess sweetness preference, while fairly extensive, may still have been too limited in scope. It was decided to examine sweetness preference using first food-item choices, the proportion of sweetened courgette consumed, and total food order, but other measures such as frequency of choice were not included. For example, measures such as frequency could provide meaningful additional information on the pattern of sweetness preference in the studied individuals. To illustrate this: a proportion of 0.75 could represent the consumption of 3 sweet courgettes and 1 unsweet courgette, but it could also refer to 12 sweet courgettes and 3 unsweet courgettes. In other words, valuable information may have been lost by omitting frequency as a measure in the current study. Using a poisson model based on frequencies with the number of overall choices as an offset term could have offered a broader perspective on sweetness preference. Additionally, although the collection order of normal diet items was measured for the gorilla group, this information was excluded from the data analysis to keep the number of tested models feasible within my study. This means, however, that potential meaningful information regarding sweetness preference has been lost. It is possible that subjects collected preferred food earliest, while actually consuming it later in the food order, as humans are often known to do (Jeong et al., 2014).

Speed-Accuracy Tradeoff

Secondly, collecting data during regular feeding time may particularly have impacted the results in the gorilla and mandrill groups. These groups only received a limited amount of food at fixed moments during the day, making it a considerable hectic setting. At the start of feeding time, individuals came running into the enclosure and foraged in a hasty manner, which can be attributed to competition for the available food sources. This meant that individuals – especially during the first minutes of feeding time – did not always appear to make deliberate foraging decisions. For example, it was observed multiple times that the youngest gorilla – who was also low in rank (see Figure A2 in Appendix A) – consumed an entire pile of courgette pieces (both sweet and nonsweet) within a few seconds. Given the hectic of regular feeding time in the gorilla and mandrill groups, it can be suggested that individuals have felt a certain extent of time pressure, which reduced their decision-making accuracy. This corresponds with the phenomenon known as the speed-accuracy tradeoff, referring to an increase in suboptimal decisions and errors when a task is performed under time pressure (Heitz, 2014). Although this phenomenon was originally studied in humans, it is also known to exist in non-human primates. It can therefore be thought that individuals may sometimes have made suboptimal feeding-decisions during regular feeding time in the gorilla and mandrill groups. This problem could be mitigated by allowing individuals more freedom and flexibility in when they consume the food item. Administering the food outside regular feeding times might already lead to a significant improvement.

Brain Size Measurement

Another methodological limitation faced by the current study is that the method used for measuring brain size was performed here for the first time and its reliability is uncertain. Although the study aimed to measure brain size as accurately as possible using skulls of the relevant species as reference material, the extent of correspondence between the results and the actual brain sizes of the studied individuals remains unknown. Regarding this point, it was particularly surprising to see that the estimated brain size differences between younger and older individuals of the same species did not always correspond with literature. For example, Mcfarlin et al. (2012) found based on brain mass data from necropsy reports that mountain gorillas show considerable brain growth in the first years of life and that brain mass should be nearing completion around the age of four. The current study, on the other hand, estimated that the brain surface area of two gorillas relatively young in age but older than four years, had not reached 60% yet. It should be noted here that western lowland gorillas are known to have considerably slower fast growth trajectories than mountain gorillas (Breuer et al., 2008). The current study also had the advantage of estimating brain size in living individuals. Yet, some discrepancies between the (limited) literature available on non-human primate brain growth trajectories and estimates from this study are surprisingly large.

Theoretical Limitations

Finally, the theoretical assumptions behind this study may have certain flaws. Although it was assumed that taste preference in humans and non-human primates have similar evolutionary origins, the preference for sweetness in human children may be an evolutionary adaptation that is not found in other species. As the human brain develops to a considerable larger extent than that of non-human primates (Gilmore et al., 2018; Sherwood et al., 2008), an evolutionary preference for sweetness to support brain development may only exist in humans. It should also again be noted that some research suggests that the preference for sweetness in humans has a cultural basis instead, as sweetness preference is thought to be associated with Western cultures and modern lifestyles (Venditti et al., 2020). For example, Sorokowska et al. (2017) found that Polish adults had a heightened preference for sweetness compared to Tanzanian hunter-gatherers. A cultural origin underlying sweetness preference in humans could explain why this preference was not found in non-human primates.

Future Research

Despite the new insights into sweetness preference in non-human primates provided by this study, many aspects have remained uncovered or can be improved. Firstly, it is recommended that future research uses a wider array of measurements to determine sweetness preference. While this study looked at first food-item choices, proportion, and total food order, measurements such as frequency of choice and total collection order should be included in future studies to examine the preference from more perspectives. This is essential as sweetness preference in non-human primates cannot be performed through verbal questioning as is often done in humans. Secondly, to prevent speed-accuracy tradeoffs future research should test sweetness preference in settings with no time-constraints. Testing during outside regular feeding times might therefore be advantageous. Preferably, individuals are tested in an individual manner to minimize the effects of social competition. However, as separation is currently not allowed under zoo regulations, competition between individuals can be reduced by spreading the food widely within enclosures. Doing this will increase the reliability and validity of future findings. Thirdly, future research could further develop the method of measuring brain size in non-human primates that was designed and performed in this study. Despite the significance of brain size and development in non-human primates and the possibilities of learning more about human behavior, relatively little is known about brain growth trajectories in these species. Because the method for assessing brain size that was developed in this study is low-cost, undemanding, and non-intrusive, future research could build further upon this method to measure non-human primate brain size in an inexpensive and ethical manner. Limitations currently existing in the method could be improved by future research to enhance its accuracy. Importantly, to get a better indication of the reliability of this method, comparing measurements to the actual skull and body sizes of anesthetized individuals could be very informative. Finally, although it was beyond the scope of this study, future research could further investigate the relationship between sex and sweetness preference, as some significant effects were found in the current study.

Conclusion

This study examined the effect of age on sweetness preference in four non-human primate species. As no significant effect was found of age, completed brain growth, or evolutionary relatedness, no support was found for the argument that the exaggerated preference for sweet food in human children has an evolutionary origin in non-human primates. Instead, the results suggest that the preference for sweetness in human children may have been a more recent human-specific evolutionary adaptation or a cultural phenomenon. More research on the relationship between age and sweetness preference in non-human primates will give us a deeper understanding on the evolutionary origins of human taste preferences and healthy living.

Acknowledgements

There are several people I would like to thank for their support throughout this project. Firstly, I want to thank the members of my research team – Floor van ‘t Hof, Inim Schenk, and Kiki Harsevoord – for their effort, collaboration, and laughter. Secondly, I would like to thank my supervisor, Karline Janmaat, for her guidance and support and for giving me the amazing opportunity to conduct research at ARTIS Zoo. I also want to thank Tonny Mulders of the University of Amsterdam and Tim van Olmen of Utrecht University for providing us with skulls and valuable insights for the development of our brain size measurement method. Finally, I wish to express my sincere gratitude to the caretakers– Iwo Nelson, Nathalie Roorda-Garius, Sandra de Groot, Teun van de Bergh, Katy Koning, Boy Roeles, Mark Barrink, and Quinten Loeff – who contributed to this project, and to all the other workers at ARTIS Zoo who made us feel at home.

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Appendix

Appendix A: Gorillas Living in ARTIS Royal Zoo

Figure A1

Pictures of the Individuals Belonging to the Gorilla Group

Note: Photographs were made by Ezzy's Artis gorilla's.

Table A1

Characteristics of the Individuals Belonging to the Gorilla Group

Name	Sex	Age (years)	Age (months)	Date of birth	Brain surface area (cm^2)	Characteristics
Dafina	Female	38	458	02-01-1987	82.38	Smaller build; Clear eyebrow bone; Browner head (than Binti)
Binti	Female	32	388	19-11-1992	112.00	Dark black fur; Biggest belly;
Akili	Male	30	365	16-10-1994	135.56	Silverback male; Pointy head
Bembosi	Male	13	165	31-05-2011	122.54	Dark black fur; Smooth nose; Long upper body
Shambe	Male	13	162	04-09-2011	121.30	Brown/red stripe on the back; Biggest of the group (except Akili)
Douli	Male	13	156	27-02-2012	131.43	Almond shaped eyes; Wrinkled nose; Often sits cross-legged
Shae	Male	9	109	21-01-2016	78.75	Relatively small male; “Serious” look; Flat back
Yanga	Female	8	100	29-10-2016	67.83	Hollow back; Browner head; Built small; Seeks eye contact
Damsi	Male	6	77	18-10-2018	75.95	Smallest of the group; Wrinkled nose

Figure A2

Normalized David's Score (Dominance Hierarchy) of the Individuals Belonging to the Gorilla Group

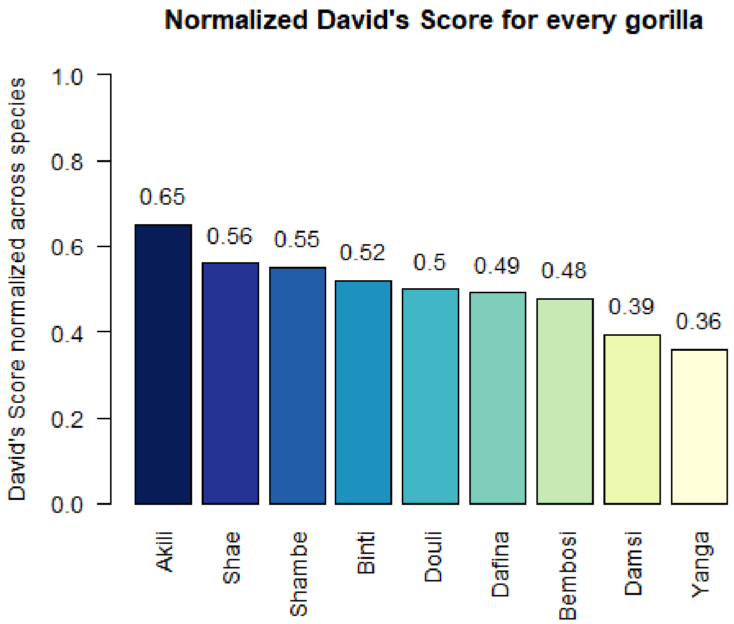


Table A2

Normal Diet of the Gorilla Group

Type of vegetable/fruit	Sugar concentration
Beet	6
Bell pepper	4.3
Bimi	0.4
Bok choy	1.6
Broccoli	0.4
Carrot	5
Celery	1
Chicory	2.4
Chinese cabbage	0
Cucumber	1.2
Endive	0.8
Fennel	2
Iceberg lettuce	1.6
Kohlrabi	4.5
Leek	3.2
Parsnip	5.5
Tomato	3.4
Red cabbage	3.2

Appendix B: Mandrills Living at ARTIS Royal Zoo

Figure B1

Pictures of the Individuals Belonging to the Mandrill Group

Note: photographs were made by Floor van 't Hof and Kiki Harsevoord.

Table B1

Characteristics of the Individuals Belonging to the Mandrill Group

Name	Sex	Age (years)	Age (months)	Date of birth	Brain surface area (cm^2)	Characteristics
Kasamo	Male	23	285	09-06-2001	86.28	Alpha male; Bright colours in the fur
N'doki	Female	22	270	29-08-2002	40.07	Second biggest of the group; Warts under the eyes
Belabo	Female	13	161	21-09-2011	41.91	"Punkhair"; Yellow eyes; Bow-legged
Bibi	Female	13	158	18-01-2012	36.34	Red nose, often met mucus; Thin hind legs
Dalila	Female	11	140	15-07-2013	35.79	White scar on the nose bridge; No hair on tip of the tail
Chipo	Female	10	125	12-10-2014	47.63	Crackled nose pattern; Whiter nose bridge
N'dulu	Female	8	101	05-10-2016	36.79	Slick back hair; Bigger posture
Denzell	Male	7	89	07-10-2017	45.39	Longer face; Bended, protruded nose; Lanky build; Visible lower teeth
Mosa	Female	6	76	27-10-2018	32.39	Smallest of the group; White stripes in fur around the rib cage
Kuskure	Male	4	57	13-06-2020	36.51	Lanky and small build; Bended nose (less than Denzell)

Figure B2

Normalized David's Score (Dominance Hierarchy) of the Individuals Belonging to the Mandrill Group

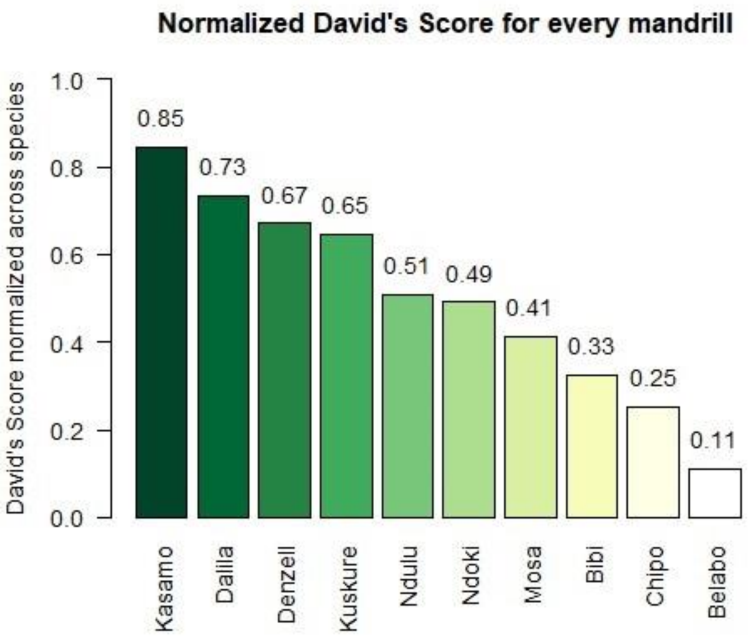


Table B2

Normal Diet of the Mandrill Group

Type of vegetable/fruit	Sugar concentration
Apple	10.4
Banana	15.5
Bell pepper	4.3
Blueberry	6
Bok choy	1.6
Carrot	5
Celeriac	0
Celery	1
Chicory	2.4
Courgette	2.4
Cucumber	1.2
Endive	0.8
Fennel	2
Grape	16,3

Iceberg lettuce	1.6
Kohlrabi	4.5
Leek	3.2
Parsnip	5.5
Red cabbage	3.2
Sweet potato	9

Appendix C: White-Faced Sakis Living at ARTIS Royal Zoo

Figure C1

Pictures of the Individuals Belonging to the White-Faced Saki Group

Note: photographs made by Floor van ‘t Hof and Kiki Harsevoord.

Table C1

Characteristics of the Individuals Belonging to the White-Faced Saki Group

Name	Sex	Age (years)	Age (months)	Date of birth	Brain surface area (cm²)	Characteristics
Noel	Male	35	422	25-12-1989	21.01	White face; Black fur
Tibiti	Female	16	195	09-12-2008	16.31	Grey fur; Thin build, less fur on belly
Castro	Male	4	49	11-02-2021	16.66	White spot above face is split in two; Darker fur

Wanakoe	Female	1	14	22-12-2023	17.52	Smaller built; Diamond shaped white spot above face

Table C2

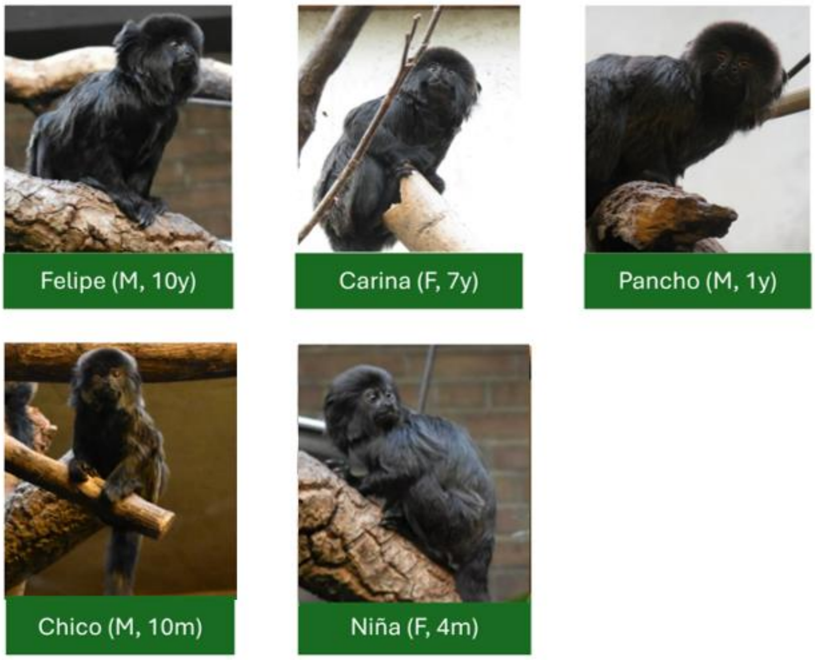
Diet of the White-Faced Saki Group

Type of vegetable/fruit	Sugar concentration
Apple	10.4
Banana	15.5
Beet	6
Bell pepper	4.3
Blueberry	6
Broccoli	0.4
Carrot	5
Celeriac	0
Celery	1
Chicory	2.4
Corn	5.3
Courgette	2.4
Mango	13.9
Papaya	7.8
Pea	1
Tomato	3.4
Grape	16,3

Appendix D: Goeldi's Monkeys Living at ARTIS Royal Zoo

Figure D1

Pictures of the Individuals Belonging to the Goeldi's Monkey Group.



Note: photographs made by Floor van 't Hof and Kiki Harsevoord

Table D1

Characteristics of the Indiviudals Belonging to the Goeldi's Monkey Group

Name	Sex	Age (years)	Age (months)	Date of birth	Brain surface area (cm^2)	Characteristics
Felipe	Male	10	122	20-12-2014	8.03	Thin tail that ends curved; Rounded head
Carina	Female	7	92	30-06-2017	7.46	Biggest; Thicker tail ending in a plume
Pancho	Male	1	15	06-12-2023	5.37	Third biggest; Looks like Felipe but with a less round head
Chico	Male	<1	10	17-05-2025	4.42	Baby face: Tail is thicker with a fluffy ending, resembling a cat's tail;
Niña	Female	<1	4	29-10-2024	3.91	Smallest.

Table D2

Diet of the Goeldi's Monkey Group

Type of vegetable/fruit	Sugar concentration
Apple	10.4
Banana	15.5
Beet	6
Bell pepper	4.3
Blueberry	6
Broccoli	0.4
Carrot	5
Celeriac	0
Celery	1
Chicory	2.4
Corn	5.3
Courgette	2.4
Mango	13.9
Papaya	7.8
Pea	1
Tomato	3.4
Grape	16,3

Appendix E: Courgette Preparation Process

Needed materials:

- One dark-green generic courgette (Curcurbita pepo) and one ‘Magda F1’ light-green courgette (Curcurbita pepo ‘Magda F1’) that is more than 11 cm long and roughly equal in thickness all around
- Face mask and hygienic gloves
- Cutting board - Sharp knife
- Granulated sugar (130 grams or 105 grams)
- Sealable containers that fit 22 courgette slices, could be distributed among several containers
- Cooking pan that fits a liter of water - Paper towels Preparations:
- Wear gloves and a facemask whenever working with the courgettes for safety reasons
- Thoroughly wash the courgettes with streaming tap water - Thoroughly wash the cooking pan, containers, cutting board and knife with dish soap and rinse with water before each step

The preparation process of the sweetened courgette began by adding either 105 grams (for light green courgette) or 130 grams (for dark green courgette) to one liter of heated water. After sucrose was absorbed in the water, it was cooled down to room temperature and distributed over two food containers. This means that both containers contained approximately 500ml of sweetened water. In preparation of the following step, both courgettes (i.e., dark green and light green) were cut into an appropriate number of 0.5cm slices. All courgette slices of one color were then distributed over the two containers containing sweetened water. The courgette slices of the other color, however, were distributed over two other containers containing both 500 ml of neutral tap water on room temperature. This was done to ensure a similar structure between the sweetened and non-sweetened courgette slices. After this, all slices were soaked in the containers for approximately 12 hours. Thus, while courgette slices of the one color were soaked in sweetened water for this time, the courgette slices of the other color were soaked equally long in neutral water. As sucrose was better absorbed in slices belonging to the middle part of the courgette, extremities of the courgettes were not used. All preparations were performed using gloves and a face mask.

Appendix F: Ethogram

Table F1

Ethogram of the Behaviors and Definitions Included in This Study

General category	Behaviour	Code	Definition
Interaction	Standing close by	Cb	Another individual within an arm length from the focal individual for at least 5 seconds.
	Stealing	St	Taking away a piece of food that another individual was holding and/or eating.
	Getting robbed	GR	Tolerated theft.
Dominance	Chasing away	CA	Coming less than an arm's length towards an individual, after which this individual leaves (outside an arm's length), without occupying its place.
	Being chased	BC	Another individual coming less than arm's length close, resulting in leaving (going outside this arm's length).
	Being displaced	BD	Moving away from previous spot after another individual approaches and takes this spot (within 2 arms lengths).
	Displacing	D	Moving towards an individual (2 arms lengths) after which that individual moves away and occupying their spot.
Investigating	Tasting	Tt	Picking up a piece of food, bringing it to the mouth and licking it.
	Sniffing	Sn	Getting the food closer than one fist to the primate's nose for more than one second.
	Holding	Hd	Holding a piece of food in hand without eating it for more than three seconds.
	Searching	Sch	Grasping/ digging/ stirring through the food pile.
	Rejecting	Rj	Not consuming a piece of food after one bite or tasting, sniffing, or holding it for the first time.
Consuming	Eating	E	Taking more than two bites or more and swallowing it. Or eating the piece as a whole in one bite.
	Collecting	C	Grabbing a piece of food and taking it to a different location without immediately eating it.

Appendix G: Brain Surface Area Measurement

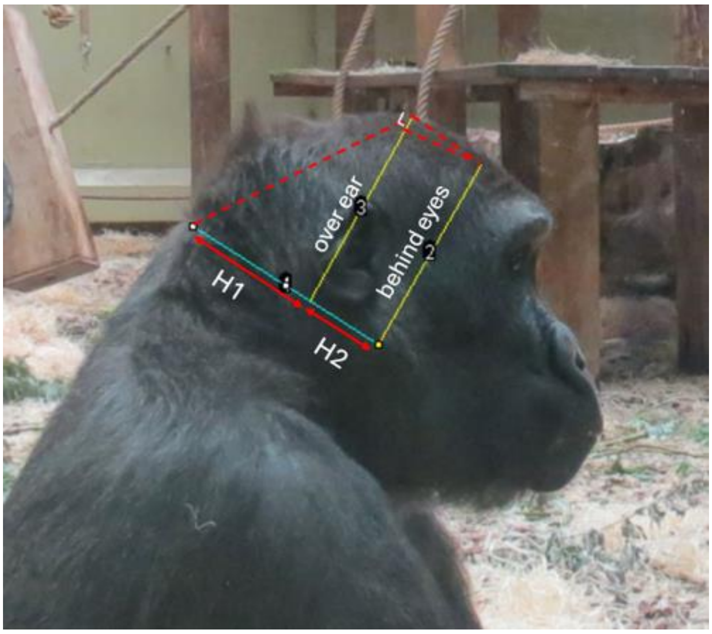
Figure G1

Measurement of Brain Surface Area and Body Length Using ImageJ

Note: picture made by Inim Schenk and Wessel de Jong Pen

Figure G2

Measurement of Brain Surface Area and Body Length Using ImageJ



Note: picture made by Inim Schenk and Wessel de Jong Pen

Appendix H: Interobserver Tests

Table H1

Results of the Interobserver Test on Eating Behaviors

	Observer 1	**Observer 2**	**Observer 3**	**Observer 4**
Observer 1	■	0.72**	0.89***	0.84***
Observer 2	0.72**	■	0.78***	0.81***
Observer 3	0.89***	0.78***	■	0.70**
Observer 4	0.84***	0.81***	0.70**	■

* p<0.05, ** p<0.01, *** p<0.001

Table H2

Results of the Interobserver Test on Rejections

	Observer 1	**Observer 2**	**Observer 3**	**Observer 4**
Observer 1	■	0.60	0.99*	0.60
Observer 2	0.60	■	0.67	1.00
Observer 3	0.99*	0.67	■	0.67
Observer 4	0.60	1.00	0.67	■

* p<0.05, ** p<0.01, *** p<0.001

Table H3

Results of the Interobserver Test on Displacements

	Observer 1	**Observer 2**	**Observer 3**	**Observer 4**
Observer 1	■	0.78**	0.85**	0.65*
Observer 2	0.78**	■	0.90**	0.71*
Observer 3	0.85**	0.90**	■	0.88**
Observer 4	0.65*	0.71*	0.88**	■

* p<0.05, ** p<0.01, *** p<0.001

Appendix I: Linear Mixed-Effects Models Assumption Check

Figure I1

Histogram of Residuals – First Choice Normal Diet Model

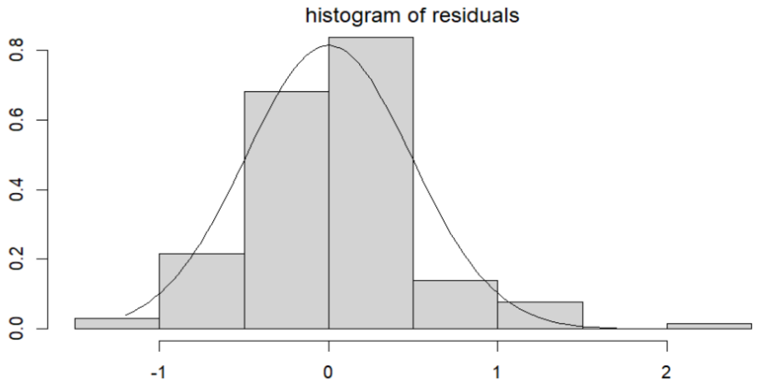


Figure I2

Q-Q Plot of Residuals – First Choice Normal Diet Model

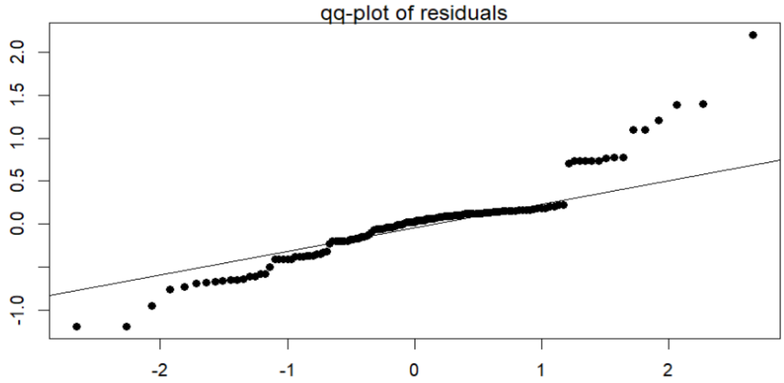


Figure I3

Residuals Against Fitted Values – First Choice Normal Diet Model

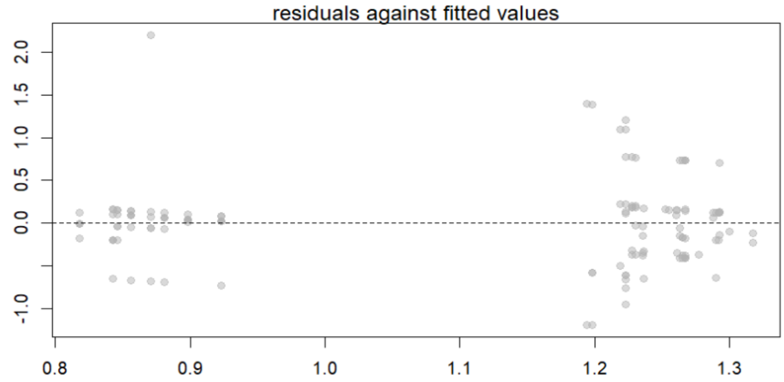


Figure I4

Histogram of Residuals – Food Order Normal Diet Model

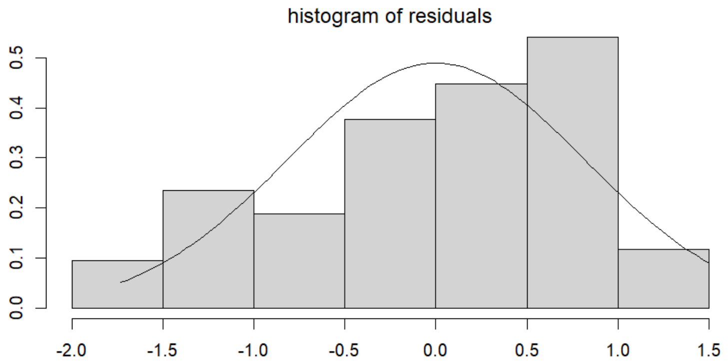


Figure I5

Q-Q Plot of Residuals – Food Order Normal Diet Model

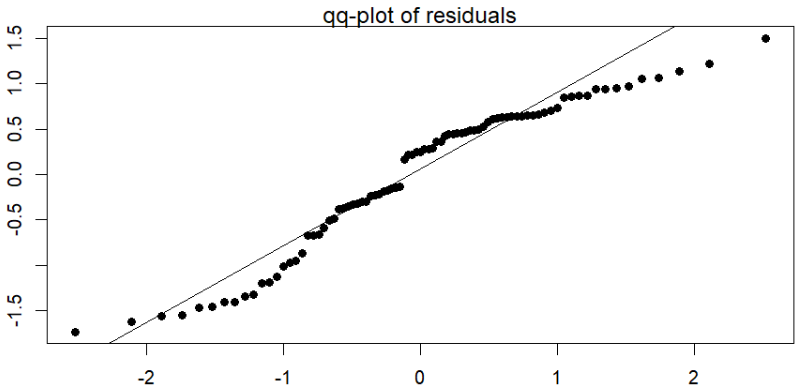


Figure I6

Residuals Against Fitted Values – Food Order Normal Diet Model