

Department of Physics, Chemistry and Biology

Master Thesis

Taste responsiveness to the 20 proteinogenic amino acids and taste preference thresholds for Glycine and L-Proline in spider monkeys (*Ateles geoffroyi*)

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## 1 Abstract

The present study assessed the taste responsiveness of four female spider monkeys (*Ateles geoffroyi*) to the 20 proteinogenic amino acids and determined taste preference thresholds for Glycine and L-Proline. To this end a two-bottle preference test of brief duration (1min) was employed. When presented at a concentration of 200 mM, the spider monkeys significantly preferred three proteinogenic amino acids (Glycine, L-Proline and L-Alanine) over fresh water whereas four other amino acids were significantly rejected (L-Tyrosine, L-Valine, L-Cysteine and L-Isoleucine). At a concentration of 100 mM, seven proteinogenic amino acids were significantly preferred (Glycine, L-Proline, L-Alanine, L-Glutamic acid, L-Aspartic acid, L-Serine and L-Lysine) whereas one was significantly rejected (L-Tryptophan). A comparison between the taste qualities of the amino acids as described by humans and taste preference/rejection responses observed with the spider monkeys suggests a fairly high degree of agreement in perception of these taste substances between the two species. When given the choice between fresh water and defined concentrations of two amino acids that taste sweet to humans the spider monkeys were found to significantly discriminate concentrations as low as 10-50 mM of Glycine and 10-40 mM of L-Proline from the solvent. This suggests that spider monkeys are similar in their taste sensitivity for Glycine and L-Proline compared to humans and slightly more sensitive compared to mice.

Keywords: proteinogenic amino acids, spider monkeys, taste responsiveness, taste preference thresholds.

## 2 Introduction

The sense of taste in nonhuman primates has been investigated both physiologically (Scott et al. 1994, Hellekant and Ninomiya 1994, Rolls et al. 1996, Rolls 1997, Rolls et al. 1998) and behaviorally (Pritchard and Norgren 1991, Laska and Hernandez Salazar 2004, Laska et al. 2001) in a variety of species and for a number of tastants. However, there is only sparse information as to the taste responsiveness of nonhuman primates for the 20 proteinogenic amino acids. This is surprising given that human studies have shown L-amino acids to have distinct and usually complex taste qualities. As proteins, and thus also amino acids which are their building blocks, are an important macronutrient it should be adaptive for nonhuman primates to be able to perceive amino acids upon ingestion. This idea is supported by studies which have shown that the composition of amino acids may affect food intake and dietary choice in mammals (Philip et al. 1987, Schiffman et al. 1981, Danilova et al. 2002)

The food selection behavior of primates suggests that they may use gustatory cues such as the salience of sweet and sour taste to assess the palatability and the nutritional value of fruit (Clutton-Brock 1977, Glaser 1989, Laska et al. 2003). The sense of taste also directs an animal to satisfy its nutritional needs and protects the body from ingesting harmful substances like toxic plant secondary compounds. When animals encounter a food item with a bitter taste they usually reject it or consume only small amounts, since foods with this taste quality may be toxic (Glendinning 1994). Food items with the taste quality "sweet", in contrast, are usually preferred by animals including human and nonhuman primates.

Spider monkeys (*Ateles geoffroyi*) are highly frugivorous (Chapman 1987, Wallace 2005) and include up to 82% of fruit in their diet (Russo et al. 2005). The remaining 18% include seeds, leaves, flower buds and animal matter (Cant 1990). Spider monkeys are the largest New World monkeys, weighing about 8 kg, with males being slightly heavier than females (see

figure 1). The area of distribution of the spider monkeys ranges from southern Mexico till Brazil (Chapman and Lefebvre 1990). Their social groups usually comprise 25 to 40 individuals (Hershkovitz 1978).

Spider monkeys have repeatedly been used in studies of taste responsiveness to sweet (Laska et al. 1998), salty (Laska and Hernandez Salazar 2004), sour (Laska et al. 2003), bitter (Laska et al. 2000) and umami (Laska and Hernandez Salazar 2004) tastes. It was found that they highly prefer sweet, salty and umami tastes and are tolerant to sour taste whereas they reject bitter taste. It was therefore the aim of the present study to assess the taste responsiveness to the 20 proteinogenic amino acids and to determine taste preference thresholds for Glycine and L-Proline, in spider monkeys. Glycine and L-Proline have been described as tasting sweet by humans and have also used in previous studies with several other species.

### **3 Materials and methods**

#### **3.1 Animals**

Testing was carried out using four female spider monkeys (*Ateles geoffroyi*) of eight years of age. They were maintained at the field station of the Universidad Veracruzana, near the town of Catemaco, in the province of Veracruz, Mexico. The animals were held under natural light conditions and were fed fresh fruits and vegetables every day. The amount of food was such that there were still leftovers present on the floor of the feeding area the next morning. No water was supplied. All animals were housed in small social groups in 25 m<sup>2</sup> enclosures with adjacent single cages. These could be closed by sliding doors, which allowed the temporary separation of animals for individual testing. All animals were born in captivity and trained to enter the single cages voluntarily. All animals had participated in previous studies using the same method (Laska, 1994, 1996, 1997, 1999, Laska et al., 2000, 2001, 2003, Laska and Hernandez Salazar 2004) and were completely accustomed to the procedure described below.



*Figure 1. Portrait of a spider monkey (Ateles geoffroyi)*

### 3.2 Stimuli

The following 20 proteinogenic amino acids were used in this study:

L-Alanine (L-Ala), L-Arginine (L-Arg), L-Asparagine (L-Asn), L-Aspartic Acid (L-Asp), L-Cysteine (L-Cys), L-Glutamic Acid (L-Glu), L-Glutamine (L-Gln), Glycine (Gly), L-Histidine (L-His), L-Isoleucine (L-Ile), L-Leucine (L-Leu), L-Lysine (L-Lys), L-Methionine (L-Met), L-Phenylalanine (L-Phe), L-Proline (L-Pro), L-Serine (L-Ser), L-Threonine (L-Thr), L-Tryptophan (L-Trp), L-Tyrosine (L-Tyr) and L-Valine (L-Val).

### 3.3 Procedure

#### Assessment of taste responsiveness to the 20 proteinogenic amino acids

A two-bottle preference test of short duration was used to determine the taste responsiveness of the spider monkeys to the 20 proteinogenic amino acids.

Tests were performed three times per day, and testing took place in the morning, approximately two hours before feeding, with 30 minute intervals between tests. For assessing the taste responsiveness to the amino acids the monkeys were given a choice between fresh water and defined concentrations of the amino acids dissolved in fresh water. To this end, two test series were performed: in the first series each amino acid was presented three times (which corresponds to three trials) at a concentration of 100 mM, and in the second series the same stimuli were presented three times each at a concentration of 200 mM. The position of the stimuli was pseudo-randomized within and between the animals in order to counterbalance possible position preferences. The monkeys were allowed to drink for 1 minute from a pair of simultaneously presented graduated cylinders of 100 ml with metal drinking spouts (see figure 2a and 2b). The volume consumed from each bottle was used to assess whether the monkeys respond to the given amino acid with a preference for or an aversion to the tastant.



Figure 2. A) one of the cylinders used in the tests for B) the two-bottle preference test.

### **Determination of taste preference thresholds**

Here, too, a two-bottle preference test of short duration (1 min) was used to determine the taste preference thresholds for two amino acids, Glycine and L-Proline. Tests were performed three times per day, and testing took place in the morning, approximately two hours before feeding, with 30 minute intervals between tests. With both amino acids, the animals were given a choice between fresh water and defined concentrations of a given amino acid dissolved in fresh water. With both substances testing started at a concentration of 200 mM and proceeded in the following steps (100, 50, 20, 10 mM, etc.) until an animal failed to show a significant preference or aversion. To define the preference thresholds more precisely, this was then followed by intermediate concentrations (e.g. of 30 and 40 mM).

To keep up the animals' motivation and their willingness to cooperate the testing of the different concentrations did not follow a strict order but was pseudo-randomized. In both test series each pair of stimuli was presented 10 times (which corresponds to 10 trials). However, if all animals preferred one of the stimuli by more than 80 % (relative to the total amount of liquid consumed) after six trials and preferred that same stimulus in at least five out of six trials, testing proceeded with the next pair of stimuli.

### **3.4 Data analysis**

#### **Assessment of taste responsiveness to the 20 proteinogenic amino acids**

The amount of the liquid consumed from each bottle in each trial was recorded for each individual. After the three trials with a given stimulus combination the volumes for each of the two stimuli were summed up and converted to percentages relative to the total amount of liquid consumed from both bottles. The criteria for a preference at the group level were as follows: the animals were only regarded as significantly preferring one of the two alternative stimuli if they (1) reached the criterion of 66.7% preference (relative to the total amount of liquid consumed) and (2) consumed more from the bottle containing the preferred stimulus in at least 10 out of 12 trials. Accordingly, the animals were regarded as significantly rejecting one of the two stimuli if (1) their preference was less than 33.3% (relative to the total amount of liquid consumed) and (2) they consumed more from the rejected stimulus in not more than 2 out of 12 trials. According to the binomial test, the ratios 12/12 and 11/12 as well as the ratios 0/12 and 1/12 correspond to  $p < 0.01$ , and the ratios 10/12 and 2/12 correspond to  $p < 0.05$ .

#### **Determination of taste preference thresholds**

The amount of the liquid consumed from each bottle in each trial was recorded for each animal. It was thereafter summed over the six or 10 trials and converted to percentages relative to the total amount of liquid consumed from both bottles. 66.7 % was taken as criterion of preference (i.e., 2/3 of the total amount of liquid consumed). An animal was only regarded as significantly preferring the amino acid over the freshwater if it (1) reached 66.7 % and (2) consumed more from the bottle containing the preferred stimulus in at least eight out of 10, or in five out of six trials, which corresponds to  $p < 0.05$  (binomial test).

## 4 Results

### 4.1 Assessment of taste responsiveness to the 20 proteinogenic amino acids

Table 1 summarizes the mean performance of the four spider monkeys in the two-bottle preference tests when presented with aqueous dilutions of the proteinogenic amino acids at a concentration of 200 mM and fresh water as the alternative stimulus. Results are ranked from the most preferred to the least preferred stimulus. With three of the proteinogenic amino acids the animals showed a significant preference whereas four of them were significantly rejected (indicated in bold typeface). With the remaining 13 proteinogenic amino acids no significant preference or rejection was found, although there were trends in either direction with some of the stimuli.

Amino acid (200 mM)	Mean $\pm$ SE	Preference
<b>Glycine</b>	<b>96.9 <math>\pm</math> 1.2</b>	<b>12 / 12</b>
<b>L-Proline</b>	<b>95.8 <math>\pm</math> 2.5</b>	<b>12 / 12</b>
<b>L-Alanine</b>	<b>92.5 <math>\pm</math> 3.6</b>	<b>12 / 12</b>
L-Glutamic acid	83.6 $\pm$ 5.8	9 / 12
L-Serine	68.7 $\pm$ 8.4	7 / 12
L-Leucine	66.2 $\pm$ 8.2	8 / 12
L-Lysine	64.6 $\pm$ 8.2	7 / 12
L-Asparagine	63.2 $\pm$ 7.8	6 / 12
L-Glutamine	59.0 $\pm$ 7.0	4 / 12
L-Methionine	50.9 $\pm$ 10.5	7 / 12
L-Histidine	50.5 $\pm$ 17.0	7 / 12
L-Threonine	49.4 $\pm$ 9.1	7 / 12
L-Arginine	47.4 $\pm$ 12.1	5 / 12
L-Aspartic acid	46.3 $\pm$ 4.8	2 / 12
L-Phenylalanine	37.7 $\pm$ 17.2	4 / 12
L-Tryptophan	37.5 $\pm$ 7.2	2 / 12
<b>L-Tyrosine</b>	<b>33.0 <math>\pm</math> 11.3</b>	<b>2 / 12</b>
<b>L-Valine</b>	<b>30.2 <math>\pm</math> 12.4</b>	<b>2 / 12</b>
<b>L-Cysteine</b>	<b>28.9 <math>\pm</math> 12.7</b>	<b>1 / 12</b>
<b>L-Isoleucine</b>	<b>27.7 <math>\pm</math> 6.6</b>	<b>1 / 12</b>

Table 1. Taste responses of the four spider monkeys when presented with the 20 proteinogenic amino acids at a concentration of 200 mM and tested against fresh water as an alternative. Bold typeface indicates amino acids that were significantly preferred or rejected.

Table 2 summarizes the mean performance of the four spider monkeys in the two-bottle preference tests when presented with aqueous dilutions of the proteinogenic amino acids at a concentration of 100 mM and fresh water as the alternative stimulus. Results are ranked from the most preferred to the least preferred stimulus. With seven of the 20 proteinogenic amino acids the animals showed a significant preference whereas one of them was significantly rejected (indicated in bold typeface). With the remaining 12 proteinogenic amino acids no significant preference or rejection was found, although here too there were trends in either direction with some of the stimuli.

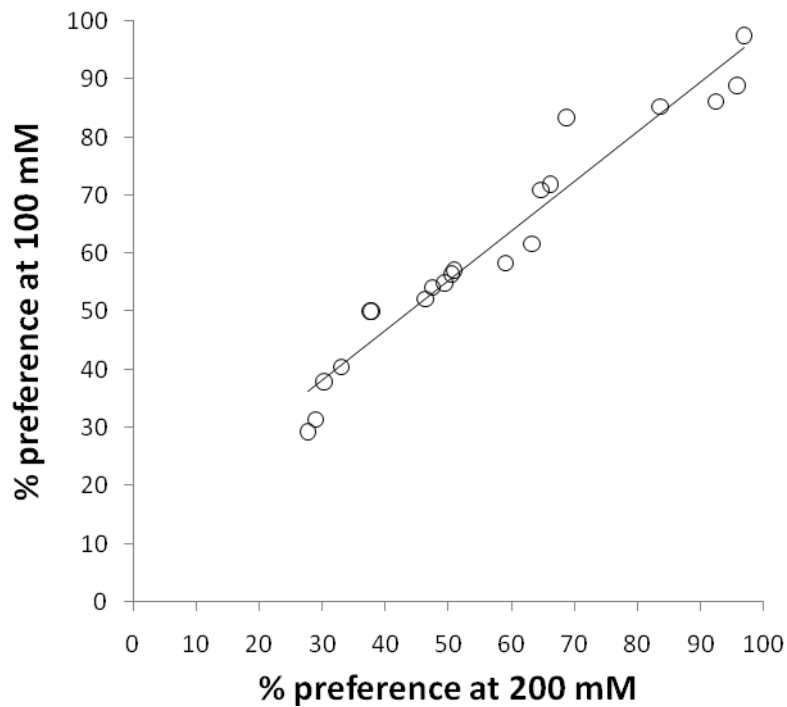
Amino acid (100 mM)	Mean $\pm$ SE	Preference
<b>L-Proline</b>	<b>97.6 <math>\pm</math> 0.8</b>	<b>12 / 12</b>
<b>Glycine</b>	<b>88.9 <math>\pm</math> 6.3</b>	<b>11 / 12</b>
<b>L-Glutamic acid</b>	<b>86.2 <math>\pm</math> 2.9</b>	<b>12 / 12</b>
<b>L-Aspartic acid</b>	<b>85.3 <math>\pm</math> 3.9</b>	<b>11 / 12</b>
<b>L-Alanine</b>	<b>83.4 <math>\pm</math> 8.5</b>	<b>11 / 12</b>
<b>L-Serine</b>	<b>71.9 <math>\pm</math> 4.3</b>	<b>11 / 12</b>
<b>L-Lysine</b>	<b>70.6 <math>\pm</math> 7.1</b>	<b>11 / 12</b>
L-Histidine	61.7 $\pm$ 11.7	7 / 12
L-Tyrosine	58.4 $\pm$ 6.5	2 / 12
L-Methionine	57.2 $\pm$ 23.1	8 / 12
L-Leucine	56.5 $\pm$ 4.4	6 / 12
L-Arginine	54.9 $\pm$ 4.6	6 / 12
L-Glutamine	54.2 $\pm$ 4.6	6 / 12
L-Asparagine	52.2 $\pm$ 14.3	5 / 12
L-Valine	50.1 $\pm$ 7.1	4 / 12
L-Cysteine	50.1 $\pm$ 8.9	4 / 12
L-Threonine	40.5 $\pm$ 5.6	3 / 12
L-Isoleucine	38.0 $\pm$ 9.2	1 / 12
L-Phenylalanine	31.4 $\pm$ 11.7	5 / 12
<b>L-Tryptophan</b>	<b>29.3 <math>\pm</math> 9.3</b>	<b>2 / 12</b>

*Table 2. Taste responses of the four spider monkeys when presented with the 20 proteinogenic amino acids at a concentration of 100 mM and tested against fresh water as an alternative. Bold typeface indicates amino acids that were significantly preferred or rejected.*



#### 4.2 Taste preference ranking between the concentrations of 100 mM and 200 mM

A comparison between the taste preference rankings of the spider monkeys obtained with the amino acids presented at 100 mM and 200 mM, respectively, showed a highly significant correlation between the two (Spearman  $r_s = 0,75$ ,  $p = 0.0012$ ) (figure 3).



*Figure 3. Taste preference ranking of the four spider monkeys with the 20 proteinogenic amino acid at the concentrations of 100 mM and 200 mM tested against fresh water. Each data point represents the mean value for the consumption of each amino acid at a group level.*

### 4.3 Determination of taste preference thresholds for Glycine

Figure 4 shows the performance of the individual spider monkeys when presented with various concentrations of Glycine and fresh water as the alternative. The individuals significantly preferred Glycine over fresh water with concentrations as low as 50 mM (Kelly), 40 mM (Piolina and Nanny) and 10 mM (Suki). With lower concentrations the animals failed to display a significant preference.

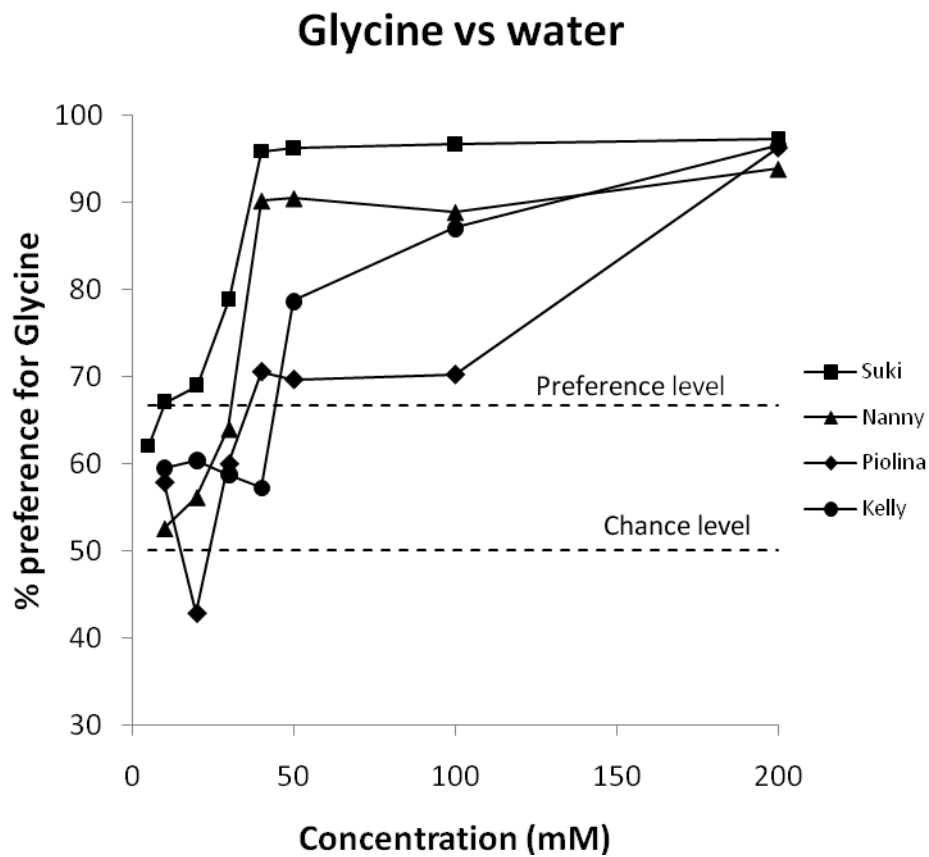


Figure 4. Taste responsiveness of four spider monkeys to various concentrations of Glycine tested against fresh water. Each data point represents the mean value of 10 test sessions of 1 min per animal.

Figure 5 shows the mean performance ( $\pm$  SD) of the spider monkeys as a group when presented with various concentrations of Glycine and fresh water as the alternative. At the group level the animals significantly preferred Glycine over fresh water with concentrations as low as 40 mM.

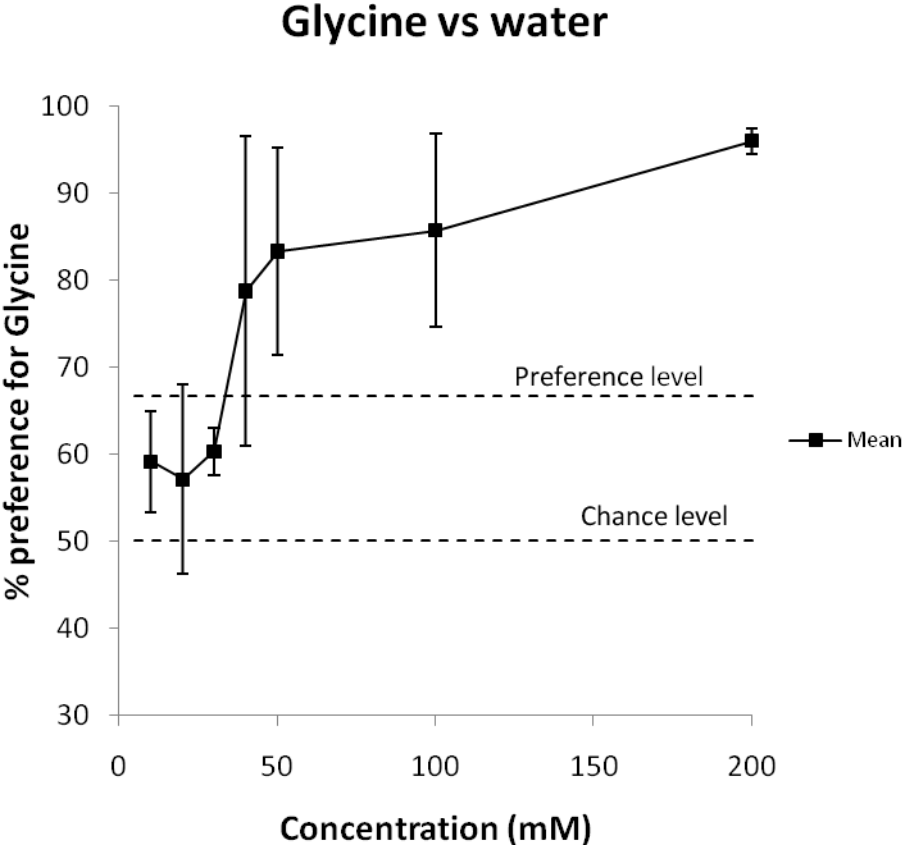


Figure 5. The mean value of the taste responsiveness of four spider monkeys to various concentrations of Glycine tested against fresh water. Each data point represents the mean value ( $\pm$ SD) of 10 test sessions of 1 min per animal.

#### 4.4 Determination of taste preference thresholds for L-Proline

Figure 6 shows the performance of the individual spider monkeys when presented with various concentrations of L-Proline and fresh water as the alternative. The individuals significantly preferred L-Proline over fresh water with concentrations as low as 40 mM (Piolina), 20 mM (Kelly) and 10 mM (Suki and Nanny). With lower concentrations the animals failed to display a significant preference.

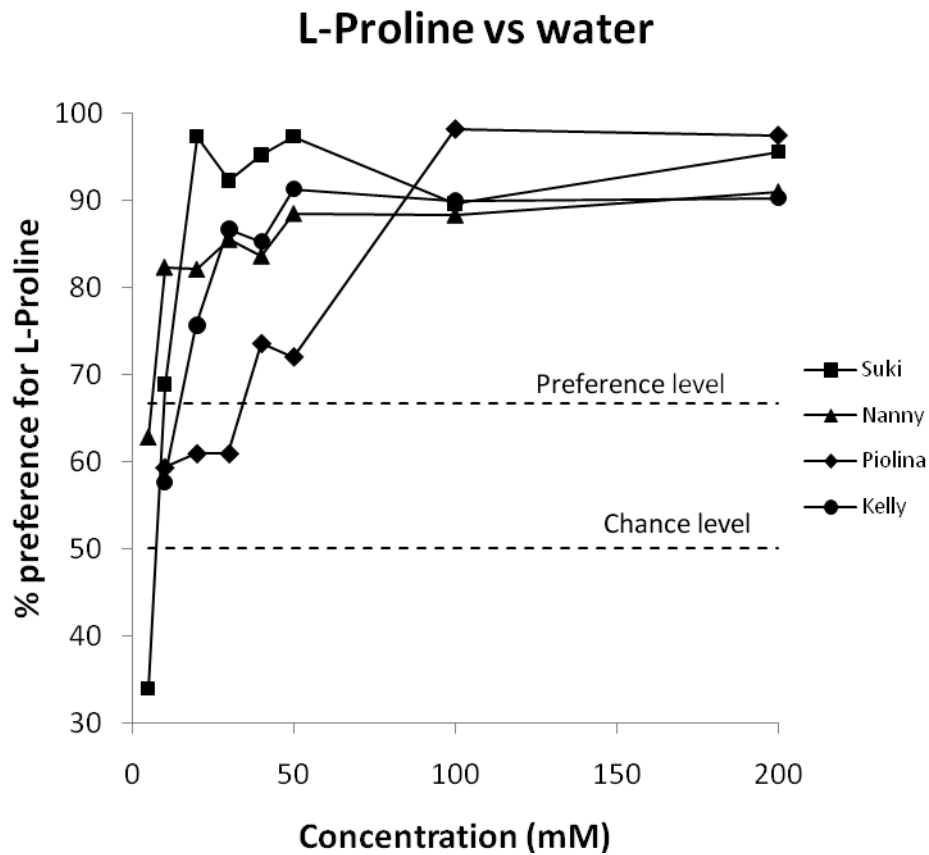


Figure 6. Taste responsiveness of four spider monkeys to various concentrations of L-Proline tested against fresh water. Each data point represents the mean value of 10 test sessions of 1 min per animal

Figure 7 shows the mean performance ( $\pm$  SD) of the spider monkeys as a group when presented with various concentrations of L-Proline and fresh water as an alternative. At the group level the animals significantly preferred L-Proline over fresh water with concentrations as low as 20 mM.

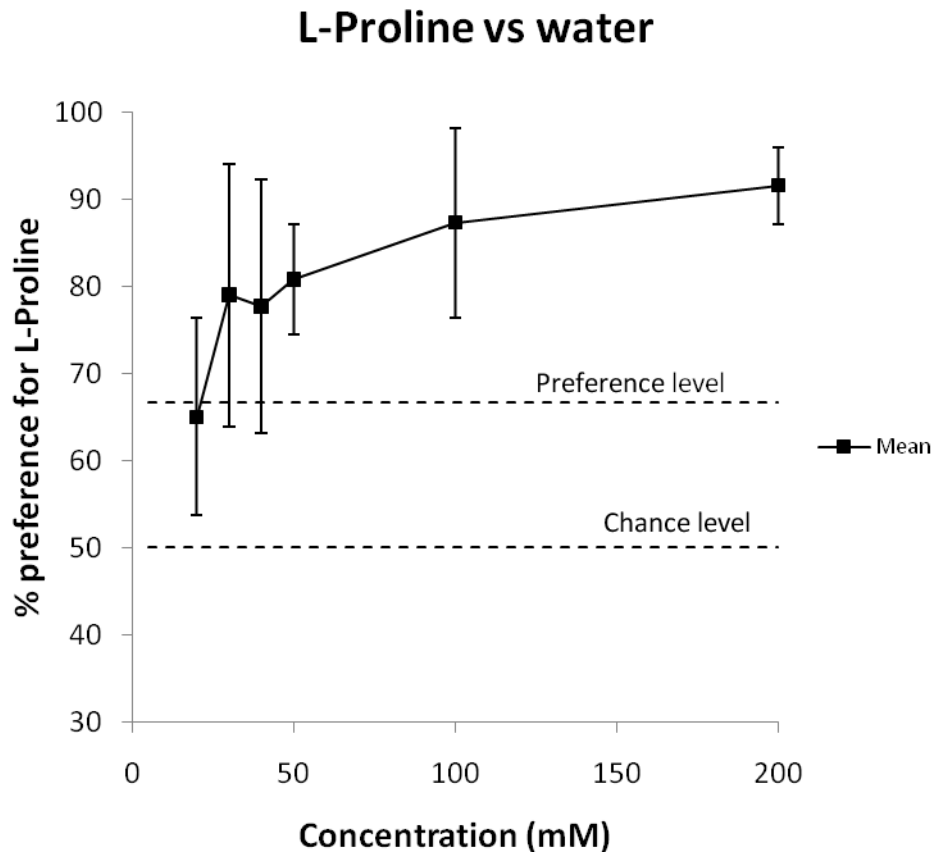


Figure 7. The mean value of the taste responsiveness of four spider monkeys to various concentrations of L-Proline tested against fresh water. Each data point represents the mean value ( $\pm$ SD) of 10 test sessions of 1 min per animal.

## 5 Discussion

The results of the present study demonstrate that the spider monkeys significantly preferred three of the 20 proteinogenic amino acids (L-Ala, L-Pro and Gly) over fresh water when presented at a concentration of 200 mM. At the same concentration four other amino acids (L-Cys, L-Ile, L-Tyr and L-Val) were significantly rejected. When presented at a concentration of 100 mM the animals significantly preferred seven of the 20 proteinogenic amino acids (L-Ala, L-Pro, Gly, L-Asp, L-Gln, L-Lys, and L-Ser) over fresh water and rejected one amino acid (L-Trp).

### 5.1 Comparison with other species: Taste responsiveness

Table 3 summarizes the responsiveness of the spider monkeys to the amino acids tested and compares them with the taste qualities as described by humans.

Amino acids	Taste qualities as described by humans	Taste responsiveness of spider monkeys at 200 mM	Taste responsiveness of spider monkeys at 100 mM
L-Alanine	Sweet; possibly complex with bitter aftertaste	<b>Preferred</b>	<b>Preferred</b>
L-Arginine	Flat to bitter; alkaline, complex		
L-Asparagine	Flat to bitter		
L-Aspartic Acid	Flat,sour,slightly bitter		<b>Preferred</b>
L-Cysteine	Sulphurous, obnoxious	<b>Rejected</b>	
L-Glutamic Acid	Unique, meaty, salty, bitter, sour, complex		
L-Glutamine	Flat, sweet, meaty, somewhat unpleasant		<b>Preferred</b>
Glycine	Sweet,pleasant,smooth, refreshing	<b>Preferred</b>	<b>Preferred</b>
L-Histidine	Flat to bitter, minerally		
L-Isoleucine	Flat to bitter	<b>Rejected</b>	
L-Leucine	Flat to bitter (similar to L-Isoleucine)		
L-Lysine	Bitter ,complex, salty, sweet		<b>Preferred</b>
L-Methionine	Flat to bitter; sulphurous, meaty or sweet		
L-Phenylalanine	Bitter, possible complex and strangling		
L-Proline	Sweet, complex with salty and sour components	<b>Preferred</b>	<b>Preferred</b>
L-Serine	Flat to sweet; possible sour, complex		<b>Preferred</b>
L-Threonine	Flat to sweet, possible bitter, sour or fatty		
L-Tryptophan	Flat to bitter		<b>Rejected</b>
L-Tyrosine	Flat to bitter	<b>Rejected</b>	
L-Valine	Flat to bitter, slightly sweet	<b>Rejected</b>	

Table 3. Taste qualities of the L-amino acids as described by humans. Data from (Schiffman et al. 1981)

Humans and other mammals are able to perceive five basic tastes: sweet, salty, sour, bitter and umami (Kinnamon and Cummings 1992, Lindemann 1996). The taste quality “sweet” is usually regarded as pleasant by humans and preferred by animals. The taste quality “bitter”, in contrast, is usually regarded as unpleasant by humans and rejected by animals. The pleasantness or unpleasantness of the other three taste qualities is largely dependent on the concentration used. Amino acids have been found to only rarely evoke a single taste quality, often they are described as having more than one taste quality and thus a mixed taste (see table 3.)

### **5.2 Comparison of taste responsiveness at 100 mM and 200 mM**

The results of the present study showed that the preferences and aversions displayed by the spider monkeys were affected to some degree by the stimulus concentration used.

Studies demonstrated that L-amino acids have a distinct and usually complex taste and that the perceived taste quality is dependent on the concentrations used. This could also plausibly explain why the spider monkeys significantly preferred more amino acids at a concentration of 100 mM compared to 200 mM as unpleasant side tastes of basically sweet amino acids might be more pronounced at higher concentrations. However, the spider monkeys also significantly rejected more amino acids at a concentration of 100 mM than in 200 mM. This could be explained if one assumes that basically unpleasant amino acids might gain a pleasant side taste with higher concentrations.

### **5.3 Comparison between humans and spider monkeys**

*Sweet tasting for humans and preferred by the spider monkeys.*

In the present study the spider monkeys showed a preference for Glycine, L-Proline and L-Alanine with both concentrations tested (200 and 100 mM), which is consistent with the human description of “sweetness” for these amino acids (Schiffman et al.1981). L-Serine is a complex amino acid that is described as tasting flat to sweet, possibly sour and L-Lysine described by humans is complex with bitter, salty, sweet taste (Schiffman et al. 1981). L-Serine and L-Lysine were both significantly preferred by the spider monkeys at a concentration of 100 mM. Both amino acids have been described by humans as having a complex taste including the quality of sweetness (Schiffman et al. 1981). According to Haefeli and Glaser (1990) L-Lysine has even a characteristic sweet taste just as L-Proline, although with a bitter aftertaste, and humans judge this taste as pleasant. Thus, five amino acids that were preferred by the spider monkeys are also described as sweet or pleasant by humans.

*Not sweet tasting for humans and rejected by the spider monkeys.*

Five out of the 20 tested proteinogenic amino acids were significantly rejected by the spider monkeys (L-Cys, L-Iso, L-Val and L-Tyr at 200 mM and L-Trp at 100 mM). Interestingly, human subjects generally describe these amino acids as tasting flat to bitter except L-Cysteine which is described as sulphurous and obnoxious tasting and L-Valine is described as having a slightly sweet after taste (Schiffman et al. 1981). Thus, all five amino acids that were rejected by the spider monkeys are also described as bitter or unpleasant by humans.

*Not sweet tasting for humans and preferred by the spider monkeys.*

Two out of the 20 tested proteinogenic amino acids were significantly preferred by the spider monkeys (L-Asp and L-Gln) despite being described as unpleasant by humans. L-Aspartic acid is described as flat, sour and slightly bitter and L-Glutamine as flat, sweet, meaty and

somewhat unpleasant (Schiffman et al. 1981). Thus, these two amino acids were preferred by the spider monkeys, despite being described as flat and unpleasant by humans.

*Sweet tasting for humans and indifferent by the spider monkeys.*

One out of the 20 tested proteinogenic amino acids was not significantly preferred or rejected by the spider monkeys (L-Thr) although human subjects describe L-Threonine to have a flat, sweet taste but also possible bitter, sour or fatty taste (Schiffman et al. 1981). According to Haefeli and Glaser (1990) L-Threonine is sweet without possessing an after taste and humans judge this taste as pleasant. Thus, although humans describe L-Threonine as pleasant the spider monkeys respond indifferently to L-Threonine.

*Not sweet tasting for humans and indifferent by the spider monkeys.*

Seven of the 20 tested proteinogenic amino acids were not significantly preferred or rejected by the spider monkeys (L-Leu, L-Arg, L-Phe, L-His, L-Asn, L-Met and L-Glu) whereas humans describe these amino acids as bitter tasting and therefore unpleasant (Schiffman et al. 1981). Thus, although humans describe these seven amino acids as bitter and unpleasant the spider monkeys respond indifferently to them.

In summary, humans describe nine out of 20 proteinogenic amino acids as sweet and/or pleasant, while the spider monkeys prefer seven out of the 20 proteinogenic amino acids.

The amino acids that both humans and spider monkeys do prefer at various concentrations are Glycine, L-Alanine, L-Proline, L-Serine and L-Aspartic acid.

The remaining 11 proteinogenic amino acids are described as having an unpleasant taste for humans (Haefeli and Glaser 1990) and the spider monkeys reject five out of the 20 proteinogenic amino acids. Interestingly the spider monkeys preferred two of the amino acids that are not described as sweet by humans, L-Lysine and L-Glutamine.

Three out of the 11 amino acids described as unpleasant by humans were also rejected by the spider monkeys, L-Isoleucine, L-Cysteine at 200 mM and L-Tryptophan at 100 mM. Thus, there is a fairly high degree of accordance between the human descriptions of the taste of the amino acid as sweet/pleasant or non-sweet/unpleasant and the behavior of the spider monkeys in terms of preference or rejection.

#### **5.4 Comparison between pigs and spider monkeys**

Using a two-bottle preference test similar to the one employed in the present study, pigs (*Sus scrofa*) were tested with 13 of the same amino acids that the spider monkeys were exposed to (Tinti et al. 2000). The concentrations used with the pigs were similar to those used in the present study. Five out of the 13 proteinogenic amino acids were preferred by the pigs (L-Ala, L-Asn, L-Glu, L-Ser and L-Thr). Three of these five amino acids (L-Ala, L-Glu and L-Ser) were also preferred by the spider monkeys. Eight of the proteinogenic amino acids tested were rejected by the pigs (L-His, L-Ile, L-Leu, L-Phe, L-Pro, L-Trp, L-Tyr and L-Val). Four of these eight amino acids were also rejected by the spider monkeys (L-Ile, L-Tyr, L-Val and L-Trp). Interestingly, one of the amino acids rejected by the pigs (L-Pro) was highly preferred at both concentrations of 100 and 200 mM by the spider monkeys. The pigs were exposed to three different concentrations, 33, 130 and 430 mM, and they rejected all of these concentrations of L-Proline. Pigs highly prefer substances that taste sweet to humans e.g. carbohydrates and although the pigs were presented with concentrations as low as 33 mM they appear to perceive the bitter after taste reported by humans with L-Proline. Thus, there are some similarities between the pigs and the spider monkeys in preferring or rejecting the taste of amino acids.



### **5.5 Comparison between house musk shrews and spider monkeys**

Using a two-bottle preference test house musk shrews (*Suncus murinus*) were tested with the same 20 amino acids that the spider monkeys were exposed to (Iwasaki and Sato 1981). 10 out of the 20 amino acids were preferred by the house musk shrew at similar concentrations as used in the present study (L-Val, Gly, L-Ala, L-Ile, L-Leu, L-Pro, L-Cys, L-Met, L-Ser and L-Thr). Four out of those (L-Ala, Gly, L-Pro and L-Ser) were also preferred by the spider monkeys. Five out of the 20 proteinogenic amino acids were rejected by the house musk shrew at similar concentrations as used in the present study (L-Cys, L-Arg, L-His, L-Asp and L-Glu). One of these five amino acids was also rejected by the spider monkeys (L-Cysteine). The house musk shrew is an insectivore and has a preference for protein rich foods. This might explain why there is only limited agreement in the taste responses between the house musk shrew and the spider monkey with amino acids.

### **5.6 Comparison between mice and spider monkeys**

Using a two-bottle preference test mice (*Mus musculus*) were tested with 14 of the same amino acids that the spider monkeys were exposed to (Iwasaki et al. 1984). Six out of the 14 amino acids were preferred by the mice at a concentration of 100 mM. Five of those (L-Ala, Gly, L-Pro, L-Glu and L-Ser) were also preferred by the spider monkeys. Three out of 14 proteinogenic amino acids were rejected by the mice at a concentration of 100 mM (L-Ile, L-Phe and L-Met). One of these three amino acids (L-Isoleucine) was also rejected by the spider monkeys.

Thus, there is a fairly high degree of accordance between the spider monkeys and the mice in the amino acids that both species preferred but less agreement with the rejected amino acids.

### **5.7 Comparison between common marmosets and spider monkeys**

Using a two-bottle preference test common marmosets (*Callithrix jacchus jacchus*) were tested with the same 20 amino acids that the spider monkeys were exposed to (Haefeli et al. 1998). Only one out of the 20 proteinogenic amino acids was preferred by the common marmosets at a concentration 500 mM (Gly). Spider monkeys also prefer Glycine at both concentrations tested of 100 and 200 mM. 19 out of the 20 proteinogenic amino acids were rejected by the common marmosets. Thus, there is a very low degree of accordance between the spider monkeys and the common marmosets in the amino acids that both species preferred but more similarities in the rejected amino acid since the common marmosets rejected all of the same amino acids as the spider monkeys. The concentrations used with the common marmosets (10, 50, 100, 200, and 500 mM) were similar to those used in the present study.

Common marmosets and spider monkeys appear to differ a lot in taste responsiveness to proteinogenic amino acids even though both species belong to the New World monkeys.

### **5.8 Comparison with other species: Taste preference thresholds**

In the present study the taste preference thresholds of the individual spider monkeys ranged between 10 and 50 mM for Glycine, and between 10 and 40 mM for L-Proline. According to Schiffman et al (1981) the human taste detection threshold value for Glycine has been reported to be 30.9 mM and for L-Proline 15.1 mM. This suggests that humans and spider monkeys are similar in their ability to detect these two amino acids. However, it is important to keep in mind that the human taste detection thresholds have been established using sophisticated signal detection methods, whereas the two-bottle preference test used with the spider monkeys provides only a conservative approximation of the species' limits of their gustatory capacities. This suggests that spider monkeys might in fact be more sensitive than humans for the amino acids tested here but further studies are needed to test this hypothesis.

The taste preference thresholds of mice have been reported to be 10 mM for Glycine and 55 mM for L-Proline (Iwasaki et al. 1984). This suggests that spider monkeys and mice are similar in their ability to detect Glycine but not in their ability to detect L-Proline.

## 5.9 Conclusion

The results of the present study fit to the general idea that dietary specialization of different species may affect the preference for or rejection of different tastants. Another idea is that phylogenetically closely related species, such as spider monkeys and humans may have a higher degree of similarities in their taste perception compared to more distantly related species. The present study confirmed that spider monkeys and humans show a fairly high degree of accordance in their taste responsiveness and are similar in their taste sensitivity for Glycine and L-Proline.

## 6 Outlook

Based on the findings of the present study, the following studies should be performed: testing the taste responsiveness to the same L-amino acids with other species would allow for conclusions as to the generality of preference or rejection responses among species. Testing the taste responsiveness to D-amino acids with the spider monkeys would allow to see if the two enantiomeric forms of a given amino acid elicit the same or different behavioral responses. And determining taste preference threshold values with other L-amino acids that taste “sweet” to humans and/or were preferred by the spider monkeys would allow for more comprehensive comparisons between the two species.

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## 8 References

- Cant J.G.H. 1990. Feeding ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. *Human Evolution* 5, 269-280.
- Clutton-Brock T.H. 1977. *Primate ecology: studies of feeding and ranging behavior in lemures, monkeys and apes*. Academic Press, New York.
- Chapman C. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica* 49, 90-105.
- Chapman C, Lefebvre L. 1990. Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour* 39, 891-896.
- Danilova V, Danilov Y, Roberts T, Tinti J, Nofre C, Hellekant G. 2002. Sense of taste in a New World monkey, the common marmoset: recordings from the chorda tympani and glossopharyngeal nerves. *Journal of Neurophysiology* 88, 579-594.

- Glaser D. 1989. Biological aspects of taste in South American primates. *Medio Ambiente* 10, 107-112.
- Glendinning J.I. 1994. Is the bitter rejection response always adaptive? *Physiology & Behavior* 56, 1217-1227.
- Hershkovitz P. 1978. *Living New World Monkeys, Platyrrhini: With an Introduction to Primates*. University of Chicago Press, Chicago.
- Haefeli R, Glaser D. 1990. Taste responses and thresholds obtained with the primary amino acids in humans. *Lebensmittel-Wissenschaft und Technologie* 23, 523-527.
- Haefeli R, Solms J, Glaser D. 1998. Taste responses to amino acids in common marmosets (*Callithrix jacchus jacchus*, *Callitrichidae*) a non-human primate in comparison to humans. *Lebensmittel-Wissenschaft und Technologie* 31, 371-376.
- Hellekant G, Ninomiya Y. 1994. Umami taste in the chimpanzee (*Pan troglodytes*) and rhesus monkey (*Macaca mulatta*). In: Kurihara K, Suzuki N, Ogawa H (Eds) *Olfaction and Taste*, 6, 365-368. Springer, Tokyo.
- Iwasaki K, Sato M. 1981. Taste preference for amino acids in the house musk shrew, *Suncus murinus*. *Physiology & Behavior* 28, 829-833.
- Iwasaki K, Kashara T, Sato M. 1984. Gustatory effectiveness of amino acids in mice: behavioral and neurophysiological studies. *Physiology & Behavior* 34, 531-542.
- Kinnamon S, Cummings C.T.A. 1992. Chemosensory transduction mechanisms in taste. *Annual Reviews of Physiology* 54, 715-731.
- Laska M. 1994. Taste difference thresholds for sucrose in squirrel monkeys (*Saimiri sciureus*). *Folia Primatologica* 63, 144-148.
- Laska M. 1996. Taste preference thresholds for food-associated sugars in the squirrel monkey, *Saimiri sciureus*. *Primates* 37, 93-97.
- Laska M. 1997. Taste preferences for five food-associated sugars in the squirrel monkey (*Saimiri sciureus*). *Journal of Chemical Ecology* 23, 659-672.
- Laska M. 1999. Taste responsiveness to food-associated acids in the squirrel monkey (*Saimiri sciureus*). *Journal of Chemical Ecology* 25, 1623-1632.
- Laska M, Hernandez Salazar L.T. 2004. Gustatory responsiveness to monosodium glutamate and sodium chloride in four species of nonhuman primates. *Journal of Experimental Zoology* 301A, 898-905.
- Laska M, Sanchez Carrera E, Rodriguez Luna E. 1998. Relative taste preferences for food-associated sugars in the spider monkey (*Ateles geoffroyi*). *Primates* 39, 91-96.

- Laska M, Hernandez Salazar L.T, Rodriguez Luna E, Hudson R. 2000. Gustatory responsiveness to food-associated acids in the spider monkey (*Ateles geoffroyi*). *Primates* 41, 175–183.
- Laska M, Kohlmann S, Scheuber H.P, Hernandez Salazar L.T, Rodriguez Luna E. 2001. Gustatory responsiveness to polycose in four species of nonhuman primates. *Journal of Chemical Ecology* 27, 1997–2011.
- Laska M, Scheuber, H.P, Hernandez Salazar L.T, Rodriguez Luna E. 2003. Sour-taste tolerance in four species of nonhuman primates. *Journal of Chemical Ecology* 29, 2637–2649.
- Lindemann B. 1996. Chemoreception: tasting the sweet and the bitter. *Current Biology* 6, 1234-1237.
- Philip M, Leung B, Rogers Q.R. 1987. The effect of amino acids and protein on dietary choice. In: Kawamura Y, Kare M.R. (Eds) *Umami: A basic taste*, pp 565-610. Marcel Dekker, New York.
- Pritchard T.C, Norgren R. 1991. Preference of Old World monkeys for amino acids and other gustatory stimuli: the influence of monosodium glutamate. *Physiology & Behavior* 49, 1003-1007.
- Rolls E.T. 1997. The representation of umami taste in the primate primary and secondary taste cortex. *Chemical Senses* 22, 779.
- Rolls E.T, Critchley H.D, Wakeman E.A, Mason R. 1996. Responses of neurons in the primate taste cortex to the glutamate ion and to inosine 5'-monophosphate. *Physiology & Behavior* 59, 991-1000.
- Rolls E.T, Critchley H.D, Browning A, Hernadi I. 1998. The neurophysiology of taste and olfaction in primates, and umami flavor. *Annals of the New York Academy of Sciences* 855, 426-437.
- Russo S.E, Campbell C.J, Dew J.L, Stevenson P.R, Suarez S.A. 2005. A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology* 26, 1017-1036.
- Schiffman S, Sennewald K, Gagnon J. 1981. Comparison of taste qualities and thresholds of D- and L- amino acids. *Physiology & Behavior* 27, 51-59.
- Scott T.R, Plata-Salaman C.R, Rolls E.T, Karadi Z, Oomura Y. 1994. Umami taste in the forebrain of the alert macaque. In: Kurihara K, Suzuki N, Ogawa H. (Eds) *Olfaction and Taste*. 6, 369-371. Springer, Tokyo.
- Tinti J.H, Glaser D, Wanner M, Nofre C. 2000. Comparison of gustatory responses to amino acids in pigs and in humans. *Lebensmittel-Wissenschaft und Technologie* 33, 578-583.
- Wallace R.B. 2005. Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. *International Journal of Primatology* 26, 1053-1075.