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The role of sucrose and sensory systems in fruit selection and consumption of *Ateles geoffroyi* in Yucatan, Mexico

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ABSTRACT

Our aim was to evaluate the role of sucrose and the role of smell, taste and touch in the selection and consumption of fruit in wild spider monkeys. We recorded the feeding bouts of 14 adults for 9 mo in the Otoch Ma'ax Yetel Kooh Reserve, Punta Laguna, Yucatan, Mexico. For each of 2346 inspections on fruits of six species the consumption or rejection and the use of touch, smell and taste was recorded. Ten fruit samples (five ripe and five unripe) from each species were collected and the sucrose concentration was determined with a refractometer. As expected, sucrose concentrations were higher in ripe than unripe fruits. The difference in sucrose concentration between ripe and unripe fruits was positively associated with the proportion of attempts on ripe fruits and the proportion of consumed ripe fruits. Furthermore, the senses of touch and taste were used more often when fruits were ripe, whereas the sense of smell was used more often when fruits were unripe. The results suggest that sensory cues and sucrose concentration play important roles in fruit selection in spider monkeys.

INTRODUCTION

Fruit is considered as a high-quality food because it is an excellent source of carbohydrates (Danish *et al*. 2006). The monosaccharides glucose and fructose and the disaccharide sucrose are the most common carbohydrates present in fruits (Karasov & Martinez del Rio 2007, Widdowson & McCance 1935), and are likely to be factors influencing fruit selection (Coleman & Downs 2012).

Frugivorous species differ in their preference for carbohydrates in relation to their nutritional needs and ability to detect them (Baker & Baker 1983, Downs *et al.* 2012, Martinez del Rio & Stevens 1989, Martinez del Rio *et al*. 1992). For example, the European starling (*Sturnus vulgaris*) has digestive adaptations that prevent the absorption of sucrose and therefore prefers fruits with higher concentrations of glucose and fructose (Martinez del Rio & Stevens 1989). In addition, the European rabbit (*Oryctolagus cuniculus*) shows a preference for maltose solutions compared to sucrose, glucose and fructose solutions of the same concentration (Laska 2002), whereas other mammals show preference for fruits high in sucrose (e.g. flying foxes, Megachiroptera, Baker *et al*. 1998, Ko *et al*. 2003, Geoffroy's tailless bat, *Anoura geoffroyi*, Jamaican fruit bat, *Artibeus jamaicensis*, little shouldered bat, *Sturnira lilium*, Herrera 1999, palm civet, *Paguma larvata*, small Indian civet, *Viverricula indica*, rhesus monkey, *Macaca mulatta*, Ko *et al*. 2003). In addition, several species of frugivorous primate are capable of detecting lower concentrations of sucrose relative to glucose or fructose (pygmy marmoset, *Cebuella pygmaea*, Glaser, 1986; Geoffroy's spider monkey, *Ateles geoffroyi*, Laska *et al*. 1996; squirrel monkey, *Saimiri sciureus*, Laska 1996; pigtail macaque, *M. nemestrina*, hamadryas baboon, *Papio papio hamadryas*, Laska 2000, Laska *et al*. 1999), and therefore sucrose may serve a role in food selection.

Many primates feed on a large variety of plant species (Richard 1985), suggesting that the choice of food depends on the nutritional content and/or degree of toxicity (Barton & Whiten 1994, Chapman *et al*. 2012). They therefore need to assess the nutritional content of food through sensory cues that provide information on the quality of the fruit such as colour, size, texture, hardness, odour and flavour (Dominy *et al*. 2004). Colour is often a long-range cue used to recruit animals from a distance (Murray *et al*. 1993, Voigt *et al*. 2004). Once animals are foraging on fruits other sensory systems, such as touch, smell and taste, may provide more useful information about the palatability and quality of the fruit.

Spider monkey species are considered ripe fruit specialists (Di Fiore *et al*. 2008, Gonzalez-Zamora *et al*. 2009), and energy content is considered a major factor in their food selection (Felton *et al*. 2009). Therefore, the detection of sugar may directly influence fruit consumption and is likely to be a criterion for the selection of food in spider monkeys (Laska *et al*. 1996). Captive Geoffroy´s spider monkeys have a remarkable sensitivity to sucrose (Laska *et al*. 1996) and are able to discriminate sucrose at lower concentrations than glucose and fructose (Laska *et al*. 1998). However, it could be argued that sucrose does not play an important role in fruit selection by spider monkeys, as it has a lower concentration than either fructose or glucose in most tested fruits (Riba-Hernández *et al.* 2003). Using Riba-Hernández *et al*.'s (2003) published sugar concentrations in the fruits of 27 species consumed by the spider monkey we found a positive correlation between glucose and fructose concentrations (r = 0.763), but no correlation between either sucrose and glucose concentrations (r = -0.096) or sucrose and fructose concentrations (r = -0.14), suggesting sucrose may have an independent influence on fruit selection in spider monkeys.

The aim of our study was to evaluate whether sucrose plays a role in the feeding decisions of the Geoffroy's spider monkey in the wild and to assess the use of senses (touch, taste and smell) in food selection. First, we tested whether sucrose concentration was higher in ripe than unripe fruits. Second, given their remarkable sensitivity to sucrose we hypothesized that Geoffroy's spider monkeys would select and consume a higher proportion of ripe fruits of the species with a larger difference in sucrose concentration between ripe and unripe fruits. Third, we hypothesized a different role of the senses of touch, taste and smell in fruit selection depending on the degree of ripeness.

METHOD

Study site and subjects

Our study was carried out in the Otoch Ma'ax Yetel Kooh protected area (20°38' N, 87°38' W, 14 m asl) located next to the village of Punta Laguna, Yucatan, Mexico. The protected area consists of 5367 ha and includes different degrees of regenerating forest. Approximately 700 ha are occupied by old-growth medium semi-deciduous forest and 2700 ha consist of 30-50-y-old successional forest. The dry season spans from December to April and the rainy season spans from May to November (Ramos-Fernandez & Ayala-Orozco 2003).

We studied one community of the Geoffroy's spider monkey (*Ateles geoffroyi*) that has been the focus of continuous research since January 1997. Thus, all community members were well habituated to the presence of observers and were individually identified. In the present study the adult individuals of the community served as subjects (see Vick 2008 for age classification). Only subjects with more than nine inspections per fruit species contributed to the analyses: six males and eight females.

Data collection

We observed the fruit selection behavior for a total of 9 mo from January 2012 to January 2013 distributing the observations roughly evenly between the dry and wet seasons. We collected data 4 d wk^{-1} during 4- or 8-h blocks between 06h00-18h00. We collected data using 5-min focal animal observations (Martin & Bateson 1993) and scored all fruit inspections by the focal animal, which included touching, smelling and tasting the fruit (Hiramatsu *et al*. 2009). We scored a fruit inspection when a focal animal performed a sensory investigation of a fruit without necessarily consuming it. We scored touch when the subject took the food in its hands or placed it against its lips with its hand. Smell was recorded each time the subject inspected a fruit by putting it within 2 cm of the front of its nose. We scored taste whenever the subject took small bites or just touched the fruit with its tongue.

Fruits were considered rejected when the monkey smelled, manipulated or tasted a fruit, but then it did not consume it. We considered fruits accepted by the monkeys when they consumed at least 75% of the fruit. Observations were made from a maximum distance of 20 m and we used Bushnell binoculars (8 × 42) to view the details of each fruit inspection because the tree canopy was relatively low (i.e. the vast majority of the trees did not reach more than 25 m in height).

We recorded at least 200 inspections on fruits of each of six tree species that changed colour over the course of ripening. The species were identified following Peña et al. (2011). Three species (*Sideroxylon capiri*, *Brosimum alicastrum*, *Spondias mombin*) changed colour from green to yellow. One species (*Croton fragilis*) changed colour from green to red. Two species changed colour twice: *Ficus ovalis* changed colour from green to yellow to red and *Dalbergia glabra* changed colour from green to yellow to orange.

To determine the concentration of sucrose we collected five ripe and five unripe fruits from each species. In the case of *Ficus ovalis* and *Dalbergia glabra* five fruits were collected for each of the colour phases of the fruits. We manually extracted the pulp and homogenized it with a mortar and pestle. We then measured the concentration of sucrose with a Master-T Refractometer (Atago®) using a Brix scale (Guillén *et al*. 2011).

Statistical analysis

To determine whether there were differences in the sucrose concentration between ripe and unripe fruits of the same species we used parametric tests as the distributions of each dataset did not violate assumptions of normality using a Kolmogorov-Smirnov test (all Ps $\geq$ .498). We used paired t-tests when fruit changed colour only once and performed within-subject analysis of variance (ANOVA) for the two species where fruit changed colour twice. We used Tukey's HSD post hoc tests to determine differences among the three colour conditions.

We performed two general linear models (GLMs) to examine the association between sucrose concentration and fruit selection and consumption. Data points were entered at the level of the individual monkey for each tree species whose fruit was selected and consumed. In both GLMs we used the difference in sucrose concentration between ripe fruits (yellow, orange or red colour depending on the species) and unripe fruits (green colour) as the independent variable. In the species where fruits changed colour more than once during ripening the values for ripe fruits were those of the yellow fruit, which had the lowest sucrose concentration between the two ripe colours. In the first GLM the dependent variable was the proportion of inspections on ripe fruits (i.e. number of inspections on ripe fruits / number of inspections on ripe and unripe fruits). In the second GLM the dependent variable was the difference between the proportion of consumed ripe and unripe fruits (i.e. the proportion of consumed fruits out of all inspections on ripe fruits - the proportion of consumed fruits out of all inspections on unripe fruits).

To examine the role of the senses of touch, smell and taste in fruit inspection we performed three further GLMs. For each GLM the dependent variable was the proportion of inspected fruits in which the monkeys used a sensory modality (i.e. touch, smell or taste). The independent variable was the ripeness of the fruit (i.e. ripe or unripe). We included fruit species as an additional independent variable to control for the effect of this variable on the relationship between fruit ripeness and the role of each sense in fruit inspection. In all GLMs the monkey identity was included as an additional fixed factor to control for between-subject variance and non-independence of data (i.e. the same monkey selecting/consuming/inspecting multiple fruits) (Tabachnick & Fidell 2007).

RESULTS

We observed 2346 inspections on fruits by the 14 subjects in which 2036 fruits were consumed. We scored 1919 inspections on ripe fruits (MEAN ± SE % of consumed fruits out of total inspections per individual: 90.2% ± 9.6%) and 427 attempts on unripe fruits (43.5% ± 39.7%).

In species in which the fruit colour changed from green to either yellow or red, ripe fruit had a significantly higher sucrose concentration than unripe fruits (Table 1). In the two species in which fruits change colour more than once sucrose concentrations differed across the three stages of ripeness (Table 1). Tukey's HSD post hoc tests revealed significant differences between green and yellow, yellow and red, and, red and green in *Ficus ovalis*, and between green and yellow, yellow and orange, and, orange and green in *Dalbergia glabra* (all $P < 0.01$ for all pairwise comparisons).

(Table 1 about here)

The first GLM revealed that the proportion of inspections on ripe fruits was positively associated with the difference in sucrose concentration between ripe and unripe fruits ($F_{1,51} = 8.02$, $P = 0.006$; Figure 1a). In the second GLM we found that the difference between the proportions of consumed ripe and unripe fruits was positively associated with the difference in sucrose concentration between ripe and unripe fruits ($F_{1,17} = 8.97$, $P = 0.008$; Figure 1b).

(Figure 1 about here)

We also evaluated how the monkeys used their senses during fruit inspection. The GLMs revealed associations of fruit ripeness with the sensory modalities. Touch ($F_{1,79} = 10.1$, $P = 0.002$) and taste ($F_{1,79} = 53.1$, $P < 0.001$) were used more often when fruit was ripe, whereas smell was used more often when fruit was unripe ($F_{1,79} = 17.0$, $P < 0.001$).
(Figure 2 about here)

DISCUSSION

We established that sucrose concentration was significantly higher in ripe than unripe fruits of the six species under consideration. As hypothesized, we found that the larger the difference in the sucrose concentration between ripe and unripe fruits the higher the proportion of inspections the monkeys made on ripe fruits. The difference in sucrose concentration between ripe and unripe fruits was also positively associated with the difference between the proportion of consumed ripe and unripe fruits. These results indicate that sucrose plays a role in both fruit selection and consumption. As hypothesized, we also found that spider monkeys rely on different sensory cues to select fruits depending on the degree of ripeness.

We found that in the fruits of each species we examined there was an increase in sucrose concentration across the different colour phases during ripening. Although our findings are not surprising as fruits undergo physical and chemical changes across stages of maturity, including sucrose concentration (Irsan 1998, Kader 1999, Moriguchi *et al.* 1990, Sabir *et al*. 2010), an increase in sucrose concentration likely leads to more frequent and successful selection of fruit (e.g. chimpanzee, *Pan troglodytes*, Reynolds *et al.* 1998). We found support for such a relationship given that the difference in sucrose concentration between ripe and unripe fruits was associated with the selection and consumption of fruit of six species in the spider monkey. This finding is in line with earlier experimental work in which the spider monkey appeared to specialize in sweetness as a criterion of fruit selection (Laska *et al*. 1996) and prefer sucrose over other sugar solutions of equal molarity (Laska *et al*. 1998). Our results confirm that the detection of sweet substances in fruits is a key factor in their selection (Laska *et al*. 1996), and that sucrose is likely to be an important factor in fruit selection in the spider monkey, despite not being a predominant sugar in many of the fruits it consumes (Riba-Hernández *et al*. 2003). Collectively, this evidence points to the proximate mechanisms for fruit selection, whereas the function is the acquisition of nutrients with high-energy impact. In particular, our findings suggest that it is likely that the spider monkey's fruit selection is based on previous knowledge, possibly learned, given that differences in sucrose concentration between ripe and unripe fruits across species is a key factor in such selection. However, future work is needed in which sucrose, fructose and glucose concentration are all measured during different fruit ripening phases to evaluate the relationship of each sugar with the selection and consumption of fruits by the spider monkey before this issue can be fully resolved.

As hypothesized, we found relationships between the use of the senses of touch, smell and taste during fruit selection depending on ripeness, which support the view that different sensory cues are useful to the spider monkey in inspecting and selecting foods as has been reported for other primates (capuchin monkey, *Sapajus apella*, Visalberghi & Neel 2010; squirrel monkey, *S. sciureus*, Dominy *et al*. 2001; spider monkey, *A. geoffroyi*, Hiramatsu *et al.* 2009, Laska *et al*. 2007). Our finding that the spider monkey sniffs unripe fruits more often than ripe fruits supports recent work showing that the spider monkey uses olfaction to inspect a fruit when visual cues do not give a reliable indication of ripeness (Hiramatsu *et al*. 2009). As previous research in captive animals has shown that the spider monkey has a high olfactory sensitivity to food odours (Hernández-Salazar *et al.* 2003, Laska *et al.* 2003, Laska *et al*. 2006), sniffing may be particularly important to verify the status of fruit ripeness.

Little research has examined the use of the sense of touch in the inspection of fruits by the spider monkey. Our finding of an increase in the use of touch when the fruit was ripe supports earlier assertions that touch is an important mechanism to inspect fruit before consumption (Dominy *et al*. 2001, Hoffmann *et al*. 2004). The sense of touch can be used to distinguish the size, shape, hardness and texture of a fruit (Dominy *et al*. 2001), which change in most fruits during ripeness. The spider monkey appears to prefer ripe fruits, as they are softer than unripe fruits (Kinzey & Norconck 1990) and the soft texture may be an indicator of ripeness (Dominy 2004). Thus, the sense of touch may be important in food selection for the spider monkey by assessing the texture that changes during fruit ripening.

The sense of taste is crucial for the selection of food as the last step in its acceptance (Garcia-Bailo *et al*. 2009) and is essential to ensure that food is safe (Dominy *et al*. 2001, Laska *et al*. 2007). We found that the spider monkey tasted fruit more frequently when it was ripe. Sweet perception resulting from simple sugars is generally elicited by ripe fruit and is associated with an energy source (Hladik & Simmen, 1996). Our findings support earlier studies on captive animals of the same species, which demonstrate that taste is important in fruit selection (Glaser 1986, Laska 1996, Laska 2000, Laska *et al*. 1996, 1999, 2007; Hladik *et al.* 2003). Thus, overall our findings on the role of sensory cues highlight the importance of smell, touch and taste in fruit selection depending on ripeness.

Although in our study we did not measure the concentrations of monosaccharide sugars present in fruits, such as glucose and fructose, we did find evidence that points to an important role of sucrose in fruit selection and consumption by the spider monkey. In addition, our findings add to the body of literature supporting that sucrose concentration is associated with conspicuous colour changes during fruit ripening. It is well understood that fruit colour is an important sensory cue that various species rely on to recognize fruit ripeness, particularly from a distance (Dominy & Lucas 2001, Regan *et al*. 2001). Our results provide evidence that other sensory cues are important for selecting fruits at close range in the spider monkey.

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Table 1. Comparisons of sucrose concentrations (g L^{-1}) (mean ± SD) in six species consumed by spider monkeys according to the fruit colour based on paired t-tests or within-subjects one-way ANOVAs.

Species*	Green	Yellow	Orange	Red	T	F	P
Sideroxylon capiri	14.4 ± 1.3	20.4 ± 3.0			4.12		0.003
Spondias mombin	8.8 ± 0.8	13.0 ± 1.6			5.25		<0.001
Brosimum alicastrum	6.4 ± 0.5	9.4 ± 1.5			4.16		0.003
Croton fragilis	8.4 ± 0.9			11.4 ± 0.5	6.39		<0.001
Ficus ovalis	4.6 ± 1.1	12.0 ± 1.0		13.2 ± 1.1		92.9	<0.001
Dalbergia glabra	6.0 ± 0.7	15.2 ± 0.8	16.8 ± 0.8			268.2	<0.001

* Tree species were determined following Peña et al. (2011)

Figure 1 llustration of the relationship between the difference in sucrose concentration (g/L) between ripe and unripe fruits consumed by spider monkeys and a) the proportion of fruit inspections on ripe fruits, and b) the differences in proportion of consumed ripe and unripe fruits. Datapoints represent responses by individual monkeys. The best fitting lines representing the relationship between the variables is shown.

Figure 2. Illustration of the use of touch, smell and taste depending on fruit ripeness during foraging and food selection. * indicates significant differences.