



## Food Preferences and Nutrient Composition in Captive White-handed Gibbons, *Hylobates lar*

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**Abstract** We aimed to assess spontaneous food preferences in captive white-handed gibbons and to analyze whether they correlate with nutrient composition. Via a 2-alternative choice test, we repeatedly presented 3 male *Hylobates lar* with all possible binary combinations of 10 types of food that are part of their diet in captivity and found the following rank order of preference: grape > banana = fig > apple > pear > honeydew melon > carrot > tomato > cucumber > avocado. Correlational analyses revealed a highly significant positive correlation between the food preference ranking and the total carbohydrate, fructose, and glucose contents of the foods ( $p < 0.01$ , respectively). With the exception of the trace mineral selenium ( $p < 0.05$ ), there was no other significant correlation with any other macro- or micronutrient. In addition, the food preferences were stable across the day because rankings obtained from tests performed at 0900, 1200, and 1500 h, respectively, did not differ significantly ( $p > 0.05$ ). Our results suggest that captive white-handed gibbons are not opportunistic, but selective feeders with regard to maximizing net gain of energy because only the content of carbohydrates, but not the contents of total energy, proteins, or lipids significantly correlate with the displayed food preferences. Further, the results suggest that captive *Hylobates lar*, in contrast to their free-ranging conspecifics, do not display marked changes in their food selection across the day.

**Keywords** food preferences · frugivory · *Hylobates lar* · nutrient composition · white-handed gibbons

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## Introduction

Most primate species are highly selective feeders and spend a considerable proportion of their time and energy searching for preferred foods (Hughes 1993). It is commonly agreed that food choices of primates are attributable to 2 principal factors: the nutritional or toxic content of the particular plant part (Barton and Whiten 1994; Freeland and Janzen 1974) and its relative spatial and temporal availability (Leighton 1993; Stevenson 2003). Several other factors such as body size or gut morphology also contribute to food selection in primates but are generally regarded as evolutionary adaptations to the aforementioned principal factors.

Several researchers reported that food selection of primates correlates negatively with the contents of plant secondary compounds such as phenolics, alkaloids, or tannins that inhibit digestion of proteins and polysaccharides or are toxic (Glander 1982; Waterman 1984; Wrangham *et al.* 1998). Conversely, only a few studies have so far demonstrated positive correlations between contents of a given nutrient and the food preferences displayed by primates (Conklin-Brittain *et al.* 1998; Milton 1998). This is surprising because optimal foraging theory predicts that natural selection will favor individuals that maximize their rate of net intake of energy or other critical nutrients and that food selection patterns observed today are thus adaptive (Stephens and Krebs 1986). However, the apparent difficulties in determining plant compounds that correlate positively with food choice in primates possibly reflect the highly complex chemical composition of potential plant food species and the trade-offs that herbivorous species thus need to make between the quest for meeting their nutritional and energetic requirements and avoiding the ingestion of too high amounts of substances used by plants to protect their potentially edible parts from predation.

A possible means to obtain information as to which nutrients might affect primate food selection positively is to present animals with food items that contain only small and thus presumably negligible amounts of plant secondary compounds and to assess whether their choice behavior correlates with any nutrient. Use of cultivated fruits is consistent with the idea because they both contain low amounts of secondary compounds and their nutrient content is well characterized (Food Standards Agency 2002; Souci *et al.* 1989). By repeatedly presenting captive spider monkeys (*Ateles geoffroyi*) with all possible binary combinations of 10 cultivated foods, Laska *et al.* (2000) showed a positive correlation between the food preferences displayed by the species and the content of total energy in the foods used. Additional studies that employed the same approach showed that like the spider monkeys, captive squirrel monkeys (*Saimiri sciureus*: Laska 2001), capuchins (*Cebus apella*: Visalberghi *et al.* 2003), and pacas (*Agouti paca*: Laska *et al.* 2003), display food preferences that correlate highly significantly with total energy content. Conversely, pig-tailed macaques (Laska 2001) prefer foods with high contents of total carbohydrates but not foods that are high in total energy content or in other sources of metabolic energy such as proteins or lipids. We speculate that differences in the degree of frugivory might account for the fact that some primate species seem to be opportunistic with regard to their preferred source of metabolic energy whereas others are not.

Like pig-tailed macaques, white-handed gibbons include a high proportion of carbohydrate-rich fruits in their natural diet (Chivers 1984) and show clear preferences toward ripe fruits, which typically have the highest content of soluble carbohydrates (Bollard 1970; Simmen *et al.* 1999). Accordingly, total carbohydrate content in foods might be an important determinant of food choice for the species (Bartlett 2007; Carpenter 1940; Jolly 1985; Raemaekers 1978; Richard 1985; Ungar 1995, 1996). Further, white-handed gibbons primarily meet their water requirement by consuming fleshy fruits and immature leaves, and they only rarely drink from open water sources (Carpenter 1940; Raemaekers 1978), which suggests that water content also may be an important factor that determines their food preference.

We aimed therefore to assess the occurrence of spontaneous food preferences in captive white-handed gibbons and to analyse whether they correlate with the abundance of macro- or micronutrients.

## Materials and Methods

### Subjects

We tested 3 male white-handed gibbons (*Hylobates lar*) of 12, 7, and 5 yr of age, respectively. All subjects were born and maintained at Kolmårdens Djurpark, Sweden. The gibbons lived in 2 enclosures 117 m<sup>3</sup> and 215 m<sup>3</sup>, respectively, joined by a corridor containing 2 test rooms 10 m<sup>3</sup> each. From one of the enclosures the gibbons had to move through the corridor to enter a test room, whereas they could enter the other test room directly from the other enclosure through a sliding door in the adjacent wall. We trained all subjects to enter the test rooms voluntarily and they were completely accustomed to the procedure. We maintained the gibbons on a 14:10-h light/dark cycle at 20–22°C. Caretakers fed the gibbons commercial primate chow and provided water *ad libitum*. Fresh fruits and vegetables were available to the gibbons *ad libitum* between 1600 and 2000 h and then removed overnight. The amount of food offered daily to the gibbons was such that leftovers were on the floor the next morning, and thus it was unlikely that ravenous appetite affected their ingestive behavior in the tests.

### Procedures

We assessed food preferences via a 2-alternative choice test. We presented the subjects with pairs of food items, and recorded their choice behavior, i.e., which of the 2 food items they consumed first. We tested gibbons singly to avoid competition affecting their choices.

We separated the gibbons for 3 sessions each day, at *ca.* 0900, 1200, and 1500 h. We chose the specific times to account for possible diurnal changes in food choice. During the sessions, the gibbons approached a 90×46 cm wooden shelf mounted on one of the walls of a test room, chose one of a pair of simultaneously presented food items, and then retreated, so that caretakers could remove the rejected food item. To prevent a gibbon from taking both food items at the same time, the food items were 20 cm apart. All foods were cubes with a side length of 1 cm so that size differences

would not affect choice behavior. Each session consisted of 20 pairwise presentations and we pseudorandomized the position of the food items, e.g. grape presented left and carrot presented right, to counterbalance possible side preferences. We generated schedules for all sessions via AMPL/CPLEX to ensure optimal spreading of all 45 possible binary combinations of 10 types of food over the sessions and days. We presented each pair of food items to a gibbon 12 times and took care never to present a food item that had been part of the previous pair.

We used the following types of food: apple (*Malus sylvestris*), avocado (*Persea gratissima*), banana (*Musa paradisiaca*), honeydew melon (*Cucumis melo*), carrot (*Daucus carota*), cucumber (*Cucumis sativus*), fig (*Ficus carica*), grape (*Vitis vinifera*), pear (*Pyrus communis*) and tomato (*Lycopersicum esculentum*). The rationale for choosing these foods was 1) that all of them are part of the gibbons' diets in captivity and thus familiar to them; 2) that data for the contents of macro- and micronutrients in these foods were available, allowing us to analyze correlations between food preferences and nutrient contents (Food Standards Agency 2002; Souci *et al.* 1989); and 3) that they differ markedly in their contents of macronutrients. With regard to 3, the contents of total energy, total carbohydrates, lipids, protein, dietary fiber, and water differed by a factor of  $\leq 21$ , 138, 235, 10, 24, and 4, respectively, between the types of food used here.

To minimize the inevitable intraspecific variation in nutrient composition, we took care always to present food items of a given type with the same degree of ripeness.

Our experiments comply with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health Publication no. 86-23, revised 1985) and also with current Swedish laws.

## Data Analysis

We recorded 1620 choices (45 binary combinations  $\times$  12 presentations per subject  $\times$  3 subjects), and established food preference rankings via 4 different criteria.

**Criterion 1 (individual level):** We assigned foods of a given type that an individual consumed first in the majority of presentations with a given binary combination, i.e., in  $\geq 7$  of 12 presentations, 1 point and the alternative 0. If a subject chose both alternatives in a given binary combination equally often, we assigned both types of food 0.5 points each. The theoretical maximum score for any type of food with the criterion is 9 (9 combinations  $\times$  1 subject).

**Criterion 2 (group level):** This criterion adopts the same assignment of points to preferred food items as criterion 1, though here we collapsed the points for all 3 subjects. Thus, the theoretical maximum score for any type of food with this criterion is 27 (9 combinations  $\times$  3 subjects).

**Criterion 3 (individual level):** We built the sum total of choices for each of the 10 types of food across all binary combinations for each individual. The theoretical maximum score for any type of food with this criterion is 108 (9 combinations  $\times$  12 presentations per subject  $\times$  1 subject).

**Criterion 4 (group level):** This criterion adopts the same procedure of building the sum total of choices as for criterion 3, though here we collapsed the data for all 3

subjects. Thus, the theoretical maximum score for any type of food with this criterion is 324 (9 combinations  $\times$  12 presentations per subject  $\times$  3 subjects).

In addition, we performed 2-tailed binomial tests using the sum total of choices for each member of a given binary combination to assess significant preferences both at the individual level, criterion 3, and at the group level, criterion 4 ( $p < 0.01$ ).

Preliminary analysis revealed that the food preference rankings obtained with the 4 criteria showed significant correlations with each other (Spearman  $r_s \geq 0.93$ ,  $p < 0.01$  for all 4 criteria), i.e., they were very similar, though not identical (*cf.* Table II); thus, for further analyses, we used only the rankings obtained via criterion 4.

We evaluated correlations between the food preference rankings and the contents of nutrients by calculating Spearman rank-order correlation coefficients  $r_s$ , which we tested for significance by computing z-scores.

We compared food preference rankings that were separately constructed for 0900, 1200, and 1500 h sessions and rankings with each other and checked for correlations via Spearman rank-order correlation coefficients.

## Results

### Food Preferences

Table I is a summary of the choice behavior of the gibbons in the food preference tests, i.e., the number of choices made by the gibbons in favor of each member of a given pair of foods. With 36 of 45 possible binary combinations, the gibbons displayed a statistically significant preference for one of the options (2-tailed binomial test,  $p < 0.01$ ). Grapes, figs, and bananas were clearly the most preferred food items and were significantly preferred over all other options ( $p < 0.01$  for all 21 combinations). The attractiveness of grapes, figs, and bananas is displayed further by

**Table I** Choice behavior of the gibbons in the food preference tests

	Grape	Banana	Fig	Apple	Pear	Melon	Carrot	Tomato	Cucumber	Avocado
Grape	X	↖	↖	↖	↖	↖	↖	↖	↖	↖
Banana	12:24	X	↖	↖	↖	↖	↖	↖	↖	↖
Fig	15:21	16:20	X	↖	↖	↖	↖	↖	↖	↖
Apple	2:34	7:29	9:27	X	↖	↖	↖	↖	↖	↖
Pear	4:32	4:32	3:33	17:19	X	↖	↖	↖	↖	↖
Melon	1:35	1:35	2:34	10:26	19:17	X	↖	↖	↖	↖
Carrot	1:35	3:33	2:34	10:26	11:25	15:21	X	↖	↖	↖
Tomato	0:36	1:35	0:36	0:36	1:35	1:35	2:34	X	↖	↖
Cucumber	0:36	1:35	0:36	0:36	0:36	0:36	0:36	2:28	X	↖
Avocado	0:36	0:36	0:36	0:36	0:36	0:36	1:35	0:27	0:12	X

The table indicates the number of choices (from  $n=3$  individuals) for each member of a given pair of food items. The first value applies to the food item to the left and the second to the food item on the top. ↖ indicates a significant preference for the food item to the left ( $p < 0.01$ ). ↗ indicates lack of significant preference for either member of a pair ( $p > 0.05$ ).

the fact that 82.4–89.2% of all possible choices were in favor of them (Table II). Avocado was clearly the least preferred food and subjects never preferred it over an alternative. Consequently, only 0.3% of all choices, and hence the lowest percentage of all options, were in favor of avocado.

### Rankings Derived from the Food Preferences

The food preference rankings derived from the gibbons' choice behavior according to the 4 criteria are in Table II. Calculations of Spearman rank-order correlation coefficients revealed that the rankings obtained with all 4 criteria correlate highly significantly with each other ( $r_s \geq 0.93$ ,  $p < 0.01$  for all 6 combinations), i.e., they are very similar, though not identical. Comparisons of the preference rankings derived from criteria 1 and 3 show that the individual gibbons displayed highly similar patterns of preference (Spearman  $r_s \geq 0.93$ ,  $p < 0.01$ ). Thus, the rank order of preference obtained with all 4 criteria applies to the gibbons both as a group and as individuals.

### Food Preferences as a Function of the Time of Day

The food preference rankings derived from the sessions at 0900, 1200, and 1500 h show close to perfect correlations with each other (Spearman  $r_s \geq 0.96$ ,  $p < 0.01$ ), i.e., they are very similar, though not identical (Table III). The fact that the gibbons' choice behavior was almost identical during the 3 sessions indicates that their food preferences were stable across the day.

### Food Preference Rankings and Nutritional Content

The Spearman rank-order correlation statistics between food preference ranking and the nutritional content of the foods are summarized in Table IV. The food preference

**Table II** Food items and their corresponding rank order of preference

Criterion 1	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	Criterion 2	S <sub>1</sub> + S <sub>2</sub> + S <sub>3</sub>	Criterion 3	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	Criterion 4	S <sub>1</sub> + S <sub>2</sub> + S <sub>3</sub>
1. Grape	8	9	9	Grape	26	Grape	89	102	98	Grape	289 (89.2)
2. Banana	7	8	8	Banana	23	Banana	79	93	95	Banana	267 (82.4)
3. Fig	9	7	7	Fig	23	Fig	103	80	84	Fig	267 (82.4)
4. Apple	5.5	5.5	5.5	Apple	16.5	Apple	63	62	72	Apple	197 (60.8)
5. Pear	5.5	4.5	4.5	Pear	14.5	Pear	64	55	58	Pear	177 (54.6)
6. Melon	3.5	4	5	Melon	12.5	Melon	48	56	57	Melon	161 (49.7)
7. Carrot	3.5	4	3	Carrot	10.5	Carrot	55	55	37	Carrot	147 (45.4)
8. Tomato	2	2	2	Tomato	6	Tomato	17	20	23	Tomato	60 (18.5)
9. Cucumber	0.5	1	1	Cucumber	2.5	Cucumber	4	7	4	Cucumber	15 (4.6)
10. Avocado	0.5	0	0	Avocado	0.5	Avocado	1	0	0	Avocado	1 (0.3)

Numbers in parentheses indicate the percentage of choices in favor of a given type of food (relative to the theoretical maximum of 324 choices/type of food). S<sub>1</sub>, S<sub>2</sub>, and S<sub>3</sub> refer to the 3 individual subjects.

**Table III** Diurnal changes in food preference rankings

0900 h	Rank	Points	1200 h	Rank	Points	1500 h	Rank	Points
Grape	1	99	Grape	1	96	Grape	1	96
Fig	2	92	Fig	2	91	Fig	3	84
Banana	3	89	Banana	3	90	Banana	2	88
Apple	4	63	Apple	4	68	Apple	5	66
Pear	5	61	Pear	5	58	Pear	4	70
Carrot	6	51	Carrot	6	52	Carrot	7	44
Melon	7	50	Melon	7	47	Melon	6	52
Tomato	8	18	Tomato	8	24.5	Tomato	8	25
Cucumber	9	10	Cucumber	9	9	Cucumber	9	10
Avocado	10	9	Avocado	10	4.5	Avocado	10	5

ranking correlates highly significantly with total carbohydrate content, and with the contents of fructose and glucose. Conversely, in the content of sucrose there is no significant correlation with the food preference ranking. The total energy content and the content of lipids and protein also failed to correlate significantly with the food preference ranking. Thus, the gibbons clearly preferred foods high in glucose and fructose but did not significantly prefer foods that are high in other energy sources such as lipids and protein. In addition, correlations between the food preference ranking and the content of water, dietary fiber, acids, and vitamins also failed to show statistical significance. This was true for all minerals except selenium, which correlates positively at the 5% level of significance with the food preference ranking.

## Discussion

Our results demonstrate that captive white-handed gibbons display marked food preferences in a 2-alternative choice situation using cultivated fruits, and that the preferences correlate significantly positively with the contents of fructose, glucose, and total carbohydrates of the sample food items. In addition, the gibbons' food preferences were stable across the day and very similar between the individuals tested.

### Evaluation of the Method Used

It is well established that several factors other than the nutritional value of a potential food item may affect an animal's choice. In a 2-alternative test situation chimpanzees, orangutans, gibbons, and rhesus monkeys usually, though not necessarily, prefer the larger of 2 pieces of fruit (Menzel and Draper 1965). We controlled for this possible bias by taking care to present our subjects with pieces of food of the same size. Similarly, side preferences may affect a subject's choice behavior and we controlled for this possibility by pseudorandomizing the position of food items.

The composition of nutrients in fruits changes with their stage of maturity (Bollard 1970; Simmen *et al.* 1999); thus, ripeness of fruits may affect food choice in primates (Redford *et al.* 1984; Richard 1985; Ungar 1995). To limit potential effects

**Table IV** Spearman rank-order correlation statistics (food preference ranking  $\times$  nutrient content

	$r_s$	$p$
<i>Macronutrients</i>		
Energy	0.48	n.s.
Water	-0.49	n.s.
Protein	-0.05	n.s.
Lipids	-0.01	n.s.
<b>Carbohydrates</b>	<b>0.92</b>	<b>&lt;0.01</b>
Dietary fiber	0.14	n.s.
Minerals	-0.18	n.s.
<i>Carbohydrates</i>		
Sucrose	-0.40	n.s.
<b>Fructose</b>	<b>0.87</b>	<b>&lt;0.01</b>
<b>Glucose</b>	<b>0.98</b>	<b>&lt;0.01</b>
<i>Organic acids</i>		
Ascorbic acid	-0.16	n.s.
Citric acid	0.14	n.s.
Malic acid	0.70	n.s.
<i>Vitamins</i>		
Vitamin A	0.50	n.s.
Vitamin B <sub>1</sub>	-0.05	n.s.
Vitamin B <sub>2</sub>	-0.12	n.s.
Vitamin B <sub>6</sub>	-0.07	n.s.
Vitamin B <sub>12</sub>	0.50	n.s.
Vitamin C	-0.16	n.s.
Vitamin D	0.50	n.s.
Vitamin E	-0.48	n.s.
Folate	-0.36	n.s.
Pantothenate	-0.36	n.s.
Biotin	-0.38	n.s.
Carotene	-0.20	n.s.
Niacin	-0.26	n.s.
<i>Minerals</i>		
Sodium (Na)	-0.42	n.s.
Potassium (K)	-0.02	n.s.
Calcium (Ca)	-0.15	n.s.
Magnesium (Mg)	-0.02	n.s.
Phosphorous (P)	-0.12	n.s.
Iron (Fe)	0.19	n.s.
Copper (Cu)	0.40	n.s.
Zinc (Zn)	-0.28	n.s.
Chlorine (Cl)	-0.04	n.s.
Manganese (Mn)	0.04	n.s.
<b>Selenium (Se)</b>	<b>0.79</b>	<b>&lt;0.05</b>

Values for the statistical measure  $r_s$  may range from +1 (perfect positive correlation) to -1 (perfect negative correlation). Energy values used are the physiological energy values derived from an aliquot of edible portion of the corresponding food item, without consideration of the individual digestibility (Souci *et al.* 1989).

of fruit maturation on choice behavior, we always presented a given type of food with the same degree of ripeness.

Differences in palatability or in novelty of the food items might also affect choice behavior (Fragaszy *et al.* 1997). To control for the factors, we took care that all types of food were familiar to the subjects and performed preliminary tests that showed that all types of food were readily taken and consumed by all subjects when presented singly, suggesting that none of them were unacceptable *per se*. Social context also affects food choice in primates (Visalberghi *et al.* 1998), which we controlled by testing our gibbons individually. In the wild, white-handed gibbons (Raemaekers 1978) and several other primate species (Thorington 1970; Whitten



1982) vary both quantity and type of consumed food with the time of day. To control for possible biases from diurnal variation in diet, we therefore spread the 12 presentations of a given binary combination of food items as evenly as possible across the sessions at 0900, 1200, and 1500 h.

Thus, we believe that the observed food preferences indeed reflect the white-handed gibbons' ability to choose between food items on the basis of perceived differences in nutrient content.

### Food Preferences in Relation to Nutrient Content

Our finding that the gibbons displayed food preferences that highly significantly correlate with total carbohydrate content, but not with total energy content, suggests that they are selective feeders with regard to energy gain. This supposition is supported by findings that wild gibbons include a considerable proportion (59–87%) of carbohydrate-rich fruits in their diets (Chivers 1984) and that they demonstrate clear preferences toward ripe fruits (Carpenter 1940; Jolly 1985; Palombit 1997; Raemaekers 1978; Richard 1985; Ungar 1995, 1996), which typically have the highest content of carbohydrates (Bollard 1970; Richard 1985).

The fact that the content of glucose and fructose correlates significantly with the gibbons' food preference ranking, whereas the content of sucrose does not, may at first seem surprising. However, humans as well as squirrel monkeys are unable to discriminate between the taste of sucrose, fructose, and glucose when their relative concentrations are adjusted (Breslin *et al.* 1994, 1996; Laska 1997), which indicates that the 3 carbohydrates are experienced as having the same taste quality. Assuming that white-handed gibbons, like humans and squirrel monkeys, are unable to discriminate between the taste quality of sucrose, fructose, and glucose, there must be an alternative explanation for our results. One might be our selection of foods presented to the subjects. In the majority of ripe fruits, the carbohydrate composition is predominated by the content of sucrose (Simmen and Sabatier 1996). However, it is not the case with grapes (Food Standards Agency 2002; Souci *et al.* 1989), in which the ratio between sucrose and fructose and sucrose and glucose in both cases is 0.06, i.e., the content of sucrose is much lower than both the content of fructose and glucose. The fact that grapes are ranked as the most preferred food, and that they have a low content of sucrose compared to most other foods tested, inevitably affects the correlation between sucrose and the food preference ranking displayed by the gibbons. As a consequence, the content of sucrose highly significantly correlates with the subjects' food preference rankings when we removed grapes from the statistical calculation while, at the same time, all other correlations remained more or less the same. Accordingly, the lack of a significant correlation between the gibbons' food preference ranking and the content of sucrose might indeed be the result of our selection of fruits.

The lack of a significant correlation between the gibbons' food preference ranking and the content of proteins and lipids could be explained by the fact that our study considered and tested only preferences for fruits and vegetables. The foods are generally poor sources of proteins and lipids (Food Standards Agency 2002; Souci *et al.* 1989) and several species of frugivorous primates therefore regularly supplement their diet with leaves or insects (Ofstedal 1991; Raemaekers 1978; Richard 1985).

Leaves contain levels of protein that are on average 5 times as high as those normally occurring in fruits and therefore constitute an excellent source of it (Waterman 1984). Insects are likewise good sources of high-quality protein and may also supply high levels of lipids (Banjo *et al.* 2006; Ramos-Elorduy *et al.* 1997), a macronutrient that is present at low levels in most leaves that primates select (Simmen and Sabatier 1996). Field studies have shown that white-handed gibbons often include both sources of protein in their diet. However, one fruit we used — avocado — contains an atypically high proportion of lipids, but was nevertheless the least preferred food.

Our finding that the gibbons displayed food preference rankings that do not correlate significantly with the content of any micronutrient, except selenium, suggests that they are not selective feeders with regard to minerals or vitamins. The finding should not be surprising given that wild plants and insects contain moderate to high levels of micronutrients (Banjo *et al.* 2006). The most likely explanation for the unexpected finding that the gibbons' food preference rankings significantly correlate with the content of selenium is that it is just a by-product of their preference for carbohydrate-rich fruits. The fact that the content of selenium correlates significantly positively with the total carbohydrate, fructose, and glucose contents of the food items ( $r_s \geq 0.77$ ,  $p < 0.01$  for all 3 combinations) supports this supposition.

Somewhat surprisingly, our results showed that the food preferences of gibbons do not correlate significantly with the content of water. Given that white-handed gibbons meet their water requirement primarily by consuming fleshy fruits and immature leaves, and only rarely drink from open water sources (Carpenter 1940; Raemaekers 1978), a positive correlation might have been expected. However, plant foods that are high in water content are typically low in carbohydrate content as well as in content of other forms of metabolic energy such as proteins or lipids (Food Standards Agency 2002; Souci *et al.* 1989). Cucumber and tomato, 2 of the least preferred types of food in our study, have the highest water content but the lowest carbohydrate content of all test options (Food Standards Agency 2002; Souci *et al.* 1989). Thus, the white-handed gibbons may trade off the content of water for total carbohydrate content of potential food items. Additional support for the supposition comes from the fact that the gibbons in the present study had access to a water spout *ad libitum* but never used it unless we changed their diet for several days to commercial monkey chow (dry food pellets) only.

### Interspecific Comparison

By employing the same method and, with few exceptions, the same types of foods as the ones we used, Laska (2001) showed that the food preferences displayed by pig-tailed macaques correlate significantly with the total carbohydrate content of the food items. In line with the findings for our white-handed gibbons, the pig-tailed macaque preference for food items does not correlate significantly with the contents of total energy, lipids, or proteins. In contrast to gibbons and pig-tailed macaques, the food preferences of spider monkeys (Laska *et al.* 2000), squirrel monkeys (Laska 2001), capuchins (Visalberghi *et al.* 2003), and a nonprimate mammal, pacas (Laska *et al.* 2003), correlate significantly with the total energy content of food items. Their

food preferences were independent of the source of metabolic energy. Captive gorillas and chimpanzees display significant correlations between their food preferences and the contents of both nonstarch sugars, i.e., soluble carbohydrates and total energy (Remis 2002). However, the 9 and 6 types of food offered to the gorillas and chimpanzees, respectively, did not include lipid-rich items such as avocado or items that differed markedly in protein contents (maximally by a factor of 4) and thus it is difficult to decide whether the preferences for sugar-rich items simply covary with energy content or not.

Laska and co-workers (2000, 2001, 2003) speculated that differences in the degree of frugivory might account for the fact that some primate species seem to be opportunistic with regard to their preferred source of metabolic energy whereas others are not. However, the data are inconclusive and further research with other species is needed to prove or disprove the hypothesis.

An alternative explanation that could possibly account for the contrast between the species and their respective preferences for different sources of metabolic energy is competition for food by sympatric animals. To minimize competition and to survive and reproduce in large communities of different species, animals have to find their own food niche (Mackinnon J. R. and MacKinnon K. S. 1980). In view of the fact that most primates (Harding 1981), as well as several other mammals and birds (Payne 1980), at least partially include fruits in their diets, it seems reasonable to assume that there is a considerable competition for them. Accordingly, frugivorous species display different preferences for food items and the respective nutrients that they contain. Alternatively, the abundance of certain plant species used as staple food by a given species might explain both inter- and interspecific differences in preferences for the main source of metabolic energy. Palombit (1997) reported that both siamang (*Hylobates syndactylus continentis*) and white-handed gibbons (*Hylobates lar*) may differ markedly in their degree of frugivory, and concomitantly in the extent of reliance on carbohydrates as a main source of metabolic energy, depending on the abundance of fig fruits in different habitats.

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