



## Great apes prefer cooked food

Victoria Wobber<sup>a,b,\*</sup>, Brian Hare<sup>b,c</sup>, Richard Wrangham<sup>a</sup>

<sup>a</sup>Department of Anthropology, Harvard University, Peabody Museum, 11 Divinity Avenue, Cambridge MA 02138, USA

<sup>b</sup>Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D04103 Leipzig, Germany

<sup>c</sup>Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27705, USA

### ARTICLE INFO

#### Article history:

Received 4 June 2007

Accepted 12 March 2008

#### Keywords:

Cooking  
Diet  
Hominid evolution  
Tubers  
Meat

### ABSTRACT

The cooking hypothesis proposes that a diet of cooked food was responsible for diverse morphological and behavioral changes in human evolution. However, it does not predict whether a preference for cooked food evolved before or after the control of fire. This question is important because the greater the preference shown by a raw-food-eating hominid for the properties present in cooked food, the more easily cooking should have been adopted following the control of fire. Here we use great apes to model food preferences by Paleolithic hominids. We conducted preference tests with various plant and animal foods to determine whether great apes prefer food items raw or cooked. We found that several populations of captive apes tended to prefer their food cooked, though with important exceptions. These results suggest that Paleolithic hominids would likewise have spontaneously preferred cooked food to raw, exapting a pre-existing preference for high-quality, easily chewed foods onto these cooked items. The results, therefore, challenge the hypothesis that the control of fire preceded cooking by a significant period.

© 2008 Elsevier Ltd. All rights reserved.

### Introduction

The advent of cooking, whether it occurred at the origin of *Homo erectus* or during the Middle Paleolithic, has been hypothesized to have had diverse effects on human physiology and behavior (Coon, 1962; Brace et al., 1987; Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Lucas et al., 2006; Wrangham, 2006). Because cooking reduces food toughness and, thus, would have allowed easier chewing and digestion, a diet of cooked food appears to have contributed to the reduction of tooth size and gut size in hominids (Aiello and Wheeler, 1995; Lucas, 2004). Small guts probably explain why modern humans fare poorly on raw diets (Kobnick et al., 1999) and why no human societies live without cooking (Wrangham and Conklin-Brittain, 2003).

Such indications of biological adaptation to cooking raise the possibility that a preference for eating cooked food is an adaptation rather than an exaptation (i.e., that the preference for cooked food evolved subsequent to the adoption of cooked diets). If so, the problem of how cooking arose is relatively complex because cooking would not necessarily have been adopted quickly after the control of fire. As Stahl (1989: 19) suggested, “use of controlled fire

as a source of warmth may have preceded systematic use of fire in food preparation by thousands or hundreds of thousands of years.” Similarly, Bellomo (1994) proposed that when fire was first controlled it was used for heat, light, and defense against predators but not for cooking.

Alternatively, cooked food may have properties that hominoid primates would find desirable even without any evolutionary exposure to cooking. If so, the control of fire would be expected to lead rapidly to cooking, as often implied or suggested (e.g., Oakley, 1963; Clark and Harris, 1985; Brace, 1995; Rolland, 2004; Wrangham, 2006).

No data are currently available to directly distinguish between these hypotheses, but human systems for food perception appear to be generally similar to those in other mammals, including primates (Dominy et al., 2001; Hladik et al., 2003). As such, the findings that rats have been shown to prefer cooked to raw starch (Ramirez, 1992) and cats prefer cooked to raw meat, provided they are familiar with cooked meat (Bradshaw et al., 2000), would suggest that this preference may have been conserved in primates. Yet no past work has investigated this question specifically.

What has been shown is that both nonhuman primates and other animals tend to prefer properties that are produced by cooking. Numerous species prefer foods that are higher in sugar, and cooking raises sugar availability in the mouth by increasing the susceptibility of starch to amylase degradation (Svihus et al., 2005; Tester et al., 2006). Apes in captivity have also been shown to finely discriminate the levels of sugar, in addition to tannins and salt in various foods or aqueous solutions (Hladik and Simmen, 1996;

\* Corresponding author. Department of Anthropology, Harvard University, Peabody Museum, 11 Divinity Avenue, Cambridge MA 02138, USA. Tel.: +1 617 496 4262; fax: +1 617 496 8041.

E-mail addresses: [wobber@fas.harvard.edu](mailto:wobber@fas.harvard.edu) (V. Wobber), [hare@eva.mpg.de](mailto:hare@eva.mpg.de) (B. Hare), [wrangham@fas.harvard.edu](mailto:wrangham@fas.harvard.edu) (R. Wrangham).

Laska et al., 1999; Hladik et al., 2003; Simmen and Charlot, 2003). In the wild as well, food choices of nonhuman primates, including apes, are well-predicted by their sugar or tannin contents, suggesting that individuals might be sensitive to these properties of a food if they were changed by cooking (Leighton, 1993; Conklin-Brittain et al., 1998; Wrangham et al., 1998). Further, cooking increases the availability of glutamate, responsible for the umami taste preference (Sasaki et al., 2007), and umami taste receptors are found widely in invertebrates and vertebrates (Bellisle, 1999). Finally, some of the textural properties to which monkeys respond are the same as those used by humans, such as viscosity, temperature, fat content, and grittiness. Perception of textural properties has in some cases been shown to be mediated in humans and nonhuman primates via similar neural mechanisms (Kadohisa et al., 2004, 2005; Rolls, 2005).

Such evidence indicates that the mechanisms of human food perception are fundamentally similar to those in other primates. Nevertheless, species preferences for any given food are unpredictable (Hladik and Simmen, 1996; Dominy et al., 2001; Hladik et al., 2003). It is, therefore, not known whether the chemical and textural changes induced by cooking would have caused Paleolithic hominids to show increased or decreased preference. However, great apes offer an opportunity to assess whether hominoids have a tendency to spontaneously prefer cooked or raw foods.

Accordingly, in this paper we report on experiments designed to establish whether great apes have an inherent preference for raw or cooked food. We tested apes' preferences by providing the individual being tested with a choice between a raw and a cooked option, then measuring how many times it picked each item. We used three different categories of food to assess apes' preferences: tubers, meat, and fruit. Each individual food might have a different prediction based on the properties of that food which are altered by cooking, thus using this variety of items allowed us to gain some insight into what factors might be influencing subjects' selectivity. In addition to testing general taste preferences in different cooked and raw foods, in *experiment 2* we also tested a few hypotheses of why subjects might prefer cooked food. We did so by manipulating the textural properties of the foods in this experiment, juxtaposing the potential taste and tactile changes caused by cooking to attempt to discern what factors would be selected by subjects in a potential preference for cooked food.

### Experiment 1: do apes prefer cooked tubers?

In this experiment, we investigated chimpanzees' preferences for cooked versus raw tubers. Tubers are an important class of food for many hunter-gatherers and have likely been significant during human evolution (O'Connell et al., 1999; Laden and Wrangham, 2005; Perry et al., 2007). They are also a category of food where the items are significantly changed in both nutritional and textural quality by cooking (Wandsnider, 1997; Wrangham et al., 1999; Laden and Wrangham, 2005). Tubers are often improved nutritionally by being cooked, since heat gelatinizes starch granules that may otherwise be incompletely digested (Ayankunbi et al., 1991; Kingman and Englyst, 1994; Tester and Sommerville, 2000; Smith et al., 2001; Lucas, 2004). Though chimpanzees in the wild occasionally eat raw tubers (Lanjouw, 2002; Hernandez-Aguilar et al., 2007), tubers are generally not elements of the chimpanzee diet. They therefore represent a relatively unfamiliar type of food for chimpanzees, for which a strong bias towards the raw or cooked items is unlikely to have been selected. The subjects in this experiment had previously tasted our test items—carrots, sweet potatoes, and white potatoes—in both their cooked and raw forms, reducing the possibility that simple fear of novelty might shift preferences away from the cooked items.

### Methods

Fourteen chimpanzees (for age and sex, see *Table 1*) were subjects for this experiment and were housed at the field station at the Yerkes Regional Primate Center in Atlanta, Georgia, USA, when they were tested. The fourteen chimpanzees had various rearing histories, with two individuals (Peony and Ericka) raised in a human family as young infants. At Yerkes all subjects were fed on a diet of monkey chow and various fruits and vegetables provided throughout each day. In the past, all of the chimpanzees had been fed various cooked foods, including the ones they were tested with in the current study. Water was available *ad libitum* during testing. Tubers were sliced across their diameter and baked in the oven at approximately 245 degrees Celsius (°C) until they were soft/edible to a human. All items in this and the subsequent experiments were at room temperature when presented.

Subjects were brought one at a time into a testing room. Each individual was presented with one food preference test consisting of five trials per day. In their first session (on the first test day), subjects were given a choice between cooked and uncooked sweet potato (*Ipomoea batatas*), then in their second session a choice between cooked and uncooked white potato (*Solanum tuberosum*), and finally in their third session cooked and uncooked carrots (*Daucus carota sativus*). Before each testing session the individual was given an introduction in which they were presented with two pieces of uncooked food and two pieces of cooked food of approximately equal size (approximately 2.5 cm diameter slices of carrot and 6.5 cm diameter slices of potato). After the subject finished eating these pieces of food the test session began.

The experimenter held a cooked piece of food in one hand and an uncooked piece of food in the other so that the subject could look, smell, and/or touch both pieces of food (the food pieces were 10–15 cm apart from each other). Once the subject had inspected the food the experimenter then slowly moved her hands out of the subject's reach while also moving them apart and stopped when the food pieces were 50–60 cm apart from each other. Once the food pieces were separated by this distance, they were moved back within reach of the subject. The subject was then allowed to touch one of the two food pieces, and was given the food piece he/she first touched. This procedure was repeated five times for each subject in each session while the position of each food type was alternated each trial and the position presented in the first trial was counterbalanced across subjects. Subjects' choices were scored live by the experimenter.

**Table 1**  
Number of choices for cooked items in *experiment 1*<sup>a</sup>

Subject	Sex	Age	Carrot	White potato	Sweet potato	All cooked
Erika	F	26	5	5	2	<b>12</b>
Barbara	F	26	1	5	5	11
Jesse	F	17	5	5	4	<b>14</b>
Sonia	F	39	5	5	5	<b>15</b>
Rita	F	12	3	0	5	8
Borie	F	35	5	1	4	10
Anya	F	19	0	0	3	<b>3</b>
Kate	F	10	5	3	5	<b>13</b>
Peony	F	31	4	4	5	<b>13</b>
Kevin	M	9	5	0	3	8
Phinneus	M	33	1	5	5	11
Travis	M	11	3	0	5	8
Amos	M	22	5	5	3	<b>13</b>
Bjorn	M	11	5	0	5	10
Mean			3.7	2.7	4.2	10.6

<sup>a</sup> The number of times each chimpanzee in *experiment 1* chose to eat the cooked food when offered a choice between cooked and uncooked carrot, white potato, and sweet potato in five test trials per food type. Scores in **bold** represent those that differ significantly from chance ( $p < 0.05$ , binomial probability, one-tailed).

## Results

Table 1 presents the food choices in each of the three testing sessions and subjects' overall choices in all three test sessions combined. Over the three test sessions 6 of the 14 subjects had an individual preference for cooked food and one subject had an individual preference for uncooked food [ $p < 0.05$ , binomial probability, one-tailed]. When all three test sessions were considered together, as a group, the subjects showed a significant preference for the cooked items [one sample t-test,  $t(13) = 3.730$ ,  $p = 0.003$ ]. As a group, when each food type is considered separately, subjects preferentially chose the cooked carrot and sweet potato [carrot:  $t(13) = 2.502$ ,  $p = 0.026$ ; sweet potato:  $t(13) = 6.104$ ,  $p < 0.001$ ] but showed no preference for the cooked or raw items with respect to the white potato (Fig. 1). When subjects' food choices with the three different food types were compared there was no significant difference across food items between the amount of cooked food that subjects chose (repeated measures ANOVA).

## Discussion

Overall, chimpanzees in this experiment preferred cooked tubers to raw tubers. These results are the first to show a preference by chimpanzees for cooked food, but the lack of preference for cooked white potatoes shows that they do not prefer all types of cooked food. Subjects were hesitant to take the initial pieces of either the raw or cooked white potato, providing a potential explanation for their indifference in that this item may simply have been inherently less interesting than the carrot and the sweet potato. Alternatively, there may not have been significant enough flavor distinctions between cooked and white potato for subjects to differentiate between the two. Neophobia was unlikely to be a factor in the white potato or the other conditions, as subjects had previously eaten all of the food items used.

In the next experiment we sought to investigate what elements of food items might influence preferences in apes, since it was unclear from the present experiment whether apes preferred the cooked taste of the items they chose selectively, or whether tactile factors were more important in determining their choices. To distinguish between these factors, we manipulated the textural properties of the food items used. We also included the other three great ape species to obtain a broader sample of apes' preferences.

## Experiment 2: why do apes prefer cooked food?

In this experiment, we aimed to investigate whether subjects in experiment 1 preferred the cooked food because of potential taste

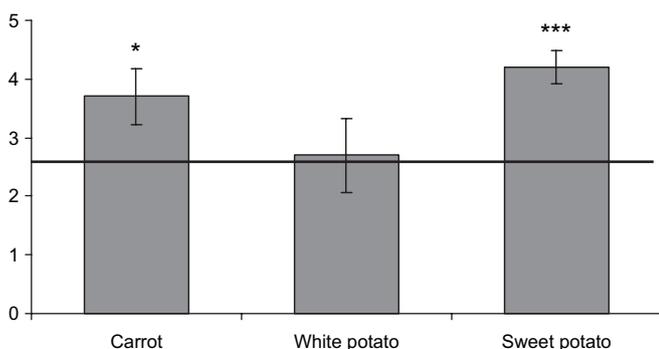


Fig. 1. Average number of trials that subjects in experiment 1 chose the cooked items with each different food item (\*\*\* $p < 0.001$ , \*\* $p < 0.01$ , and \* $p < 0.05$  with one sample t-test).

changes resulting from the nutrient changes of cooking, or whether other factors contributed to such a preference. Potential factors changed by cooking other than taste which may have affected preferences included: 1) food being made less tough by cooking, defining toughness as the ease of propagating a fracture in a piece of food (Lucas, 2004), and 2) food requiring less chewing before swallowing. Ease of chewing is distinct from toughness in that, in this instance, selectivity acts not on the texture but on the relative speed at which one can eat, which is a function of texture but also other factors, such as particle size which can be changed by cooking and processing. Thus, it was necessary to tease apart whether apes used the textural index of toughness or simply the reduction in the amount of chewing required in their selection of different items.

To test these two hypotheses, we presented apes with choices between food items that had been manipulated along these two factors. We used carrots as a test item, because chimpanzees had shown a strong preference for this item in its cooked state in experiment 1. We presented, alongside cubes of carrot, carrots which had been mashed (using a blender) to represent an item which was both less tough and required little chewing before swallowing, and carrots which had been grated (using a standard cheese grater) to represent an item which would require less chewing before swallowing because of decreased particle size but which was no less tough than the regular pieces of carrot.

We presented the subjects with the following six pairwise comparisons (see Methods for exact size of pieces used and cooking specifications): raw whole versus cooked whole (abbreviated henceforth as RW-CW), raw grated versus cooked whole (RG-CW), raw mashed versus cooked whole (RM-CW), cooked grated versus cooked whole (CG-CW), cooked mashed versus cooked whole (CM-CW), and cooked grated versus cooked mashed (CG-CM). We tested three potential hypotheses governing performance in these conditions, the predictions of which are depicted in Table 2 (along with the actual results for each condition). These hypotheses are not mutually exclusive, as multiple factors could shape performance in each condition; rather, these conditions were designed to assess the relative importance of each in selecting food items.

### Hypothesis 1: prefer cooked taste

If subjects use the potential nutrient and general taste changes accompanied by cooking as a stronger index of selection than textural factors, they should prefer the cooked food to raw in each of the conditions juxtaposing a cooked and raw item, and should be indifferent in the conditions with two cooked items.

### Hypothesis 2: prefer less tough

If subjects select mainly on the basis of toughness, they should prefer the cooked item to raw when both are cubes (CW over RW) since cooked carrot is less tough than raw carrot. Further, they should prefer the CW item to the RG item, since grating does not reduce the toughness of the raw carrot. In the case of the CG item, subjects should be indifferent between this and the CW item, because again the grating should not change toughness and in this instance both items are cooked and, thus, should have similar degrees of toughness. In the RM-CW condition, subjects should either be indifferent between RM and CW, since in this instance the raw item is decreased in toughness, or should prefer the RM to the CW, since we did not measure the exact degree to which mashing reduced toughness and, thus, could not say whether we in fact made the RM less tough than the CW (we merely aimed to reduce toughness in the raw item rather than to perfectly match it with the texture of the cooked item, hence this small degree of imprecision in the predictions of the hypothesis). Finally, according to this hypothesis subjects should prefer the less tough item when both items presented in the choice are cooked (CM over CW and CM over CG).

**Table 2**  
Hypotheses, predictions, and results for experiment 2<sup>a</sup>

Hypothesis	Predicted preferred food in a given condition					
	RW-CW	RG-CW	RM-CW	CG-CW	CM-CW	CG-CM
1. Prefer cooked taste	CW	CW	CW	Indif	Indif	Indif
2. Prefer less tough	CW	CW	RM/Indif	Indif	CM	CM
3. Prefer less chewing	CW	RG/Indif	RM/Indif	CG	CM	Indif
Actual preferences	CW	CW	Indif	CW	Indif	CM

<sup>a</sup> Hypotheses in experiment 2 as to which carrot item subjects should prefer depending on what factor they use to form their preferences, and the actual results for each condition. “Indif” represents a condition where subjects should be indifferent between the two items. The abbreviations for the carrot pieces are as follows: RW = raw whole, CW = cooked whole, RG = raw grated, RM = raw mashed, CG = cooked grated, and CM = cooked mashed.

### Hypothesis 3: prefer less chewing

If subjects select based on reducing the amount of chewing required, they should prefer the cooked item to the raw when both are cubes (CW over RW), since the less tough cooked carrots should require less chewing than the raw carrots. When the cooked cube is presented with a texturally manipulated raw item (RG or RM), subjects should either prefer the easier to chew item (with both the grated and mashed being easier to chew than the plain cube of the raw item), or be indifferent, since again we could not quantify how much the grating and mashing increased ease of chewing relative to cooking. Subjects should also prefer the texturally manipulated items when these items are presented along with the cooked whole item (CG over CW and CM over CW), since cooking increases the ease of chewing of both items, but the textural manipulations further augment the ease of chewing. Finally, subjects should be indifferent when offered two texturally manipulated items (CG-CM) since both will be relatively easy to chew.

### Methods

Twenty-three individuals (fourteen chimpanzees, three bonobos, two gorillas, and four orangutans) at the Wolfgang Koehler Primate Research Center (WKPRC) at the Leipzig Zoo participated in this experiment, although not all individuals participated in all conditions. The apes at the WKPRC receive cooked food as a part of their normal diet, with cooked beef and pieces of bread supplementing their regimen of fruit and vegetables. These apes are occasionally (less than once a month) fed cooked carrot but do not receive any cooked fruit or vegetables on a regular basis.

In this experiment, the food items were placed on a sliding table (rather than being held in the experimenter's fists as in experiment 1), with the sliding function of the table enabling the food options to be kept far enough away that subjects could not obtain them until the moment of choice. The subject sat across from the experimenter, behind a Plexiglas panel that had holes at the height of the table through which the subject could extend its fingers to make a choice. The experimenter began each trial by placing small squares of plastic on the two sides of the table, lined up with holes in the Plexiglas. Each square of plastic corresponded to a certain food item, so that the tastes of various items were not mixed by placing them in the same location on the table.

After the experimenter placed the plastic squares, she offered subjects a “taste” piece of each food item (see below for piece sizes). She first offered them a small piece of the left food item and subsequently placed a larger “choice” piece of that item on the left plastic square, then offered the subject a small piece of the right item and placed the choice item on the right-side plastic square. Subjects were required to take these taste items in order for a trial to begin, ensuring their motivation and reminding them what items they were choosing between since it was not necessarily visually apparent. Subjects received the six conditions mentioned above: RW-CW, RG-CW, RM-CW, CG-CW, CM-CW, and CG-CM. If subjects did not take the taste items for a given condition before

every trial, they did not continue with that condition. However, they did continue with the other conditions in which they participated, leading to slightly different sample sizes for each condition.

Subjects were tested in two different sessions that occurred on two different days. On each test day, subjects were presented with 24 trials, four of each condition. Thus, overall, there were eight trials for each condition. The order in which conditions were presented and the side on which each food item appeared were counterbalanced within and across subjects.

For the “whole” conditions, the piece offered was a 2 cm<sup>3</sup> cube of either raw or cooked carrot. The carrot in the “grated” conditions was grated using a standard cheese grater, and the amount given matched the size of the cube. The “mashed” conditions involved carrot which had been put in a blender, along with one-half cup water to allow some congealing of the mixture. The amount of mashed carrot given again matched the size of the cube. Cooked items were boiled for five minutes, before being either grated or mashed, respectively.

### Results

Subjects' individual choices are shown below in Table 3, with the general result of each condition and how this matches with the predictions of the hypotheses shown in Table 2. Subjects significantly preferred the cooked item to the raw when both items were cubes [RW-CW: one sample t-test,  $t(22) = 4.212$ ,  $p < 0.001$ ] and when the raw item was grated [RG-CW:  $t(16) = 11.579$ ,  $p < 0.001$ ], but were indifferent between the RM and CW items. Thus, the results of these three conditions supported the “prefer softer” hypothesis, since subjects preferred the CW to raw items except when it was paired with the mashed item. However, the results of the CG-CW and CM-CW conditions did not support this hypothesis, as subjects significantly preferred the CW [ $t(16) = 11.579$ ,  $p < 0.001$ ], and were indifferent to the choice between CM and CW. Finally, subjects strongly preferred the mashed carrot to the grated carrot [CG-CM:  $t(16) = -4.045$ ,  $p = 0.001$ ; see Table 2 for how these results fit in with the hypotheses].

The same trends seen in group averages can be seen when examining the number of individuals in each group who showed an individual preference for a given item, as revealed by a binomial test of their performance—in this instance, only individuals who chose a given item on eight out of eight trials would be considered as showing a significant preference ( $p < 0.05$ ) for that item. Nine individuals significantly preferred the cooked item by this measure in the RW-CW condition, as did nine individuals in the RG-CW condition (though not the same nine individuals). Five individuals showed significant preferences for the CW over both the RM and CM (the same five individuals showed significant preferences in both conditions).

Species differences could not be assessed using an ANOVA due to the small sample sizes in the bonobo and gorilla groups, but qualitative analysis of individual performance suggested

**Table 3**  
Number of choices for cooked whole (or cooked grated) in *experiment 2*<sup>a</sup>

Subject	# of trials picking cooked whole (CW)					# picking cooked grated (CG)
	RW-CW	RG-CW	RM-CW	CG-CW	CM-CW	CG-CM
<b>Chimpanzee</b>						
Alex	7	–	–	–	–	–
Alexandra	6	6	5	7	7	6
Dorien	4	–	–	–	–	–
Fifi	7	<b>8</b>	7	<b>8</b>	7	1
Fraukje	5	<b>8</b>	<b>8</b>	<b>8</b>	<b>8</b>	7
Frodo	5	<b>8</b>	7	<b>8</b>	4	<b>0</b>
Jahaga	7	<b>8</b>	<b>8</b>	<b>8</b>	<b>8</b>	1
Patrick	4	7	4	<b>8</b>	5	1
Pia	<b>8</b>	<b>8</b>	<b>8</b>	7	<b>8</b>	<b>0</b>
Riet	6	–	–	–	–	–
Sandra	5	<b>8</b>	<b>8</b>	<b>8</b>	<b>8</b>	2
Swela	5	–	–	–	–	–
Trudi	5	<b>8</b>	<b>8</b>	<b>8</b>	<b>8</b>	5
Unyoro	4	–	–	–	–	–
<b>Bonobo</b>						
Kuno	5	<b>8</b>	5	7	5	1
Limbuko	7	<b>8</b>	3	7	5	<b>0</b>
Yasa	3	7	5	<b>8</b>	2	<b>0</b>
<b>Gorilla</b>						
Bebe	4	6	2	<b>8</b>	3	1
Viringika	4	–	3	–	1	–
<b>Orangutan</b>						
Dokana	5	7	4	7	7	4
Dunja	5	4	2	5	3	1
Padana	5	7	3	5	2	<b>0</b>
Pini	3	6	2	5	1	<b>0</b>

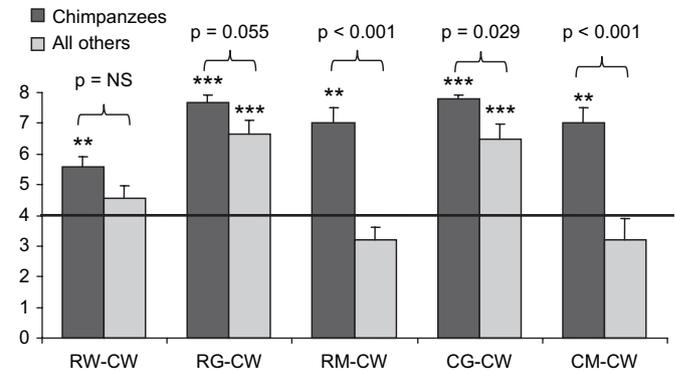
<sup>a</sup> The number of trials (out of eight) where subjects chose the cooked whole carrot (or, in the last condition, the grated carrot). Scores in **bold** represent those that differ significantly from chance ( $p < 0.05$ , binomial probability, two-tailed). Dashes represent a condition in which the subject did not participate. Abbreviations as in Table 2.

a distinction between chimpanzees and nonchimpanzees. Of the nine individuals who significantly preferred the cooked item in the RW-CW item, seven were chimpanzees. Further, seven of the nine individuals who preferred the CW to the RG were chimpanzees, and all five of the individuals who preferred the CW to the RM and CM were chimpanzees. Analysis of overall performance comparing chimpanzee and nonchimpanzee groups for each condition revealed that in most conditions chimpanzees chose the cooked whole option significantly more often than the other species [independent samples t-test, RG-CW:  $t(15) = 2.084$ ,  $p = 0.055$ ; RM-CW:  $t(16) = 5.896$ ,  $p < 0.001$ ; CG-CW:  $t(15) = 2.766$ ,  $p = 0.014$ ; CM-CW:  $t(16) = 4.464$ ,  $p < 0.001$ ; Fig. 2].

There were no significant differences in subjects' preferences between their two test sessions, as shown by a paired sample t-test comparing each individual's performance on each condition in the two sessions.

## Discussion

Overall, subjects preferred the cooked piece of carrot to the raw piece of carrot in the one condition where textural properties were not manipulated, replicating and extending the finding from *experiment 1* to the other great apes. In the grated condition, subjects generally preferred the cooked whole option, and in the mashed condition subjects were mainly indifferent between cooked and raw options. There were species differences in these conditions, in that chimpanzees were less inclined to choose the mashed or the grated options than were the other species. Overall, subjects preferred the mashed carrot to the grated, with all species showing a dislike for the grated option. These results make it



**Fig. 2.** Comparison of preferences between chimpanzees and other apes in *experiment 2*. Numbers of trials on which subjects chose the cooked whole option, comparing chimpanzees and all three other apes grouped together (\*\*\* $p < 0.001$ , \*\* $p < 0.01$ , and \* $p < 0.05$  with one sample t-test. Abbreviations as in Table 2).

difficult to distinguish between the “cooked taste” and “prefer softer” hypotheses.

The species differences found here may have reflected distinctions in neophobia rather than in actual taste preference, though taste distinctions between species would not be unexpected given past work showing differing thresholds for various nutrients across apes (Simmen and Charlot, 2003). Greater neophobia in chimpanzees was suggested by the fact that five chimpanzees refused to participate in either the grated or mashed conditions, whereas only one of the other apes refused (Table 3). This population of chimpanzees had been shown in previous work to take novel food items fairly readily (Addessi and Visalberghi, 2006), but it is possible that the novel textures of the carrot created neophobia to a greater degree. Though capuchins have been shown to be less neophobic towards familiar foods manipulated in their visual and olfactory properties than towards completely novel foods (Visalberghi and Addessi, 2000), it is possible that chimpanzees differ in this preference. Further, the chimpanzees at the WKPRC were in a biomedical laboratory prior to their arrival at the Leipzig Zoo, while this was not the case for the other apes, which have lived in zoos their entire lives. This provides a potential explanation for the heightened neophobia among chimpanzees due to their background with a restricted diet and numerous potentially frightening novel stimuli.

Because of the possible effects of neophobia in the present experiment, we designed the next experiment to better control the novelty of the items presented, and to extend the findings of cooked preferences to other food groups.

## Experiment 3: do apes prefer all cooked foods?

This experiment provided great apes with choices between raw and cooked meat, and raw and cooked apple (*Malus domestica*). We controlled for neophobia in this experiment because one of these items was familiar in its raw form (apple) and the other was familiar in its cooked form (meat). Thus, this juxtaposed preferences determined by taste/texture and those which would be determined by familiarity with the test items.

## Methods

Fifteen chimpanzees, five bonobos, two gorillas, and five orangutans at the WKPRC participated in *experiment 3*. The procedure for this experiment was similar to that of *experiment 2*, with a few exceptions. Again, the sliding table was used, and subjects were offered “taste” pieces of each food item before each trial.

However, in the previous experiment, subjects were required to take this taste piece on every trial in order to continue with that trial, while in this experiment the different pieces of food could be visually discriminated (using color, rigidity) so if subjects took the taste piece on the first trial, they continued with all trials even if they did not take future taste pieces. If subjects refused to even take one taste piece of a given food item, they did not continue with trials of that food item but continued with the other item. Thus, some subjects only participated in either the meat or the apple conditions.

Subjects were again tested in two different sessions which occurred on two different days. For each session, subjects received 8 meat trials followed by 8 apple trials (or vice versa), thus resulting in 16 trials per session and 16 total trials for each condition across the two sessions. Thus each subject received 16 trials of raw versus cooked meat and 16 trials of raw versus cooked apple, with meat and apple never being presented together in the same trial. The order of conditions for each session (eight meat trials first versus eight apple trials first) and the side on which each food item appeared were again counterbalanced within and between subjects.

For both the meat and the apple, the cooked items were boiled for 10 min. Each food item was cut into 2 cm<sup>3</sup> cubes. The meat used was beef, which subjects were familiar with in its cooked form. Both cooked and raw pieces of apple were cut so as not to have any skin. As in the previous experiment, pieces of plastic were placed on the table so as not to cross-contaminate food items.

## Results

The results for each individual subject are shown below in Table 4. Overall, subjects significantly preferred the cooked meat pieces [one sample t-test,  $t(17) = 6.735, p < 0.001$ ], but chose the cooked and raw pieces of apple equally. Subjects also chose the cooked beef significantly more often than they themselves chose the cooked apple (for those individuals who participated in both conditions), suggesting that subjects were distinguishing between the two foods rather than certain individuals being cooked-biased and others not [paired sample t-test,  $t(16) = 2.765, p = 0.014$ ]. In looking at the number of individuals who significantly preferred each item ( $p < 0.05$  with a binomial test; in this instance, a significant preference was 13 or more out of 16 trials), a higher percentage of individuals preferred the cooked meat than individuals who preferred the cooked apple, with 11 out of 18 individuals (61.1%) significantly preferring cooked meat and only six out of 26 (23.1%) preferring cooked apple. No individuals significantly preferred raw meat, but two individuals (7.7%) preferred raw apple to cooked apple. The two subjects who preferred the raw apple also preferred the cooked meat, suggesting a potential effect of neophobia in these individuals since these were the two familiar items.

As in the previous experiment, species comparisons with an ANOVA were not possible. However, again, distinctions between the chimpanzees and the other apes were apparent in the number of individuals showing significant preferences in each condition. Every one of the 8 chimpanzee subjects participating in the meat condition showed a significant preference for cooked meat, whereas only 3 of the 10 other subjects did so. In contrast, 3 of 15 chimpanzee individuals preferred the cooked apple while 3 of the 11 other apes did so, suggesting that species differences were not as large a factor in this condition. Mean group performance also supported the notion that chimpanzees chose the cooked meat significantly more often than did individuals of the other species [independent samples t-test,  $t(16) = -3.722, p = 0.002$ ], though both groups significantly chose the cooked meat when analyzed separately [one sample t-tests, chimpanzees:  $t(7) = 29.000, p < 0.001$ ; nonchimpanzees:  $t(9) = 3.192, p = 0.011$ ; Fig. 3]. No

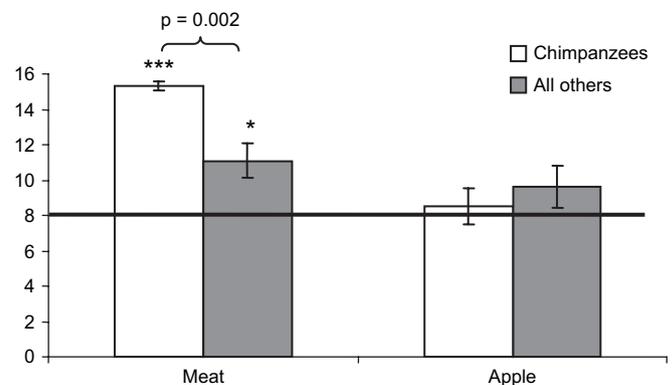
**Table 4**  
Number of choices for cooked item for experiment 3<sup>a</sup>

Subject	# of trials picking cooked	
	Meat	Apple
<b>Chimpanzee</b>		
Alex	–	8
Alexandra	<b>15</b>	<b>15</b>
Annet	–	11
Dorien	–	12
Fifi	<b>15</b>	8
Fraukje	–	8
Frodo	–	6
Jahaga	<b>16</b>	10
Lome	<b>15</b>	<b>1</b>
Patrick	<b>15</b>	6
Pia	–	<b>15</b>
Riet	<b>16</b>	7
Sandra	<b>14</b>	10
Trudi	<b>16</b>	3
Unyoro	–	8
<b>Bonobo</b>		
Joey	–	7
Kuno	8	10
Limbuko	10	12
Ulindi	–	4
Yasa	<b>15</b>	9
<b>Gorilla</b>		
Bebe	12	11
Viringika	<b>15</b>	<b>2</b>
<b>Orangutan</b>		
Bimbo	8	–
Dokana	11	<b>16</b>
Dunja	10	<b>13</b>
Padana	<b>15</b>	10
Pini	7	11

<sup>a</sup> The number of trials (out of 16) where subjects chose the cooked food item. Scores in **bold** represent those that differ significantly from chance ( $p < 0.05$ , binomial probability, two-tailed). Dashes represent a condition in which the subject did not participate.

significant difference was present in the apple condition between chimpanzees and non-chimpanzees.

Performance across sessions was analyzed to determine whether subjects showed consistent preferences equally on the two separate test days. No significant differences were present for either the meat or the apple conditions, thus revealing that subjects did have fairly stable preferences. Further, there were no differences in performance between subjects who received the meat conditions first and those who received the apple conditions first (independent samples t-test).



**Fig. 3.** Comparison of preferences between chimpanzees and other apes in experiment 3. Numbers of trials on which subjects chose the cooked option, comparing chimpanzees and all three other apes grouped together ( $***p < 0.001$ ,  $**p < 0.01$ , and  $*p < 0.05$  with one sample t-test).

Since not every subject took the taste piece every time, analyses were performed to compare the subjects that took the taste piece on every trial to those that took it on at least one trial but then did not consistently take the taste piece over the course of the session. There was a significant difference between these two groups in the meat condition, with subjects who did not always take the taste piece (i.e., refused to take the raw piece as a taste item) choosing the cooked item significantly more often than subjects who always took the taste piece of the raw item [independent samples t-test,  $t(16) = 4.177, p = 0.001$ ]. These distinctions in fact fell exactly along species lines, with 10 individuals only sometimes taking the taste piece in the meat condition, these being the 8 chimpanzee and 2 gorilla subjects, and the 8 subjects from the other two species always taking the taste pieces. In the apple condition, there was no distinction between subjects who always took the taste piece and those who did not take it consistently.

### Discussion

Apes in this experiment preferred the cooked beef to the raw beef, but showed no discrimination between raw and cooked apple. These preferences were constant across two separate test sessions, and there were differences between species in that chimpanzees chose the cooked meat significantly more than did the other species.

These results suggested that neophobia was not the sole factor affecting subjects' performance in previous experiments, as subjects in this experiment did not selectively choose the familiar item in the apple condition (the raw item) but rather showed indifference between the raw and cooked options. This indifference is somewhat logical, as apple can be fairly easily eaten and digested in its raw form as compared to raw meat. As such, it may have been that, similar to the white potato in [experiment 1](#), there was not enough distinction between the cooked and raw apple to cause subjects to have a significant preference. Thus, these results further supported the notion that apes tend to prefer cooked food to raw, but potentially only when there are significant changes induced by cooking.

Though these results indicate that neophobia was not responsible for the apes' response to cooked apples, neophobia might have nevertheless influenced their response to raw beef. In order to address the effects of neophobia in the meat condition, in the next experiment we tested a population of chimpanzees that was equally unfamiliar with cooked and raw meat.

### Experiment 4: do chimpanzees prefer novel cooked items?

This experiment again provided subjects with a choice between cooked and raw beef. We tested chimpanzees that were not given meat as a part of their regular diet, and as far as was known had never eaten cooked meat (see [Methods](#) section below for a more detailed description of these chimpanzees' history and diet).

### Methods

Ten individuals from the Tchimpounga Chimpanzee Sanctuary in Congo Republic participated in this study. Because these animals arrived at the sanctuary from unknown conditions, usually having been confiscated or found as orphans, we cannot be sure whether they had ever eaten cooked meat in their lifetimes. However, these chimpanzees are not fed cooked meat as a part of their regular diet, and since the individuals tested had all been at the sanctuary for at least five years at the time of testing and most arrived as infants, it is reasonable to say that these individuals were equally unfamiliar with cooked and raw meat. Although somewhat unlikely, it is possible that the chimpanzees had tasted raw meat by catching

small animals in the forest; thus, if anything the cooked meat would be more novel to this population. The chimpanzees at Tchimpounga do receive cooked plantains and rice on a regular basis.

The procedure of this experiment was nearly identical to that of [experiment 3](#), except that the apple conditions were eliminated and subjects only received one session rather than two, since preferences in the previous experiments had been shown to be constant over the course of two sessions. The test session consisted of 12 trials, and food placement on each side was alternated and counterbalanced between subjects for which food (raw or cooked) appeared first on which side. Beef was again used, and again cut into 2 cm<sup>3</sup> cubes then boiled for 10 min. Similar to [experiments 2](#) and [3](#), pieces of plastic were placed on the table so as to not cross-contaminate the tastes of the raw and the cooked meat. In addition, this experiment used the same criteria as [experiment 3](#) to determine participation in each trial—subjects did not have to take the “taste” piece offered on every trial, but simply had to take it on the first trial in order to be able to participate in the test.

### Results

Results are shown in [Table 5](#). Overall, subjects significantly preferred the cooked meat [one sample t-test,  $t(9) = 5.589, p < 0.001$ ]. Six of the 10 subjects preferred the cooked meat individually [binomial test,  $p < 0.05$ ; in this instance, choosing cooked on at least 10 of the 12 trials], and no subject significantly preferred the raw meat. Most subjects took the “taste” pieces on nearly every trial, with only three individuals refusing the taste piece more than once.

### Discussion

These results demonstrated that even among a group of chimpanzees that were not fed cooked meat on a regular basis, individuals still showed a significant preference for cooked over raw beef. Thus, neophobia does not account for their preference, nor can it entirely account for the preference of the Leipzig chimpanzees seen in [experiment 3](#).

### General discussion

Overall, great apes in these experiments preferred cooked foods to raw, from tubers to meat. However, they did not prefer all foods cooked, being indifferent as to the choice between raw and cooked apple and between raw and cooked white potato. Neophobia could not be eliminated as a contributing factor in some results but, in [experiment 4](#), chimpanzees that were equally unfamiliar with cooked and raw beef still preferred the cooked item. Subjects' preferences remained stable across test sessions and across test

**Table 5**

The number of trials (out of 12) in which subjects picked the cooked meat ([experiment 4](#)). Scores in **bold** represent those that differ significantly from chance ( $p < 0.05$ , binomial probability, two-tailed)

Subject	# of trials picking cooked
Chimpie	<b>11</b>
Christophe	<b>12</b>
Elikia	<b>11</b>
Kola	6
Maya	7
Mbolo	8
Ramsay	9
Sobebe	<b>12</b>
Yoko	<b>11</b>
Yoro	<b>11</b>
Mean	9.8

populations, suggesting that food choices were not strongly shaped by past experience. The different properties being used to select the cooked items were also strongly salient across individuals and populations. This implies something inherently preferable about the effects of cooking which is immediately discernable.

These results support the hypothesis that great apes perceive and prefer properties of cooked food relative to raw, in the case of both starchy foods and meat. It was unclear which properties apes were sensitive to in the cooked food. The results of experiment 2 suggested that subjects may have used texture to discriminate between the carrots of different manipulated consistencies. Yet apes' lack of preference for items such as cooked apple, which is softer than raw apple, showed that other factors were involved as well. It is important to note that in both cases where the cooked item was not preferred over the raw (white potato and apple), individuals did not prefer the raw item, but were simply indifferent between the two options. This implies that apes may have chosen the cooked item only when that item seemed significantly better, with the white potato and apple not showing large enough differences between cooked and raw to create a preference distinction. Future work can investigate which properties of food items altered by cooking are the most salient in determining preferences.

It is important to note that our experiments were not designed to investigate what sort of preferences would have been found if the apes had been given extended experience with the cooked items, thus potentially using the post-ingestional consequences to change their preferences. This has been examined in mammals, including humans (Birch et al., 1990; Labouré et al., 2001; Visalberghi et al., 2003). As such, one future area of research would be to investigate whether nonhuman apes will also adapt their preferences based on the digestive and nutritional consequences of eating (e.g., caloric intake, etc.).

There were some species differences in the results. Past work had demonstrated that taste thresholds for tannins and sugars differ among great ape species (Laska, 2001; Remis and Kerr, 2002), but many of the differences seen here may simply have been a result of the chimpanzees being more neophobic than the other apes. For example, the chimpanzees preferred the cooked meat to the raw meat more strongly than the other species. However, in the conditions where neophobia was not an issue, chimpanzees' preferences resembled those of the other apes. This suggests that great apes in general prefer the properties present in cooked food rather than chimpanzees having any stronger of a preference.

Overall, our findings conform to evidence that wild chimpanzees choose seeds that have been heated by wild fires (Brewer, 1978), demonstrating that great apes possess a preference for cooked items. These preferences may be widespread in mammals, as shown by the evidence for rats and cats preferring cooked items (Ramirez, 1992; Bradshaw et al., 2000), and as would be expected from the improved quality of cooked items. Most likely, therefore, early hominids prior to their control of fire possessed these preferences as well. This, in turn, suggests that cooking would have spread quickly after it arose, with preferences for the properties of cooked food being exapted from ancestral traits rather than having developed as an adaptation to eating cooked food. If the former had been the case, this would have suggested that cooking may not have spread until human taste preferences could shift to select these foods. Thus, the evidence that this preference is conserved over evolutionary history supports the notion that early hominids were likely to have cooked their food soon after possessing control of fire, as they would have readily preferred any items prepared by this method.

## Acknowledgements

We thank the caretakers at the Wolfgang Koehler Primate Research Center at the Leipzig Zoo and at the Tchimpounga

Chimpanzee Sanctuary in the Congo Republic, especially Jean Maboto and Bernard Moubaka. Thanks also to Terry Burnham and Jessica Ganas for help in collecting data at Yerkes, and to Lisa Pharoah, Rebeca Atencia, and Keith Brown for facilitating research at the Tchimpounga Sanctuary. Finally, thanks to Katherine Duncan and Rachel Carmody for discussions regarding the manuscript. The research of the second author (B.H.) is supported by a Sofja Kovalevskaja Award received from The Alexander von Humboldt Foundation and the German Federal Ministry for Education and Research. These experiments complied with the laws of the countries in which they were performed.

## References

- Addessi, E., Visalberghi, E., 2006. How social influences affect food neophobia in captive chimpanzees: a comparative approach. In: Matsuzawa, T., Tomonaga, M., Tanaka, M. (Eds.), *Cognitive Development in Chimpanzees*. Springer-Verlag, Tokyo, pp. 246–264.
- Aiello, L., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36, 199–221.
- Ayankunbi, M., Keshinro, O., Egele, P., 1991. Effect of methods of preparation on the nutrient composition of some cassava products—Garri (Eba), Lafun, and Fufu. *Food Chemistry* 41, 349–354.
- Bellisle, F., 1999. Glutamate and the UMAMI taste: sensory, metabolic, nutritional and behavioural considerations. A review of the literature published in the last 10 years. *Neurosci. Biobehav. Rev.* 23, 423–438.
- Bellomo, R.V., 1994. Methods of determining early hominid behavioral activities associated with the controlled use of fire at Fxj 20 Main, Koobi Fora, Kenya. *J. Hum. Evol.* 27, 173–195.
- Birch, L., McPhee, L., Steinberg, L., Sullivan, S., 1990. Conditioned flavor preferences in young children. *Physiol. Behav.* 47, 501–505.
- Brace, C.L., 1995. *The Stages of Human Evolution*, fifth ed. Prentice-Hall, Englewood Cliffs, New Jersey.
- Brace, C., Rosenberg, K., Hunt, K., 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. *Evolution* 41, 705–720.
- Bradshaw, J., Healey, L., Thorne, C., MacDonald, D., Arden-Clark, C., 2000. Differences in food preferences between individuals and populations of domestic cats *Felis silvestris catus*. *Appl. Anim. Behav. Sci.* 68, 257–268.
- Brewer, S., 1978. *The Chimpanzees of Mt. Asserik*. Knopf, New York.
- Clark, J.D., Harris, J.W.K., 1985. Fire and its role in early hominid lifeways. *Afr. Archaeol. Rev.* 3, 3–27.
- Conklin-Brittain, N., Wrangham, R., Hunt, K., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int. J. Primatol.* 19, 971–998.
- Coon, C.S., 1962. *The History of Man: From the First Human to Primitive Culture and Beyond*, second ed. Jonathan Cape, London.
- Dominy, N.J., Lucas, P.W., Osorio, D., Yamashita, N., 2001. The sensory ecology of primate food perception. *Evol. Anthropol.* 10, 171–186.
- Hernandez-Aguilar, R., Moore, J., Pickering, T., 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proc. Natl. Acad. Sci.* 104, 19210–19213.
- Hladik, C., Pasquet, P., Danilova, V., Hellekant, G., 2003. The evolution of taste perception: psychophysics and taste nerves tell the same story in human and nonhuman primates. *C.R. Palevol.* 2, 281–287.
- Hladik, C., Simmen, B., 1996. Taste perception and feeding behavior in nonhuman primates and human populations. *Evol. Anthropol.* 5, 58–71.
- Kadohisa, M., Rolls, E., Verhagen, J., 2004. Orbitofrontal cortex: neuronal representation of oral temperature and capsaicin in addition to taste and texture. *Neuroscience* 127, 207–221.
- Kadohisa, M., Rolls, E., Verhagen, J., 2005. Neuronal representations of stimuli in the mouth: the primate insular taste cortex, orbitofrontal cortex and amygdala. *Chemical Senses* 30, 401–419.
- Kingman, S., Englyst, H., 1994. The influence of food preparation methods on the *in-vitro* digestibility of starch in potatoes. *Food Chemistry* 49, 181–186.
- Koebnick, C., Strassner, C., Hoffmann, I., Leitzmann, C., 1999. Consequences of a long-term raw food diet on body weight and menstruation: results of a questionnaire survey. *Ann. Nutr. Metab.* 43, 69–79.
- Labouré, H., Saux, S., Nicolaidis, S., 2001. Effects of food texture change on metabolic parameters: short- and long-term feeding patterns and body weight. *Am. J. Physiol. (RCP)* 280, R780–R789.
- Laden, G., Wrangham, R., 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *J. Hum. Evol.* 49, 482–498.
- Lanjouw, A., 2002. Behavioural adaptations to water scarcity in Tongo chimpanzees. In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 52–60.
- Laska, M., 2001. A comparison of food preferences and nutrient composition in captive squirrel monkeys, *Saimiri sciureus*, and pigtail macaques, *Macaca nemestrina*. *Physiol. Behav.* 73, 111–120.

- Laska, M., Scheuber, H., Sanchez, E., Luna, E., 1999. Taste difference thresholds for sucrose in two species of nonhuman primates. *Am. J. Primatol.* 48, 153–160.
- Leighton, M., 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14, 257–313.
- Lucas, P.W., 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.
- Lucas, P.W., Ang, K.Y., Sui, Z., Agrawal, K.R., Prinz, J.F., Dominy, N.J., 2006. A brief review of the recent evolution of the human mouth in physiological and nutritional contexts. *Physiol. Behav.* 89, 36–38.
- Oakley, K., 1963. On man's use of fire, with comments on tool-making and hunting. In: Washburn, S.L. (Ed.), *Social Life of Early Man*. Methuen, London, pp. 176–193.
- O'Connell, J.F., Hawkes, K., Jones, N.G.B., 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.* 36, 461–485.
- Perry, G., Dominy, N., Claw, K., Lee, A., Fiegler, H., Redon, R., Werner, J., Villanea, F., Mountain, J., Misra, R., Carter, N., Lee, C., Stone, A., 2007. Diet and the evolution of human amylase gene copy number variation. *Nature Genetics* 39, 1256–1260.
- Ramirez, I., 1992. Is starch flavor unitary—evidence from studies of cooked starch. *Physiol. Behav.* 52, 535–540.
- Remis, M., Kerr, M., 2002. Taste responses to fructose and tannic acid among gorillas (*Gorilla gorilla gorilla*). *Int. J. Primatol.* 23, 251–261.
- Rolland, N., 2004. Was the emergence of home bases and domestic fire a punctuated event? A review of the Middle Pleistocene record in Eurasia. *Asian Perspect.* 43, 248–280.
- Rolls, E., 2005. Taste, olfactory, and food texture processing in the brain, and the control of food intake. *Physiol. Behav.* 85, 45–56.
- Sasaki, K., Motoyama, M., Mitsumoto, M., 2007. Changes in the amounts of water-soluble umami-related substances in porcine longissimus and biceps femoris muscles during moist heat cooking. *Meat Science* 77, 167–172.
- Simmen, B., Charlot, S., 2003. A comparison of taste thresholds for sweet and astringent-tasting compounds in great apes. *C. R. Biol.* 326, 449–455.
- Smith, C., Martin, W., Johansen, K., 2001. Sego lilies and prehistoric foragers: return rates, pit ovens, and carbohydrates. *J. Arch. Sci.* 28, 169–183.
- Stahl, A.B., 1989. Comment on James (1989). *Curr. Anthropol.* 30, 18–19.
- Svihus, B., Uhlen, A.K., Harstad, O.M., 2005. Effect of starch granule structure, associated components, and processing on nutritive value of cereal starch: a review. *Anim. Feed Sci. Technol.* 122, 303–320.
- Tester, R.F., Qi, X., Karkalas, J., 2006. Hydrolysis of native starches with amylases. *Anim. Feed Sci. Technol.* 130, 39–54.
- Tester, R., Sommerville, M., 2000. Swelling and enzymatic hydrolysis of starch in low water systems. *J. Cereal Sci.* 33, 193–203.
- Visalberghi, E., Addessi, E., 2000. Response to changes in food palatability in tufted capuchin monkeys, *Cebus apella*. *Anim. Behav.* 59, 231–238.
- Visalberghi, E., Janson, C.H., Agostini, I., 2003. Response toward novel foods and novel objects in wild *Cebus apella*. *Int. J. Primatol.* 24, 653–675.
- Wandsnider, L., 1997. The roasted and the boiled: food composition and heat treatment with special emphasis on pit-hearth cooking. *J. Anthropol. Archaeol.* 16, 1–48.
- Wrangham, R., 2006. The cooking enigma. In: Ungar, P. (Ed.), *Early Hominin Diets: The Known, the Unknown, and the Unknowable*. Oxford University Press, New York, pp. 308–323.
- Wrangham, R., Conklin-Brittain, N., 2003. Cooking as a biological trait. *Comp. Biochem. Physiol.* 136, 35–46.
- Wrangham, R., Conklin-Brittain, N., Hunt, K., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* 19, 949–970.
- Wrangham, R., Jones, J., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.* 40, 567–594.