

Food Neophobia and Social Learning Opportunities in Great Apes

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Abstract

Finding food resources and maintaining a balanced diet are major concerns for all animals. A compromise between neophobia and neophilia is hypothesised to enable animals to enlarge their diet while limiting the risk of poisoning. However, little is known about how primates respond to novel food items and whether their use is socially transmitted. By comparing how four different species of great apes respond to novel food items, we investigated how differences in physiology (digestive tract size and microbial content), habitats (predictability of food availability), and social systems (group size and composition) affect their response toward novelty. We presented two familiar foods, one novel fruit, four novel aromatic plants from herbal medicine, and kaolin to captive chimpanzees (*Pan troglodytes*), western gorillas (*Gorilla gorilla*), Bornean orangutans (*Pongo pygmaeus*) and Sumatran orangutans (*Pongo abelii*). We recorded smelling, approach-taste delays, ingestion, interindividual observations, and food transfers with continuous sampling. We found that behaviors differed between the apes: chimpanzees were the most cautious species and observed their conspecifics handling the items more frequently than the other apes. Close observations and food transfers were extremely rare in gorillas in comparison to orangutans and chimpanzees. We suggest that a low neophobia level reflects an adaptive response to digestive physiological features in gorillas and to unpredictable food availability in orangutans. Social interactions appeared to be predominant in chimpanzees and in both orangutan species to overcome food neophobia. They reflect higher social tolerance and more opportunities for social learning and cultural transmission in a feeding context.

Introduction

Finding food resources and maintaining a balanced diet are major concerns that all animals must face for their survival. Several studies investigating novelty in primates have shown that their first response toward novel foods combines neophilia, i.e., curiosity, and neophobia, i.e., reluctance, inducing total or partial cautiousness (Fu *et al.* 2013; Johnson 2000; Kawai 1960; Rozin 1976; Visalberghi *et al.* 2003a). These types of responses are hypothesized to enable the animals to enlarge their diet while limiting the risk of poisoning, the so-called “omnivore’s dilemma” (Rozin 1976; Milton 1993). Another adaptive strategy is to learn from conspecifics’ feeding behavior, thus decreasing the risk of sampling potentially toxic items themselves (Giraldeau *et al.* 1997). Socially aided learning (*sensu* Heyes 1994) has indeed been shown to help primates overcome their neophobia and to underlie the establishment of dietary habits (Gustafsson *et al.* 2011; Lonsdorf 2006; Masi *et al.* 2011; Tarnaud and Yamagiwa 2008; Visalberghi and Addessi 2001).

Great apes adapt to different habitats and to fluctuations in food availability by exploiting a great variety of food sources including fruit, leaves, stems, flowers, seeds, honey, invertebrates, and sometimes even

vertebrates: chimpanzees (*Pan troglodytes*: Boesch and Boesch 1989; McGrew *et al.* 1988; Nishida and Uehara 1983), gorillas (*Gorilla gorilla*: Deblauwe *et al.* 2003; Masi *et al.* 2009; Rogers *et al.* 2004; Tutin *et al.* 1991), Bornean orangutans (*Pongo pygmaeus*), and Sumatran orangutans (*Pongo abelii*: Galdikas 1988; Knott 1998; Rodman and Schwartz 1988; Utami and van Hoof 1997). They are also exposed to important anthropogenic modification of their environment (Junker *et al.* 2012; Wich *et al.* 2008). However, despite the importance of neophobia and social learning for understanding how apes acquire and broaden their diet, only four studies have addressed this question experimentally in chimpanzees (Addessi *et al.* 2006; Matsuzawa and Yamakoshi 1996; Ueno and Matsuzawa 2005; Visalberghi *et al.* 2002), with only one in orangutans (Gustafsson *et al.* 2011) and none in gorillas or bonobos. This is surprising, as these issues have been tested extensively in a number of other species, e.g., birds (Sherwin *et al.* 2002), fishes (Swaney *et al.* 2001), monkeys (Visalberghi and Addessi 2001; van de Waal *et al.* 2013), pigs (Figueroa *et al.* 2013), and rats (Galef and Whiskin 2008).

Some observations from the field suggest that wild chimpanzees are conservative and unwilling to taste and accept novel foods (Nishida and Uehara 1983; Takasaki 1983). In the landmark study initiated by Matsuzawa and Yamakoshi (1996), wild chimpanzees accustomed to cracking oil-palm nuts were assessed on their neophobia toward panda and coula nuts. Only 8 of the 14 adults showed any interest in the coula nuts and only 2 in the panda nut. Conversely, juveniles showed greater interest in both nuts by attempting to explore them through either sniffing or nibbling (Biro *et al.* 2003). Other experiments conducted on captive chimpanzees have confirmed these interindividual differences among adults (Addessi *et al.* 2006; Visalberghi *et al.* 2002); some of them were cautious toward novel food whereas others showed a higher propensity to accepting them. Recent studies have highlighted that beside neophobia, reluctance to adopt new foraging strategies may be due to conservatism and conformity (Hopper *et al.* 2011; Hrubesch *et al.* 2009). Two experiments specifically addressing the question of social influence (Addessi *et al.* 2006; Ueno and Matsuzawa 2005) have confirmed the lower neophobia of juveniles. However, while noting many interindividual observations toward conspecifics, they did not find any clear effect of observation on the observers' tendency to explore novel foods.

Surprisingly, although neophobia is hypothesized to have been selected to prevent any risk of poisoning, none of these studies have included vegetative parts of plants in their experiments, even though they often contain the most concentrated amount of bitter secondary compounds such as alkaloids and tannins (Glander 1982; Vining 1990) and are part of the diet of all great apes (Cousins and Huffman 2002; Knott 1998; Krief *et al.* 2006). This could be particularly relevant because, along with the number of exposures (Birch and Marlin 1982; Sullivan and Birch 1994; Visalberghi and Addessi 2000; Wardle *et al.* 2003), the palatability of items determined by tastes such as sweetness or bitterness is known to affect both neophobia and social learning (Carruth *et al.* 2004; Gosset and Roeder 2001; Johnson 2007; Remis 2002, 2006). In addition to vegetative parts of plants, a peculiar low-quality food item found to be widespread among animals is soil. Geophagy has been described in *ca.* 30 species of primates including great apes (Williamson *et al.* 1990). One of the main hypotheses explaining this behavior is its role in alleviating digestive disorders (Reid 1992; Vermeer and Ferrell 1985; Wiley and Katz 1998). A recent study suggested

that soil may also increase the bioactivity of certain plants when ingested concomitantly (Klein *et al.* 2008). Thus, a propensity to ingest soil may give us some clues regarding digestive tolerance to secondary compounds.

The unique experiment investigating neophobia toward novel plants was carried out on captive orangutans (Gustafsson *et al.* 2011). By presenting several vegetative parts of plants, the authors noted a low level of neophobia associated with a high level of social tolerance and social interactions. They hypothesized that adaptations to unpredictable environments particular to that species could explain this flexibility. Orangutans are known to subsist on lower quality foods during food scarcity, and their low neophobia may explain how they manage to broaden their diet when fruits become rare to comprise low-quality food items such as bark, leaves, and soil (Knott 1998). Variable environments can select for flexibility, reflected by low neophobia (Greenberg 1990). Other experimental studies indirectly studied apes' responses toward a novel plant by focusing on the behavior of leaf swallowing (Huffman and Hirata 2004; Huffman *et al.* 2010; Menzel *et al.* 2013). These studies confirmed the interindividual differences in neophobia and suggested that some individuals were more likely to be the demonstrator than others.

Do great apes present similar behavior toward novel food items? How do they differ in their tendency for social observations in that context? To tackle these questions, we presented two familiar foods, one novel fruit, four novel aromatic plants belonging to the French Pharmacopoeia, i.e. included in the list of legal therapeutic plants published by the French health authority, and a novel clay mineral (kaolin), to chimpanzees (*Pan troglodytes*), western gorillas (*Gorilla gorilla*), and Bornean and Sumatran orangutans (*Pongo pygmaeus* and *Pongo abelii*). We aimed to use a systematic approach with a larger sample of apes than has been tested previously for reactions to new foods. Comparing these species is relevant when considering how they differ in their diet, habitat, and social system. Compared to other apes, gorillas are more folivorous and less frugivorous. In response to the high fiber and low available energy content of leaves as food, gorillas have evolved a greater tolerance to bitter taste, a larger body size, a richer intestinal fauna in a longer gut permitting microbial fermentation, and correspondingly longer gut retention times than other apes (Chivers and Hladik 1980; Collet *et al.* 1984; Lambert 1998; Remis 2000, 2006; Simmen and Charlot 2003; Tutin *et al.* 1991). Therefore, considering neophobia as a strategy to avoid poisoning, gorillas, being well adapted to tolerate high and regular amounts of secondary compounds, should show a lower neophobia level. Orangutan food availability is highly unpredictable (Fleming *et al.* 1987; Knott 1998, 2005; van Schaik and Pfannes 2005) compared to the relative seasonality of chimpanzee and gorilla environments (Tutin *et al.* 1991; Wrangham *et al.* 1998; Yamagiwa and Basabose 2006). During food shortages, orangutans have to rely on fall-back foods such as fibrous vegetation, bark, and soil (Delgado and van Schaik 2000; Knott 1999). Thus, according to the Greenberg hypothesis (Greenberg 1990), orangutans would also show lower neophobia. In contrast, chimpanzees, being specially adapted neither to a folivorous diet nor to nonseasonal habitats, should be the most neophobic species.

Finally, social learning opportunities are expected to vary with social structure. Although chimpanzees usually belong to large multimale–multifemale communities whose mean party size is around five

individuals (Boesch *et al.* 1996; Goodall 1986; Itoh and Nishida 2007; Nishida 1970), western gorillas live in stable one-male, multifemale groups of around nine individuals (Parnell 2002; Remis 1997), and Bornean and Sumatran orangutans have been described as semisolitary species that rarely form parties of more than two individuals (Delgado and van Schaik 2000; Galdikas 1985). As a result, we expect a higher propensity for social learning in gorillas and chimpanzees compared to orangutans. Moreover, if social learning is used to obtain information, more social interactions should be observed with novel items compared to familiar ones.

Methods

Study Sites and Subjects

We tested 60 apes housed in the French zoos Beauval (BE), La Palmyre (LP), and La Boissière du Doré (BD) (Table I). We tested two groups of chimpanzees ($N_{BE} = 15$, $N_{LP} = 9$), three groups of gorillas ($N_{BE} = 7$, $N_{LP} = 3$, $N_{BD} = 5$), two groups of Bornean orangutans ($N_{BE} = 7$, $N_{LP} = 4$), and one group of Sumatran orangutans ($N_{BD} = 10$). Dominant individuals in each group were assessed by their caregivers.

Table I: Study subjects in each zoo

	Chimpanzees						Western gorillas					
Zoo	Mature male		Mature female		Immature		Mature male		Mature female		Immature	
	Name	Age	Name	Age	Name	Age	Name	Age	Name	Age	Name	Age
BE	Joseph	24	LaVieille	48	Makury	7	Asato	16	Inge	27		
	Gamin	18	Charlotte	31	Bazu	7			Kabinda	25		
			Micheline	29	Rachel	7			Tamarilla	21		
			Baraka	28	Ann	5			Sheila	16		
			Julie	25								
			Bonobo	25								
			Gypso	20								
LP			Domi	18								
	Tsavo	14	Lily	20	Lulu	5	Bongo	18	Yola	16		
	Benji	13	Christmas	14					Ybana	9		
	Leo	11	Isabelle	13								
BD			Melie	11								
							Atanga	12			Nbia	4
							Yeboah	9			Ndove	4
						Vimoto	8					
	Bornean orangutans						Sumatran orangutans					
Zoo	Mature male		Mature female		Immature		Mature male		Mature female		Immature	
	Name	Age	Name	Age	Name	Age	Name	Age	Name	Age	Name	Age
BE	Muda	24	Christina	21	Bayu	4						

			Manis	17	Suli	4						
			Janah	16								
			Mandy	8								
LP	Sandai	15	Lotus (<i>hybrid</i>)	33								
			Tiba	32								
			Molly (<i>hybrid</i>)	17								
BD							Major	46	Manis (<i>hybrid</i>)	32	Kawan	5
							Jambi	11	Jane	24	Kembali	5
									Moni	21		
									Flora (<i>hybrid</i>)	17		
									Minak	11		

BE = Beauval; LP = La Palmyre; BD = La Boissière du Doré: BD.

The subjects were pooled into three broader classes: juveniles, adult males, and adult females, based on body size. We did not consider infants in the analyses because they were too dependent on their mothers to get access to the items using their own initiative.

Apes had access to enclosures with indoor and outdoor facilities and all groups were fed with different fruits and vegetables. Caregivers regularly enriched their diet with branches of oak, birch, hornbeam, and hazel trees. All individuals had a natural light–dark cycle because of the large windows in their indoor enclosures. We conducted this study between November 2007 and June 2008 to limit interference by visitors, who were more frequent during the summer period. All experiments represent 84 h of observation. They complied with protocols approved by the scientific and animal care committee of each zoo and adhered to the French legal requirements.

Procedure

Items Presented

To evaluate the effect of novelty and palatability, we sent a questionnaire about the apes' food preferences and usual diet to the caregivers at each of the zoos. Based on their replies, we selected the following items:

- 1) One familiar and less palatable item to control for novelty: turnip root (*Brassica rapa*, 28 kcal per 100 g of raw food, USDA nutrient database 2009)
- 2) One familiar and palatable item to evaluate the possible confounding effect of competition: apple fruit (*Malus pumila*, 52 kcal per 100 g of raw food, USDA nutrient database 2009)
- 3) One novel and palatable item: sapota fruit (*Manilkara zapota*, 83 kcal per 100g of raw food, USDA nutrient database 2009). We considered this fruit palatable because of the features shared with the familiar and palatable fruit (pulpy, sweet, and highly caloric)
- 4) Four novel and less palatable items: stems with leaves of four aromatic plants from herbal medicine: basil (*Ocimum basilum* with digestive properties, 23 kcal per 100 g of fresh plant, USDA nutrient database 2009), chervil (*Anthriscus cerefolium* with diuretic properties, 17.8 kcal per 100 g of fresh plant, Ciquel 2008), coriander (*Coriandrum sativum* with digestive properties, 23 kcal per 100 g of fresh plant, USDA nutrient database 2009), and sage (*Salvia officinalis* with digestive properties, nutrient data not available). Vegetative plant parts were considered less palatable than fruits because they usually contain a less soluble form of sugar (Hladik *et al.* 2002) and higher concentrations of secondary compounds (Vining 1990). The plants we used are not toxic, were available throughout the study period, and belong to the French Pharmacopoeia.
- 5) One mineral: kaolin (white clay). In the wild, geophagy usually involves clay that is similar in chemical composition to the clay mineral kaolinite (Mahaney *et al.* 1996). Therefore, we also presented kaolin to all groups except the LP orangutans for logistical reasons.

All items were kept fresh in zoo refrigerators during the study period and were never stored for >5 d. Although it is very unlikely, the apes may have eaten the experimental items when housed at previous zoos. If so, it would probably have been only very occasionally because they are not part of the usual zoo diet. Therefore, at worst, the novel items may have been very unfamiliar rather than novel for some individuals.

Experiments

Before the beginning of the experiment period, we conducted several preliminary experiments with mint, apple, and turnip, during 1 wk, to habituate the apes to the procedure, the observer, and the camera device and to adapt the procedure to each zoo's conditions, such as enclosure size and staff, as well as apes' schedules. We standardized the amount according to the individuals' weights as estimated by each zoo's veterinarians to ensure that we gave a similar quantity of plants to all groups. To avoid satiating the subjects or disrupting their diet, we gave the equivalent of *ca.* 5g of plants per 30 kg of subject and one apple, turnip, or sapota per 70 kg of subject. We cut both fruit and turnips into homogeneous pieces of 2 cm³. We mixed kaolin powder (1 g of clay for 1 kg of subject) with water (1 kg/0.5 L) to give it a muddy texture that the subjects could handle.

While subjects were waiting in an adjacent enclosure, we distributed each item in *ca.* 10 heaps along a 1.5-m line to allow all individuals to access it. Experiments began from the opening of the sliding door. We held three sessions of presentation for each item separately. Each experiment lasted for a maximum of 30 min or until the complete ingestion of the items presented. We conducted one experiment per day for each group and we randomized the order of plants presented. Each experiment took place in the indoor facility, except for the LP orangutan group, where experiments took place in the outdoor facility. Apes' behaviors were recorded with two video cameras, one fixed and the other mobile and handled by the observer. To avoid biases due to hunger or satiety, experiments started from 30 min to 1 h after the animals' feeding time.

Data Collection

Response to Novel Food

By rewinding the videos and focusing on a different individual with each viewing, we used the focal animal continuous sampling method (Altmann 1974) to record behaviors related to food processing (approach, sniffing, tasting, and ingesting; see Table II for definitions).

Table II

List of actions used by great apes to discover, evaluate, and eat food items presented

Behavior	Description
Food processes	
Approach	The focal ape is oriented toward the item and approaches it to <30 cm from its face.

Behavior	Description
Sniffing	The focal ape is oriented toward the test item with its nose ≤ 5 cm of the test item.
Tasting	The focal ape picks up the item with its mouth and/or licks or chews it.
Rejection	The focal ape moves away or drops the item after taking, sniffing, or tasting it.
Ingestion	The focal ape visibly consumes a part of the item and does not reject it.
Social interactions	
Close observation	The ape looks toward an item possessor with < 20 cm between both heads.
Begging	The ape directs a specific posture such as an extended hand or lips to an item possessor.
Offering	The ape gives a part of the item without previous begging.
Active sharing	The ape gives a part of the item with previous begging.
Relaxed claim	The ape takes without protest or resistance from the possessor.
Stealing	The ape takes with protest and resistance from the possessor.

Because of the limited quantity of plants on offer, we did not consider ingestion rates, duration, and number of occurrences, as these variables were too dependent on the subjects' arrival order. Low visibility during the initial approach prevented us from recording the precise quantities ingested for all individuals accurately. We analyzed the proportion of individuals smelling the novel items (sniffers), the proportion of individuals ingesting the items among those who took them (consumers), and the time elapsed between approach to < 30 cm from the item and tasting (approach-taste delay) for each item.

Social Learning Opportunities

We also noted close interindividual observations and food transfers. We analyzed the proportion of individuals observing their conspecifics (observers). In line with Jaeggi *et al.* (2008) and de Waal (1989), we discriminated four categories of food transfers: "offering," "active sharing," "relaxed claim," and "stealing" (see Table II for more details). For each interaction, we noted down which was the initiator, i.e., giver, beggar, and robber, and which was the solicited conspecific. To investigate whether some individuals were mainly observers or whether they were preferentially selected as models by their conspecifics, we calculated two scores for each individual corresponding to the mean percentage of the group members he or she observed (observation score) and the mean percentage of group members by which the individual was observed (demonstration score). We calculated these scores for the three presentations of the familiar foods pooled together, of the sapota fruit, of the four aromatic plants pooled together, and of the kaolin. One of us (E. G.) and someone not involved in the experiments recorded and analyzed all of the data. A κ coefficient index of > 0.8 for all variables recorded ensured the reliability of measures.

Statistical Analysis

To tease apart novelty from palatability, we used the turnip presentation as the control condition because it was the least palatable item, and was familiar to all species and individuals. For each ape species, we used Linear Mixed-Effects models (LME) with binomial distribution to examine the effects of the items and sessions on the proportions of sniffers, consumers, and observers. We used another LME with Poisson distribution to evaluate the effect of items and sessions on the approach-taste delays. Then, to make cross-species comparisons we used additional similar LMEs to examine the effects of the “item” and the interaction “item × species” during the first session of presentations on the proportions of sniffers, consumers, and observers. *Post hoc* analysis consisted of fitting additional LMEs to make pairwise comparisons between ape species on the interaction “item × species.” We included the terms “identity,” “zoo,” and “rearing condition” (natural mother or human) as random factors.

Because the sample size was too small to include all variables within a single model, we used LMEs to evaluate the effect of “session” separately for each item and each species on sniffers, approach-taste delays, consumers, and observers. We also used LMEs to compare the response between each sex–age class during the first presentation of the two familiar items pooled together and the four novel plants pooled together to have a sufficiently large sample. Random factors also included “item” in these analyses. All LMEs were fitted using R (v. 2.14.1; R Development Core Team 2011).

Results

Response to Novel Foods

Chimpanzees

The proportion of sniffers during the first session was higher for all novel items than for the familiar and less palatable item, the turnip, except for chervil (Fig. 1, Table III). Sniffers decreased significantly across the three sessions for all novel items except chervil (sapota: from 27% to 0%, basil: from 82% to 14%, chervil: from 23% to 14%, coriander: from 73% to 5%, sage: from 77% to 14%, kaolin: from 77% to 18%). Approach-taste delays were higher for kaolin than for turnip (Fig. 2, Table III). The delay increased significantly across sessions only for apple, although it remained very low (from $1 \pm \text{SE } 1 \text{ s}$ to $7 \pm \text{SE } 10 \text{ s}$) (Table III). The proportion of consumers was fewer for all of the novel and less palatable items compared to turnip (Fig. 3, Table III). There were no significant individual differences (Table III).

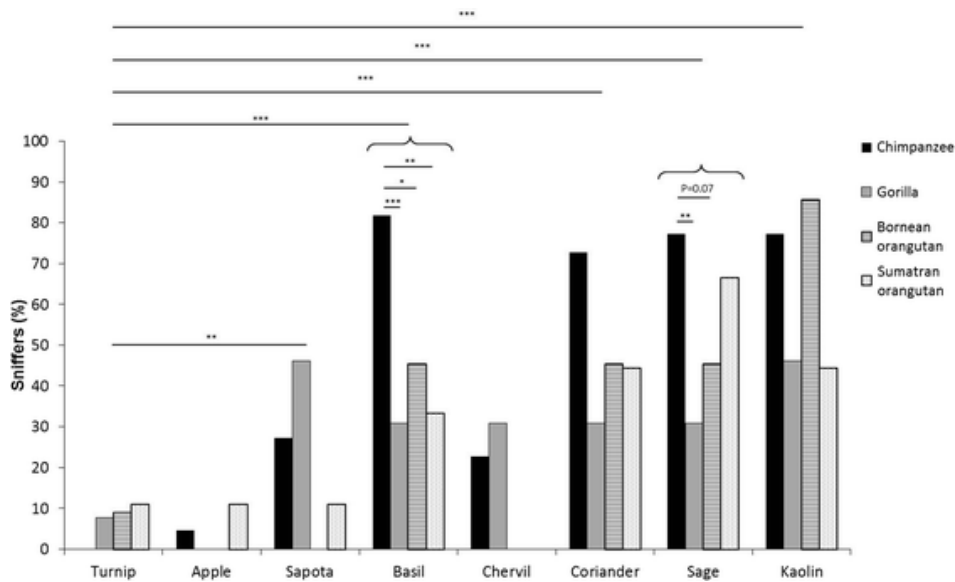


Fig. 1: Proportion of “sniffers” for each experimental food item presented (turnip, apple, sapota, basil, chervil, coriander, sage, kaolin) for groups of chimpanzees, gorillas, and Bornean and Sumatran orangutans during the first presentation. For each item, the significance of its comparison with turnip is noted above. When the interaction item \times species was significant, we note the significant differences between each ape species below the brace (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Table III: Linear mixed models testing the effect of food item at the first session of presentation, and the effect of session number and individual differences on the proportions of sniffers, approach-taste delays (s), and proportions of consumers and observers in chimpanzees

Fixed effects	First session			Trend across sessions			Interindividual differences	
	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	0			-1.472 ± 1.485	0.759	0.387		
Apple	5	1	0.323	0 ± 1.059	0	1	0.56	0.576
Sapota	27	4.487	0.04	-15.748 ± 49.94	9.627	0.003	—	—
Basil	82	65.258	<0.001	-2.199 ± 0.495	29.368	<0.001		
Chervil	23	3.17	0.082	-0.885 ± 0.728	0.757	0.387		
Coriander	73	40.385	<0.001	-11.201 ± 3.977	38.884	<0.001		
Sage	77	50.717	<0.001	-1.609 ± 0.404	23.698	<0.001	0.283	0.755

Kaolin	77	50.717	<0.001	-1.756 ± 0.428	19.63	<0.001	—	—
Approach -taste delays	Delay ± SE	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	1 ± 0			0.638 ± 0.057	0.352	0.555		
Apple	1 ± 1	2.171	0.151	1.015 ± 0.126	8.297	0.006	2.747	0.08
Sapota	17 ± 61	1.087	0.304	1.073 ± 0.075	0.025	0.875	—	—
Basil	52 ± 168	1.541	0.224	-0.178 ± 0.027	0.024	0.878		
Chervil	259 ± 672	2.675	0.116	-3.632 ± 0.117	1.942	0.176		
Coriander	53 ± 125	2.951	0.097	-0.991 ± 0.057	0.625	0.436		
Sage	87 ± 227	2.421	0.129	-0.458 ± 0.024	0.21	0.649	0.494	0.613
Kaolin	80 ± 159	4.199	0.049	-1.337 ± 0.044	4.037	0.05	—	—
Consumers	%	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	100	0	1	0	0	1		
Apple	100	0	1	0	0	1	0.23	0.795
Sapota	100	0	1	0	0	1	—	—
Basil	67	8.014	0.008	0.972 ± 0.662	2.343	0.134		
Chervil	71	6.233	0.021	-1.699 ± 1.004	0.306	0.586		
Coriander	35	29.333	<0.001	1.599 ± 0.943	3.539	0.069		
Sage	75	5.36	0.027	-1.323 ± 0.603	1.892	0.176	3.002	0.055

Kaolin	73	5.796	0.022	1.086 ± 0.615	3.642	0.063	—	—
Observers	%	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	32			0.116 ± 0.244	0.371	0.544	0.362	0.698
Apple	27	0.104	0.748	0.189 ± 0.218	1.444	0.234		
Sapota	59	3.405	0.072	-0.037 ± 0.191	0.094	0.76	—	—
Basil	59	3.405	0.072	-0.125 ± 0.205	0.81	0.371	4.539	0.013
Chervil	14	2.074	0.157	-0.125 ± 0.376	0.148	0.701	—	—
Coriander	55	2.333	0.134	-0.547 ± 0.275	6.88	0.011		
Sage	68	6.4	0.015	-0.199 ± 0.201	2.338	0.131		
Kaolin	55	2.333	0.134	-0.081 ± 0.202	0.36	0.551	—	—

Individual differences are pooled for familiar plants and novel aromatic plants.

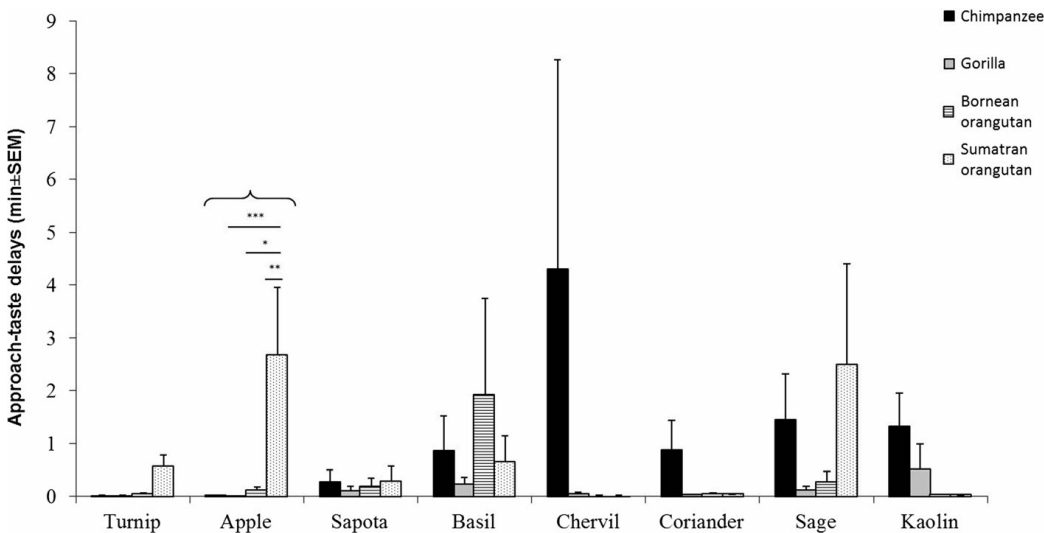


Fig. 2: Approach-taste delays (mean ± SEM) for each experimental food item presented (turnip, apple, sapota, basil, chervil, coriander, sage, kaolin) for groups of chimpanzees, gorillas, and Bornean and Sumatran orangutans during the first presentation. For each item, the significance of its comparison with turnip is noted above. When the interaction item × species was significant, we note the significant differences between each ape species below the brace (**P* < 0.05; ***P* < 0.01; ****P* < 0.001).

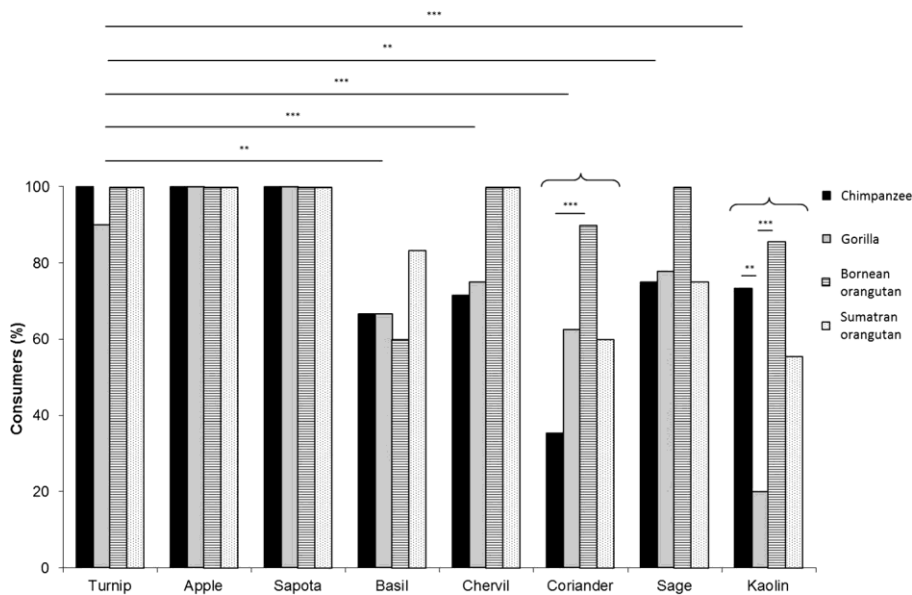


Fig. 3: Proportion of “consumers” for each experimental food item presented (turnip, apple, sapota, basil, chervil, coriander, sage, kaolin) for groups of chimpanzees, gorillas, and Bornean and Sumatran orangutans during the first presentation. For each item, the significance of its comparison with turnip is noted above. When the interaction item \times species was significant, we noted below the brace the significant differences between each ape species ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$).

Gorillas

At the first sessions, the proportion of sniffers was higher for sapota and kaolin compared to the familiar and less palatable item, the turnip (Fig. 1, Table IV). We noted a significant decrease of sniffers across sapota fruit presentations only (from 46% to 0%). Approach-taste delays did not differ significantly between the novel and familiar items and consumers were significantly fewer compared to turnip for kaolin only (Fig. 2, Table IV). These variables did not vary significantly across sessions.

Table IV: Linear mixed models testing the effect of food item at the first session of presentation, and the effect of session number and individual differences on the proportions of sniffers, approach-taste delays (s), and proportions of consumers and observers in western gorillas

Fixed effects	First session			Trend across sessions			Interindividual differences	
	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	8			0 ± 0.889	0	1		
Apple	0	1	0.327	1.024 ± 1.528	0.401	0.531	0.187	0.831
Sapota	46	5.556	0.027	-1.965 ± 0.733	8.466	0.006	—	—

Basil	31	2.25	0.147	-0.387 ± 0.626	0.207	0.652		
Chervil	31	2.25	0.147	-0.812 ± 0.678	0.917	0.344		
Coriander	31	2.26	0.148	-0.292 ± 0.534	0.207	0.652		
Sage	31	2.27	0.149	-0.821 ± 0.561	2.13	0.153	0.153	0.859
Kaolin	46	5.556	0.027	-0.68 ± 0.464	1.484	0.231	—	—
Approach-taste delays	Delay \pm SE	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	1 ± 0			0.148 ± 0.193	0.245	0.625		
Apple	1 ± 0	0.65	0.435	0.357 ± 0.203	1.423	0.247	0.3	0.746
Sapota	7 ± 16	1.088	0.311	-1.171 ± 0.179	1.169	0.291	—	—
Basil	15 ± 21	3.851	0.069	-0.806 ± 0.112	1.655	0.217		
Chervil	3 ± 4	2.453	0.141	-0.328 ± 0.169	0.169	0.688		
Coriander	2 ± 2	2.869	0.114	1.028 ± 0.192	2.039	0.175		
Sage	7 ± 12	2.471	0.138	0.374 ± 0.127	0.043	0.838	0.38	0.688
Kaolin	31 ± 90	0.944	0.345	-0.009 ± 0.044	0.621	0.446	—	—
Consumers	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	91			15.25 ± 122.66	0.589	0.45		
Apple	100	0.583	0.458	0	0	1	7.213	0.004

Sapota	100	1.106	0.306	-15.17 ± 84.63	1.177	0.288	—	—		
Basil	67	1.938	0.183	-0.016 ± 9.072	0.001	0.981				
Chervil	75	0.667	0.426	-0.39 ± 1.762	0.132	0.721				
Coriander	63	1.512	0.236	-0.185 ± 0.901	0	1				
Sage	78	0.49	0.49	18.33 ± 6750.53	2.143	0.161			10.198	<0.001
Kaolin	20	17.64	<0.001	1.201 ± 0.968	1.761	0.207	—	—		
Observers	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P		
Turnip	0			0 ± 1.714	0	1	0.786	0.467		
Apple	8	1	0.327	0.305 ± 0.561	0.329	0.569				
Sapota	8	1	0.327	-0.834 ± 1.018	0.766	0.387			—	—
Basil	8	1	0.327	-19.06 ± 19283	1.521	0.225			0.253	0.777
Chervil	8	1	0.327	-19.06 ± 19283	1.521	0.225				
Coriander	23	3.6	0.07	-1.06 ± 0.738	3.192	0.082				
Sage	23	3.6	0.07	-1.06 ± 0.738	3.192	0.082				
Kaolin	23	3.6	0.07	-19.36 ± 924	5.286	0.027	—	—		

Individual differences are pooled for familiar plants and novel aromatic plants.

We observed individual differences in the proportion of consumers during the presentations of the familiar items and the aromatic plants (Table IV). Differences for the familiar items were due to the lower proportion of adult females ($N = 6$, 25%) compared to adult males ($N = 5$, 90%; $F = 14.632$, $df = 1$, $P = 0.001$). Conversely, differences in the ingestion of novel plants were due to the higher proportion of adult

females (75%) compared to adult males (25%, $F = 13.884$, $df = 1$, $P < 0.001$) and juveniles (13%, $F = 13.081$, $df = 1$, $P < 0.001$).

Bornean Orangutans

The proportion of sniffers was higher for kaolin compared to turnip during the first sessions (Fig. 1, Table V). The proportion of sniffers decreased significantly across the three sessions for coriander and kaolin (coriander: from 45% to 9%, kaolin: from 86% to 0%, Fig. 2, Table V). We noted no significant differences for the approach-taste delays. The proportion of consumers of basil was lower than for turnip (Fig. 3, Table V). We observed no significant differences between age–sex classes (Table V).

Table V: Linear mixed models testing the effect of food item at the first session of presentation, and the effect of session number and individual differences on the proportions of sniffers, approach-taste delays (s), and proportions of consumers and observers in Bornean orangutans

Fixed effects	First session			Trend across sessions			Interindividual differences	
	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	11			-23.25 ± 9114.69	1.525	0.226		
Apple	0	1	0.329	15.15 ± 117.6	0.769	0.387	2.591	0.101
Sapota	0	1	0.329	-23.25 ± 9115	1.525	0.226	—	—
Basil	45	4	0.059	-0.967 ± 0.518	3.413	0.074		
Chervil	0	1	0.329	-23.25 ± 9115	1.525	0.226		
Coriander	45	4	0.059	-1.669 ± 0.8	4.709	0.038		
Sage	45	4	0.059	-1.008 ± 0.552	3.875	0.058	0.262	0.771
Kaolin	86	22.752	<0.001	-22.17 ± 51.26	20.52	<0.001	—	—
Approach-taste delays	Delay \pm SE	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	3 ± 3			$0.448 \pm$	1.292	0.266	0.269	0.767

				0.14				
Apple	7 ± 13	0.909	0.354	-0.441 ± 0.121	0.004	0.951		
Sapota	11 ± 28	0.985	0.335	-0.446 ± 0.088	0.657	0.426	—	—
Basil	115 ± 329	1.176	0.293	-1.339 ± 0.048	1.376	0.252		
Chervil	1 ± 1	0.662	0.432	2.192 ± 0.19	1.413	0.26		
Coriander	3 ± 2	0.213	0.65	0.911 ± 0.111	2.369	0.142		
Sage	17 ± 39	1.274	0.273	0.404 ± 0.043	0.363	0.552	0.278	0.759
Kaolin	2 ± 1	0.538	0.475	0.633 ± 0.159	1.288	0.271	—	—
Consumers	Delay ± SE	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	100			-15.38 ± 127.65	0.019	0.891		
Apple	100	0	1	0	0	1	0.635	0.541
Sapota	100	0	1	0	0	1	—	—
Basil	60	6	0.025	0.873 ± 0.703	0.751	0.394		
Chervil	100	0	1	0	0	1		
Coriander	90	1	0.331	-0.304 ± 2.531	0.24	0.63		
Sage	100	0	1	-0.48 ± 0.609	0.608	0.443	1.798	0.179
Kaolin	86	1.471	0.244	-0.047 ± 17.533	0.012	0.913	—	—
Observers	%	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>

Turnip	27			-0.834 ± 0.588	2.818	0.103		
Apple	27	0	1	0 ± 0.46	0	1	0.957	0.402
Sapota	64	3.077	0.095	-0.693 ± 0.367	7.896	0.009	—	—
Basil	18	0.238	0.631	0.189 ± 0.437	0.234	0.632		
Chervil	9	1.176	0.291	0 ± 0.5	0	1		
Coriander	18	0.238	0.631	0.253 ± 0.508	0.29	0.594		
Sage	55	1.667	0.211	-0.384 ± 0.367	1.755	0.195	5.808	0.006
Kaolin	86	7.692	0.014	-0.479 ± 0.359	5.7	0.028	—	

Individual differences are pooled for familiar plants and novel aromatic plants.

Sumatran Orangutans

The proportion of sniffers was higher for sage only compared to turnip during the first sessions (Fig. 1, Table VI). The proportion of sniffers did not vary significantly across the three sessions. Approach-taste delays did not differ significantly between turnip and the other items but decreased across sessions for apple (Fig. 2, Table VI). The proportion of consumers was lower than that of turnip for coriander and for kaolin (Fig. 3, Table VI).

Table VI: Linear mixed models testing the effect of food item at the first session of presentation, and the effect of session number and individual differences on the proportions of sniffers, approach-taste delays (s), and proportions of consumers and observers in Sumatran orangutans

Fixed effects	First session			Trend across sessions			Interindividual differences	
	%	F (df = 1)	P	Estimate \pm SE	F (df = 1)	P	F (df = 2)	P
Turnip	11			-23.42 ± 10159.6	1.531	0.228		
Apple	11	0	1	-23.42 ± 10159.6	1.531	0.228	0.37	0.697

Sapota	11	0	1	-0.901 ± 1.059	0.773	0.388	—	—
Basil	33	1.231	0.284	-0.252 ± 0.505	0.234	0.633	4.184	0.024
Chervil	11	1	0.332	0.545 ± 0.760	0.346	0.562		
Coriander	44	2.571	0.128	-1.313 ± 0.79	3.497	0.073		
Sage	67	7.692	0.014	0 ± 0.638	0	1		
Kaolin	44	2.571	0.128	-0.376 ± 0.582	0.234	0.633	—	—
Approach–taste delays	Delay ± SE	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	54 ± 75			0.82 ± 0.056	2.544	0.124	0.315	0.735
Apple	160 ± 205	2.106	0.169	-3.658 ± 0.233	5.274	0.035		
Sapota	18 ± 44	1.276	0.278	-1.976 ± 0.21	1.124	0.301		
Basil	39 ± 78	0.138	0.716	-2.84 ± 0.156	0.122	0.733	6.302	0.009
Chervil	2 ± 1	0.893	0.369	0.512 ± 0.387	1.514	0.254		
Coriander	3 ± 2	1.759	0.212	0.133 ± 0.258	0	1		
Sage	150 ± 343	0.676	0.424	-1.03 ± 0.037	1.366	0.256		
Kaolin	2 ± 2	3.793	0.07	0.27 ± 0.053	0.082	0.777	—	—
Consumers	%	<i>F</i> (df = 1)	<i>P</i>	Estimate ± SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	100			0	0	1	0.581	0.572

Apple	100	0	1	-0.081 ± 1.24	0.004	0.951		
Sapota	100	0	1	0.078 ± 1.471	0	1	—	—
Basil	71	1.56	0.234	18.43 ± 6822.9	1.213	0.291	8.679	<0.001
Chervil	100	0	1	-0.635 ± 1.203	0.246	0.631		
Coriander	60	5.143	0.043	18.27 ± 8038.32	2.639	0.139		
Sage	67	2.647	0.125	-0.443 ± 0.602	0.516	0.481		
Kaolin	56	6.4	0.022	1.296 ± 0.768	2.257	0.146		
Observers	%	<i>F</i> (df = 1)	<i>P</i>	Estimate \pm SE	<i>F</i> (df = 1)	<i>P</i>	<i>F</i> (df = 2)	<i>P</i>
Turnip	11			0.723 ± 0.476	4.348	0.047	2.177	0.148
Apple	56	4.571	0.048	-0.233 ± 0.356	0.852	0.365		
Sapota	56	4.571	0.048	$0. \pm 0.297$	0	1		
Basil	33	1.231	0.284	-0.253 ± 0.508	0.301	0.588		
Chervil	0	1	0.332	0.834 ± 1.018	0.773	0.388		
Coriander	22	0.364	0.555	-0.834 ± 0.763	1.744	0.199	0.139	0.871
Sage	67	7.692	0.014	0.094 ± 0.311	0.215	0.647		
Kaolin	44	2.571	0.128	0.285 ± 0.312	2.077	0.162		

Individual differences are pooled for familiar plants and novel aromatic plants.

Sumatran orangutans showed individual differences during the aromatic plant pre- presentations for smelling,

approach-taste delays, and ingestion (Table VI). Fewer adult males sniffed these items ($N = 2$, 0%) compared to adult females ($N = 5$, 50%; $F = 9.079$, $df = 1$, $P = 0.006$) and juveniles ($N = 2$, 38%, $F = 4.2$, $df = 1$, $P = 0.06$). Adult males also showed higher approach-taste delays ($N = 2$, mean delay = $496 \pm SD 700$ s) than adult females ($N = 5$, mean delay = $22 \pm SD 40$ s, $F = 8.26$, $df = 1$, $P = 0.015$) and juveniles ($N = 2$, $30 \pm SD 74$, $F = 4.527$, $df = 1$, $P = 0.071$). Finally, adult males ingested no items ($N = 12$, 0%), although adult females ($N = 5$, 45%, $F = 6.078$, $df = 1$, $P = 0.021$) and juveniles did ($N = 2$, 88%, $F = 49$, $df = 1$, $P < 0.001$).

Cross-Species Comparison

During the first session of each experiment, the proportion of sniffers was higher for all novel items except chervil compared to the familiar and less palatable item, the turnip (see Table VII and Fig. 1). The interaction “item \times species” was significant for basil and sage. *Post hoc* analysis revealed that the proportion of sniffers was significantly higher in chimpanzees compared to gorillas (basil: $F = 8.907$, $P < 0.001$; sage: $F = 6.884$, $P = 0.002$), Bornean orangutans (basil: $F = 3.883$, $P = 0.026$), and Sumatran orangutans (basil: $F = 6.231$, $P = 0.004$).

Table VII: Linear mixed model testing the effects of food “item” and the interaction between food item and ape species (chimpanzees, western gorillas, and Bornean and Sumatran orangutans) on the proportions of sniffers and consumers, approach-taste delays, and the proportion of observers

	Apple		Sapota		Basil		Chervil		Coriander		Sage		Kaolin	
Sniffers	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Intercept	6.011	0.016	22.99	<0.001	22.99	<0.001	22.99	<0.001	64.0819	<0.001	79.926	<0.001	91.389	<0.001
Item	0.668	0.416	7.096	0.009	43.395	<0.001	3.753	0.055	36.778	<0.001	48.35	<0.001	61.766	<0.001
Item * species	0.255	0.956	1.402	0.221	3.414	0.004	0.565	0.757	1.791	0.108	2.324	0.038	1.777	0.112
Approach-taste delays	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Intercept	8.434	0.005	8.729	0.004	4.489	0.037	1.559	0.217	5.489	0.022	5.94	0.017	7.828	0.006
Item	2.054	0.156	0.547	0.462	2.815	0.098	2.167	0.147	1.395	0.242	3.76	0.056	3.642	0.06
Item * species	6.758	<0.001	1.129	0.353	0.521	0.79	1.024	0.420	1.601	0.160	0.958	0.459	1.550	0.173
Consumers	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Intercept	6925.45	<0.001	8792.12	<0.001	491.82	<0.001	884.146	<0.001	478.89	<0.001	731.626	<0.001	507.854	<0.001
Item	0.831	0.365	1.061	0.306	16.401	<0.001	6.326	0.015	30.989	<0.001	8.165	0.005	31.055	<0.001

	Apple		Sapota		Basil		Chervil		Coriander		Sage		Kaolin	
Item * species	1.101	0.369	1.246	0.291	0.382	0.888	0.996	0.436	2.963	0.012	0.466	0.831	3.738	0.003
Observers	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Intercept	35.749	<0.001	67.336	<0.001	47.093	<0.001	19.352	<0.001	44.396	<0.001	79.321	<0.001	64.13	<0.001
Item	0.846	0.36	11.067	0.001	3.349	0.07	2.721	0.102	3.157	0.079	17.034	<0.001	11.69	<0.001
Item * species	2.109	0.059	3.297	0.005	3.372	0.004	1.495	0.187	2.206	0.048	2.409	0.032	2.50	0.027

We included identity, zoo (Beauval, La Palmyre, La Boissière du Doré) and rearing condition as random factors.

Approach-taste delays during the first session did not differ significantly between the items (Table VII, Fig. 2). The interaction “item × species” was significant for apple. *Post hoc* analysis revealed that approach-taste delay in Sumatran orangutans was higher compared to chimpanzees ($F = 10.551, P < 0.001$), gorillas ($F = 4.295, P = 0.024$), and Bornean orangutans ($F = 5.463, P = 0.009$).

Finally, all individuals consumed apple and sapota at the first session. The proportion of consumers was significantly lower for all novel and less palatable items (Table VII, Fig. 3). The interaction “item × species” showed a significant effect for coriander and kaolin. *Post hoc* analyses revealed that the proportion of Bornean orangutans consuming coriander was higher compared to chimpanzees ($F = 9.85, P < 0.001$). For kaolin, there were fewer consumers in the gorilla group compared to chimpanzees ($F = 7.817, P = 0.001$) and Bornean orangutans ($F = 8.985, P < 0.001$).

Social Learning Opportunities

Chimpanzee

The proportion of individuals observing their conspecifics was significantly higher for sage than for other items (Fig. 4, Table III). Observers decreased significantly across sessions for coriander only (from 55% to 18%). We noted significant differences between sex–age classes for aromatic plant presentations only. The proportion of observers was higher for juveniles ($N = 5, 75%$) compared to adult males ($N = 5, 30%, F = 9.679, df = 1, P = 0.004$) and adult females ($N = 5, 46%; F = 5.059, df = 1, P = 0.028$). Dominant individuals were the main demonstrators during presentations of familiar items, the sapota fruit, and the aromatic plants to BE group and during the kaolin presentations to LP group. Otherwise, adult females were the main demonstrators. The main observers were juveniles for all items at BE and for all items except aromatic plants, for which the dominant group was females at LP (Table VIII).

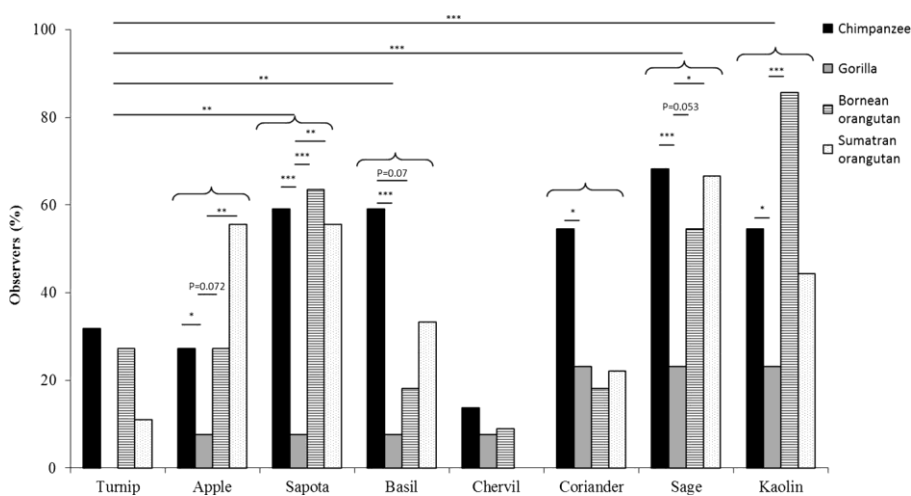


Fig. 4: Proportion of “observers” for each experimental food item presented (turnip, apple, sapota, basil, chervil, coriander, sage, kaolin) for groups of chimpanzees, gorillas, and Bornean and Sumatran orangutans during the first presentation. For each item, the significance of its comparison with turnip is noted above.

When the interaction item \times species was significant, we note the significant differences between each ape species below the brace (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Table VIII: Main demonstrators and observers for different food item with their age–sex classes, name, and score (% , mean \pm SD) for groups of chimpanzees, gorillas, and Bornean and Sumatran orangutans at Beauval (BE), La Palmyre (LP), La Boissière du Doré (BD) zoos

	Main demonstrators				Main observers			
	Familiar items	Sapota	Aromatic plants	Kaolin	Familiar items	Sapota	Aromatic plants	Kaolin
Chimpanzees								
BE (N=14)	Dominant male Joseph: 17 \pm 20	Dominant male Joseph: 36 \pm 26	Dominant male Joseph: 36 \pm 16	Adult female Julie: 17 \pm 18	Juvenile Makury: 10 \pm 8	Juvenile Makury: 21 \pm 12	Juveniles Bazu and Ann: 10 \pm 10	Juvenile Makury: 21 \pm 7
LP (N=8)	Dominant female Lily: 29 \pm 10	Dominant female and male Lily and Tsavo: 42 \pm 26	Adult female Mélie: 24 \pm 24	Dominant female Lily: 88 \pm 13	Juvenile Lulu: 27 \pm 12	Juvenile Lulu: 33 \pm 14	Dominant female Lily: 13 \pm 12	Juvenile Lulu: 58 \pm 7
Gorillas								
BE (N=5)	—	Dominant male Asato: 8 \pm 15	Adult female Kabinda: 4 \pm 10	—	—	Adult female Inge: 8 \pm 15	Adult female Dominant male Sheila and Asato: 2 \pm 7	—
LP (N=3)	Adult female Yola: 17 \pm 41	—	Adult female Yola: 17 \pm 31	Adult female Yola: 17 \pm 29	Adult female dominant male Ybana and Bongo: 9 \pm 20	—	Adult female Ybana: 9 \pm 20	Dominant male Bongo: 17 \pm 29
BD (N=)	Dominant male	—	Dominant male	Adult males	Adult male	—	Adult male	Adult male

	Main demonstrators				Main observers			
	Familiar items	Sapota	Aromatic plants	Kaolin	Familiar items	Sapota	Aromatic plants	Kaolin
5)	Vimoto: 4 ± 10		Vimoto: 16 ± 12	Atanga and Yeboah: 8 ± 15	Yeboah: 4 ± 10		Yeboah: 6 ± 11	Dominant male Yeboah and Vimoto: 8 ± 15
Bornean orangutans								
BE (N=7)	Adult female Janah: 14 ± 20	Adult female Cristina: 33 ± 29	Adult female Cristina: 17 ± 29	Adult female Cristina: 56 ± 35	Juvenile Suli: 17 ± 15	Juvenile Suli: 28 ± 10	Juvenile Suli: 15 ± 22	Juvenile Suli: 39 ± 42
LP (N=4)	Adult females Dominant male Molly, Tiba, and Sandai: 17 ± 28	Adult females Molly and Tiba: 56 ± 51	Adult females Molly and Tiba: 25 ± 28		Adult female Lotus: 22 ± 34	Adult female Dominant male Molly and Sandai: 33 ± 33	Adult female Lotus: 17 ± 22	
Sumatran orangutans								
BD (N=9)	Adult female Moni: 33 ± 17	Adult female Moni: 56 ± 11	Adult female Moni: 13 ± 22	Adult female Moni: 41 ± 17	Juveniles Kembali and Kawan: 31 ± 18	Juvenile Kembali: 42 ± 13	Juvenile Kembali: 13 ± 18	Adult female Flora: 31 ± 6

Gorillas

The proportion of observers did not differ significantly between turnip and other items (Fig. 4, Table IV). We noted no significant differences between sex–age classes in gorillas. In fact, we recorded very few interindividual observations and demonstrators, and observers appeared to be equally distributed between adult males and females (Table VIII).

Bornean Orangutans

At the first presentation, the proportion of observers was higher for kaolin compared to turnip (Fig. 4, Table V). Then, observers decreased across presentations (sapota: from 64% to 9%, kaolin: from 86% to 29%). We noted significant individual differences for the aromatic plants presentations (Table V). This difference was due to the lower proportion of observers for adult females ($N = 7$, 11%) compared to juveniles ($N = 2$, 63%; $F = 12.46$, $df = 1$, $P = 0.001$). In both groups the main demonstrators were adult females for all items, whereas in BE group ($N = 7$), the juveniles were the main observers. In LP group ($N = 4$), which had no juveniles, the main observers were equally distributed between males and females (Table VIII).

Sumatran Orangutans

The proportion of observers was higher for apple, sapota, and sage compared to turnip (Fig. 4, Table VI). The proportion of observers increased across turnip presentations (from 11% to 56%). We noted no significant differences between sex–age classes in Sumatran orangutans (Table VI). However, the main demonstrator was an adult female, while the main observers were juveniles for all items except kaolin, for which it was another adult female (Table VIII).

Cross-Species Comparison

The proportion of individuals observing their conspecifics was higher for sapota, basil, sage, and kaolin (see Table III and Fig. 4). The interaction “item \times species” was also significant for all novel items except chervil. *Post hoc* analysis showed fewer observers in gorillas for almost all items compared to chimpanzees (apple: $F = 2.843$, $P = 0.042$; sapota: $F = 8.947$, $P < 0.001$, basil $F = 8.947$, $P < 0.001$; coriander: $F = 4.308$, $P = 0.017$, sage: $F = 6.932$, $P = 0.002$, kaolin: $F = 4.308$, $P = 0.017$), Bornean orangutans (apple: $F = 2.795$, $P = 0.072$; sapota: $F = 8.986$, $P < 0.001$; sage: $F = 3.150$, $P = 0.053$, kaolin: $F = 8.335$, $P < 0.001$), and Sumatran orangutans (apple: $F = 6.366$, $P = 0.004$; sapota: $F = 6.366$, $P = 0.004$; sage: $F = 4.142$, $P = 0.023$; kaolin: $F = 4.308$, $P = 0.017$). The proportion of observers never exceeded 23% in gorillas (Fig. 4).

Food Transfers

Compared to chimpanzees and both orangutan species, we observed very few food transfers in gorillas (Fig. 5). The only observations were when an adult female from BE group “stole” pieces of sapota fruit from her infant on three occasions.

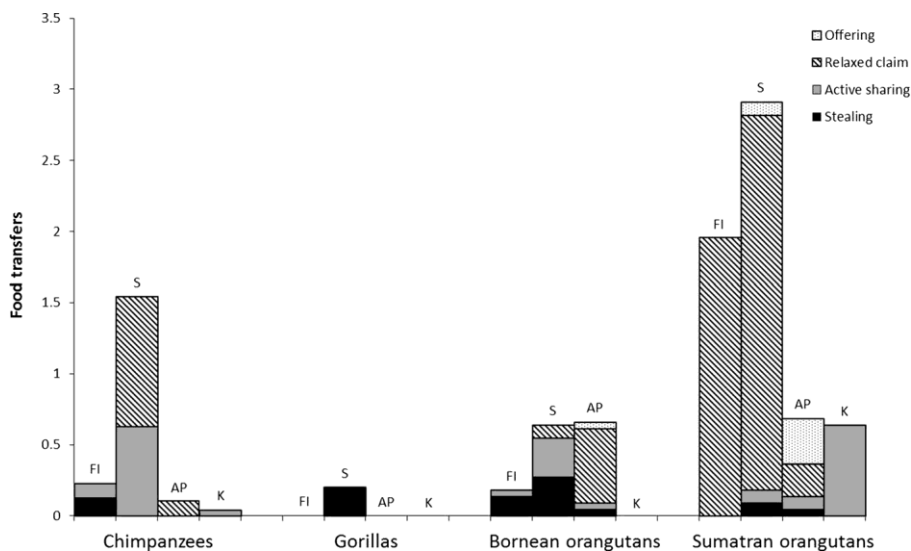


Fig. 5: Mean of food transfers as a proportion of mean group size observed for each ape species and for each type of food item (FI = familiar items, S = sapota fruit, AP = aromatic plants, K = kaolin). The proportions of each type of food transfers are indicated inside the bar for each type of food item.

In chimpanzees, food transfers occurred through active sharing and relaxed claims, especially with the sapota fruit. Stealing only involved familiar items while transfers of aromatic plants and kaolin were only made via relaxed claims. Adult males never initiated food transfers.

In Bornean orangutans, food transfers involved sapota fruit and the four aromatic plants. We observed two cases of “offering” with the sage. Otherwise, orangutans transferred aromatic plants via “relaxed claims” (35 cases of 40). All sex–age classes initiated transfers irrespective of the item, and they were especially directed to adult females (35 cases of 40).

We recorded the majority of food transfers in Sumatran orangutans (104 occurrences). We observed 15 cases of offerings, which occurred with novel items only (1 case for sapota and 14 cases for aromatic plants). The majority of transfers with the familiar food and sapota were relaxed claims and were performed by one adult female (68 cases of 82) through a peculiar behavior. She chewed these items throughout the experiments and accepted stealing directly from her mouth by several individuals through long “kisses,” i.e., lips of both individuals in contact for >5 s: 39 times for apple and 29 times for sapota fruit. Even if we exclude these “kisses,” transfers were initiated by all age–sex classes and were especially directed to adult females (26 cases out of 37).

Discussion

Response to Novel Foods

Chimpanzees, western gorillas, and both orangutan species showed similar behaviors toward familiar items. The majority of individuals tasted them very quickly and displayed very little explorative behavior before ingestion, confirming that the quantities offered and their arrangement were adapted to limit

monopolizations. The majority of great apes ingested the novel sweet fruit (sapota) quickly and demonstrated very little explorative behavior before consumption. However, when novel foods had poor nutritive content and low palatability, the ape species differed in their response. This result supports the hypothesis that nutritional value affects the neophobic response (Carruth *et al.* 2004; Johnson 2007). Despite the absence of negative experiences with novel foods during life in captivity, apes expressed cautiousness toward the vegetative parts of some novel plants, reflecting each species' predispositions.

Chimpanzees sniffed almost all novel items more than the familiar ones. Moreover, they ingested two novel aromatic plants less frequently in the first session compared to other ape species. Age and sex did not significantly affect food neophobia. This is in contrast with results of previous studies, in which adult chimpanzees were more neophobic than juveniles (Biro *et al.* 2003). The fact that we used vegetative parts of plants instead of more nutritive food may explain this contrast. In the wild, adult individuals show more frequent and more diverse consumption of unusual and bioactive plants compared to juveniles (Masi *et al.* 2011). Thus, in line with previous experimental studies, our study confirmed chimpanzees' cautiousness when eating novel plants. As highlighted by Yamagiwa and Basabose (2006), chimpanzees never stop being primarily frugivorous even when fruit is scarce. With a low propensity for folivory the nutritional strategy of chimpanzees is to obtain an optimal mix of nutrients while avoiding toxic secondary compounds (Glander 1982; Milton 1993). At the behavioral level, this appears to be translated through neophobia. The secondary compounds present in the diverse plants may also explain why the response of chimpanzees differed between the different novel plants presented.

Unlike chimpanzees, gorillas consumed the novel aromatic plants with little prior exploration. Adult males appear to be the main consumers of familiar items while adult females were the main consumers of novel aromatic plants. Females, being lower ranked than males, may have developed a propensity to try all possible edible items as the adult males monopolise the most palatable ones. Moreover, female gorillas usually leave their natal community at maturity and may transfer to another community more than once. As a result, they may be adapted to broadening their diet via lower neophobia (Harcourt and Stewart 2007). Interestingly, unlike the other species, very few gorillas ingested kaolin. Unlike chimpanzees, geophagy, which is assumed to alleviate digestive disorders, has rarely been described in the literature for western gorillas (Williamson *et al.* 1990). These results are in line with our hypothesis related to physiological features, which predicted a strong propensity for testing novel plants in gorillas because of their higher ability to digest vegetative plant parts and higher tolerance to secondary compounds, resulting in a lower risk related to novel plant ingestion. When gorillas use pith and leaves during periods of fruit scarcity, these items comprise all of their diet (Doran *et al.* 2002; Remis *et al.* 2001; Tutin *et al.* 1991).

Finally, in line with our hypothesis related to ecological characteristics, both orang-utan species also appeared less cautious than chimpanzees, showing few smelling behaviors for novel aromatic plants and short approach-taste delays. Their higher propensity to accept the sapota fruit, aromatic plants, and kaolin

quickly confirmed their low neophobia, which may be adapted to the unpredictability of food availability particular to their habitat (Gustafsson *et al.* 2011). Bornean orangutans manifested a slightly higher propensity to ingest the novel plants than Sumatran orangutans. Moreover, Sumatran orangutans appeared more cautious toward sapota than their Bornean cousins, based on the approach-taste delay. Also, although Sumatran adult males did not smell the aromatic plants before tasting them, they took longer to taste the novel plants and were less likely to ingest them, suggesting a lack of interest in these items, and low neophobia. In the wild, Bornean orangutans have a higher proportion of cambium feeding, whereas Sumatran orangutans have higher insect feeding, suggesting higher propensities to taste low-nutritive items in Bornean orangutans. A low habitat quality in Borneo is usually proposed as the main cause of differences of dietary pattern between two species (Delgado and van Schaik 2000).

Social Learning Opportunities

We noted significant differences in social interactions between familiar and novel items, in line with what we predicted from a social learning perspective. Moreover, this difference may be underestimated because close individual observations aimed at gathering information could not be unequivocally disentangled from begging aimed at provoking food transfers, perhaps explaining their occurrence during familiar item presentations. This is also reflected by the fact that we observed active sharing and stealing especially with familiar food or with novel fruit. In contrast, aromatic plants involved relaxed claims.

In chimpanzees, we noted individual observations regularly during all presentations. In line with previous studies, juveniles were the main observers and initiated the majority of food transfers in each group. However, several adults also performed a high number of close observations, suggesting that they may continue to integrate information by social learning throughout their life (Biro *et al.* 2003; Masi *et al.* 2011; Ueno and Matsuzawa 2005). The main demonstrators for almost all items were the dominant individuals of each group, independent of sex. The influence of the demonstrators' social rank on the transmission of dietary habit is in line with the "prestige effect" in chimpanzee social learning (Horner *et al.* 2010). Similarly, Hopper *et al.* (2011) found that the behavior of a dominant female could influence chimpanzees' food choice. Such social learning bias could be particularly adaptive when faced with possibly poisonous plants (see Gosset and Roeder (2001) for similar observations on lemurs). When faced with unfamiliar plants in the wild, the favorite demonstrators were adults between 25 and 40 yr old (Masi *et al.* 2011), suggesting a possible mix between "copy older" and/or "copy successful individuals" social learning strategies (Laland 2004). Our findings, that ecologically less competent juvenile chimpanzees were the main observers and solicited more food transfers, support this notion. Being more cautious than the other ape species, such a social learning strategy may allow chimpanzees to overcome their initial neophobia, as well as providing an optimal choice of novel items to test to profit from their beneficial properties, such as carbohydrates and prophylactic compounds, while avoiding possible poisonous molecules. In support of this, neophobic behaviors such as sniffing decrease across sessions for almost all the novel items,

suggesting that neophobia may decrease rapidly within the social group. Gorillas did not seem eager to exchange or look for information from their conspecifics despite their more cohesive social groups, and we recorded almost no observations or food transfers for this species. The low observation and demonstration scores observed also suggest a lack of any social learning strategies in the gorillas we studied. Such rarity of interactions in gorillas has been described in the wild (Masi *et al.* 2009, 2011; Watts 2003). Differences in social tolerance have also been suggested to influence the differential speed of learning between captive chimpanzees and gorillas when confronted with a novel “termite fishing” task (Lonsdorf *et al.* 2009). However, our sample included only two juveniles, which were in a bachelor group, so their low sociality could be due to “carer” absence and the probable stressful presence of blackback males. Several observations of wild western gorillas suggest a high level of interaction between mothers and youngsters, especially via food sharing (Maestriperi *et al.* 2002; Nowell and Fletcher 2006). These studies also highlighted the fact that suckling is still tolerated, even though juvenile gorillas show low levels of contact with their mother once the juvenile is capable of traveling independently, probably to forearm against potential fruit shortages (Nowell and Fletcher 2007). Interestingly, long lactating periods are very likely to help them develop a taste for bitter compounds and adapt more easily to a folivorous diet. Evidence for such learning has already been suggested in humans (Mennella and Beauchamp 2005; Schaal 2005) and highlights the relationship between gorillas’ ontogenetic niche and diet acquisition. In addition to their digestive physiological adaptation to a herbivorous diet, postnatal exposure to bitter taste via a longer lactating period may help gorillas to discover novel sources of foods and ingest large amounts of vegetation without being poisoned. Such adaptations, reflected by their low neophobia, appear to be sufficiently efficient to prevent any propensity for complex social learning strategies.

All our observations of “offering” occurred in orangutan groups and all individuals interacted socially in both species, although juveniles had the highest observer scores. Orangutans directed their “offers” toward adult females, suggesting that they may continue to consider them major referents, even after weaning. A previous study based on a token-exchange task found that transfers were more frequent in orangutans than in chimpanzees and gorillas (Pelé *et al.* 2009). In the wild, food transfers, studied especially between infants and mothers, decreased to weaning age and focused on a few food items that remain difficult for the offspring (Jaeggi *et al.* 2008, 2010). Interestingly, orangutans did not transfer rare foods more than familiar ones in these studies. However, encounters with novel foods could not be fully covered under wild conditions. In the present study, which addressed this point, we observed more food transfers during novel food presentations than during familiar ones, suggesting increased food interest on the first encounter with a novel item. Thus, our observations confirm the social tolerance of orangutans and suggest many opportunities for social learning when confronted with novel foods. Indeed, cultural transmission of diet preferences has recently been reported in the wild, revealing the important role of social learning in orangutans’ diet acquisition (Jaeggi *et al.* 2010). It is important to note that high rates of social interactions in orangutans have been described, especially in rehabilitation centres and zoos (van Schaik *et al.* 2003). Although captive conditions may lead to increased sociality, large numbers of wild orangutans concentrate

in areas with a locally high abundance of fruit (Mackinnon 1974; Sugardjito *et al.* 1987; te Boekhorst *et al.* 1990). The picture emerging from these studies suggests that when orangutans are confronted with novel foods they may show a low neophobia and a strong disposition to monitor their conspecifics. Such optimal learning processes are conducive to allowing the apes to incorporate potential novel foods during solitary periods while taking full advantage of their conspecifics' knowledge during their rare encounters. The simultaneous tendency for individual and social learning probably reflects orangutans' adaptations to the seasonal and interannual declines in fruit availability that are peculiar to their habitat.

Finally, we observed more food transfers and almost all "offering" in the Sumatran orangutans. It has been hypothesized that Sumatran orangutans are less vulnerable to seasonal fluctuation compared to their Bornean cousins because of higher soil fertility and, indeed, densities of orangutans in Sumatra are twice as high as in similar habitats on Borneo (van Schaik 1999; van Schaik *et al.* 1995, 1996b). Habitat productivity and orangutan density are very likely to have selected for behavioral traits. For example, tool use and manufacture in wild orangutans have been observed in the swamps of northwestern Sumatra (Fox *et al.* 1999; van Schaik *et al.* 1996a). According to several authors, these behaviors are direct reflections of greater gregariousness and social tolerance (Fox *et al.* 1999; van Schaik and Knott 2001; van Schaik *et al.* 2003). The fact that we noted more frequent social interactions in Sumatran orangutans than in Bornean orangutans in our study supports the hypothesis that this contrast may be taxonomically based.

By involving unusual plants, this study may provide fresh insight into self-medication in great apes. Once tasting a novel item, instantaneous and postingestive feedback is the most effective way of integrating the novel food into the usual diet (Bernstein 1999; Laska 2001; Laska *et al.* 2000; Matsuzawa and Hasegawa 1983; Matsuzawa *et al.* 1983; Milton *et al.* 1993; Visalberghi *et al.* 2003b). Therefore, if a healthy individual experiences a flavor and falls ill, it will subsequently treat the taste as poison. Conversely, a sick individual tasting the same flavour during its convalescence may associate the taste with its recovery and integrate it into its diet as medication (Garcia *et al.* 1955; Green and Garcia 1971). Interestingly, rats that have learned that one food is toxic can ignore their personal experience in favor of the presumably toxic food after interacting with "demonstrator" rats that have eaten that food (Galef and Whiskin 2008). Such reliance on socially acquired information, despite conflicting personal information, with low palatable curative items may be useful in case of an epidemic. Considering gorillas' propensity to try novel plants, it is not surprising that their usual diet is regularly enriched with medicinal plants (Cousins and Huffman 2002; Masi *et al.* 2011). In contrast, chimpanzees were more cautious with regard to novel aromatic plants than gorillas and seemed to look for information before consuming the plants. These features may be the basis for traditional use of certain plants in wild chimpanzee communities. Both species of orangutans were also very interested in the novel plants. Because wild individuals must often broaden their diet to face periods of low food availability in their natural environments, their propensity to try unusual items might be more adapted to environmental constraints of food scarcity than to medicinal use. Consequently, the discrimination between usual foods and medicine that would allow for the acquisition of a medicinal

repertoire of plants should be more developed in chimpanzees, followed by orangutans and gorillas. This last assumption would be most interesting to investigate in the wild.

Limitations

The items selected as “novel and less palatable” may not have equally low palatability for all ape species. Future studies should measure taste thresholds for items offered and control for texture, appearance, and odor to disentangle the diversity of factors that define palatability for each ape species. Moreover, the plants we offered were not particularly bitter or toxic. However, not all bitter compounds are necessarily toxic (Glendinning 1994), and toxic substances, such as the lethal alkaloid dioscorine, may sometimes be tasteless (Hladik and Simmen 1998; Hladik *et al.* 2002; Maga and Rousseff 1990). Therefore, we considered that a basic level of neophobia toward vegetative parts of plants should have been selected independently of the plant bitterness. Illness may be a strong driver to taste items with secondary compounds. No subjects were sick during this study, but replicating this experiment with sick individuals may be a promising avenue in future research.

The choice of turnip as a control item could be problematic as its texture may represent a confounding variable. A vegetative plant part would have been more appropriate. However, caregivers considered candidates such as salad or chicory very palatable items for two gorilla and one orangutan groups. As we only considered delays before tasting and the proportion of sniffers, consumers, and observers, we believe that turnip is still an appropriate control. The texture effect would have been problematic for other measures, such as chewing time or other manipulative activities, which we did not measure.

An improved experimental design would have considered an equal number of each type of food item, e.g., four novel and less palatable items vs. four familiar and palatable items vs. four familiar and less palatable items vs. four novel and more palatable items. This would avoid the possible bias caused by preferences for a particular familiar food. For logistical reasons (similar food for all apes and available in all zoos during the whole study period), this could not be achieved here.

Our sample size was large compared to previous experimental studies on this topic. However, differences in rearing and living conditions between zoos and group composition could also have affected our results. Our results may also be biased by particular individuals and should therefore be confirmed in more groups. Future studies could replicate this work in sanctuaries to control for group size and composition and to avoid the biasing effect of enclosure and site-specific features with individuals used to the same diet.

The presence of two hybrids in one Bornean and one Sumatran orangutan group may have reduced the differences between both species.

Finally, we did not include infants in our analyses because of their limited locomotor activity. Future studies should be designed explicitly to investigate the development of neophobic and neophilic tendencies during infancy in great apes, such as in the pioneering work of Ueno and Matsuzawa (2004).

Perspectives

The individual differences we observed could not always be explained by age–sex class or dominance rank. Diverse personality dimensions that may influence interaction with novel items and foraging strategies have been now identified in great apes, such as boldness, openness, curiosity, and exploration tendencies (Carter *et al.* 2013; Hopper *et al.* 2014; Massen *et al.* 2013). A promising avenue for future research is to investigate how personality differences between and within each ape species affect their responses to novel items.

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