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**CONSIDERATIONS ON FIELD METHODS USED TO ASSESS
NON-HUMAN PRIMATE FEEDING BEHAVIOUR AND HUMAN FOOD INTAKE
IN TERMS OF NUTRITIONAL REQUIREMENTS**

Measuring food intake has been a major issue in our multidisciplinary research team, where anthropologists and primatologists worked together aiming at the objective of a better understanding of food preferences and choices in various contexts, especially in environmental settings where indigenous, spontaneous, species can cover most of the nutritional requirements. The idea of merging primatological studies with an anthropological approach resulted from the search of methods to differentiate what part of the feeding behaviour is exclusively determined by biological factors and what is shaped by the sociocultural context including symbolic aspects, which can become a major force determining food choices in human groups. This important anthropological basis of human feeding behaviour was the major concern of Igor de Garine, who conducted field studies, mostly in Africa, during the second half of the 20th century (Garine, 1972; 1993). When I met Igor De Garine at the end of the seventies, and when we decided to construct a research team together, I had conducted fieldwork on several wild primate species, with the aim of understanding the origin and the evolution of feeding behaviour (Hladik, 1988). Of course, the differences in our approaches have never been excessively different, since non-human primates share with humans several traits that are now considered as 'cultural' (see, for instance, the review by Jolly, 1999), whereas some human cultural traits have been understood as biologically adaptive (Pasquet et al., 1993).

Indeed, one of the topics in which our respective primatological and anthropological approaches converged was methodology, for example how to measure accurately feeding behaviour and food intake, in order to compare different ethnic groups, or, among non-human primates, different species? Since the time of early field studies our research team has been reshaped and renewed — including young researchers on food perception — under the leadership of Serge Bahuchet, with whom we have conducted surveys of food production in various environments, either 'natural' or partly reshaped by human settlements (Bahuchet *et al.*, 1990). However, the methodology remains a central issue of the field approaches of feeding behaviour (Simmen *et al.*, 2004). In this context some of the new techniques recently introduced in the field will be presented and discussed in relation to the experience of previous fieldwork.

Methods for measuring food intake in non-human primates

The field methods used by primatologists to compare feeding behaviour of different primate species, or groups living in various environmental conditions, must be adapted to peculiar aims since no previous approach allows accurate results in

both the fields of biology and behaviour, both are necessary to understand the global phenomenon of feeding. The measurement of the actual food intake of wild primates is particularly time consuming and can be done only in a few places where the conditions of visibility are exceptionally good. This is why, in most instances, only the feeding time is recorded, generally with an indirect statistical method (periodical scans of individuals), which allows comparison of behavioural traits, but not necessarily that of the diet.

For instance, during an early primatological survey in Sri Lanka (Hladik, 1977), undertaken with a team of the Smithsonian Institution which included students of the University of Peradeniya, we were able to follow a targeted animal, from dawn to dusk, in some study areas. This was possible in the Sacred Area of Polonnaruwa, where buddhist pilgrims have been in peaceful contact with the monkeys for centuries. In such places, where natural vegetation is partly open, the conditions of visibility allowed the observer to record the exact number of fruits eaten, or the number of mouthfuls when the animal was feeding on large flower bunches or packs of young leaves. It was sometimes necessary to use a tape recorder when the feeding activity was too fast to allow the taking of notes. Calculation of the food ingested during a day necessitates samples to be collected, fruits, flowers and leaves to be weighed and for the mouthfuls including a small number of young leaves and/or flowers, to be reproduced as accurately as possible, after comparing estimates of different observers. Although collecting, weighing, and preparing food samples for further biochemical analysis necessitated almost as much time as the daytime observation, the co-operation and relay at mid-day of the observers allowed them to obtain the series of data presented in Figure 1 (each dot along the time axis is a full day of observation), for two species of leaf monkeys, *Semnopithecus entellus* and *S. senex*. The food intake of another species of primate, the toque macaque (*Macaca sinica*) was also recorded in the same area, with the same method, during a period also covering the entire seasonal cycle.

The tables I and II, show examples of the results obtained after full days of observation, during which we have been able, with the help of my colleagues of the Smithsonian Institute (Susan Ripley, Rudy Rudran, Wolfgang Dittus, and their Ceylonese Students) working on territorial and social behaviour of the same primate species, to compare the results obtained with various techniques. It is particularly interesting to consider the feeding time, obtained either by scans (statistically showing the time spent feeding on various food items) — or by the actual recording of the time spent feeding

Sample eaten	Time spent feeding		Amount ingested, fresh weight		Amount ingested, dry weight	
	(min)	(%)	(g)	(%)	(g)	(%)
Mature leaves of <i>Adina cordifolia</i>	57	30.0	165	30.0	56.0	29.8
Mature leaves of <i>Schleichera oleosa</i>	40	21.1	150	27.3	86.7	46.1
Young leaves and shoots of <i>Schleichera oleosa</i>	52	27.4	115	20.9	22.9	12.2
Young leaves of <i>Garcinia spicata</i>	27	14.2	70	12.7	7.1	3.8
Leaf flushes (and some flowers) of <i>Walsura piscidia</i>	9	4.7	30	5.5	9.0	4.8
Green fruits of <i>Adina cordifolia</i>	5	2.6	20	3.6	6.3	3.3

Table I — Comparison of the results obtained with various field methods for the measurement of food intake by one *Semnopithecus senex*, observed in Sri Lanka, in April, during one day, from 6:30 to 18:30.

by one targeted animal during the whole day. The comparison thus includes the feeding time and our results calculated in terms of the actual weight (in grams) eaten by one individual primate during the same day.

- In Table I, concerning the feeding behaviour of *Semnopithecus senex*, the results of various calculations do not much differ, either when considering the feeding time, or the food intake, at least in terms of the percentage of fresh weight of leaves of various tree species that were eaten vs the percentage of feeding time spent on these plant species. This may show the interest in using the easy method of scan sampling for recording feeding time, when the speed of feeding is even for plucking, crushing and swallowing leaves, by the whole group of primates.

- However, the other example of a full day of records of the feeding behaviour of *Semnopithecus entellus* (Table II), observed after the Monsoon rains have stopped, when fruits were available in large amounts, shows a such large difference between the percentage of feeding time and that of the actual food intake (for instance 28% vs 77% for the fruits of *Ficus benghalensis*), that we can consider the comparison of feeding time as totally irrelevant for a research on the diet. The discrepancies are even more important for primates (such as macaques) feeding on insect and/or other invertebrates for which the foraging time could be extremely important and the weight of food obtained is low — for instance, in a period of 10 minutes, either 50 to 100 g of fruit is eaten, or 1 or 2 g of small insects are obtained by active foraging — but insects provide fat and protein necessary for a balanced diet.

Sample eaten	Time spent feeding		Amount ingested, fresh weight		Amount ingested, dry weight	
	(min)	(%)	(g)	(%)	(g)	(%)
Fruits of <i>Ficus benghalensis</i>	36	28.1	1200	77.3	250.9	71.2
Fruits of <i>Drypetes sepiaria</i> (stones not included in weight)	19	14.8	126	8.1	31.5	8.9
Fruits of <i>Schleichera oleosa</i>	20	15.6	68	4.4	22.1	6.3
Fruits of <i>Walsura piscidia</i> (with seeds eaten)	11	8.6	24	1.5	6.4	1.8
Fruits of <i>Alseodaphne semecarpifolia</i>	10	7.8	40	2.6	9.8	2.8
Young leaves of <i>Streblus asper</i>	5	3.9	4	0.3	0.7	0.2
Young leaves of <i>Tamarindus indica</i>	10	7.8	13	0.8	2.9	0.8
Flowers of <i>Tamarindus indica</i>	2	1.6	3	0.2	0.8	0.2
Leaves of <i>Alangium salvifolium</i>	6	4.7	60	3.9	23.1	6.6
Leaves of <i>Mimosa pudica</i>	9	7.0	14	0.9	4.3	1.2

Table II — Comparison of the results obtained with various field methods for the measurement of food intake by one *Semnopithecus entellus*, observed in Sri Lanka, in June, during one day, from 5:30 to 18:30.

Accordingly, to compare the annual variation of food intake by two different species as shown in Figure 1, it was crucial to utilise the quantitative method based on the fresh weight actually ingested. Furthermore, this type of comparison allows one to investigate the energy balance in relation to the food choices and the relative use of various plant parts and plant species, and the chemical composition of these foods. While there is a parallel trend in the seasonal variation of the diet of both primate species due to seasonal availability of fruits and leaves resulting of the monsoon cycle, the computation shows that the two species obtain the major part of their annual diet from a different set of products. *Semnopithecus senex* is the most folivorous at any time of the year and obtain 70% of its annual food intake from the three most common tree species, especially *Adina cordifolia*, whereas *Semnopithecus entellus* eats more fruit and includes ten tree species (including those used by *S. senex*) to make 70% of its annual intake (Hladik, 1981).

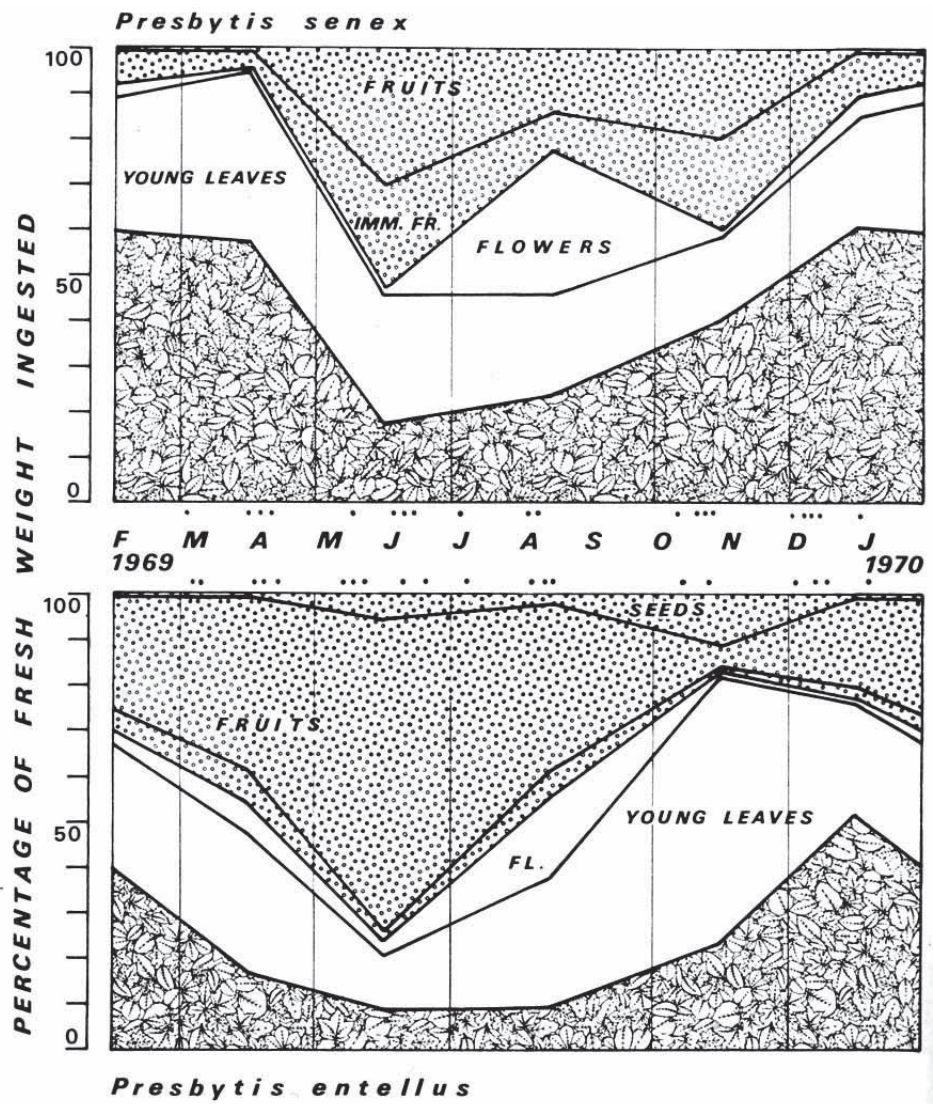
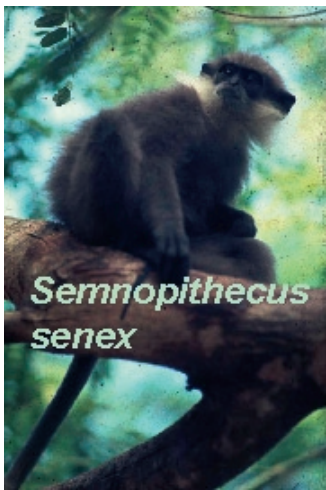


Figure 1 — Comparison of the seasonal variation of food intake of two species of primates, *Semnopithecus senex*, (upper), and *Semnopithecus entellus*, (lower) in their natural forest habitat. Each dot along the time axis represent a full day of continuous observation focused on one species and followed by a day for collecting and preserving food samples. The field technique used allows to compare cumulative percentages of actual weights of various foods ingested (along the vertical axis), which vary throughout the seasonal cycle; nevertheless, at any time, *S. senex* is more folivorous than *S. entellus*. Such a specific difference in food choice, also concerned with the type of food plants, correspond to a difference in energy intake, linked to group size and range size (After Hladik, 1977).

In short, one species (*S. senex*) feeds on the most abundant plant parts that provide a low energy return. This is linked to a strategy of low energy expenses, with small groups of 4 to 7 individuals living in small territories (2 to 7 hectares). The other species (*S. entellus*), which lives in larger groups (including 12 to 25 individuals) in larger territories (10 to 15 hectares) obtain a richer diet by spending more energy on moving and finding plant parts providing more energy, especially sweet fruits. The comparison has also been made with the macaque (*Macaca sinica*) living in the same forest with an even higher investment of energy providing a richer diet; however the comparison of the two species of *Semnopithecus* is particularly interesting to consider as a model, because these two species have a similar body weight, and, finally, with

an energy investment totally different can reach a similar population density by using a quite different strategy of energy balance.

Considering these published results on the primate diet, that are not easy to produce and not very abundant in the current literature, I was recently extremely surprised by the comments of one of the referees of a paper submitted to an international journal by my colleagues, who obtained reliable and complete results on the actual food intake of a lemur species inhabiting a dry forest in the North West of Madagascar. The referee was asking “ but why the standard method (scan sampling) has not been used? ”. In this case, the lemur species is mainly frugivorous, implying that a method based on feeding time (scan sampling) is not at all adequate. Because it does not require as much field work as recording the actual food intake, and statistical comparisons are easier, the most used method of sampling is based on feeding time, and most published studies resulted of the use of this field method. Is this a criterion for considering it as a standard?

Methods for measuring energy expenditure

Recent field methods used in primatology could involve more sophisticated techniques. This is the case of studies on energy expenditure carried on in the south of Madagascar. These studies currently follow the work of Rasamimanana *et al.* (2006) showing that among ringtailed lemurs (*Lemur catta*) the dominance of female is not directly linked to energy expenditure. The energy expenditure of male and female *L. catta* calculated by Rasamimanana has been based on the factorial method, which consists of adding the time spent for various activities affected by a factor representing the level of energy spent (for instance, during walking slowly, or for running) related to body size. Such factors have to be determined for each type of activity (see the review by Pasquet, 2004). Although this requires several tests in the field, the factorial method has been utilised for studies in anthropology allowing comparison of different ethnic groups in Africa (Pasquet and Koppert, 1993).

For the studies on the ringtailed lemurs (*Lemur catta*) and on other lemur species of Madagascar, it was not easy to evaluate the accuracy of the factorial method, since it implies adding a series of estimates of energy expenditure, for species whose metabolism slightly differs from that of other primates. Accordingly, the field study that started in 2006, aiming at an accurate measurement of energy expenses, was based on doubly labelled water (water including the stable isotopes deuterium and oxygen 18), a method which is also used for anthropological studies, but which was rarely utilized in the field, and never for wild lemurs. The animals have to be captured (a syringe with ketamine is thrown with a blowpipe) and doubly labelled water is incorporated into the bloodstream. After a few days (4 days in this case), the animal has to be re-captured for someone to take another sample of its blood.

The technique consists of measuring the turnover of two isotopes: deuterium (^2H) and oxygen 18 (^{18}O) over the period of 4 days in order to estimate the quantity of carbon dioxide produced and thus the energy expended during this period of time. The energy expenditure is calculated according to the difference in the proportions of deuterium and oxygen 18 found in the blood at the start and at the end of such a field experiment. Of course, the analysis of the blood samples in terms of stable isotopes requires the know-how of a specialized laboratory and the cost of such analysis (including that of doubly labelled water) implies a careful planning for studies on non human primates as well as for studies in anthropology.

Diet and energy expenditure in human populations

In fieldwork concerning human diet and energy balance, although the backgrounds where human populations are embedded are as much socioculturally as biologically determined, the environmental and biological conditions involve issues that are partly similar to those that we have to face for primatological studies.

The actual measurement of the food ingested could be extremely precise, although the quantitative method requires an important investment in time by a scientific team and should be carefully prepared in terms of contacts and collaboration with the local population that might eventually consider this type of approach as too much invasive. For instance, in the comparative studies conducted in Cameroon on the Yassa, the Mvae, and the Bakola Pygmies (Koppert *et al.*, 1993), the individual portions were actually weighed, as well as the uneaten remains. The information — concerning food intake of 40 persons in each village and 33 persons in the Pygmy camps — was stored for computation by an iterative process, with a program that was developed by Koppert. This peculiar computation was necessary, because, in several instances, the food was taken from a communal dish (that was weighted), and the expected distribution among the participants has to be calculated. And the results allowed one to compare the seasonal cycle of food intake (Fig. 2) in these various groups utilising different parts of the available food resources, in relation to practices, knowledge, and beliefs.

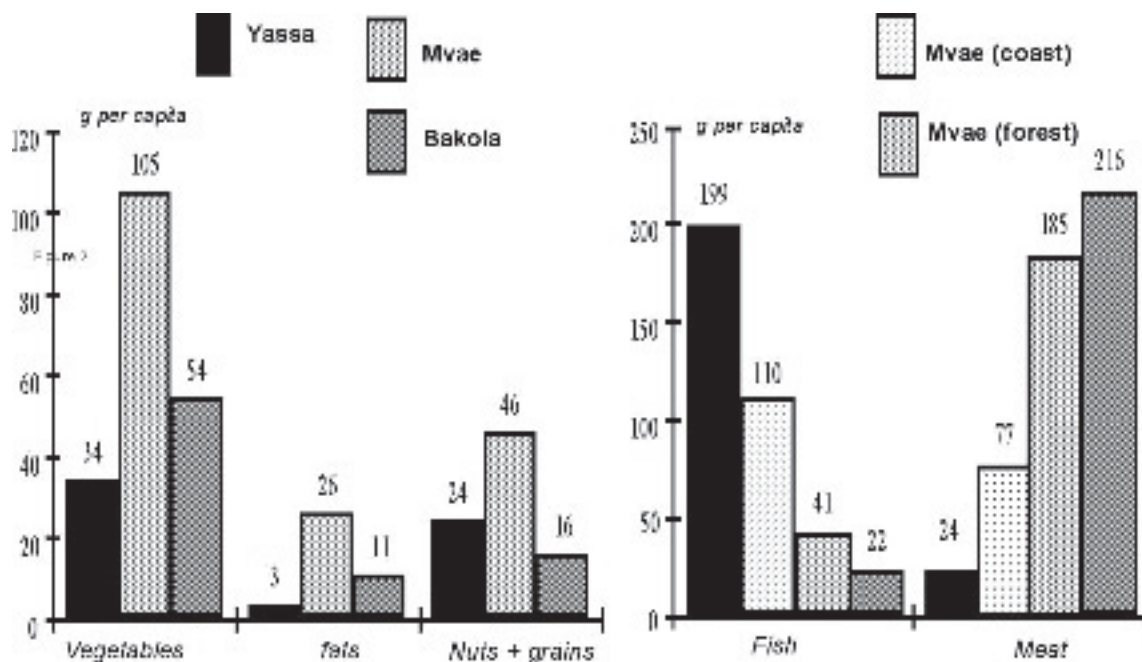


Figure 2 — Relative importance of different food classes in four populations of southern Cameroon, as percentages of the total intake, respectively for vegetable (left) and meat or fish (after Koppert *et al.*, 1993).

Before such field studies, some of the anthropologists of our team, who had previously studied social structures and way of life of the ethnic group, had to spend as much time as necessary to prepare the place where the field work on food anthropology could be undertaken. For instance, in the Cameroonian areas where the above described studies have been carried on, meetings were organised under the

authority of the Chief of the village, to obtain a consensus of the inhabitants, some of whom, in turn, would benefit of temporary paid jobs for participating in the weighing of foods. However, the limit of our inputs in terms of money or other gifts was to avoid interfering with the food system that we were actually measuring. This is a classical issue concerning even the physicists who know that there is a limit when measuring the trajectory of a particle, since the actual system of measurement might change the trajectory. In our case, we had to be sure that most benefits obtained by the villagers from our study were preferentially invested in the roofing or other improvement of their housing, or for children education, etc., rather than for canned food, that was indeed rarely bought and used in the villages where we investigated food anthropology.



Figure 3 — An accurate measurement of the individual food intake in a communal dish. The dish is placed on a precision scale (one gram for 30,000 g) protected in a trunk with a thin PVC sheet and dryer. The operator, whose micro-computer is also protected from humidity, records the weight of each helping for each participant.

The most accurate measurement of individual food consumption in a communal dish might imply wider interference between the system of measurement and what is actually measured. It was carried on during a field study among the Ngbaka of the Central African Republic (Koppert and Hladik, 1990). A fast and precise electronic scale — a material which is currently very common in food shops, but was an expensive device for laboratory at this time — was connected to a micro computer, all these materials being carefully protected against humidity (Fig. 3). As the participants were picking up the food in the communal dish (either the meat dish, or the dish with yam or cassava), each of the event was recorded after an immediate calculation (by the computer) of the difference in weight of the communal dish before and after taking the food. Thus the field assistant obtained, for each participant, the exact weight actually ingested. The shape and duration of the meal is also recorded by this method. Although requiring a total involvement of the participants in the field research and a period of habituation to forget the unusual setting, the results were fruitful in ethnological terms. The communal dish appears as a way to mask the social status of the participants,

since no individual part of the dish is obviously attributed. Whereas the social status generally results as an attribution of a large portion of protein to the adults (especially to the adult males), masking the actual intake of the participants in a communal dish is a way to provide a better share to the children who need a larger portion of protein. Indeed the children actually obtain, in the communal dish, enough protein to cover their nutritional requirements. This social and nutritional function of the communal dish could be verified by such a sophisticated field method. However, this type of exceptional study needs a deep involvement of the participants, who must be sufficiently relaxed to forget the technical context for a while. This was allowed by the network of exchanges and emphatic social links between the team of anthropologists that were established during the years preceding such studies.



Figure 4 — A Douglas bag receiving the exhaled gas during a specific activity (here preparation of manioc) to determine the energy expenditure for calculation of the energy budget, in a village of southern Cameroon.

The results of the actual food intake can be easily converted in terms of energy, using the FAO tables and/or the results of analysis of food samples collected during the field study. Nevertheless, a study of the energy budget also requires measurements of the energy expenses. The techniques for such measurements are very similar to those described above for non-human primates, and again, the factorial method is the one most frequently utilised. In this case the accuracy can be satisfactory, when the energy expense during each type activity is measured. This was performed by recording the production of carbon dioxide during the activities (such as walking, chopping wood with machete, harvesting manioc, etc.) performed by a subject wearing a mask connected to a Douglas bag (Fig. 4), and analysing the carbon content of the exhaled gas (Pasquet and Koppert, 1993).). Again, the technical sophistication of the methodology, that should be partly forgotten by the habituated observed person, necessitates a previous approach by the team of anthropologists, in order to reach a local consensus, with mutual benefits for carrying out the study.

In southern Cameroon, in the different villages where such measurements have been performed (in parallel with the quantitative study of the diet described above), there was a survey of the time allocation conducted on a total of 87 subjects (26 Yassa men and 18 Mvae men, 22 Yassa women and 21 Mvae women). Each subject was followed by a local assistant, to record, minute-by-minute activities. The results allowed one to compare activity levels and patterns on work day, as well as the seasonal variation of the activity levels. Those were, as expected, related to the level of energy intake that was calculated according to seasonal variation of food intake, but large differences have been found between fishermen Yassa and among Mvae, with the women showing significantly higher energy expenses during the major dry season, when most time is devoted to agricultural tasks.

The human energy budget has also been studied with the method of the doubly labelled water, which, in this case, is carefully sipped in a glass by a subject in order to estimate the quantity of carbon dioxide produced and thus the energy expended during a standard period of time. This accurate but expensive method was used in northern Cameroon to study the energy balance during a period of traditional intensive overfeeding, the *Guru Walla* (Pasquet *et al.*, 1992). The aim of this study, that was coupled with a social anthropological approach, was to legitimate the induction of some energy-wasting adaptive process (*luxusconsumption*, or dietary induced thermogenesis) during this extreme case of overfeeding.

Field studies on taste perception and feeding behaviour

Field methodology also shows parallel issues for studies on taste perception among non-human primates and human populations. However, whereas verbal communication allows a simplified approach of what is perceived by *Homo sapiens*, for all other primates, studies of taste perception imply a long period of testing to obtain statistically significant results.

Moreover, most studies on non-human primates have to be carried out under laboratory conditions, in order to provide access to tasting solutions to an isolated animal. The 'two-bottle test' allows one to determine the difference of consumption between two solutions and, after varying the concentrations (a process that can take several months). The taste threshold is the minimum concentration of a solution (for instance of sucrose) which is differentiated from pure water (Simmen *et al.*, 2004).

Field studies on taste perception are thus exceptional in non-human primates. A study on the perception of tannins could be carried out recently on a group of ringtailed lemurs (*Lemur catta*) freely ranging on a large enclosure. In this enclosure, the animals can be followed and the 'two-bottle test' provided in protected boxes giving access to the identified target animal (Simmen *et al.*, 2006). A 'two-bottle test' on free ranging lemurs was also carried on in the south of Madagascar (Simmen, 2004) at the edge of the forest, showing the threshold to acid solution of a young lemur, who later is going to feed on the very acidic pulp around the seeds of the tamarind tree (*Tamarindus indica*).

Interestingly, such measurements of the taste responses correspond to the measurements that, in non-human primates, could have been carried out on the taste nerve. In the most recent research, the recording of the taste responses to solutions in contact with the tongue have been done on isolated nerve fibres (Hellekant and

Danilova, 2004) and, in some instances directly on the neurones of the taste areas of the brain of a macaque (Rolls, 2004).

Nobody could even think of carrying out such investigations on humans; however, a non invasive approach of human taste perception, that is easy to carry on in field conditions, led to parallel conclusions about taste sensitivity (Hladik *et al.*, 2003). A total of 412 subjects were tested in Africa, Asia, and Europe. The test solutions of pure compounds (fructose, sucrose, citric acid, sodium chloride, quinine, tannin, etc.) were tested at random, but starting from the most diluted solutions in series prepared with local drinking water. In such blind tests (Fig. 5), the subject, who has to name, in his/her own language, the quality of the taste, at first perceives the most diluted solution as pure water and can name the taste quality only when the concentration is higher. The lowest concentration correctly named for a given substance is considered as the taste recognition threshold and is among the most important parameters playing a basic role in individual responses to foods.



Figure 5 — Determination of the taste thresholds for various pure compounds in diluted solutions in a village of southern Cameroon.

As for non-human primates, the human taste responses to solutions of pure compounds are not measurements of levels of responses to what has been considered as 'basic tastes' (salty, sweet, bitter, or acid). Such 'basic tastes' are approximate definitions in various languages, but do not correspond to what is shown by the experiments described above, each taste signal (even for a pure compound) involving simultaneously several types of taste fibres. Testing taste sensitivity with various compounds is just a way to investigate the functioning of the whole taste system, especially when comparing the relationships between the responses to various compounds. Such a comparative approach afforded by interdisciplinary field researches was conducted by our team in anthropology and in primatology, led us to consider the former and recent impacts of evolutionary trends on the taste system. It helps to explain the present condition of *Homo sapiens* and the relationships with the cultural parameters that strongly interfere with food preferences and food choices.

A major consequence of natural selection among primates is the dichotomy of the taste system, allowing to discriminate what is potentially harmful (the bitterness of several alkaloids or the astringency of tannins) from what is beneficial and provide energy, especially the various sugars present in the fruit pulp of the angiosperms that evolved in parallel with primates during the Caenozoic (Hladik *et al.*, 2003). These evolutionary trends also explain the possible utilisation of plant secondary compounds that are harmful and efficient for protecting the plant, but useful as 'preventive medicine' when eaten in small amount by the great apes and can avoid the infestation by parasites (Krief *et al.*, 2005). In such cases, this eventually leads towards cognition and social learning.

Finally, the history of humankind has been deeply marked by cooking foods and by the utilisation of salt, the most common food additive used to improve the taste of cooked foods. But why salt and salty taste has such an impact in the collective representations of most civilisations, whereas no selective trend had ever induced salt perception in primates? Since the concentration of sodium chloride is below recognition threshold in natural products (except along the seashore, where exceptionally some wild primates live), the functioning of our taste system is based on the gene pool of most remote ancestors than primates, especially fishes. And this former ability to perceive salt allowed some of our *Homo* ancestors (not necessarily *H. sapiens*) to make a great discovery in improving food taste (Hladik, 2006). The pleasurable utilisation of such improved foods, in the context of social contacts, is certainly at the origin of civilisation.

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