Relationship Between Feeding Time and Food Intake in Hamadryas Baboons (*Papio hamadryas*) and the Value of Feeding Time as Predictor of Food Intake

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The relationship among time spent feeding, number of feeding bouts, feeding bout length, and the amount of food ingested was determined in a study of 18 hamadryas baboons (*Papio hamadryas*) at the German Primate Center (DPZ). There was considerable within- and between-subject variation in all four variables. Feeding time and number of feeding bouts could explain only 30% and 40%, respectively, of the variation in the ingested amount of food. No relationship was found between feeding bout length and amount of food ingested. The reason for these weak relationships is the high within- and between-subject variation in ingestion rate. If the amount of ingested food is estimated by multiplying mean ingestion rates of various subject categories by feeding time, deviations from true amounts range from 8% to 50%. A prediction of feeding success solely by measuring feeding time or number of feeding bouts is therefore not recommended and an estimation of food intake from ingestion rates and feeding time has to be treated with caution. Zoo Biol 18:495–505, 1999. © 1999 Wiley-Liss, Inc.

Key words: *Papio hamadryas*; food intake; feeding time; foraging studies; behavioral methods

INTRODUCTION

Food selection and feeding success of primates and the consequences for their survival and reproduction are the focus of many recent studies [Janson, 1988; Altmann, 1998]. Food distribution in time and space is believed to be a major force that drives the evolution of social systems in primates through different forms and degrees of competition [Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997]. Another aspect is the ecologic role of primates in their habitat as consumers and seed dispersers

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[Chapman, 1995; Garber and Lambert, 1998]. A balanced and optimal feeding is also vital to the captive management of primates. In this case, not only the composition of diets is of importance, but the form of food presentation as well. The distribution of food can have major influence as a mean for tension reduction in groups or for environmental enrichment and well-being [Snowdon, 1989; Reinhardt and Roberts, 1997].

For most questions related to studies on foraging and feeding, the individual food intake (energy or nutrient) is the crucial factor [Altmann, 1998], for example, to compare the foraging success of individuals or to estimate the amount of plant matter consumed in a forest. However, estimation of individual food intake is difficult, because identifying, counting, weighting, and/or measuring of ingested food items creates many practical problems, and the sources of measuring errors are numerous, particularly under natural conditions [Hladik, 1977]. For reasons of practicability and convenience, an approximation to actual food intake is often used, by measuring the time spend feeding. It is obvious that there must be a certain relationship between the time spent feeding and the amount ingested. Yet the magnitude of this relationship is rarely established [Nakagawa, 1997]. In particular, if more than one type of food is used, feeding time is not acceptable as an estimate of the food intake, because feeding rate may differ considerably among food items [Hladik, 1977]. If feeding times of different food types are lumped together, even a negative relationship between feeding time and ingested amount of food or energy may be the result [Koenig et al., 1997]. A systematic inter-specific comparison of the relationship between feeding time of various diet components (percentage of total feeding time) and ingested mass of the same components (percentage of total diet mass) provided by Kurland and Gaulin [1987] revealed a very close relationship between feeding time and ingested mass for one type of food (e.g., leaves). Yet, for other types they found an underestimation of 30% (e.g., fruits) or an overestimation of 600% for animal matter in the diet.

The aim of this study was to analyze the relationship between food intake and other variables that are used to estimate food intake in other studies, e.g., feeding time, number and length of feeding bouts, and ingestion rate. The analysis is based on data of individual food intake and feeding time that were independently collected in a controlled situation, in which only one species (hamadryas baboons) was fed only one food type. The question is, how reliably can we predict feeding success (defined as nutritional or energy intake per feeding session) by simply measuring feeding time, number of feeding bouts, or feeding bout length under such controlled conditions? Furthermore, the consequences of the estimations of food intake by multiplying ingestion rates by feeding time are examined. Results of this study can aid in understanding possible data errors and their impact on food intake of free-ranging primates.

METHODS

The study was conducted at the German Primate Center (DPZ) with a group of 18 hamadryas baboons. The group consisted of two adult males, seven adult females, one sub-adult female, seven juveniles, and one infant organized in two one male units (Table 1). The enclosure included an outdoor area of 170 m2 and an indoor area of 20 m2. Except times when the enclosure was cleaned or the food was distrib-

TABLE 1. Hamadryas baboons of the DPZ and their theoretical energy requirements

Baboon	Age class	Omu	Body mass (kg)	Energy requirement (kJ d^{-1})
M1*	Adu	1	30.5	4,793.9
M2*	Adu	2	32.7	5,050.0
F1*	Adu	1	18.5	3,416.3
F2*	Adu	1	17.5	3,282.1
F3*	Adu	1	15.2	2,965.8
F4*	Adu	1	16.3	3,118.5
F5*	Adu	1	17.0	3,214.3
F6*	Adu	2	18.3	3,389.6
F7*	Adu	2	14.2	2,824.6
M3	Juv	1	6.5	1,678.4
M4	Juv	1	6.4	1,661.0
M5	Juv	1	4.2	1,238.0
M6	Inf	1	1.6	684.9
F8	Subadu	2	13.5	2,607.4
F9	Juv	2	10.3	2,298.3
F10	Juv	1	8.4	1,997.3
F11	Juv	1	7.4	1,832.0
F12	Juv	1	5.5	1,501.2
Group			244.0	47,553.6

M, male; F, female; Omu, member of one-male unit 1 or 2; Adu, >5 years, Subadu, 5 years; Juv, <3 years; Inf, <1 year.
*Included in analysis.

uted, the baboons had free access to all parts of the enclosure. The standard diet for the hamadryas baboons at the DPZ included fruit, vegetables, seeds, and, as the staple food, monkey pellets, a commercial monkey diet (SSNIFF®, Spezialdiäten GmbH, Soest, Germany). They were fed twice a day in the outdoor enclosure and they needed normally 30 to 40 minutes to finish the food. During the study period, however, the baboons were fed only with the monkey pellets to control for differences among food types and to make counting of food intake easier. In a 5-day pilot study, the baboons had time to adapt to the new food composition. Also during this phase, the reliability of the observation methods were tested. The daily energy requirements of the group were calculated to determine the daily amount of food (pellets) they needed.

The daily energy requirements of the baboons were calculated following Altmann's [1998] procedure. The basal metabolic rate was set at 354 $M^{0.75}$ kJ d^{-1} [Hemmingsen, 1960; in Altmann, 1998] where M is body mass in kilograms. Body masses of the baboons were taken during the week before the study started. The baboons were 50% to 80% heavier than free-ranging hamadryas baboons [Kummer, 1968]. The energy requirement for locomotion was estimated as 10.7 $M^{0.684}$ kJ km^{-1} and the average distance traveled by a DPZ baboon in the enclosure was 1.8 km per day [Zinner, 1993]. For juveniles and pregnant females, 21 kJ g^{-1} was added (the amount they gained per day) [Payne and Waterlow, 1971] for growth. The average growth rate was estimated as follows: body mass (grams) minus average body mass at birth (800 g) divided by age (days). Thus, the juvenile and infant baboons experienced an average growth rate of approximately 8.0 g d^{-1}, resulting in an energy requirement for growth of 168 kJ d^{-1}. This was a 70% to 80% higher growth rate than it was reported for free-ranging olive [Nicolson, 1982; in Altmann, 1998] or yellow baboons [Altmann and Alberts, 1987]. The fetal average growth rate was approxi-

mated to calculate the energy requirement for gestation. Body mass at birth (800 g) plus an estimation of 200 g of placental tissues divided by average gestation length of 180 days resulted in 5.6 g d^{-1} for fetal growth, which equals an energy requirement for mothers of at least 116.7 kJ d^{-1}. The daily energy requirement for the entire group was therefore calculated as 47,554 kJ. The pellets had a cylindrical form of 1.0 cm × 2.0 cm and an average mass of 2 ± 0.3 g. Their energy content was 12.4 kJ g^{-1}, which translated into a basic requirement of 3,835 g pellets per day for the 18 baboons. Protein and other nutritional requirements were over-satisfied by this amount. To make sure that all baboons were able to appease their energy requirements, they were offered 6,000 g pellets per day.

The food was distributed equally in one large patch of approximately 80 m^2 in the outdoor enclosure and the baboons were allowed 45 minutes to feed. After 45 minutes, the baboons were locked in the indoor area for some minutes and the pellets, which were not eaten by them, were collected and weighed again. The difference between offer and the residual was the likely amount of food (pellets) eaten by the group.

Eighteen consecutive feeding sessions were observed and the behavior of the entire group was recorded by video to achieve simultaneous behavioral protocols for each adult member of the group. Video tapes were subsequently analyzed second by second. Further details of the data transformation are given in Zinner [1993].

The following variables were measured:

1. Amount of food ingested (grams): Each ingested pellet was counted and the number was multiplied by 2 g. The number of pellets was corrected for the number of pellets that were taken out of pouches and not reingested.
2. Feeding time (seconds): The time spent on manipulation and ingestion of pellets was recorded to the nearest second, including the time when contents of pouches were manipulated and re-ingested.
3. Feeding bout length (seconds): The time from the beginning to the end of a feeding bout was recorded to the nearest second. A feeding bout started when a baboon touched a pellet with its hand or mouth. The bout was terminated when the baboon interrupted manipulation or ingestion of pellets for at least 5 seconds.
4. Number of feeding bouts: The number of feeding bouts as defined above was counted.
5. Ingestion rate (grams s^{-1}): Amount of ingested food (grams) divided by feeding time (seconds) within 45 minutes.

Statistics

The data presented here meet the criteria for parametric tests. For correlation, Pearson's *r*, was used. When necessary, correlation coefficients were averaged after a Fisher *Z*-transformation, and they were compared by using the coefficient of determination *r*^{2} [Martin and Bateson, 1993]. Variances were expressed as coefficients of variance (cv). Inter-individual differences were tested using a one-way analysis of variance (ANOVA), by treating each individual as a group. The magnitude of effect (*rm*) [Friedman, 1968, 1982] for each ANOVA was calculated as follows:

$$r_m = \sqrt{\frac{dfN(F-1)}{dfN(F)+dfD}}$$

where F = F value from ANOVA, dfN = degrees of freedom of the numerator, and dfD = degrees of freedom of the denominator. Correlations and ANOVAs were carried out with the respective modules of STATISTICA® 5.0. The alpha level was set at 0.05 for all analyses.

RESULTS

During the 5-day pilot study, I tested the reliability of the observation method and the resulting calculation of food intake. I compared the difference between food offer (6,000 g per day) and the residual of food after the feeding session with the amount of food calculated from direct observation and counting of ingested pellets. In the 5 days, the mean residual was 1,126.4 g, which corresponds to a likely intake of the group of 4,873.6 ± 153.4 g pellets. In contrast, the average calculated amount determined by direct observation and counting of ingested pellets was 4,962 ± 140.4 g. The deviation between the two methods to determine food intake of the group was only 1.8 ± 0.5%, which showed that the estimation of food intake by direct observation and counting of ingested pellets was highly reliable. Therefore, the slight overestimation of food intake by direct observation was disregarded during the subsequent study period.

During the study period, the group ingested on average 4,053 g pellets per day, i.e., they took 5.7% more than the estimated basic requirement of 3,835 g. Compared with a 4-week period before the study, no significant behavioral changes were observed. Most important, there was no reduction of play behavior in juveniles and infants, which is a first indicator of energy deficiency [Southwick, 1967; Barrett and Dunbar, 1992]. Thus, it is assumed that the overall energy and nutritional intake of the baboons were not diminished by the experimental feeding regime, which was not intended and not expected.

The main feeding parameters of the nine adult hamadryas baboons of the DPZ are given in Table 2. On average, an adult baboon ingested 210.7 g of pellets per 45-minute feeding session. Within each session, they spent 772.0 seconds feeding, which represents 28.6% of the feeding session. The number of feeding bouts was 53.7 and the average bout length was 14.9 seconds. There was considerable within- (17% to 59%) and between-individual (16% to 64%) variation in all parameters.

Because of the substantial within- and between-individual variation, the relationship between the amount of food ingested and the other feeding parameters was also highly variable (Figs. 1–3). The average correlation coefficient (after Fisher Z-transformation) for amount of food ingested by feeding time was 0.55, and for amount ingested by number of feeding bouts it was 0.63. No correlation existed between amount ingested and length of feeding bouts (r = –0.01). In other words, even under this controlled feeding condition, only 30% (12% to 61%) of the variance in food intake was explained by feeding time (Fig. 1) and 40% (17% to 64%) by the number of feeding bouts (Fig. 2).

What could be expected if one uses feeding time or number of feeding bouts instead of amount of food ingested to determine inter-individual differences in feed-

TABLE 2. Food intake and feeding parameters of nine adult hamadryas baboons per 45 minute feeding session

Ind	Intake (g)		Feeding time (s)		No. of bouts		Bout lengths (s)	
	Mean	cv	Mean	cv	Mean	cv	Mean	cv
M1	225.0	0.30	372.9	0.55	31.2	0.45	12.7	0.54
M2	169.2	0.30	189.7	0.42	27.7	0.37	7.1	0.41
F1	172.9	0.26	527.7	0.33	34.4	0.40	17.0	0.41
F2	236.2	0.23	1,054.2	0.20	57.8	0.38	20.4	0.36
F3	244.4	0.34	1,224.3	0.38	80.7	0.45	16.5	0.32
F4	204.2	0.32	889.1	0.44	62.4	0.60	15.9	0.49
F5	255.4	0.24	1,558.7	0.19	75.1	0.43	23.9	0.46
F6	170.7	0.27	523.7	0.27	51.9	0.28	10.2	0.19
F7	218.4	0.17	607.8	0.26	62.4	0.25	10.0	0.23
Total	210.7	0.16	772.0	0.57	53.7	0.35	14.9	0.36

Average food intake (grams of pellets), feeding time (seconds), number of feeding bouts, bout length (seconds), and the respective coefficients of variance (cv) (18 feeding sessions; M, male; F, female; Ind, individual).

ing success? The consequences are demonstrated by a comparison of the magnitudes of effect (*rm*) [Friedman, 1968, 1982] in the following example. The question is, are there differences in feeding success among the nine adult hamadryas baboons? Three one-way ANOVAs were performed with individual as the independent variable and amount of food ingested, feeding time, and number of feeding bouts as dependent variables. The sample size for each individual was 18. The resulting *rm* were compared.

The magnitudes of effect differed among the three ANOVAs (Table 3). In this
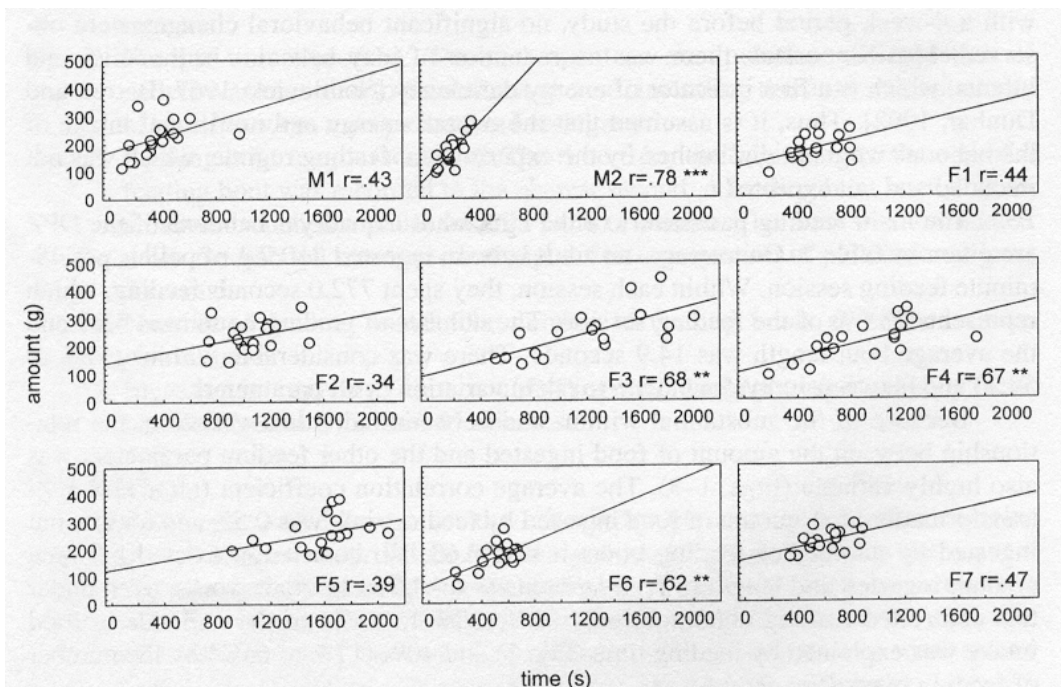

Fig. 1. Amount of food (g) ingested by feeding time (s) for each adult hamadryas baboon (18 feeding sessions; **$P < 0.01$; ***$P < 0.001$).
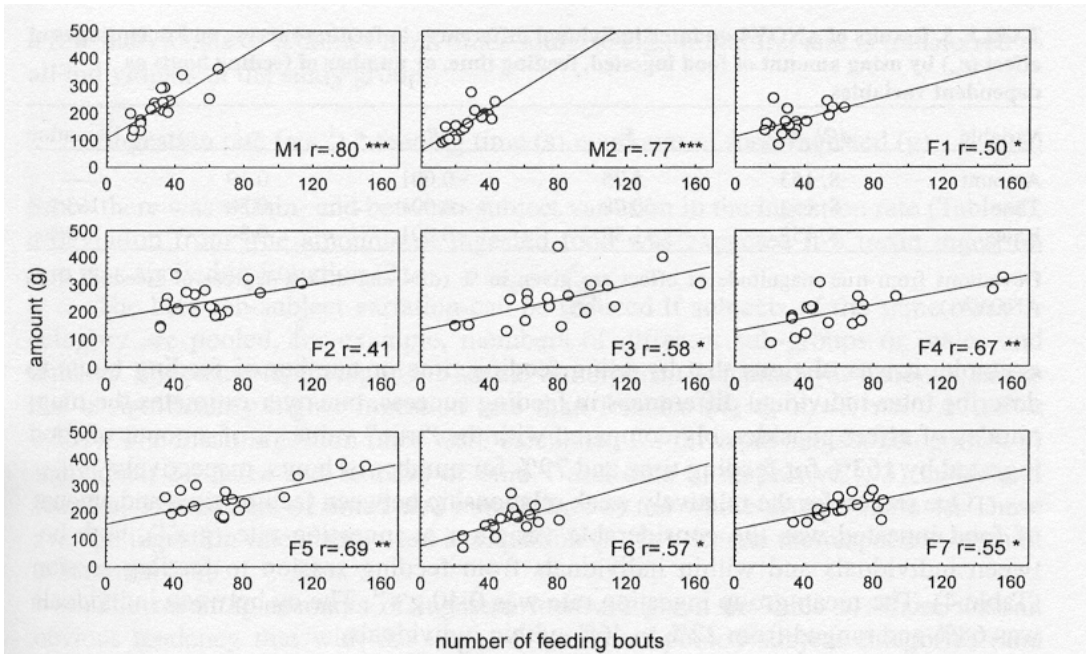
Fig. 2. Amount of food ingested (g) by number of feeding bouts for each adult hamadryas baboon (18 feeding sessions; *P < 0.05. **P < 0.01, ***P < 0.001).
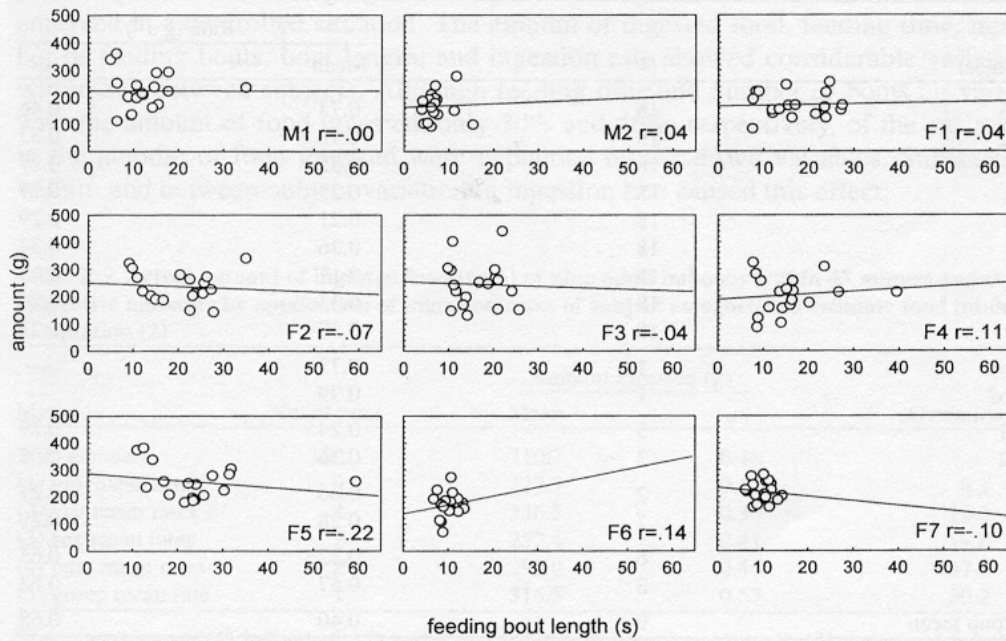

Fig. 3. Amount of food ingested (g) by feeding bout length for each adult hamadryas baboon (18 feeding sessions)

TABLE 3. Results of ANOVA on inter-individual differences in feeding success and magnitudes of effect (r_m) by using amount of food ingested, feeding time, or number of feeding bouts as dependent variables

Variable	dfN, dfD	F	P	r_m^2	Deviation
Amount	8, 153	5.75	<0.001	0.19	—
Time	8, 153	50.78	<0.001	0.50	163%
Bouts	8, 153	11.39	<0.001	0.34	79%

Deviations from true magnitude of effect are given in % (dfN and dfD = degrees of freedom from ANOVAs).

example, it was obvious that by using feeding time or number of feeding bouts to describe inter-individual differences in feeding success, one over-estimates the magnitudes of effect considerably compared with the "true" value *rm* of amount of food ingested by 163% for feeding time and 79% for number of bouts, respectively.

One reason for the relatively weak relationship between feeding time and amount of food ingested was the considerable variation in ingestion rate (g s–1), both between individuals and within individuals from feeding session to feeding session (Table 4). The mean group ingestion rate was 0.40 g s^{-1}. The cv between individuals was 68% and ranged from 22% to 46% within individuals.

If actual food intake cannot be measured precisely or if it is too time- and energy consuming, a frequently used method to get an estimate of food intake is to determine a mean ingestion rate and multiply it by feeding time following Equation (2). The mean ingestion rate is often obtained in a short preliminary study with only

TABLE 4. Ingestion rates (g s^{-1} feeding time) of nine adult hamadryas baboons during 18 feeding sessions with the respective coefficients of variance (cv)

Subject	N	Rate (g s^{-1}) Mean	cv
M1	18	0.73	0.46
M2	18	0.99	0.33
F1	18	0.35	0.27
F2	18	0.23	0.27
F3	18	0.21	0.29
F4	18	0.26	0.34
F5	18	0.17	0.25
F6	18	0.34	0.26
F7	18	0.38	0.22
mo1	1	0.73	—
mo2	1	0.99	—
fo1	5	0.24	0.29
f02	2	0.36	0.08
m	2	0.86	0.21
f	7	0.28	0.29
o1	6	0.32	0.65
o2	3	0.57	0.63
Group mean	9	0.40	0.68

M, male; F, female. Ingestion rates pooled by various subject categories.
mo1, male of omu1; mo2, male of omu2; fo1, females of omu1; fo2, females of omu2; m, males; f, female; o1, members of omu 1; o2, members of omu2.

a few individuals or it comes from other sources, e.g., literature, and is transferred to all individuals of the study group.

$$\text{ingestion rate (g s}^{-1}) * \text{feeding time (s)} = \text{amount of food ingested (g)} \qquad (2)$$

Since there was within- and between-subject variation in the ingestion rate (Table 4), a deviation from true amounts of ingested food was expected if a mean ingestion rate was applied in Equation (2).

The between-subject variation can be reduced if subjects of the same class or category are pooled, for example, members of different sub-groups or males and females. For example, owing to the sexual dimorphism in hamadryas baboons, males had a significantly higher ingestion rate than females ($n_m = 2$, $n_f = 7$; $t = 7.17$; $P < 0.001$). The mean ingestion rates were calculated for different subject categories: 1) individual, 2) males and females of omu 1 and omu 2, respectively, 3) males and females, 4) members of omu1 and omu 2, and 5) the whole group (Table 4). These average ingestion rates were used in Equation (2) to estimate the respective amount of ingested food.

The resulting amounts of ingested food are given in Table 5. There was an obvious tendency that with the larger diversity of pooled subject categories (and smaller number of included ingestion rates), the deviations from true values increase. Depending on the respective applied ingestion rate, the mean amount of ingested food of an adult hamadryas baboon was over-estimated by 8% to 50%.

DISCUSSION

Aspects of the foraging behavior of hamadryas baboons were observed and analyzed in a controlled situation. The amount of ingested food, feeding time, number of feeding bouts, bout length, and ingestion rate showed considerable variation within and between subjects. Although feeding time and number of bouts co-varied with the amount of food ingested, only 30% and 46%, respectively, of the variation in the amount of food ingested were explained by these two variables. Substantial within- and between-subject variation in ingestion rate caused this effect.

TABLE 5. Actual amount of ingested food (true) of nine adult baboons within 45 minues and the respective amounts by application of ingestion rates of subject categories to estimate food intake in equation (2)

Method	No. of rates	Amount ingested (g)		Deviation %
		Mean	cv	
True amounts	162	210.7	0.16	
(1) ind. mean rates	9	227.7	0.16	8.1
(2) s+o mean rates	4	236.5	0.30	12.2
(3) sex mean rates	2	252.4	0.41	19.8
(4) omu mean rates	2	290.0	0.46	37.6
(5) group mean rate	1	316.5	0.57	50.2

The categories are (1) individual, (2) males and females of omu 1 and omu 2, (3) males and females, (4) members of omu1 and omu 2, and (5) the whole group.
No. of rates, number of different ingestion rates that are included in the calculation; deviation (%) from true amount.

If such a relatively weak relationship is found under controlled conditions, with only one standardized food type, it is possible that under field conditions with various food types and restricted observation conditions, the effect of error can be much greater [Hladik, 1977]. One has to be very cautious by estimating foraging success exclusively by feeding time or number of feeding bouts. As shown in the example above, inter-individual differences are likely to be over-estimated. In other studies, an over or under-estimation may be presumably true as well as other effects, for example, seasonal variation or sex differences. Nevertheless, feeding time is a very useful and important variable in other contexts, for example, for the determination of time budgets [Caraco, 1979; Altmann, 1980; Harcourt and Stewart, 1984; Heiduck, 1997].

One possible approximation of the true values of feeding success may be the inclusion of a mean ingestion rate. Multiplying this rate by feeding time would result in an approximation of the amount of food ingested. Yet, ingestion rates also show substantial within- and between-subject variation and even if one is able to determine ingestion rates for some individuals of a group, it is not advisable to transfer these values to the entire group. This analysis shows that using pooled ingestion rates results in significant deviations from true values of food intake. The greater the diversity of pooled subject categories is, the higher is the deviation. Therefore, it is advisable to break down subject categories as much as possible, i.e., the use of mean ingestion rates of males and females or adults and juveniles for an estimation of food intake will yield results that are closer to true values than overall group means.

Although the measurement of feeding time is necessary for specific research questions related to time budgets or time constraints [Dunbar, 1992], the optimal method to estimate feeding success, defined by amount of food ingested, is the direct counting, measuring, or weighing of food items. If food intake has to be estimated by feeding time and a mean ingestion rate, the use of mean ingestion rates of smaller subject categories will provide more reliable results.

CONCLUSIONS

1. In a group of nine adult hamadryas baboons, substantial between- and within subject variation was found the amount of food ingested, feeding time, number of feeding bouts, feeding bout length, and ingestion rate.

2. Feeding time and number of feeding bouts could explain only 30% and 46%, respectively, of the variation in the ingested amount of food.

3. A prediction of feeding success solely by measuring feeding time or number of feeding bouts is not recommended.

4. An estimation of feeding success by multiplying feeding time by mean ingestion rates will provide more reliable results if mean ingestion rates are derived from smaller subject categories, e.g., sex classes, instead of overall group means. Deviations from actual food intake range from 8% to 50% depending on the subject categories.

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