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Food quality, spatial deployment, and the intensity of feeding interference in yellow baboons (*Papio cynocephalus*)

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Summary. Optimization models lead one to predict that the energy invested in competitive interference with feeding should increase as the quality of the contested food increases. This prediction was tested in a study of feeding interruptions involving juvenile yellow baboons (*Papio cynocephalus*) in Amboseli National Park, Kenya. For each of the 50 foods eaten by these young primates, 6 measures of food quality (energy content, protein content, yield, yield rate, processing value, and dispersion) and one measure of the spatial deployment of baboons (number of neighbors) were examined for correlations with 4 measures of the frequency and intensity of interruptions (interruption rate, probability of unsuccessful attempts, probability of appropriation, and probability of agonistic behavior). Disperson of food and the proximity of neighboring baboons had little or no effect on the frequency or intensity of interruptions. Food quality had negligible effects on the probabilities of appropriation and agonistic behavior. Yield characteristics were the best predictors of the success of attempted interruptions: attempts were least likely to be successful when processing the food was time-consuming. These results suggest that (1) the interrupter decides whether to interrupt on the basis of increasing its probability of winning the contest and decreasing its cost, and (2) the victim decides whether to resist on the basis of the time that has been and must be invested in harvesting the contested food item.

Introduction

Interference during foraging, including approach and avoidance, spatial displacement, and fighting, is often interpreted as a manifestation of competition for food (Wilson 1975). The cost of interference of this kind can range from temporary disruption of a feeding bout to severe injury, either to the actor or to the reactor, or to both. Feeding interference is likely to be most frequent and intense among animals, such as some nonhuman primates, that live in permanent social groups. These interactions may be an evolutionary constraint that counters selective forces (e.g., protection from predation) favoring sociality (Bertram 1978; Rubenstein 1978). In some populations, interference with foraging is thought to have far-reaching demographic and ecological consequences (Dittus 1977, 1979; Wrangham 1980). If these contests are competitive interactions over food, then the energy invested in initiating and resisting interference should increase as the quality of the contested food increases. That is, the tendency to interfere or to resist should be proportional to the potential payoff to the winner of the contest (Parker 1974; Maynard Smith 1982).

Yellow baboons (*Papio cynocephalus*) live in permanent multimale, multifemale groups and are highly synchronized social foragers (Altmann and Altmann 1970). Interruptions of the feeding bouts of one individual (the "victim") by another (the "interrupter") are commonly observed. These interactions are sometimes accompanied by agonistic behavior on the part of one or both participants. During a study of feeding interruptions involving juvenile yellow baboons, interrupters that appropriated their victims' food or feeding sites consistently fared worse – not only worse than the optimum predicted on the basis of harvesting characteristics of the food, but also worse than they would have done by finding their own feeding sites without interference (Altmann and Shopland, ms. submitted). In addition, only one-quarter of feeding bouts terminated by interruption were followed

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by appropriation of the victim's food. Together, these results suggest that, for juvenile baboons, interruptions may not primarily reflect competition for a particular food item or feeding site. Instead, they may be (1) agonistic contests used in the establishment and maintenance of rank in an age class undergoing transitions in dominance status, (2) interactions whereby the interrupter increases its relative foraging success by lowering the success of a competitor, or (3) both of these. Interrupters did not appear to be selective with respect to timing; that is, in most cases the timing of interruptions did not differ significantly from a temporal distribution that is independent of the onset of the feeding bout. Are interrupters also nonselective with respect to food quality?

Several studies have addressed the influence of resource quality on the decision to escalate a contest for that resource. Most of these studies have focused on contests for one kind of resource that varies in quantity or quality – e.g., nectar (Ewald 1985), fish of different sizes (Enquist et al. 1985), shellfish in beds of different densities (Goss-Custard et al. 1984), nest sites (Robinson 1985), or web sites (Maynard Smith and Riechert 1984). Little attention has been given to the effects of resource quality on contests between omnivores like baboons, for which decision-making involves assessment of a wide spectrum of plant and animal foods. Here I test the null hypothesis that, for juvenile baboons, the frequency and intensity of feeding interruptions are independent of the quality of the victim's food. I examine both indirect effects, through the spacing of neighbors during foraging, and direct effects of quality on intensity.

Adult baboons, because more experienced, are likely to be more efficient foragers than are juveniles and therefore would be more suitable subjects for a test of optimization models of foraging. My primary goal was not the testing of such models per se, but the determination of the role of interruptions in the socioeconomic world of these young, "upwardly mobile" animals. Optimization models provided one framework for such an investigation.

Methods

Field methods

I observed the foraging behavior of a group of yellow baboons (Alto's Group) in Amboseli National Park, Kenya. Group size ranged from 37 to 46 individuals during the study period, 30 January to 29 August 1980. Amboseli is chiefly a short-grass savanna with several permanent waterholes and interspersed woodlands of *Acacia xanthophloea* and *A. tortilis*. Characteristics of the study area and of the baboon group are described in detail elsewhere (Altmann and Altmann 1970; Western and van Praet 1973; Altmann et al. 1977; Post et al. 1980).

Criteria for feeding and feeding interruptions can be summarized as follows:

1. Feeding bout. Began when the baboon touched the food and ended when the animal had broken contact with the food for 2 s or longer. No feeding bout included more than one food type.

2. Food unit. The smallest unit of a particular food type ordinarily brought to the mouth in a single hand-to-mouth movement.

3. Feeding site. The smallest food-containing area that could be used by a single baboon from one location.

4. Spontaneous. Apparently independent of the behavior of other baboons.

5. Successful interruption. The termination of the victim's feeding bout in response to (1) the approach of the interrupter, (2) the appropriation by the interrupter, with or without accompanying agonistic behavior, of the victim's food item or feeding site, or (3) the aggressive behavior of the interrupter toward the victim without subsequent appropriation of the food. Agonistic behavior (aggressive and submissive acts) was scored as defined by Hausfater (1975). Spatial displacements of baboons not engaged in feeding bouts were not scored as interruptions.

6. Unsuccessful attempt at interruption. An interaction in which one baboon directed aggression at or attempted to appropriate the food of another, without a subsequent take-over.

Observations were made on foot at a distance of 3 to 10 m from the focal individual. I chose 12 baboons (1 subadult, 2 adolescent, and 3 juvenile males; 3 adolescent and 3 juvenile females) at random as focal animals; for simplicity, I refer to these subjects as "juveniles" throughout. I watched one focal individual per sample day. A juvenile was considered "in sight" as long as I could see each food item as it was eaten. I gathered two kinds of samples of foraging behavior:

1. 876 *focal-animal samples* (Altmann 1974) of 20 min each (total of 15,124 min in sight), one sample being conducted each hour from 0700 h to 1800 h with the exception of the 1200 h. On a MORE event recorder (Observational Systems, Inc.), I recorded two types of samples on alternating sample days. In one, the focal animal was observed continuously throughout the sample. In the other, I switched observation to the interrupter if it appropriated the focal animal's food; when the interrupter's bout ended, I resumed observation of the focal animal. At the onset of each feeding bout, I recorded the time, initiation type (spontaneous or by interruption; if by interruption, with or without aggressive and submissive behavior), the identity of the victim (if applicable), and the food type. During the bout I noted the time at which each food unit disappeared into the mouth and the beginning and ending times of any intervals in which the subject was out of sight. At the end of the bout, I recorded the time, termination type (spontaneous or by interruption, with or without agonistic behavior and appropriation), and the identity of the interrupter (if applicable).

2. 175 *nearest-neighbor samples* of 10 min each (total of 1750 min in sight), conducted between focal-animal samples on one-third of sample days. Intervals were timed with a stopwatch; data were recorded on prepared checksheets. Each sample consisted of 11 point samples, at 1-min intervals, in which I recorded the following information on the focal animal: (1)

Table 1. Summary statistics for variables of food quality, spatial deployment, and interruption intensity

Category	Variable	Mean	S.D.	Range	*N*	Transformation used
Food quality	Energy content (kJ/100 g)	626.6	412.6	184 – 1454	33	None
	Protein content (g/100 g)	7.6	5.3	1.2 – 20.8	34	Log
	Yield (food units)	5.1	5.1	1.0 – 32.7	50	Log
	Yield rate (food units/min)	0.3	0.2	0 – 1.2	50	Log
	Dispersion	1.6	0.6	1 – 3	50	None
	Processing value	1.6	2.5	−2.1 – 11.0	50	Square root
Spatial deployment	Number of neighbors	4.7	2.8	0 – 11	40	None
Interruption intensity	Interruption rate (no./100 min)	14.5	13.7	0 – 69.5	50	Square root
	Probability of unsuccessful attempts	0.09	0.13	0 – 0.47	43	Arcsine
	Probability of appropriation	0.45	0.33	0 – 1.00	43	Arcsine
	Probability of agonistic behavior	0.27	0.26	0 – 1.00	43	Arcsine

identity of and distance to nearest neighbor, (2) number of baboons within a 5-m radius, (3) activity state (feeding or not feeding), and (4) food type (if applicable).

Data analysis

The data collected in focal-animal and nearest-neighbor samples were sorted by food type. Of 63 identifiable foods used by baboons during samples, 13 were eaten during fewer than 10 bouts each (all focal animals pooled); these were dropped from the analysis. For each of the remaining 50 foods, I calculated values for the following variables:

A. Food quality

1. Energy content. kJ/100 g wet mass (Appendix).

2. Protein content. g protein/100 g wet mass (obtained from Altmann et al. 1987).

3. Yield. Mean number of food units eaten during a spontaneously terminated bout.

4. Yield rate. Mean number of food units consumed per min in a spontaneously terminated bout.

5. Processing value. A measure of the length of time required to process the food (Appendix).

6. Dispersion. A score of 1 if the food was clumped, 2 if it was more or less uniformly distributed, and 3 if it could not be classified as clumped or uniform. Class 3 foods were dropped from the analysis. A food was considered clumped if it was distributed in patches that could accommodate several baboons but not the whole group, and within which the density of food units was high (e.g., mats of the prostrate herb *Trianthema ceratosepala*). A food was scored as uniformly distributed if it occurred in large stands that could accommodate the entire baboon group without crowding; the density of food units within the stand could be high or low (e.g., high–green grass blades on the plains during the wet season, low–seeds scattered on the ground in *Acacia tortilis* woodland). The use of the number of baboons accommodated was an objective rule of thumb that reflected a preliminary judgment of clumping by eye.

B. Spatial deployment

1. Number of neighbors. Mean number of baboons within a 5-m radius of the focal individual.

C. Interruption intensity

1. Interruption rate. Number of attempted interruptions per 100 min when the focal animal was in sight and feeding on that food.

2. Probability of unsuccessful attempts. The proportion of all attempted interruptions that were unsuccessful.

3. Probability of appropriation. The proportion of all successful interruptions in which the interrupter appropriated the victim's food.

4. Probability of agonistic behavior. The proportion of all successful interruptions in which interrupter, victim, or both showed agonistic behavior.

The values of each of these 11 variables for the 50 foods are available on request from the author. Values that were not normally distributed were transformed as noted in Table 1.

Results

Ranges of and relationships among food characteristics

The foods eaten by juvenile baboons incorporated a wide range of plant and animal parts, including seeds, fruits, flowers, gums, leaves, and underground portions of plants, dung, insects, and vertebrate flesh. As one would expect from the dietary diversity of these young omnivores, the range of values for the six measures of food quality is great (Table 1). Similarly, values for variables of spatial deployment and interruption intensity exhibit a wide range (Table 1). This large spread of values should be ideal for detecting correlations between quality and intensity variables. It should be noted, however, that missing values (from lack of proxi-

Table 2. Coefficients of correlation among quality, spatial, and intensity variables

	Interruption rate	Probability of unsuccessful attempts	Probability of appropriation	Probability of agonistic behavior	Number of neighbors
Energy content	−0.20	−0.10	0.26	−0.34	0.04
Protein content	−0.27	−0.11	0.21	−0.32	−0.08
Yield	−0.13	−0.28	0.07	0.03	−0.08
Yield rate	−0.20	−0.58***	−0.13	0.06	−0.16
Processing value	0.10	0.35*	−0.04	−0.13	0.18
Number of neighbors	0.16	−0.09	−0.17	−0.23	–

Transformed values used to calculate Pearson correlation coefficients; * $P<0.05$; *** $P<0.001$

mate analyses, etc.) reduce the sample sizes for some pairwise and most multiple correlations.

No strong correlations among variables of interruption intensity were found. In contrast, some significant correlations among food quality variables existed. Not surprisingly, energy content was significantly correlated with protein content ($r=0.62$, $P<0.001$), and yield, yield rate, and processing value were all intercorrelated ($r=0.5$–0.7, $P<0.001$). These correlations suggested the use of multiple regression to distinguish the separate contributions (if any) of each quality variable to predicting the intensity variables (see below).

Dispersion

Because dispersion was scored as a categorical, not a continuous, variable, it was treated separately from all other quality variables. Using a *t*-test on transformed values, I first tested the null hypothesis that the mean number of neighbors was the same for clumped and uniformly distributed foods. Then I tested similar null hypotheses of equality of means for each of the variables of interruption intensity.

The mean number of baboons within 5 m of a focal juvenile did not differ significantly between clumped and uniform foods. That is, on the scale studied here, dispersion of food appeared to have no effect on dispersion of baboons. Likewise, clumping of food was not associated with significantly higher frequencies of successful interruptions, unsuccessful attempts, appropriation, or agonistic behavior.

Number of neighbors

To examine the relationship of variables of spatial deployment with those of food quality and of interruption intensity, I calculated Pearson correlation coefficients for pairs of variables (Table 2). Significance tests showed no significant correlations of number of neighbors with quality or intensity variables. Spatial deployment of baboons appeared to have no effect on the frequency or intensity of interruptions, and vice versa.

Nutritional value and yield characteristics

For each pair of quality and intensity variables, I computed the Pearson correlation coefficient, as above (Table 2). Food quality had no detectable effect on the rate at which interruptions were attempted or the probability that a take-over would occur. Interruptions tended to result in agonistic behavior less often when the victim fed on foods of high energy and protein content, although this tendency did not reach statistical significance. The most striking correlations involved yield characteristics. The probability of unsuccessful attempts showed a strong negative correlation with yield rate and a weaker positive correlation with processing value. These results suggest that interrupters are more likely to encounter successful resistance from their intended victims when the latter are feeding on hard-to-process foods, i.e., those with a low yield rate.

Yield characteristics have thus far been defined in terms of food units. For 18 of the foods included in the analysis above, conversion factors of g/food unit were available (S. Altmann in prep.). Fifteen of these foods were corms and green leaves of grasses and sedges, a group of foods on which interruption rates were especially high. For these 15 species-parts I calculated yields and yield rates in mass and in energy and then performed the same correlation analysis as above.

Neither the total yield per bout (kJ) nor the yield rate (kJ/min) in energy had a significant effect on any measure of the frequency and intensity of interruptions. In contrast, attempted interruptions were more likely to fail for grasses with a low yield rate in g/min ($r=-0.59$, $P<0.05$). This result conforms with the results for yield rate in food units

Table 3. Results of multiple regression analysis

Dependent variable	Independent variables[a]						r^2	F	DF	P	Significant regression coefficients[b]
	EC	PC	YD	YR	PV	NN					
	x	x	x	x	x	x	0.16	0.51	6,16	NS	None
Interruption rate			x	x	x	x	0.20	1.84	4,30	NS	None
	x	x					0.07	0.90	2,23	NS	None
			x	x	x		0.17	2.74	3,39	NS	YR: −2.18*
Probability of	x	x	x	x	x	x	0.45	2.21	6,16	NS	YR: −0.99*
unsuccessful			x	x	x	x	0.43	5.74	4,30	**	YR: −0.62**
attempts	x	x					0.01	0.15	2,23	NS	None
			x	x	x		0.35	7.11	3,39	***	YR: −0.62**
Probability of	x	x	x	x	x	x	0.36	1.51	6,16	NS	None
appropriation			x	x	x	x	0.10	0.80	4,30	NS	None
	x	x					0.07	0.90	2,23	NS	None
			x	x	x		0.07	0.96	3,39	NS	None
Probability of	x	x	x	x	x	x	0.30	1.16	6,16	NS	None
agonistic			x	x	x	x	0.07	0.56	4,30	NS	None
behavior	x	x					0.14	1.94	2,23	NS	None
			x	x	x		0.02	0.24	3,39	NS	None

Transformed values used

[a] EC = energy content, PC = protein content, YD = yield, YR = yield rate, PV = processing value, NN = number of neighbors

[b] Independent variables for which the regression coefficient differs significantly from zero; $*P<0.05$; $**P<0.01$

when all 50 foods were included; it supports the conclusion that, to victims, processing time is more important than energy harvest.

Multiple regression of intensity on quality and spatial variables

To separate the contributions of individual variables of quality and spacing to the prediction of intensity variables, I used multiple regression (BMDP 1983 procedure 6R). A stepwise technique would have included in the analysis only cases without missing values. Instead, I selected 4 subsets of independent variables, for which a minimum of 18 and a maximum of 42 cases could be included. Then I performed a regression of each dependent variable (i.e., measures of interruption intensity) on each subset of independent variables. This procedure had some of the qualities of stepwise regression in that it examined the relative contribution of each variable as a predictor; at the same time it retained the information in cases with missing values. The subsets of independent variables were as follows:

1. Nutritional value (energy content, protein content), yield characteristics (yield, yield rate, processing value), and spatial deployment (number of neighbors);
2. Yield characteristics and spatial deployment only;
3. Nutritional value only; and
4. Yield characteristics only.

The results of this regression analysis are given in Table 3.

For the most part, the regression analysis supports the conclusions drawn from the correlation analysis: (1) the number of neighboring baboons has little or no effect on the frequency or intensity of interruptions; (2) food quality is a poor predictor of probabilities of appropriation and of agonistic behavior; and (3) yield rate is a good predictor of the probability that attempted interruptions will be unsuccessful. Yield rate also has a weak negative effect on the rate at which interruptions are attempted.

Discussion

Each interruption is the product of decisions by two individuals. The interrupter must decide whether to initiate the contest, whom to interrupt, whether to escalate if it encounters resistance, and whether to take over the food. The victim must decide whether to resist or to yield, and how long and how energetically to resist if it meets with escalation from the interrupter. To what extent does the quality of the potential victim's food influence these decisions? The results reported above indicate that the component of quality most likely to affect decision-making is the rate at which the food can be harvested. The nutritional value and dispersion of the food appear to have negligible effects, as does the number of potential interrupters or victims close by. Apparently, the decisions to at-

tempt or to resist an interruption are more likely to be influenced by food quality than are the decisions to escalate, appropriate, or prolong resistance. The correlation and regression analyses presented above suggest the following interpretation: the interrupter's decision is based on criteria qualitatively different from those used by the victim; nevertheless, the decisions of the contestants are not independent.

The victim's decision appears to be based on the value of time. Because baboons are omnivores, they consume parts of many plants with well-developed adaptations against herbivory; circumventing these adaptations often requires long handling times (Hamilton et al. 1978). Moreover, groups often undertake long day-journeys (Altmann and Altmann 1970). In order to keep up with the group, a foraging baboon constantly takes the risk of having to terminate its feeding bout as the group moves on. Also, time spent on foraging cannot be used for other activities, such as grooming, mate guarding, and resting, that may contribute directly or indirectly to survival and reproductive success. For these reasons, the time devoted to processing a food item can be regarded as an investment.

A contest between owner and challenger is usually weighted in favor of the owner (Parker 1974; Maynard Smith and Riechert 1984). Part of this "property advantage" may be independent of the value of the contested object (Sigg and Falett 1985); nevertheless, the victim's time investment in a food item or patch probably contributes to this asymmetry in resource-holding potential (Parker 1974). The more time required to process a food that the victim has begun to harvest, the more likely the baboon should be to resist an interruption successfully.

The availability of alternative food sources has been shown to increase the tendency to withdraw from feeding interference (e.g., Berkson and Schusterman 1964; Parker 1974). A baboon group is ordinarily on the move throughout the day, and its food resources are patchy on a large scale (Post 1982). Therefore, at any particular moment the alternative food items available to a victim are likely to be only of the same food type. If the food is easily processed, the victim should be more prone to abandon it to the interrupter and to begin on a new item or site. If, however, the food is difficult to process, giving it up will force the victim to repeat prolonged handling on another item.

Interrupters appeared to interfere with their victims, not to gain a food item, but to maintain dominance status or to decrease the foraging success of a competitor (Altmann and Shopland, ms. submitted). The latter is accomplished both by causing the victim to lose its food and by depleting its time resources (Jones 1983). If interruptions are dominance contents, a baboon should be most likely to initiate interference if its probability of winning the contest is high. Juvenile baboons most frequently intervene in fights or form agonistic alliances when they are likely to win (Cheney 1977; Walters 1980); the same may be true for initiating interruptions. Baboons may determine (either through learning or through an expectation based on their own experience with harvesting times) that they will probably encounter resistance from victims feeding on hard-to-process foods; they should avoid trying to interrupt these individuals. Alternatively, if interruptions are mechanisms by which an interrupter raises its relative foraging success by lowering that of the victim, the interrupter will receive the highest net benefit when its own cost (i.e., the probability of having to invest energy in aggression) is low. Again, the foods with lowest cost will be those associated with a low probability of resistance from the victim, that is, those that can be processed relatively quickly.

In the above interpretation of interruption sequences, the concept of decision points (Enquist et al. 1985), or transitions between the owner's and the challenger's behavior, may be useful. Food quality chiefly affects decision points early in the sequence. The victim makes its decision on the basis of the time it must invest and has invested in its food. The interrupter assesses its probability of success, which is partially determined by the victim's decision. The interrupter's assessment may follow either from trial-and-error learning of the relative processing values of foods and consequent probabilities of success, or from subtle behavioral signals from the victim that indicate its willingness to risk possible aggression by resisting. The low average probability of unsuccessful attempts (0.09, Table 1) suggests that interrupters are fairly competent at making these assessments.

Unexpectedly, the frequency and intensity of interruptions were independent of the dispersion of food and competitors. In an observational study of wild brown hares *Lepus europaeus* (Monaghan and Metcalfe 1985) and in an experimental study of captive rhesus macaques *Macaca mulatta* (Southwick 1967), clumping of food led to an increased frequency of agonistic behavior and appropriation of food by interruption. In foraging groups of oystercatchers *Haematopus ostralegus* (Vines 1980; Goss-Custard et al. 1984), mallards *Anas platyrhynchos* (Harper 1982), and Japanese macaques *Macaca fuscata* (Furuichi 1983), the lo-

cal density of conspecifics affected or was affected by interruption rates.

The interpretations presented here require a few caveats. Because this study was observational and not experimental, I could not control several variables, in particular hunger and relative dominance status, that may influence asymmetries between contestants. Hunger has been shown to raise levels of both aggressive feeding interference and resistance to it (Berkson and Schusterman 1964; Southwick 1967; Wasserman and Cruikshank 1983; Ewald 1985). A relatively high-ranking victim may be less likely to receive aggression from the interrupter than is a lower-ranking one (Dittus 1977; Post et al. 1980; but see Janson 1985). The effect of dominance status on interruptions is now under investigation for these same juveniles. Limitations on the focus of this study also call for cautious interpretation of the results. First, I did not consider the quality of the food with respect to nutrients other than protein. Moreover, all analyses were based on the *intrinsic* value of the food type, not on the actual value of a particular food item. Second, data were collected only on interruptions involving at least one juvenile; the results may not necessarily apply to feeding interference among adult baboons. For example, the energetic and, possibly, hormonal stress caused by interruptions may be relatively more severe for pregnant or lactating females than for juveniles.

The evolution of female-bonded groups of primates, such as baboons, may be the consequence of competition among adult females for high-quality foraging patches containing a limited number of feeding sites (Wrangham 1980). Among young yellow baboons, however, feeding interruptions do not appear to reflect this kind of competition. Rather, these interactions seem to be a form of pure interference, or of competition for social status, which, once consolidated, may translate into energetic gains at later stages of maturation (e.g., Whitten 1983). Whether interruptions confer such gains on adult baboons remains to be seen.

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Appendix

Energy content =
[3.40(g protein/g wet mass) + 8.37(g lipid/g wet mass)
+ 3.92(g carbohydrate/g wet mass)]/0.239 kJ/100 g

Formula from S. Altmann (pers. comm.); proximate analyses from Altmann et al. (1987).

$$\text{Processing value} = \text{mean}\left[\left(\frac{\Sigma t_i}{n} - t_0\right) - \frac{t_\omega - t_0}{2}\right],$$

where t_0 = time at which spontaneously initiated bout begins, t_ω = time at which spontaneously initiated bout ends, t_i = time at which the ith food unit in the bout is consumed, and n = number of food units consumed in bout. High positive values indicate hard-to-process foods.

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