Still More on Predatory Behavior in Nonhuman Primates

by Geza Teleki

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Though I agree with much that Washburn and Ciochon (1974) have to say about common causes of controversy among anthropologists, their claim that scientists who arrive at opposing conclusions have access to the same information is not entirely convincing—not, at least, in the arena of current debate about the frequency (Gaulin and Kurland 1976), the normality (Reynolds 1975), and the evolutionary significance (Burton 1975) of chimpanzee predatory behavior. To be sure, the information provided in an original source is “the same,” and even the access may in most cases be “the same”; but accuracy of citation is altogether another matter. The misunderstanding caused by what Washburn and Ciochon (1974:765) view as “culturally determined scientific tradition” is often nothing less, in my experience, than inaccurate citation of someone else’s observations. I refer in this particular instance to De Pelham and Burton’s comments on primate predation (CA 17:512–13). My reports on chimpanzee predatory behavior (Teleki 1973b, b, 1975) do not contain what has been attributed to me by De Pelham and Burton. I urge those interested in their hypothesis about the proximate causes of chimpanzee predatory behavior in Gombe National Park, Tanzania, to check their use of data against the original source material.

The logic whereby De Pelham and Burton delineate and explicate the complicated issue of potential relationships between chimpanzee predation and banana provisioning is to be commended. There would be more to commend, however, and to employ in theoretical models if their logical presentation had been founded upon an accurate portrayal of the original field observations. De Pelham and Burton begin by contrasting the following pieces of information:

1. “It is significant that Goodall’s (1963) first reports of vertebrate meat-eating noted only three episodes in two years.”
2. “In 1968–69, 30 episodes of predatory behaviour were observed (Teleki 1973a): all of these took place within 150 yards of the banana-feeding area.”

Having set up this rate dichotomy, they proceed to seek a linkage between banana eating and mammal eating on the grounds that both increased between 1961–62 and 1968–69. They arrive at the following conclusion: “We are suggesting that predation at Gombe may be in large part attributed, not to the context of artificial feeding, but to the chemical imbalance imposed by this mineral overload in the food provided.”

So it might have been if Gombe chimpanzees had actually increased their predatory rate from 3 to 30 kills over the eight years that they were heavily provisioned with bananas. There is, to my knowledge, no evidence that such an increase occurred. On the contrary, evidence is presented in my monograph (Teleki 1973a:52–59) that the number of mammals killed by the Gombe study population does not vary much from year to year, with or without banana provisioning.

Given the large amount of information produced since 1962 on the predatory habits of Gombe chimpanzees, Goodall’s early report can hardly be considered more than a preliminary statement. Goodall herself provided much additional information in a later monograph (Van Lawick-Goodall 1968), containing other kinds of evidence (fecal analysis, carcass transportation, etc.) showing that annual predation frequencies were higher than 3 cases even before banana provisioning became commonplace in 1966–67. These data, together with other previously unpublished information drawn from the Gombe files, were summarized in my monograph, in which I conservatively estimated that the local chimpanzee community killed about 10 mammals per annum throughout the 1960–70 study period (using a base figure of 95 known kills and some incidental evidence). In the same monograph I pointed out the many difficulties involved in estimating predation rates and repeatedly cautioned readers not to rely on the figures until better data became available.

Only one conspicuous change was positively documented for the final years of the 1960–70 study period: the chimpanzees emphasized one specific prey species, baboons, in lieu of the five other species routinely exploited. This shift in prey selection was particularly marked during 1968–69 and can probably be attributed, as stated in my monograph (Teleki 1973a:107–8), to the banana-provisioning procedure. This does not, as far as I can see, constitute evidence for major fluctuations in predation rates. In the absence of solid evidence for a rate increase between 1961–62 and 1968–69, the entire hypothesis proposed by De Pelham and Burton becomes a moot affair.

Two additional inaccuracies require attention. By referring to 30 episodes without drawing a distinction between successful kills and attempted kills, De Pelham and Burton give readers the impression that I observed 30 successful kills in a 12-month span. The fact is that I recorded only 12 kills between March 1968 and March 1969. As stated in the monograph (p. 107), “the 12 kills recorded in 1968–69 are in reasonable accord with the general average of 10 kills per year for the decade.” I can therefore see no reason to speculate about the nutritional causes of a large rate increase wrought by “chemical imbalances” imposed by a “mineral overload.” Indeed, if attempted kills and successful kills had been noted with equal rigor during every year of the decade, the “three episodes in two years” become even less representative of an annual predation rate. Calculations of predatory success rates from such variable data are especially unreliable, however, as I point out in the monograph (p. 53), because “observation at Gombe has not always been continuous, because staffing fluctuates yearly, and because unsuccessful predation is less likely to be noticed consistently.”

Why, then, do De Pelham and Burton disregard all my qualifying statements about the reliability of the numerical data and even fail to distinguish between kill numbers and episode numbers?

The only graceful way out of the false dichotomy presented by De Pelham and Burton would be to argue for a caus
linkage between banana eating and baboon eating, these being the only phenomena for which rate increases are documented (Wrangham 1974, Teleki 1973a). I leave it to my colleagues to determine what, if any, “chemical imbalances” are compensated for when Gombe chimpanzees overindulge in baboon meat—as opposed to colobus monkey, blue monkey, redtail monkey, bushpig, and bushbuck meat.

The second error concerns the claim that all 30 episodes were logged within 150 yards of the provisioning station. The relevant sentence in my monograph (p. 55) reads: “All of the 30 observed episodes occurred in the lower portion of Kakonde Valley, most within 150 yards of the feeding area.” The terms “all” and “most” are not synonymous in the monograph, where I also note that additional predatory events had occurred outside the valley but were not included in the sample of 30 because behavioral data were incomplete. This may in fact be a rather minor point, but does serve to illustrate how original data can be misrepresented so as to stack the hypothesis deck in favor of preferred conclusions.

The risks involved in applying simple causal models to complex dietary situations have been discussed elsewhere (Strum 1976). Suffice it to note here that De Pelham and Burton’s reference to a nutritional study by Hladik and Viroben (1974), who are cited because they postulate some similarities in the diets of chimpanzees in Gabon and Tanzania (i.e., Gombe), can be questioned on the grounds that the Gabon study involved only five chimpanzees who were reintroduced, from captivity, to an island sanctuary on the Ivindo River. Chimpanzee dietary habits are not similar everywhere in equatorial Africa (Teleki 1974; see also Baldwin and Teleki 1973), and the results of a short study on rehabilitated chimpanzees are not necessarily representative of the species.

I would therefore urge those who seek biochemical (De Pelham and Burton) or bioenergetic (Gaulin and Kurland 1976) solutions to the predation propensities of Gombe chimpanzees to be more cautious, both in the use of field data and in the generation of extrabehavioral dietary models. The effects of banana provisioning upon behavioral, social, nutritional, medical, and demographic parameters among the Gombe chimpanzees have also been discussed elsewhere (Teleki 1973a; Wrangham 1974, 1975; Teleki, Hunt, and Pfifferling n.d.), and it is entirely probable that predatory behavior is one among many chimpanzee traits affected by this research technique. Solutions to these problems are not speeded along, however, when the field data are considered malleable.

Reply

by Alison de Pelham and Frances D. Burton

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If Teleki finds his own data so “variable,” why then is he secure about his “average” of 10 per annum, based not only on observed kills (46) but on “incidental evidence,” while criticizing us for lumping the data for observed kills and observed attempts? (or predatory behaviour?) Presumably, if the monograph was published, it was for the purpose of instruction, and with the hope that others might utilize the material. While Teleki correctly criticizes us for saying that all of the 30 predatory episodes occurred within 150 yards of the banana-feeding area, he neglects our qualifying comment a little farther on, “Since the majority of predatory episodes occurred in the context of banana feeding, . . .”

He objects to our utilization of Hladik and Viroben’s (1974) study of western chimpanzees on the basis that the subjects were “rehabilitated” animals and suggests that we should have known better than to cite such incomparable material. The single line in that study which describes the group states: “La constitution d’un groupe de chimpanzés due à l’initiative du Pr. Grassé (Mission Biologique au Gabon, à partir de 1963) nous a permis d’entreprendre, en 1970–1971, une étude quantitative du régime alimentaire dans le milieu naturel.” We understand this to mean “The establishment of a group of chimpanzees, initiated by Professor Grassé (Biological Mission in Gabon since 1963), permitted us to undertake, during 1970–1971, a quantitative study of diet in the natural environment” (we have purposely kept the translation literal). Either research is to be limited to original research, or we may continue to utilize data as it is published. Those who have particular expertise in a field undoubtedly will be closer to the original sources and undoubtedly will have knowledge not reflected in publications. Researchers who utilize published material must rely on its validity.

Our substantive issue with Teleki is twofold: it concerns biochemical influence on behaviour (banana eating) and whether or not there was an increase of predatory behaviour in conjunction with banana feeding. He states (1973:109): “Since eating bananas is not known to stimulate an urge for meat, it would seem reasonable to assume that predatory behavior has more functions than those of nutrition.” The first part of this statement we contest outright; the data cited in our paper suggest the contrary. The second part of the statement is indisputable; almost any behaviour of higher primates has more than one function, or cause. Teleki (1973) notes that 19 cases of killing after bananas were fed happened after one hour and that some initiators had eaten more than 20 (p. 109); thus 19 cases out of 21 in the study period were clearly associated with high consumption of bananas, and the kills occurred within a short time after consumption.

The second point at issue is whether or not there has been an increase in meat eating (and predatory behaviour) among chimpanzees. We accept Teleki’s caveat (p. 109), “The simple fact that more episodes of unsuccessful predation were observed in the 1968–1969 period than at any other time during the decade probably indicates that observer experience and efficiency does play a significant role in the general picture.” Data on predation offered by Van Lawick-Goodall and by Teleki are shown in table 1. Teleki’s estimate of an average yearly kill rate of 10 is based on “95 kills recorded in 10 years” (p. 57), although he states that only 46 were observed (p. 53). For the period 1968–70, he notes 21 observed kills; adding this to Van Lawick-Goodall’s 28 for the period 1960–67 yields a total of 49 for the decade. Combining Van Lawick-Goodall’s data on fecal remains and remains brought into the study area with the observed kills would produce a yearly rate of 11, as compared with Teleki’s 8. Counting all successful kills (including fecal remains, etc.) and all attempts, the annual rate is 13 for 1960–67 and 18 for 1968–70. Table 2 records the data on kills in relation to banana provisioning in this period. Goodall’s data show a rate of 1.5 kills per annum before banana feeding and 4.2 with

**TABLE 1**

<table>
<thead>
<tr>
<th>Study Period</th>
<th>Observed Kills</th>
<th>Observed Attempts</th>
<th>Fecal Remains</th>
<th>Remains Brought in</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960–67</td>
<td>28 (4)</td>
<td>14 (2)</td>
<td>38</td>
<td>11</td>
<td>91 (13)</td>
</tr>
<tr>
<td>1968–70</td>
<td>21 (8)</td>
<td>23 (9)</td>
<td>11</td>
<td>44</td>
<td>14 (18)</td>
</tr>
</tbody>
</table>


Note: Teleki does not give information on fecal remains and remains brought into the study area. Van Lawick-Goodall’s data on these points are included here, although there is some doubt as to whether all such remains were actual kills and as to whether some of them duplicated observed kills. Figures in parentheses are the annual rates implied by the figures to the left.

108 CURRENT ANTHROPOLOGY
banana feeding, an almost threefold increase. On the basis of Teleki's data, we obtain a rate of 12 kills per year with bananas and 6 per year without, an apparent twofold increase in the presence of banana feeding. Attempted kills with banana feeding, according to Teleki, amounted to 18 per year, while without banana feeding the annual rate was 3.3. Evaluating observed kills, attempts, or their sums (table 1), there is clearly a trend toward increase in rate of predatory behaviour in association with banana eating (table 2). Teleki notes (pp. 54-55) that the decrease in observed kills between the first 12 months and the last 18 months of the study period "was perhaps connected with the feeding reduction initiated in June 1968... and less consistent observation... by the lower chimpanzee attendance rate that accompanied the reduction of banana distribution."

While "a comparison of kill rates in the periods shows that banana feeding probably affected the type of prey captured more than the yearly rate of predation" (p. 55), we think it significant that in the study period, during banana feeding, 10 of the kills occurred so soon after huge consumption; this suggests that the baboons were prey of choice because they were close by. Yearly rates do not reflect the acceleration-deceleration associated with banana feeding and reduction. Under provisioning with seven banana days a week, the predation observed between mid-March and mid-June of 1968 totalled 14 cases in 3 months (p. 107). After reduction to one or two banana days every two weeks, the incidence dropped to 5 cases in 5 months (p. 107). When it rose again, between mid-November and mid-March, the incidence was 11 cases in 4 months, or 2.8 per month. In our paper we said (p. 512), "The fact that predation rises again after a plateau in provisioning has been reached may be attributed to habit, or to renewed sensitivity to lower thresholds of intake." The speculation that something in bananas influences such predatory behaviour was new only in its application to the Gombe chimpanzees. As Teleki suggests, it is perforce a "null" point and must remain so until detailed physiological studies can refute or support the hypothesis. We insisted, and maintain in accordance with Strum (1976), that the phenomenon is complex and its explanations must be multiple.

The suggestion of biochemical influence is not a particularly new approach, and we need not cite here the enormous volume of, for example, nutritional data (vitamins, enzymes, stress, allergies) that have been documented. The nature of science, we need not inform our colleagues, is to proceed with hypotheses that are not "true," but disprovable. If the speculation has heuristic value in suggesting complicated sociobiological processes rather than simplistic recourse to aggression, etc., it will have served its purpose.

### Table 2

<table>
<thead>
<tr>
<th>Study Period</th>
<th>Observed Kills</th>
<th>Observed Attempts*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960–61, no bananas (Goodall 1963)</td>
<td>3 (1.5)</td>
<td>–</td>
</tr>
<tr>
<td>1962–67, bananas (Van Lawick-Goodall 1968)</td>
<td>25 (4.2)</td>
<td>–</td>
</tr>
<tr>
<td>March 1968–March 1969, bananas (Teleki 1973)</td>
<td>12 (12.0)</td>
<td>18 (18.0)</td>
</tr>
<tr>
<td>March 1969–August 1970, no bananas (Teleki 1973)</td>
<td>9 (6.0)</td>
<td>5 (3.3)</td>
</tr>
</tbody>
</table>

Note: Figures in parentheses are the annual rates implied by the figures to the left.

*Attempts by period are not available for the Goodall and Van Lawick-Goodall data.

### References Cited


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### On Symbolic Interpretation

By Gerard F. Kennedy

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Jarvie (CA 17:687–91) has created something akin to the Batesonian metalegix which begins, according to my recollection, "Daddy, why do things get in a muddle?" (Bateson 1972). Jarvie’s essay is a conversation between himself and Leach. The alleged objective of the conversation is to consider the limits of symbolic interpretation in anthropology, but the conversation, it turns out, is limited to the anthropology of Leach. I finished the metalegix with the distinct feeling that there are indeed limits to symbolic interpretation, especially when one limits discussion to one anthropologist, or, to put it more exactly, to one's interpretation of one anthropologist. Hence, in keeping with Bateson’s definition of a metalegix, the conversation is itself engineered and structured in such a way that it reveals something about the nature of the problem being discussed. The limits here being discussed are not the limits of anthropology, but the limits of Jarvie’s and Leach’s perspectives on virgin birth, grace before meals, “Eeeny, meany, miny min,“ etc.

Jarvie chooses Leach as the object of his criticism because in his estimation “Leach’s work makes argument not just worthwhile, but possible.” Leach is thus proposed as the exemplar scholar in this field, and all others are dismissed with what