Primate Predation and Bioenergetics

Strum (*1*) explains the high frequency of predation by baboons as the result of social tradition. We suggest that ecology, and bioenergetic considerations in particular, are fundamental in determining whether such behavior can arise and be maintained.

Merely to ascribe a high frequency of a particular behavior to the existence of a local tradition does not elucidate its ultimate causes regardless of the proximate mechanisms that spread or maintain the behavior in the population. Moreover, unless the spread of a behavioral trait is attributable to particular diffusion mechanisms, the concept of tradition is completely uninformative. Indeed, given appropriate environmental conditions, the appearance of facultative adaptive responses (*2*) may follow a similar time course: the adaptation appearing in first one, and later more individuals.

Growth, maintenance, and reproduction all require energy intake. Those individuals most efficient at energy capture (other things being equal) will be the fittest by making either more time or more energy (or both) available for reproduction and predator avoidance; natural selection will optimize feeding strategy. Thus, an animal is expected to include in its diet those food items with the highest net energy yield per unit handling time (*3*). But for any animal, the energetic cost of handling some potential food items will be too high to permit their use regardless of gross nutritive value. The cost of handling some such items may cease to be prohibitive if the net energy yield of other food items (the bioenergetic base) is increased. In theory, populations within a species can be placed along a continuum with respect to their members' ability to exploit items with high handling costs. At one end of this continuum are populations whose members are unable to meet minimum maintenance requirements; at the other extreme are populations that, as a result of provisioning or exploitation of domesticated foods, have an artificially expanded bioenergetic base.

A food item is optimal when its net energetic yield per unit time is maximal. And an optimal diet is one in which the organism's energetic requirements (for some unspecified time period) are met by the inclusion of only those optimal food items. The spatial distribution of food items, both density and dispersion (that is, patchiness), is translated by the mobile predator into its temporal pattern of prey encounter. Hence the frequency of any item included in the diet will be proportional to its relative density in the predator's habitat (*3*). That the baboons at Gilgil (*1*), and, for that matter, the chimpanzees at the Gombe National Park (*4*, *5*), prey on other animals can be understood in terms of the altered bioenergetic base of these populations. The high frequency of their predatory behavior is a function of the altered spatial distribution of acceptable prey.

Baboons spend most of the day foraging in open country, and their movements are restricted by the distribution of water (*6*). Otherwise suitable forage patches cannot be exploited if too distant from water sources. The study site at Gilgil is a cattle ranch, and the owners have altered the habitat to this end (*7*). By introducing permanent standing water and by eliminating lelechuet scrub, the ranchers have in effect increased the available forage area (patch size) and decreased interpatch distance. The concomitant reduction in the time and energy costs of travel between forage patches results in higher foraging efficiency for the resident baboons.

Because large carnivores have been systematically shot and trapped out, the Gilgil baboons encounter suitable animal prey at a higher than normal rate. Moreover, since the rate of predation on baboons themselves has diminished, time and energy allocated for predator avoidance are proportionately reduced. Finally, the baboons are released from the interference aspects (*8*) of interspecific competition with other predators.

The fact that adult males take more and larger prety and were the first to exhibit predatory behavior may also have a bioenergetic basis. In addition to having a mechanical advantage, larger animals are energetically more efficient than smaller ones. For example, Taylor *et al.* (*9*) have shown that the minimum cost of running, measured in oxygen consumption (milliliters per gram-kilometer), decreases with increasing body weight. Hence, a small increase in the bioenergetic base will more readily allow a larger individual (at Gilgil, adult male baboons) to exploit items with high handling costs (such as ungulates). In contrast to adult males, smaller animals (females and juveniles) will have higher ratios of handling cost to energy input and hence smaller optimal and maximal prey sizes.

Table 1. Summary of the stepwise multiple regression. The dependent variable is the percentage of animal food in the diet in each month; β is the normalized regression coefficient.

Weighted dietary contribution (D') of:	Multiple r	β
Open *Uapaca* forest	.410	–0.716
Riverine thicket	.531	1.546
Open *Pericopsis* forest	.566	–6.798
Riverine *Syzygium* forest	.857	6.530
Open *Monotes* forest	.869	0.325
Riverine *Vitex* forest	.888	–0.275
Riverine *Cordia* forest	.896	–0.145

We predict that a stable equilibrium in the frequency of predation will be reached as interference competition with conspecifics progressively negates the benefits gained in taking animal prey.

The arguments presented above are theoretical and necessarily formulated in the absence of certain relevant information. Nevertheless, they are testable given data on baboon time budgets and the biomass of baboons, their predators, competitors, and potential prey at Gilgil and other study sites.

The unusually high frequency of chimpanzee predation at the Gombe National Park (*5*, *10–12*) can be understood in similar terms. Provisioning of the chimpanzees with bananas had made their predatory behavior energetically feasible. Baboons, also attracted to the bananas, were brought into close proximity with chimpanzees and became the preferred prey (*5*).

Suzuki's report on chimpanzee ecology at the Kasakati Basin in Tanzania (*12*) contains some data sufficient for a preliminary evaluation of the bioenergetic hypothesis. As predicted, meat-eating in this natural habitat is infrequent; thus, our sample size is small and results of the statistical analysis are only suggestive. These data are analyzed by means of a stepwise multiple regression technique (*13*) in which the dependent variable is percentage of animal food in the diet and the independent variables are of the form:

$$D'_j = \frac{D_j}{\left(H_j / \sum_{i=1}^{n} H_i \right)}$$

where H_j is the size of the jth habitat in square kilometers, D_j is the percentage of food obtained in the jth habitat as estimated from fecal analyses, and H_j contributes to ΣH_i if and only if the associated $D_j \neq 0$. The sample consists of 15 cases, each representing a monthly pattern of foraging. Each independent variable, D'_j, represents the percentage contribution to the diet of a particular habitat type, in a given month, corrected for the relative size of that habitat. Thus the values of D' approximate foraging efficiency in any month. Table 1 presents a summary of the multiple regression. More than 80 percent of the variance in the amount of animal prey taken is explained by the variance in D' ($F = 4.09$; d.f. = 7, 7; $.01 < P < .05$). In addition, Suzuki (*10*), in reporting the few cases of predation by chimpanzees at the Budango Forest, states that this behavior did not occur when food was scarce.

Since the recent emphasis on the significance of hunting in human evolution (*14*), various objections have been raised (*15*). Lee's answer to his own question, "What do hunters do for a living?" is, "They gather" (*16*). Nevertheless, if there is validity in a carnivore model for hominid evolution (*17*), it is essential to separate convergent adaptation from fortuitous similarity. In baboons, chimpanzees, and perhaps Pleistocene hominids, meat contributes to the diet. The ecological factors that lead to predation in extant nonhuman primate populations are, however, quite different from those postulated as having altered the diet of early hominids. In the case of living primates, an expanded bioenergetic base may make the utilization of animal food possible; in contrast, our hominid ancestors are never characterized as having exploited an enriched habitat (*18*). Unlike the Gilgil baboons, early hominids would not have been free from interspecific competition with carnivores (*19*). Minimization of interference competition between hominids and contemporary carnivores (presumably nocturnal and crepuscular forms) could have been achieved if the former occupied a midday hunting niche. However, exploitative competition is not thereby reduced. Finally, Pleistocene hominids were themselves subject to predation (*20*) with concomitant demands on their time and energy.

We are understandably preoccupied with the evolution of our own species. The study of living primates may provide insight into the selective pressures operating on our ancestors in that they can serve as models for the reconstruction of hominid behavior. However, this is only informative when the biological mechanisms underlying the behavior of living forms are understood. The importance of bioenergetics and feeding strategy to adaptation should not be ignored.

STEVEN J. C. GAULIN
JEFFREY A. KURLAND*
Department of Anthropology,
Harvard University,
Cambridge, Massachusetts 02138

References and Notes

1. S. C. Strum, *Science* **187**, 755 (1975).
2. G. Underwood, *Evolution* **8**, 365 (1954); P. B. Medawar, *New Biol.* **11**, 10 (1951).
3. T. W. Schoener, *Annu. Rev. Ecol. Syst.* **2**, 369 (1971). We intend a more general meaning for the terms "handling time" and "handling cost" than that employed by Schoener. Under "handling" we subsume the pursuit, subduing, and processing of food items.
4. J. Goodall, *Anim. Behav. Monogr.* **1**, 161 (1968); J. van Lawick-Goodall, *In the Shadow of Man* (Houghton Mifflin, Boston, 1971).
5. G. Teleki, *The Predatory Behavior of Wild Chimpanzees* (Bucknell Univ. Press, Lewisburg, Pa., 1973); *Sci. Am.* **228**, 32 (January 1973).
6. S. A. Altmann, *Baboon Ecology: African Field Research* (Univ. of Chicago Press, Chicago, 1970).
7. R. S. O. Harding, *Am. J. Phys. Anthropol.* **38**, 587 (1973).
8. R. S. Miller, *Brookhaven Symp. Biol.* **22**, 63 (1969). Direct interaction between competitors, for example, aggressive encounters, is termed interference competition; indirect effects, for example, the reduction of a common resource, is termed exploitative competition.
9. C. R. Taylor, K. Schmidt-Nielsen, J. L. Raab, *Am. J. Physiol.* **219**, 1104 (1970).
10. A. Suzuki, *J. Anthropol. Soc. Nippon* **79**, 30 (1971).

→ T. Nishida, *Primates* **9**, 167 (1968); V. Reynolds and F. Reynolds, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rhinehart & Winston, New York, 1965), pp. 368–424.

→ A. Suzuki, *Primates* **10**, 103 (1969).

13. N. Nie, D. Bent, C. H. Hull, *Statistical Package for the Social Sciences* (McGraw-Hill, New York, 1970).
14. For example, I. DeVore and S. L. Washburn, in *African Ecology and Human Evolution*, F. C. Howell and F. Bourliere, Eds. (Aldine, Chicago 1963), pp. 335–367; S. L. Washburn and C. S. Lancaster, in *Man the Hunter*, R. B. Lee and I. DeVore, Eds. (Aldine, Chicago, 1968), pp. 293–303.
15. C. J. Jolly, *Man* **5**, 1 (1970); W. G. Kinzey, *Am. Anthropol.* **76**, 680 (1971); B. Kurten, *Not from the Apes* (Random House, New York, 1972).
16. R. B. Lee, in *Man the Hunter*, R. B. Lee and I. DeVore, Eds. (Aldine, Chicago, 1968), pp. 30–48; R. B. Lee, *Natl. Mus. Can.* **230**, 73 (1969).

→ G. B. Schaller and G. R. Lowther, *Southwest. J. Anthropol.* **25**, 307 (1969).

18. Descriptions of the paleoecology: G. Bond, in *African Ecology and Human Evolution*, F. C. Howell and F. Bourliere, Eds. (Aldine, Chicago, 1963), pp. 308–334; B. Campbell, *Human Evolution* (Aldine, Chicago, 1974); G. J. H. McCall, B. H. Baker, J. Walsh, in *Background to Evolution in Africa*, W. W. Bishop and J. D. Clark, Eds. (Univ. of Chicago Press, Chicago, 1967), pp. 191–220.
19. The carnivore fauna of Plio-Pleistocene Africa is discussed by R. F. Ewer [in *Background to Evolution in Africa*, W. W. Bishop and J. D. Clark, Eds. (Univ. of Chicago Press, Chicago, 1967), p. 109]; L. S. B. Leakey [in *ibid.*, pp. 7–29; *Olduvai Gorge 1951–1961, I* (Cambridge Univ. Press, Cambridge, England, 1965)].

→ C. K. Brain, *S. Afr. Archaeol. Bull.* **24**, 170 (1969).

21. After this comment was submitted, V. Reynolds [*Man* **10**, 123 (1975)] offered a parallel critique questioning the relevance of predation by the Gombe chimpanzees for the reconstruction of early hominid behavior. We thank C. Gaulin, R. Kurland, A. Santa Luca, J. Szlanski, A. Walker, the referees of this comment, and, in particular, I. DeVore for comments on an earlier draft; J. Sodergren for statistical advice; and S. Strum for helpful criticism. Order of authorship was determined by a best-of-seven squash match (4-3).

* Present address: Department of Anthropology, Pennsylvania State University, University Park 16802

31 March 1975; revised 9 September 1975

I agree with Gaulin and Kurland that "the importance of bioenergetics and feeding strategy to adaptation should not be ignored." Elsewhere (*1–5*), primate predation at Gilgil, Amboseli, and Gombe has been treated in greater depth within a social and ecological framework.

Gaulin and Kurland see a problem with my use of the word "tradition" (*6*). I did not reify the concept of tradition by making it into a causal mechanism. Nor do I believe that the descriptive meaning of the term, as I have used it, is in any way inconsistent with its usage in the anthropological and ethological literature (*7, 8*). Wilson's recent definition (*9*) is illustrative:

> The ultimate refinement in environmental tracking is tradition, the creation of specific forms of behavior that are passed from generation to generation by learning. . . . It can be initiated, or altered, by a single successful individual. It can spread quickly, sometimes in less than one generation, through an entire society, or population. . . .

My report was a brief, interim description of changes in predatory behavior by the Gilgil baboons and some of the social factors involved. Definable mechanisms of diffusion do indeed exist. These are in the form of specific social relationships between individuals in the troop, which are the basis for observational and imitative learning, and greatly influence an individual's opportunities to participate in predatory behavior. Some characteristics of these relationships facilitate the propagation of a new behavior, such as predation, while other aspects place limitations on the degree and course of behavioral elaboration (*1*).

Processes of social facilitation and imitative and observational learning have been described for many species (*9, 10*), for baboons in differing habitats (*11, 12*), and for this particular troop (*1*). Given the above, I find "tradition" a useful descriptive term when applied to baboon predation at Gilgil.

On the other hand, I have some difficulty with the ambiguity of Gaulin and Kurland's use of the term "facultative adaptive response." If they use it descriptively, then they are simply substituting one term for another, neither more nor less informative.

If they are classifying the phenomenon as that type of adaptation which can change, as opposed to a "fixed" adaptation where behavior is obligatory (*13*), then several questions still remain. How and why did the behavior occur in the first individual? In successive individuals? Why do some individuals of the same age and sex class adopt the new behavior and not others? What influences the rate of acquisition or change? What influences its differential expression in groups of the same species under similar conditions (*1, 8*)?

It may be that Gaulin and Kurland are proposing an alternative hypothesis—that every baboon has the innate potential to engage in predatory behavior, with genetically variable thresholds. If this is the case, each baboon independently adopts predatory behavior and, in addition, there is a random order of occurrence within the population which is independent of an animal's relationship to others. This would, as they claim, produce the same time course as the one I described: the behavior appearing first in one and then in several individuals. However, since I have data on observational and imitative learning influencing changes in an individual's predatory behavior (*1*), and since the pattern of change in the group as a whole does not appear to be random with reference to the behavior of others, I think we must treat this alternative view as having minimal explanatory value.

While I agree with the need for an ecological framework within which to evaluate primate predation (*1*), there are, nonetheless, difficulties with the arguments and model presented by Gaulin and Kurland. Most ecologists agree that optimization is likely a real phenomenon; few agree on just how it operates or at what level (the individual, population, or species). If at the individual level, is it simply energy maximization, or does it involve nutrient complementarity, use of time, fitness strategies involving intraspecific interference, and so forth (*14–17*)? Optimization at higher levels, involving coevolution (*18*), interspecies interference competition (*15*), or group selection (*16*) may work against individual optimization, for example, making predators responsible (prudent) in their energy acquisition.

Higher level models of optimization of course subsume more variables and so approach closer to "reality." But these complex models are more difficult to construct and to analyze mathematically (*19*).

Simple energy models (*14*) are the easiest to use but, for the most part, are based on Gaulin and Kurland's assumption: "all other things being equal." Even ignoring the above-mentioned difficulties, there is still a problem with such an assumption when a system is in a nonequilibrium state (as is the case with Gilgil baboons).

In considering the application of Gaulin and Kurland's model to baboon predation, perhaps the most telling difficulties arise when we contrast predation by baboons at Amboseli and Gilgil.

Amboseli, in recent years, has suffered high mortality of its predominant vegetation as a result of a rise in the water table (*20*). During this habitat deterioration the plant community has been transformed from a hydrophytic to a xeromorphic form. This is a habitat in which baboon populations should not practice predation, according to Gaulin and Kurland. Also, Amboseli still has a full and abundant complement of natural predators which provides conditions of interspecific "interference competition" and requires time and energy for predator avoidance by baboons. Hence, Amboseli has conditions of food scarcity, or low bioenergetic base, interference competition, and predation on baboons. Contrary to expectations, Amboseli baboons do practice predatory behavior on species similar to those at Gilgil and in essentially the same form (*1, 2, 12*). Comparison of normalized predatory rates between Amboseli and Gilgil sites during 1970 to 1972 reveals that rates were similar (*2*) although habitat conditions were radically different.

Strict application of simple bioenergetic models contrasts with current suggestions that specific nutrients or toxins, rather than proteins or calories, are limiting factors or important determinants of foraging strategies in general and predatory behavior in particular (*2, 14, 21*). Hausfater (*2*), for example, suggests that baboon predation at Amboseli may reflect the need for vitamin B_{12} since the temporal patterning of predatory rate fits a lognormal model of vitamin deficiency. In this way, as Schoener states (*14*), "The need for a balanced diet may also affect selectivity, sometimes causing items with greatest caloric yield to be underselected. . . ."

Slatkin and Hausfater's (*22*) comparison of time budgets of solitary and group-living males at Amboseli indicates that immediate social factors also influence foraging decisions and durations. They suggest that discussion of items such as resource patchiness must take into consideration "social variables" for group-living species.

At Gilgil I documented changes in predatory patterns between two study periods (*1, 23*). Habitat modification occurred before both studies, and rainfall, foraging patterns, and prey density were essentially similar (*24*). Widespread participation, extended hunting, elaborate strategies, food sharing, and the like were not present earlier but were present or developed during the second study period. How does one account for this within the bioenergetic model that is being proposed, or for the existing variation in prey species profiles between different troops that share the same habitat with extensive home range overlap?

The argument about the relationship of prey size to predator size—in this case, differences in prey selection by adult males and other baboons—requires the demonstration of a threshold for prey size and handling costs. This must be followed by evidence that the threshold falls between the boundary limits for adult males and other baboons. While the running efficiency of animals of differing sizes may be representative of a class of important variables, it does not constitute a demonstration of either the existence of a threshold or its discriminating function.

Furthermore, sexual dimorphism in baboons and its relationship to bioenergetics is still controversial (*25*), and the interaction between predator size and foraging strategies has been argued in several directions (*14*). In fact, females and juveniles at Gilgil do take large prey such as young Thomson's gazelles. The limitation does not appear to be the size of the prey, but age- and sex-related patterns of social interaction and foraging, which restrict movement away from the troop by females and immatures (*1*). Prey size is of greater consequence in determining the range of prey which baboons can take than in predicting whether the baboon predator will be male or female (*1*).

Gaulin and Kurland predict that a "stable equilibrium in the frequency of predation" will be reached as the result of interference competition among conspecifics. At Gilgil, other processes may be instrumental in affecting the stability of the predatory rate before interference competition can be operative.

Some of the initial success of baboon predators at Gilgil may have resulted from the previously "peaceful" relations between baboons and their prey. As predation increased, effective strategies and concerted hunting behavior also increased. Frequently hunted ungulate herds responded with increased wariness, greater flight distance, and protective maneuvers. Thus, approach and capture became more difficult for a baboon predator, which negated the previous advantage gained by improved hunting skills. In this manner, a feedback system is established which resets the parameters of the predator-prey interaction (*1*).

Individual participation scores for male baboons fluctuate over time (*1*). These shifts are intimately tied to a male's social relationship with other males and his sexual relationship with estrus females occurring outside of a predatory context. For male baboons, social and sexual interactions take precedence over predatory behavior. As a result, perturbations within the social system are reflected in the overall amount of predation by the troop (*1*).

Discussion of data on chimpanzee predation is better left to others (*3–5, 26*). I will simply mention that once provisioning stopped at Gombe, predation by chimpanzees continued at the same rate. The rate of chimpanzee predation on baboons has been linked to the provisioning procedure (*3, 4*). As expected, without provisioning there was a shift in prey preference from baboons to colobus, which reflected changes in the frequency of contact between the different primate species.

During the peak period of provisioning, 19 of the 30 predatory episodes described by Teleki (*3*) occurred immediately after the chimpanzees had eaten large quantities of bananas. At best, this timing of predatory events might be explained in terms of nutrient complementarity needs, if single-factor explanations are required. On the bases of dry-weight analysis of chimpanzee foods at Gombe, Wrangham (*4*) found that bananas rank low both nutritionally and in terms of protein. He also suggests a link between disease and provisioning due to several factors, among them protein deficiency resulting from extensive banana feeding (*3*). Teleki correlates demographic trends in the Gombe population with provisioning schedules. Highest mortality and lowest natality appear at times of greatest provisioning (*27*).

The nature of chimpanzee predation has been explained by Wrangham (*4*) in terms of ecological factors such as opportunities presented by specific spatial configurations of the environment, and in terms of differential "vulnerability" of the prey species. Wrangham points to the nutritional, but not caloric (that is, energy), importance of chimpanzee predation, while Teleki (*3, 5*) emphasizes its social function.

The construction and interpretation of Gaulin and Kurland's multiple regression is also somewhat misleading. They did not use all of Suzuki's data on foraging and habitats (*28*). The basis of their selection, and its possible bias, remains unstated and unexamined. Furthermore, their use of "habitat" is confusing for they use it to refer to the entire Kasakati Basin when they are arguing one point, and then they use it to refer to portions within the basin when they are making another point. In fact, all of the habitats in table 1 in their comment are from the same area.

The prediction that "meat-eating in this natural habitat [meaning all of Kasakati] is infrequent" is not tested by the multiple regression that they perform. The regression describes the variance for meat-eating using habitats within the study "habitat."

The prediction that the variance in animal prey taken is explicable in terms of differences in foraging efficiency (habitats within the Kasakati "habitat") would be better tested by including all of Suzuki's data or by a data base that contained more than two cases of predation.

It is not the case that their regression demonstrates either the relationship between low bioenergetic yield and low predation or the relationship between foraging efficiency and the frequency of meat-eating. Since good data exist from other study sites with which to test these hypotheses, it is curious that Gaulin and Kurland should choose these particular data.

In summary, the bioenergetic considerations put forward by Gaulin and Kurland do not alone provide enough information to help predict the course of baboon predation at Gilgil or elsewhere. Primate predation cannot be linked simply to (i) expansion of the bioenergetic base of a population, (ii) absence of interference competition, and (iii) absence of predation on the primate predator.

While ecological variables are necessary and important in the development of primate predation (although the exact relationship is yet to be determined), social and individual variables are also of immediate importance (*1*), in this as in other cases of behavioral variation and innovation (*8, 26*). Not all ecological opportunities can be exploited. For social animals, existing social systems represent "preadaptations" for certain types of exploitative opportunities and obstacles for others. Furthermore, within social systems, certain classes of individuals are "preadapted" for new behaviors while others are not (*1*).

The fit between predatory behavior and a lognormal model that Hausfater (*2*) found for Amboseli baboons indicates, regardless of the vitamin B_{12} arguments, that several factors are acting multiplicatively with respect to each other and in relationship to environmental factors in determining predatory behavior. This is an appropriate point from which to build an appreciation of the complexity of variables involved in primate predation.

Since Gaulin and Kurland's evaluation of the applicability of primate predation to understanding human evolution is based on the interpretations that their model provides, the difficulties with their statements are self-evident. In Teleki's review (*5*) of the data on primate subsistence patterns, his synthesis of nonhuman primate predation and human hunting provides a broad, comparative framework for appraising evolutionary developments within the human adaptation.

Evolutionary processes are compromise processes, making a fit between what is ideally best and what is actually possible. Considerations of what is possible should at the very least include anatomical, psychological, social, and ecological factors. It is because I support such a multifactoral approach that I welcome Gaulin and Kurland's remarks on the ecological dimension of primate predation, especially if my earlier report left them with the impression that I considered this area either nonexistent or unimportant.

S. C. STRUM

Department of Anthropology, University of California, San Diego, La Jolla 92023

References and Notes

1. S. C. Strum, *Natl. Geogr.* **147**, 672 (1975); paper presented at Symposium on the Evolutionary Biology of Primates, Los Angeles, 1975; G. Teleki and R. Harding, Eds., *Primate Subsistence Patterns and Human Evolution* (Columbia Univ. Press, New York, in press); S. C. Strum and R. Harding, *Nat. Hist.*, in press.
2. G. Hausfater, *Behaviour*, in press.
3. G. Teleki, *The Predatory Behavior of Wild Chimpanzees* (Bucknell Univ. Press, Lewisburg, Pa., 1973); R. Wrangham, *Primate Eye* **2**, 6 (1974); *Anim. Behav.* **22**, 83 (1974).
4. R. Wrangham, thesis, Cambridge University, Cambridge, England (1975).
5. G. Teleki, *J. Hum. Evol.* **4**, 125 (1975).
6. S. C. Strum, *Science* **187**, 755 (1975).
7. M. Herskovits, *Man and His Works: The Science of Cultural Anthropology* (Knopf, New York, 1966); A. Hultkrantz, *International Dictionary of Regional European Ethnology and Folklore: General Ethnological Concepts* (Rosenhilde & Bagger, Copenhagen, 1960), vol. 1, pp. 229–234; M. Mead, *Growing Up in New Guinea* (New American Library, New York, 1930); P. Phillips and G. Willey, *Am. Anthropol.* **55**, 615 (1953).
8. E. Menzel, Ed., *Symposium, 4th International Congress of Primatology*, vol. 1, *Precultural Primate Behavior* (Karger, Basel, 1973).
9. E. O. Wilson, *Sociobiology: The New Synthesis* (Belknap, Cambridge, Mass., 1975).
10. J. Alcock, *Ibis* **3**, 308 (1969); P. Klopfer, *Am. Nat.* **91**, 61 (1957); *Behaviour* **17**, 71 (1961); T. Struhsaker, *Univ. Calif. Berkeley Publ. Zool. No. 82* (1967); W. Thorpe, *Learning and Instinct in Animals* (Methuen, London, 1963).
11. K. R. Hall, *Symp. Zool. Soc. London.* **10**, 1 (1963); H. Kummer, *Primate Societies: Group Techniques of Ecological Adaptation* (Aldine, Chicago, 1971).
12. S. Altmann and J. Altmann, *Baboon Ecology* (Univ. of Chicago Press, Chicago, 1970).
13. G. Underwood, *Evolution* **8**, 365 (1954).
14. E. Pianka, *Evolutionary Ecology* (Harper & Row, New York, 1974); R. Ricklefs, *Ecology* (Chiron, Newton, Mass. 1973); T. Schoener, *Annu. Rev. Ecol. Syst.* **2**, 369 (1971).
15. T. Case and M. Gilpin, *Proc. Natl. Acad. Sci. U.S.A.* **71**, 3073 (1974); R. Miller, *Ecology* **45**, 256 (1964).
16. M. Gilpin, *The Theory of Group Selection in Predator-Prey Communities* (Princeton Univ. Press, Princeton, N.J., 1975).
17. T. Schoener, *Ecology* **49**, 123 (1968); *Brookhaven Symp. Biol.* **22**, 103 (1969); *Am. Nat.* **103**, 277 (1969); *Theor. Popul. Biol.* **4**, 56 (1973).
18. M. Rosenzweig and R. MacArthur, *Am. Nat.* **97**, 209 (1963).
19. M. Gilpin, *Theor. Popul. Biol.* **5**, 333 (1974).
20. D. Western and C. Van Praet, *Nature (London)* **241**, 104 (1973).
21. A. Coelho, C. Bramblett, L. Quick, paper presented at the meeting of the American Anthropological Association, Mexico City, 1974; K. Glander, in *Socioecology and Psychology of Primates*, R. Tuttle, Ed. (Aldine, Chicago, 1975); R. Moss, *Symp. Zool. Soc. London* **21**, 207 (19 C. Smith, *Ecol. Monogr.* **38**, 31 (1968); L. Tinbergen, *Arch. Neerl. Zool.* **13**, 265 (1960).
22. M. Slatkin and G. Hausfater, *Primates*, in press.
23. Evaluation of the significance of predatory "rates" is difficult. "Rate" is a necessary statistic for longitudinal comparisons of predation within a group and comparisons between groups, sites, and even species. However, differences in conditions, duration, and methods of observation between studies and sites may be an important source of differences in reported rates. For this reason, I prefer to base my discussion of baboon predation at Gilgil primarily on changes which were observed in the "form" of predatory behavior (who participates, when, where, techniques, and so forth.).
24. L. Blankenship and S. Quortrup, *J. S. Afr. Wildl. Manage. Assoc.* **4**, 185 (1974); R. Harding, thesis, University of California (1973); E. Ables, personal communication; S. C. Strum, personal observation.
25. A. Coelho, *Primates* **15**, 263 (1974).
26. J. van Lawick-Goodall, *In the Shadow of Man* (Houghton Mifflin, Boston, 1971).
27. G. Teleki, *Folia Primatol.*, in press.

A. Suzuki, *Primates* **10**, 103 (1969).

29. Further research was supported by grant 963 from the University of California Academic Senate. I thank N. Bishop, G. Hausfater, and G. Teleki for their critical comments. Special thanks are due to M. Gilpin, whose lengthy discussions with me were extremely helpful. I also thank S. Gaulin and J. Kurland for incorporating some of my previous criticisms into the current version of their comment.

31 October 1975