

Primate Predation: Interim Report on the Development of a Tradition in a Troop of Olive Baboons

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Abstract. A troop of olive baboons, *Papio anubis*, has developed systematic predation, which includes hunting and sharing of meat. Although meat-eating among nonhuman primates—baboons and chimpanzees especially—had been discovered in earlier field studies, systematic predation had been reported for chimpanzees and humans only. Starting as an adult male activity in the olive baboon troop, this tradition rapidly expanded to include capture and consumption of prey by adult females and juveniles of all ages and both sexes. Infants eat but have not been observed to capture prey.

Although there are isolated reports of meat-eating in nonhuman primates, systematic predation has been observed only recently (1, 2). Meat-eating by baboons and chimpanzees appears to be restricted to limited populations. The present study provides evidence concerning the way in which a tradition of predation can develop within a group of nonhuman primates.

From December 1972 until January 1974 I conducted a field study of the social behavior of a troop of free-ranging olive baboons (*Papio anubis*) near Gilgil, Kenya. This troop had been studied by Harding (3) in 1970 to 1971 and by 1973 averaged 7 adult males, 21 adult females, and 38 immatures. Harding observed 47 cases of baboon predation on small animals in 1032 hours of observation, the highest rate of predation reported for any primate other than man. The prey were

Cape hares (*Lepus capensis*), birds of various species, and the young of diverse antelopes: Thomson's gazelles (*Gazella thomsoni*), dik-dik (*Rhynchotragus kirki*), steinbok (*Raphicerus campestris*), and impala (*Aepyceros melampus*). All but three cases of predation were the result of adult male activity; in all but one case, adult males were the only consumers of the meat.

Although the primary focus of my study was intratrop social dynamics, I observed 100 cases of predation by baboons in 1200 hours of observation. In addition to this increased predatory rate, important changes in the pattern of predation had also taken place (4).

With minor exceptions the list of species preyed upon by the baboons remained the same as in the earlier study period, although prey preferences were different (Table 1). The propor-

Table 1. Prey species caught in the 1971 to 1972 study and the 1972 to 1974 study. The numbers of prey caught by male, female, and juvenile baboons are given for the later study.

Species	Prey caught, 1970-1971	Prey caught, 1972-1974				
		Total	By males	By females	By juveniles	Captor unidentified
Thomson's gazelle	16	33	24	1	1	7
Hare	12	41	22	9	9	1
Bird	4	11	3	1	6	1
Dik-dik	8	7	4	3		
Other ungulates:	7					
Steinbok		6	6			
Impala		1	1			
Klipspringer		1	1			
Total	47	100	61	14	16	9

tion of ungulates eaten, including Thomson's gazelles and dik-diks, decreased by 18 percent between the two periods of observation, whereas that of hares and birds increased by 18 percent (5).

More significant than these fluctuations in prey preferences, however, were the concurrent changes in the nature of participation in predatory acts, both meat-getting and meat-eating. In the 1970 to 1971 study, adult males did 94 percent of the killing and 98 percent of the eating, while adult females, the only other class to participate, did 6 percent of the killing and 2 percent of the eating (2). During my study year, males did 61 percent of the killing; females, 14 percent; and juveniles, 16 percent; 9 percent of the kills were unidentified as to captor. This change in participation may have contributed to the difference in the prey profile since males and other age and sex classes differed in the type of prey taken (Table 1).

All adult males participated in at least some meat-eating phases of predatory events, but individual scores ranged from that of an animal that ate meat in 63 percent of the kills to that of an animal that ate meat in only 11 percent of the kills (6). In all, at least one adult male was present at 93 percent of predatory episodes, with at least one male eating meat in 91 percent. Some males were more active in capturing their own prey while others were more persistent at getting meat that others had captured. A single male was the most frequent captor and consumer during both study periods, although the identity of the individual changed from the first to the second study. Other changes in male participation patterns were related to the im-

migration, emigration, and death of males, and individual participation in predation was not independent of social variables such as relationship between males, amount of tension in the group, and so forth (4).

At the outset of the second study period, adult females were already participating more in all stages of predation than they had at the close of the first. During the second period, females attended the consumption phase of 68 percent of kills and obtained meat in 52 percent, although not all females are represented in these figures. Only specific individual females were interested in meat, and those that did the most capturing were not the same ones that obtained portions of meat captured by others (7). The range of individual participation in meat-eating for females overlapped that for males, with some females participating in consumption more than some males (6). Also, one female had a higher score for capture than two of the seven males. If measures of meat-eating and meat-getting are evidence of an individual's motivation, the interest of some females in meat equaled or exceeded that of some males.

The major developments in juvenile and infant participation in predatory episodes occurred during my study. Early, infrequent cases of juveniles attending carcass consumption with their mothers rapidly gave way to a pattern of frequent attendance (and participation when possible), once the young animal had been successful in obtaining meat. In addition, kills were focal points of social interaction for large male juveniles, and mixed juvenile play groups often approached and investigated kill sites. Individual rates of attendance increased markedly once

meat was successfully obtained, regardless of the way an animal was introduced to the kill site (6). An increase in juvenile capture rate was associated with increased frequency of juvenile participation in consumption. Juveniles usually preyed on birds and hares, but by the end of the study they had successfully captured a young Thomson's gazelle as well.

Infants also participated in meat-eating but were never seen to capture their own meat. Infants attended 54 percent and obtained meat at 18 percent of all meat-eating episodes (6). Two separate patterns of infant involvement were apparent. First, those infants that were still in close association with their mothers and appeared to be mainly attracted initially to the mother and not the kill had the highest meat-eating scores. Nonetheless, as they gained some independence from their mothers, these infants attended kills more often than others of similar age. Second, some older infants began their participation independently as members of play groups as described for juveniles. Attendance by older infants of either category usually did not coincide with the presence of their mothers. Furthermore, those infants with high scores for meat-eating were also those with special relationships (8) with adult male major consumers of the kill (9).

Many of the kills witnessed by Harding (2) were the result of accidental or fortuitous capture of concealed prey. He also observed several instances in which adult males left the troop to investigate a nearby herd of Thomson's gazelles or detoured through areas where other prey species might be found; prey were captured on several of these occasions.

Important differences in the pattern of predation were observed in the second study and resulted from increases in the distance traveled and time spent away from the troop by males in pursuit of prey. Individuals ranged up to 3.2 km from the periphery of the troop and spent up to 2 hours in "hunting" behavior, with or without success. The same individual prey might be repeatedly hunted on successive days until it was captured, the troop changed its ranging pattern, or the prey matured to the point that it could run faster than the baboons, often only a matter of a few days. A successful relay system of chasing prey, at first employed

accidentally, was quickly adopted as a hunting strategy by adult males. Subsequent episodes in which this rudimentary cooperative technique was used were much more successful than those in which only one baboon pursued a prey animal (4, 10).

In many ways, baboon predatory behavior is now comparable to that described for chimpanzees (1, 11), although baboons do not exhibit the elaborate sharing behavior of chimpanzees engaged in meat-eating. Nevertheless, the carcass of the baboon prey was shared, after a fashion, since it often passed from one individual to another when participants aggressively displaced each other or became satiated and lost interest. At the same time, bits and pieces of meat and bone, which were dropped during normal social interactions around the kill, were consumed by the hangers-on.

In addition, I witnessed several incidents that, although more rudimentary than the chimpanzee pattern in that they were not preceded by elaborate communicative gestures, qualified as sharing. This sharing was of two types, that between a female and her offspring and that between an adult male and an adult female. The adult pairs were sometimes involved in a consort (that is, sexual) relationship and sometimes not. In both types of sharing, members ate in close proximity either from the same pile of meat or from the same piece of meat simultaneously. Frequently, one individual moved to allow another access to the meat. Such

behavior was not exhibited by the baboons in any other circumstances (including other feeding situations).

These observations on baboon predation add further detail to our knowledge of the development of social traditions in a nonhuman primate group. The data also yield important information on the elaboration, sophistication, and success of predation in a primate species without tools or language. At the same time, they may illustrate the limitations which the lack of these advantages imposes on primate hunting patterns. In this manner, observations of meat-getting and meat-eating in nonhuman primates are relevant to an understanding of the evolution of hunting in *Homo sapiens* (4).

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References and Notes

1. R. A. Dart, *Symp. Zool. Soc. Lond.* 19, 49 (1953); J. van Lawick-Goodall, *In the Shadow of Man* (Collins, London, 1971); G. Teleki, *The Predatory Behavior of Wild Chimpanzees* (Bucknell Univ. Press, Lewisburg, Pa., 1973).
2. R. S. O. Harding, *Am. J. Phys. Anthropol.* 38, 587 (1973); paper presented at the 9th International Congress of Anthropological and Ethnological Sciences, Chicago, 1973; paper presented at the meeting of the American Anthropological Association, New Orleans, 1973.
3. All data on baboon predation in the earlier study period are taken from Harding (2). Harding also includes details of the study area.
4. S. C. Strum, in preparation.
5. Predatory episodes ranged from a few minutes to several hours, depending on the prey species. The baboon seldom ate the prey at the capture site, but transported it in its mouth to the shade, toward the group, or away from approaching males. The baboon

usually did not kill the prey until eating it, but the prey often suffered a broken neck during transport and died.

6. Only 91 of the 160 predatory episodes were used in calculating scores for attendance and meat-eating since identification of participants in the remaining episodes was not comparable. Scores are adjusted to the length of an individual's membership in the troop and the number of kills during that time. In this way percentage figures are comparable across individuals despite the fact that 2 males, 2 females, and 4 infants died, 11 infants were born, 3 males and 1 juvenile immigrated, and 3 males emigrated during the study period. Individual attendance scores range from 23 to 73 percent for males, 2 to 41 percent for females, 3 to 19 percent for juveniles, and 2 to 27 percent for infants. Individual meat-eating scores range from 11 to 63 percent for males, 0 to 32 percent for females, 0 to 11 percent for juveniles, and 0 to 7 percent for infants. At least one juvenile obtained 54 percent of the kills and obtained meat in 27 percent of kills. Meat-eating was scored as 0 if none occurred and 1 if any occurred, irrespective of the type of eating (carcass or scraps) or of the time spent in meat-eating (4).
7. The pattern differs from that of males in that males with a high score in capture also had a relatively high score in consumption, whereas the opposite is true for females.
8. S. C. Strum, in preparation; T. W. Ransom and B. S. Ransom, *Folia Primatol.* 16, 179 (1971).
9. Other factors limited participation scores in meat-eating phases of predatory episodes. Because only adult males ventured regularly beyond the periphery of the troop, participation in kills by other age and sex classes was contingent upon their occurring within or near the troop. Some kills were 3.2 km from the troop, while others, although closer, went unobserved by most troop members. The total figures for participation of females, juveniles, and infants do not reveal the great increase in their participation during the year.
10. Although predatory behavior represents an increasingly larger investment of time, meat still makes up only a small proportion of the baboon diet.
11. J. van Lawick-Goodall, *Anim. Behav. Monog.* 1, 161 (1968); G. Teleki, *Sci. Am.* 238, 32 (January 1973).
12. Supported by NSF grant GS-35180. I thank Mr. and Mrs. A. Cole and the government of Kenya for making this research possible, and R. S. O. Harding, L. F. Muckenfuss, T. W. Ransom, and M. E. Spiro for their critical comments.

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