

OMNIVOROUS PRIMATES

Gathering and Hunting in
Human Evolution

Edited by
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NOTES

1. Note that this representation does not differ from the classical system with three axes at 60° used by MacKinnon and MacKinnon (1978).
2. Perpendicular axes are more convenient for plotting diagrams, and they are used here to obtain dietary values that can be compared to the measures of gut differentiation discussed in the next section.
3. The mean values on axis 0x (+25, +12, and -5, respectively) provide a useful approximation of dietary divergence.
4. Similar but less precise correlations have been found after calculating the total area available for absorption in the small gut of different primate species: for folivorous forms, the index approaches +100, and it may reach as low as -100 for animalivores.
5. Similarly, no folivores were found among the primitive reptiles of the Permian (Halstead, 1969; Olson, 1966).
6. Other physiological changes, such as seasonal birth periods, are also known to occur in most species.

Shirley C. Strum

8. Processes and Products of Change: Baboon Predatory Behavior at Gilgil, Kenya

As the search for hominid origins has intensified in the last two decades, so has the attempt to find an animal model for the predatory component of early hominid behavior. Various animals have been proposed as representative of the early hominid adaptation, including baboons (e.g., B. Campbell, 1966; Dart, 1963; DeVore and Washburn, 1963; R. Fox, 1967; C. J. Jolly, 1970; Oakley, 1961), social carnivores (e.g., Crook, 1966; Peters and Mech, 1975; Pfeiffer, 1969; Schaller and Lowther, 1969; P. Thompson, 1975), and chimpanzees (e.g., Crook and Gartlan, 1966; Kortlandt, 1972; Kortlandt and Kooij, 1963; Lancaster, 1968; Reynolds, 1966; Teleki, 1975).

These models have been inadequate because our understanding of the evolution of behavior has been rudimentary, the relevant data have been sparse, and we have tended to underestimate the behavioral variability of a predaceous species. Early hominids were at the same time primates, social predators, and anatomically transitional forms; therefore a precise analogue, whether animal or human, can never exist. Yet the study of nonhuman primates and social carnivores can illustrate the basic interplay between an organism and the complexity of its environment and help us to generate hypotheses about the evolution of the subsistence patterns which we now recognize as unique to humans. By understanding processes, we can better comprehend the products of evolutionary change.

Essential to such an understanding is knowledge about the behavior that led to the inclusion of large animals as prey, a significant difference from predatory behavior of living nonhuman primates. This article presents data on the predatory behavior of one baboon troop that had been under almost continuous observation for 7 years at the time of writing. These data provide specific areas of contrast with other primate predators, including human ones. More important, they illustrate how predation may be affected by the individual, social, and ecological contexts of a group-living primate species, as well as the processes that initiate, facilitate, or inhibit changes in this particular behavior.

THE STUDY SITE

The data presented here were collected on Kekopey Ranch near Gilgil, Kenya, roughly 115 km northwest of Nairobi in the Great Rift Valley, an area of high-altitude savannah with volcanic soils. Descriptions of this area and its climate have been published elsewhere (Blankenship and Field, 1972; Blankenship and Qvortrup, 1974; Harding, 1976). The ranch covers some 182 km², but the baboons under study live within a central area of about 73 km². About 52% of this area is grassland (40% preexisting, 12% the result of recent bush removal), while the remaining 48% is bush of varying densities, dominated in most areas by leleshwa (*Tarchonanthus camphoratus*). The volcanic soil, in combination with sufficient water, can produce good grassland, but relatively low rainfall between 1970 and 1977 resulted in periodic drought conditions and low grassland productivity.

During the past 20 years the area has been altered for cattle raising by bush clearing and construction of a system of cattle troughs that bring water into previously dry areas. A large biomass of wildlife coexists with the cattle. In addition to the baboon population, of interest to the present discussion is the abundance of several antelope species (Thomson's gazelle, impala, reedbuck, steenbok, dikdik, klipspringer, duiker), Cape hares, and numerous predatory and nonpredatory birds.

Large carnivores have been shot or trapped since the early part of this century, but despite their reduced numbers, hyena, lion, and cheetah have occasionally preyed on the cattle. A sizable leopard population still remains, along with three species of jackals, bat-eared fox, and feral domestic dogs that hunt in packs.

Baboon and ungulate populations have increased rapidly, probably as a result of ecological modifications at Kekopey (additional grassland and water plus lowered predator density). Although a rough estimate of 50 Thomson's gazelle in the central area in 1956 (A. and T. Cole, personal communication) is probably imprecise, the order of magnitude seems correct. By the middle of 1970 the population had expanded to 2,000 (Blankenship and Qvortrup, 1974). At this time, in the central area there also were approximately 1,400 impala, 1,000 reedbuck, 200 zebra, 100 buffalo, and 150 eland, in addition to the smaller antelope species.

In 1970, seven baboon troops were identified in this area, with group sizes ranging from 35 to 125 and a population density of 10.3 baboons/km² (Harding, 1973b), at the upper range for "savannah" baboons. Since 1970 most baboon troops have doubled in size, and many have split. In 1977 there were a minimum of 12 troops within the same area, yielding a density of roughly 19 baboons/km².

Although it was a cattle ranch, Kekopey remained "wild" in many respects. The human population was sparse and dispersed, consisting of a

dozen cattle herders and their families, the ranch owners, and occasional groups of migrant charcoal burners, temporary residents when a new area was being cleared of bush. Harassment of wildlife or contact between wildlife and humans remained minimal, unlike in other areas in Kenya. Ecological modification was slight but critical because it opened up new opportunities for wildlife as well as cattle.

THE GROUP AND STUDY METHODS

One group of baboons in the Kekopey population has been under close observation since September 1970, when R. S. O. Harding began the initial study. This group (PHG) has been studied by a succession of 11 scientists with only one break in continuity, August 1974–March 1975. Between 1970 and 1977, the period covered by this report, the troop grew from an average of 49 individuals to 63 animals in 1973, 84 in 1975, and 91 in 1976 (table 8.1). This increase is the result of both an excess of births over deaths and some male immigration; the number of adult females has remained fairly constant.

Harding was the first to document extensive predatory behavior in PHG (1973a, 1974, 1975), and later researchers have extended his observations (Strum, 1975a,b, 1976a,b; N. Chalmers; H. Gilmore; L. Scott; D. Manzollilo; M. Demment, personal communications).

Predation has never been the focus of any PHG studies, but because of excellent observation conditions and the frequency of the behavior, data on baboon predation have been collected during each study. The differences in methodology, orientation of observers, and focus of projects have had an unavoidable effect on the predation data. As a result, my discussion of PHG predatory behavior relies most heavily on my own data collected

Table 8.1. Age-sex classes

	1970-1971	1973	1975	1976-1977
Adult males	4	7	10	10
Subadult males	2	—	2	5
Adult females	18	19	21	21
Juveniles	15	24	32	39
Infants	10	13	19	16
Total	49	63	84	91
Observation hours	1,032	1,200	250	792.5

Note: Figures given here represent mean numbers of animals for each observation period. Study periods are those of Harding (10/70-10/71) and Strum (12/72-1/74; 6-8/75; 8/76-4/77).

during three periods: December 1972 to January 1974 (referred to here as "1973"); June to September 1975; and a third period beginning in August 1976. I report here on data collected through April 1977.

Systematic sampling was used for the main topics during each of my three studies, but data on predatory behavior were collected in an *ad lib* manner (J. Altmann, 1974). Routine sampling was interrupted for any instance of predatory behavior, and potential episodes and factors thought to be important to this behavior were monitored continuously. Notes on predatory episodes were taken in narrative style, and individual sequences were photographed.

ELEMENTS OF BABOON PREDATORY BEHAVIOR

Predation, like any complex behavior, is dynamic and varies over time, depending on the context and participants. Among PHG baboons this variability is quite marked. Although it is difficult to characterize the PHG predatory pattern for the entire period since 1970, some basic elements exist; I will briefly review them before discussing how this behavior has changed.

Prey Species

With minor exceptions, the species preyed on by PHG baboons have remained the same over the years, but the proportional representation of these animals (the prey profile) differs from year to year (table 8.2). Not all available prey species are captured, and baboon troops in the same population differ in their selection of prey. The PHG baboons capture the young of several antelope species (Thomson's gazelle, impala, dikdik, steenbok, reedbuck, klipspringer) plus individuals of all ages of the smaller antelopes, such as dikdik and steenbok. Cape hare and button quail, several smaller ground-nesting birds, and some tree-nesting bird species are also frequent prey.

Methods of Capture

Teleki (1973a) distinguishes opportunistic and systematic predation in primates, a classification based on the mode of pursuit employed by the predator. Dividing predatory episodes into three stages (pursuit, capture, and consumption), he also identifies three behaviorally distinct modes of pursuit: seizure, chase, and stalk. Opportunistic predation takes place when "no systematic searching or stalking activities precede the capture" (1973a:50). Nonhuman primate predation is said to include hunting when there is deliberate searching, or the presence of chase or stalk as modes of pursuit.

Table 8.2. Prey species

	1970-1971		1973		1975		1976-1977	
	No.	%	No.	%	No.	%	No.	%
Thomson's gazelle (<i>Gazella thomsoni</i>)	16	34	33	33	—	—	9	20
Dikdik (<i>Rhyncotragus kirki</i>)	8	17	7	7	2	13	5	11
Steenbok (<i>Raphicerus campestris</i>)	1	2	6	6	1	6	1	2
Impala (<i>Aepyceros melampus</i>)	1	2	1	1	—	—	—	—
Klipspringer (<i>Oreotragus oreotragus</i>)	—	—	1	1	—	—	—	—
Antelope, <i>sp. indet.</i>	5	11	—	—	—	—	—	—
Hare (<i>Lepus capensis</i>)	12	25	41	41	9	56	24	53
Bird	1	2	11	11	4	25	5	11
Small mammal, <i>sp. indet.</i>	3	6	—	—	—	—	1	2
Total	47	100	100	100	16	100	45	100

Note: These figures should be compared with caution, since different observation methods were used in 1970-1971 and the other three periods, and different numbers of observation hours were involved in each period (see table 8.1).

PHG baboons captured prey both opportunistically and systematically, although the ratio between these two approaches varied from year to year. Opportunistic capture consisted of simple seizure of exposed prey. Systematic capture exhibited varying degrees of sophistication, the extremes of which I have arbitrarily classified as *simple* and *complex* hunting (cf. "extended hunting"; Strum, 1976a). *Simple hunting* required active searching and either stalking or chasing of the prey. It involved only one baboon predator, pursuit lasted less than 10 minutes, and the distance the predator traveled from the troop was less than 300 m. *Complex hunting* involved more than one predator, the pursuit lasted more than 10 minutes (table 8.3), and the distance the predator traveled to contact the prey ranged from 300 to 1,600 m, although the predator might travel up to 4,000 m during the course of the hunt.

There are intermediate cases, and the assignment of such cases to the simple or complex category was based on variables such as predatory intent (e.g., watching prey or predatory activities of other animals) persistence over time or space, and comparison with the initial predatory pattern. Most of the significant deviations from the initial pattern were termed complex hunting for purposes of analysis. However, some episodes were classified as simple hunting although the baboon predator involved had traveled more than 300 m, because the prey was contacted only incidentally, in the course

Table 8.3. Duration of Thomson's gazelle hunts (1973)

	Successful (n = 24), minutes	Unsuccessful (n = 26), minutes
Total	1145	620
Range	10-120	5-85
Mean	—	24
Mode	60	10, 20
Median	50	30

Note: The sample of successful hunts includes 7 simple hunts, 13 complete complex hunts, and 4 lengthy complex hunts, the beginning of which could not be observed. The unsuccessful sample refers to complex hunts only (see text for definition of "simple" and "complex" hunts).

of a search for something else. In addition, many single-predator episodes were classified as complex hunting if the baboon hunter covered more than 450 m in order to contact a prey animal *and* spent more than 15 minutes in pursuit without any other feeding activity. If a stalk was followed by a sequential chase by several baboons, the episode was classified as complex hunting regardless of the time spent in pursuit. Finally, if the prey was contacted less than 300 m from the point where the predator first began to hunt but the pursuit involved more than one predator and lasted more than 10 minutes, the episode was designated a complex hunt.

It is difficult to distinguish between types of hunting that lie along a continuum of behavior, but the contrasts between types of hunting at either end of the continuum are clear. I suggest that one baboon moving 3 m to pursue a small animal for a few minutes and five male baboons moving synchronously over 1,600 m to contact a prey animal, then spending 2½ hours in following, scattering, searching, and chasing, represent different hunting patterns. Figure 8.1 provides basic data on complex hunting episodes observed in 1973.

Chances for opportunistic capture arose during the day, as the troop searched for vegetable foods. Because hares and infant antelopes attempted to avoid detection by remaining concealed and immobile, a baboon often fed as close as 10 cm to a potential prey before it ran away. However, concealment may not be as effective a defense against baboon predators as it is against predators that rely on movement cues.

Not all successful kills were the result of accidental discoveries. In simple hunting, two methods of active searching were employed. In the first, a baboon left the troop to approach a nearby herd of Thomson's gazelle, then moved through the herd and scrutinized the surrounding area. These searches sometimes resulted in the location and successful capture of infant gazelles. Since dikdik and steenbok prefer denser cover and are not clearly visible to the baboons during troop movement, searching also included

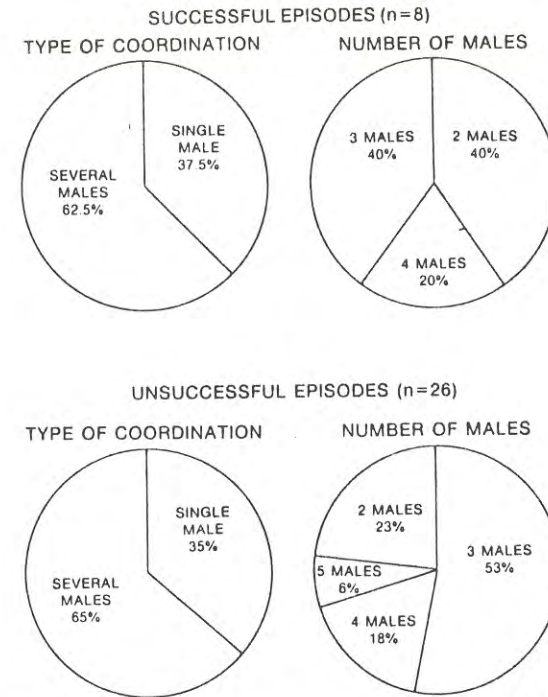


Figure 8.1. Complex hunting on Thomson's gazelle by Gilgil baboons (1973). Five episodes of complex hunting that were not observed in their entirety are omitted here.

detouring through thickets, with the result that prey was flushed, chased, and sometimes captured.

Active pursuit also characterized simple hunting, although it was not always successful. For example, male RD spotted a juvenile hare 225 m away and began to pursue it. As soon as RD had closed the distance to 150 m, the hare took off, with RD chasing it in a zigzag path at full speed for 4 minutes. As he was about to grab it, the hare dashed into a hole, some 450 m from the point where the chase had begun. RD tried to follow into the hole but lost the hare. He sat above the hole for 2 minutes, then tried probing it again, but gave up after 2 minutes more. RD was able to close the distance between himself and the hare and, had the hare not ducked into the hole, RD would have caught it.

At times, fortuitous episodes seemed to stimulate more systematic efforts:

A female baboon chases a hare that has raced out from among the bushes in which the baboons are feeding. Several females and juveniles take up the chase, all rushing

at it from different directions. From 245 m away, male RD sees the commotion and runs to intercept the hare, chasing it over 400 m. In the chase, the hare runs past several other baboons who try for it but miss, and RD is the only one to really pursue. Ten minutes later RD gives up, having lost the hare in a thicket. The troop has moved quickly through the neighboring area and RD turns back to rejoin the troop. RD eyes several large herds of tommies as he walks very slowly toward the troop. RD then walks obliquely towards the troop and more directly towards a herd of tommies, glancing back at another herd as he goes. He has been searching through all the clumps of grass and low bushes as he doubles back. The hare has circled around and hidden itself out of RD's path. In this process of searching, RD walks past a very small tommy which is "freezing" in the grass. He doesn't see it but after he moves 30 m away, the tommy gets up and runs off. This catches RD's attention and he sits down, gazing at the baby. A female tommy runs after the baby, moving it even further away from the baboon. RD, standing bipedally to observe the infant, changes his direction and walks towards the tommy and away from the baboon troop.

RD devoted the next 20 minutes to tracking the baby, trying to close the distance between them, as Thomson's gazelle from two herds raced back and forth in front of him. He surveyed other herds as he moved past them, but persisted in following the small gazelle. He finally gave up.

RD's behavior at the end of this example verges on what I have termed complex hunting, for it was systematic hunting, sophisticated in its searching and chasing techniques, and pursuit was persistent and prolonged. Complex hunting could also involve more individuals, greater expenditure of time and effort, and more coordination and strategy, and was quantitatively, if not qualitatively, different from simple hunting. Complex hunting was directed only toward Thomson's gazelle. Two hours could be spent searching, stalking, and chasing, and the same prey animal could be pursued on several days, as the baboon troop revisited an area during its daily movements.

The involvement of many baboons in complex hunting was often accidental, as when several baboons, beginning independently, all converged on the same prey animal simultaneously. But at times activities were coordinated among hunters. For instance, since adult male baboons continually monitor the behavior of other troop members, particularly other adult males, behavior sequences on the following pattern occurred. An adult male baboon looks up from feeding and sees a herd of Thomson's gazelle at a distance. He stops foraging and sits with his gaze fixed at that distant point. Then, beginning either with the closest male or with the male who first observed the alert male's behavior, recognition spreads among the troop's males. When the first male walks off in the direction of the gazelle herd, the others watch him as he moves toward the prey. Once capture appears imminent, the other males might move out to join him. If the predatory event occurs far from the troop, the observing males often move to new positions that allow them a better view.

Sometimes, other males moved toward a distant herd only seconds after the first male had started in that direction. They concentrated on the same prey animal or on other prey, but they also used the presence of other hunters to their advantage by taking over a chase when the previous hunter tired, or by purposefully chasing their own target in the direction of other hunting baboons.

Timing of the chase was critical. Male baboons are rapid runners, but they seemed able to sustain top speed for only about 5 minutes. Sequential chases by several males enabled pursuit to be conducted at top speed for a much longer period, and initial errors in timing could often be overcome if more than one baboon were involved.

Kill and Consumption

The actual moment of capture was not always observable. However, in those instances for which there are data, baboons did not attempt to kill the prey before eating it. Usually, baboons grabbed an antelope and began eating on the soft underbelly, whether the animal was still alive or dead. The prey animal might remain alive for as long as 10 minutes after consumption began, but more often it died as it was being transported from the place it was seized to the first eating site. Although prey was captured with the hands, it was carried in the mouth, usually by the neck, and as a result a broken neck was often the cause of death. I have never observed what appeared to be a purposeful kill bite, although twice a killing bite was inflicted, seemingly accidentally.

Holding the antelope to the ground with both hands and feet, the consumer took the first bite from the underbelly. After the viscera were eaten, the meat on the ribs, the vertebral column, and the limbs was consumed. In the process of eating the limbs, the baboon often turned the skin inside out. The consumer alternated between these various parts of the body until only the limbs and head remained. Once the fleshy parts were gone, the consumer had to exert more and more effort to free the meat from bones and skin. Force was applied by using the incisors to pull in opposition to the hands and feet. The head was consumed last, although marrow eating often followed brain consumption and the carcass might be reexamined for further edible portions. Before the brain was attempted, the ears and eyes were eaten.

The brains of prey were not always eaten. Baboons consumed the brains of smaller species, such as Cape hares, as a matter of course, but they often left the brains of the larger antelopes intact. Two factors were influential: the age of the individual prey animal and the identity of the baboon consumer. The PHG baboons used several techniques to extract the brain from larger prey: crunching, cracking with canines, and entry through the upper palate. The crunching technique was primarily used on infant antelopes, whose thin bones were easily cracked. Their skulls fit easily

between the baboons' molar teeth, while positioning of larger prey was more difficult and might be impossible. When the entire skull of the prey was placed between the molars of the consumer and pressure was applied, the braincase cracked into small pieces. Usually the brain was sucked out or licked off the pieces of bone to which it adhered, but fingers might be used to scoop out the remainder. Eating away at the bones of the face and upper palate also allowed the brain to be sucked out. Sometimes several techniques were tried if the first was unsuccessful. Most often, attempts at crunching the skull were followed by attempts to enter through the palate.

The condition of the carcass of an antelope eaten by a baboon was distinctive and possibly diagnostic: the pelt was split from underneath, with portions of limb bones still attached, but all other bones were no longer articulated. Sometimes the pelt appeared to have been turned inside out, the result of the baboons' attempts to break limb bones for their marrow without separating the tough skin from the bones. Around the pelt might be found fragments of skull and facial bones (often the mandible was broken into two segments), and limb bones, either whole or with ends broken off. Scattered throughout the area were bits of ribs and vertebrae.

Consumption of hares and birds was not so systematic. Baboons often crammed small items into their mouths in one movement, or, if they had been eating leisurely, bolted their prey when approached by another potential consumer. The remains of birds and hares were seldom more than a bit of fluff or feathers.

Some baboons apparently did not know how to dispatch prey once they had caught it. For example, having wounded a young Thomson's gazelle during capture, a subadult male licked the wounds as he held down the prey. When he picked up the gazelle and attempted to feed, he did so at the forelimb, then at the elbow, but with little success (baboon teeth and hands seem to have difficulty penetrating the hide of most ungulate prey except in the thin-skinned underbelly). When he next tried to bite into the back, he obtained only fur. The male then tried unsuccessfully to bite through the skin in several other regions, and returned to licking the wounds. At last he managed to break the skin and pull the shoulder joint through, using the incision his initial wounds had made, but even so, 10 minutes after he had begun, he still had obtained little from the carcass of his prey. After 20 minutes of consumption, the male finally bit into the underbelly and fed easily.

Prey Response

Hares. Cape hares employed two methods of escape from a baboon. Remaining immobile ("freezing") was the simplest method and occurred both in the open, where the hare was in plain view, and in denser cover, where the hare was partially concealed. Baboons often passed very close to

a "freezing" hare without apparently noticing it. In these cases I could not determine whether the camouflage was effective or whether the baboon had no predatory interest at the time. Hares also escaped by running away either at high speed in a straight line or in a zigzag motion. Zigzagging occurred only during active and close pursuit by a baboon and appeared to be an effective means of predator avoidance.

Baboons never were observed engaging in complex hunting for hares, but long chases could follow an unsuccessful short lunge. If a hare disappeared from view during the pursuit, a baboon might search in bushes or clumps of grass over an area of about 0.5 ha, the longest search lasting 40 minutes but most averaging 5 minutes. Sequential chasing of a hare occurred once in 1973, when several males converged on the prey from different directions, each taking up the chase at appropriate intervals. As was often the case with Thomson's gazelle, the prey had outrun the first baboon that pursued it and probably would have escaped if additional baboons had not intervened.

Birds. The usual mode of pursuit for solitary birds was simple seizure, although one stalk was observed. Prey animals ranged from nestlings to fully adult members of several species. A bird being preyed upon did not actively defend itself, nor did conspecifics come to its aid; furthermore, birds did not obviously avoid baboons as hares did. Bird eggs are not considered under the category of predation in this study (although others have included eggs as prey; e.g., Hausfater, 1976), but baboons consistently and frequently searched for and obtained eggs. As a result they were mobbed by adult birds attempting to defend their nests (particularly crowned plovers, *Stephanibyx coronatus*). These maneuvers occurred regardless of whether the baboons were actively raiding a nest or not, but the behavior seldom deterred any but the smallest baboons.

Ungulates. The literature refers to the peaceful coexistence of and symbiotic relationship between baboons and ungulates (e.g., DeVore and Hall, 1965; Struhsaker, 1967). Predation on impala (*Aepyceros melampus*) was rare among PHG baboons, perhaps because capture of all but the youngest infants was so difficult. Young impala were defended by their mothers, occasionally successfully. In general, the two species intermingled and responded to each others' alarm signals, although not consistently.

Thomson's gazelle (*Gazella thomsoni*) have several methods of general predator avoidance, including simple running, doubling back, stotting (a form of stiff-legged prancing), jumping, and crossing (Walther, 1969). Vigilance, approach to the predator, coalescence into larger herds, concealment, and lying down (without complete immobility) are also employed. PHG baboons normally preyed on gazelle fawns approximately 1 week old or younger. Fawns usually lay concealed when left by their mothers during the first week of their life, which allowed the mother to

move off to feed, either singly or with a female herd. The mother then returned to her fawn for nursing, leaving it hidden again in a place where it would stay until her return. Females sometimes defended their young once the baboons had captured them. This defense was rarely effective, but it sometimes delayed consumption of the prey for a few minutes, as the predator moved to avoid the charge of the female gazelle. Once the fawn stopped vocalizing, its mother's interest appeared to cease. For most of the study period, Thomson's gazelle herds did not show flight or avoidance of PHG baboons. Between June and December of 1973, however, when complex hunts were frequent, those herds in which baboons had hunted recently or frequently became vigilant, wary, and fled quickly. This behavioral change occurred as little as 1 week and as much as 4 weeks after an initial complex hunt.

Other species of antelope (dikdik, steenbok, reedbuck) did not usually avoid baboons. When not being preyed upon, these animals peacefully fed close to the baboons without signs of wariness or nervousness. Since these species were not objects of complex hunting and were infrequently preyed upon, they may not have regarded baboons as potentially dangerous predators.

Interactions With Other Predators

Lions have been eliminated and leopard numbers have been reduced at Kekopey; baboons were only seen in contact with smaller predatory species. Interactions with jackals, tawny eagles, Egyptian vultures, and ground hornbills resulted from competition around baboon kills. For example, jackals repeatedly tried to gain access to a Thomson's gazelle carcass while the baboons still possessed it. The baboons usually responded by avoidance but at times aggressively attacked the jackals. During these encounters, jackals had a better chance of getting the carcass because the baboon consumer temporarily abandoned it. Ground hornbills competed in a similar manner, but the only baboons they could intimidate were immatures (up to about 4 years of age).

Participants

The degree to which age-sex classes and individual baboons took part in predation has varied over the years at Kekopey (table 8.4). As a result, no one study period is representative of a general pattern. Trends in participation are discussed later, but the following general characteristics of PHG baboon predatory behavior are presented as an introduction.

Adult males, adult females, and juveniles (of both sexes) all captured prey animals; infants did not, although they did eat meat. Adult males made more kills than females, but during some periods juveniles captured nearly as many animals as adult males.

Table 8.4. Age-sex class of known captors

	Thomson's Gazelle	Dikdik	Other ungulates	Hares	Birds	Total	
						No.	%
1970-1971							
Males	16	8	10	9	1	44	94
Females	—	—	—	3	—	3	6
Juveniles	—	—	—	—	—	0	
Total	16	8	10	12	1	47	
1973							
Males	24	4	8	22	3	61	67
Females	1	3	—	9	1	14	15
Juveniles	1	—	—	9	6	16	18
Total	26	7	8	40	10	91	
1975							
Males	—	1	1	2	—	4	29
Females	—	—	—	3	—	3	21
Juveniles	—	—	—	4	3	7	50
Total	—	1	1	9	3	14	
1976-1977							
Males	2	—	—	5	1	8	19
Females	1	1	—	4	1	7	25
Juveniles	3	2	—	6	2	13	46
Total	6	3	—	15	4	29	

Note: Predatory episodes in which the identity of the captor could not be determined are excluded here.

Male, female, and juvenile baboons¹ generally employed different modes of pursuit. Complex hunting was entirely an adult male activity, but for other age-sex classes, the type of pursuit (stalk, chase, or seizure) appeared to be consistent with the prey items taken most frequently by that class (fig. 8.2; table 8.5).

The adult males heavily involved in capturing prey were similarly involved in consumption. Only certain adult females showed definite interest in predation, but those who captured the most were not necessarily those who obtained meat captured by others. The range of individual participation in predatory behavior for adult males and adult females overlapped, with several females capturing and consuming more than some of the males.

Although the amount of meat that each individual obtained may have been quite small, meat-eating was widespread, particularly during 1973. In that year, for example, 58 members of the troop (76%) ate meat; participation ranged from individuals who ate in 63% of the predatory episodes to those who ate in only 1%. Interest in meat was even higher than

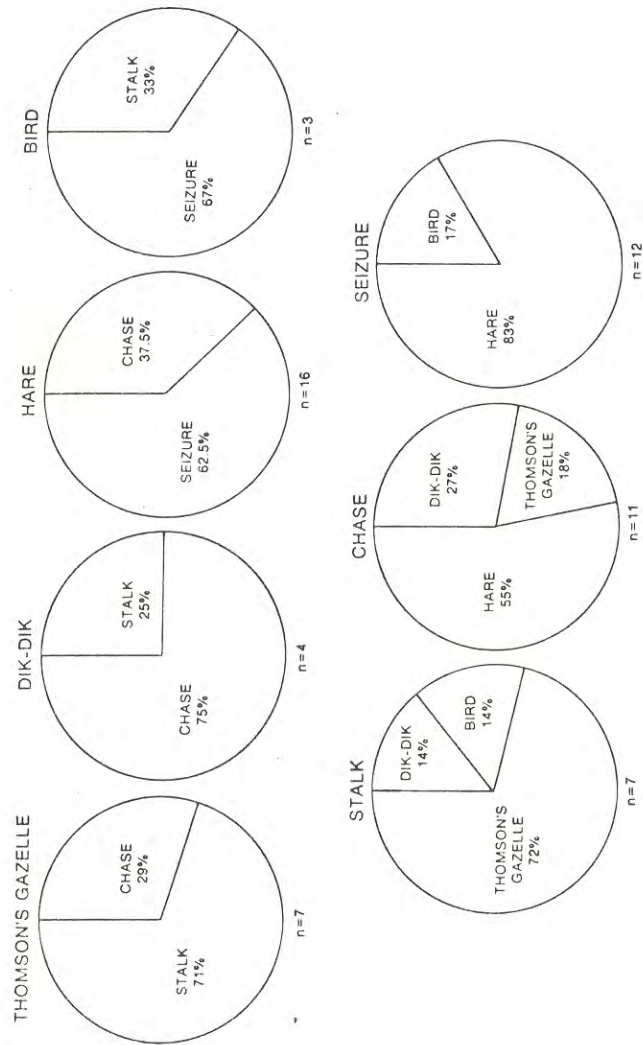


Figure 8.2. Modes of pursuit exhibited by Gilgil baboons (1973) when hunting various prey species. Figures for Thomson's gazelle are based on observed episodes that did not involve complex hunting.

Table 8.5. Mode of successful pursuit by different age-sex classes of captors (1973)

Age-sex class	Stalk		Chase		Seizure		Total	
	No.	%	No.	%	No.	%	No.	%
Male	6	55	2	18	3	27	11	100
Female	—	—	6	67	3	33	9	100
Juvenile	1	10	3	30	6	60	10	100
Total	7	—	11	—	12	—	30	—

Note: These data are based on the 30 episodes in which the entire pursuit was observed and which did not involve complex hunting.

this figure indicates, for when attendance at kills in 1973 is examined rather than success in obtaining meat, it is evident that 96% of the troop attended some predatory episode. (Attendance is defined here as visual orientation toward a kill and physical presence within 7.6 m of it.) Each of these troop members attended at least 2% of the episodes in 1973, but some individuals attended as many as 75%.

The data on capture and consumption show marked sexual differences. Adult males killed more frequently, and they alone practiced complex hunting. These differences did not stem from differential access to prey as the result of different locations within the troop (detailed in Strum, 1976a) but from significant differences in behavioral patterns. However, the dynamics of participation of individual males and females are not what might be predicted from the capture data.

The Male Pattern

Fluctuations in the predatory behavior of individual adult males were related to their interactions with other adults, male and female. For example, when a male was in sexual consort with a receptive female and then conflict occurred between maintaining proximity to the female and eating meat, the male chose to continue consortship. At times the male appeared to be deliberating, looking back and forth between the meat and the female, but finally chose to follow the female. In 1973, I observed 35 cases of conflict between consort and meat-eating behavior during predatory episodes. Resolution of such conflicts ranged from consort males entirely ignoring meat-eating opportunities to males allowing their consort females to have, keep, and eat the carcass. Even males with very high predatory scores chose estrous females over meat. Adult males following a consort pair also found themselves in situations where opportunities for consort behavior and meat-eating occurred simultaneously. Their response was similar to that of the consort male except for occasions when there was a large number of following males, when one

might approach a kill site for a brief period; however, he quickly followed the consort group whenever it moved.

During unstable periods in a relationship between two adult males, their participation in predation dropped noticeably, resuming only after the uncertainty was resolved. This was particularly apparent after the arrival and subsequent integration of a new male in the troop, which involved resident males in a series of dyadic interactions.

Adult male participation in predatory behavior was clearly influenced by social factors. While male scores for all aspects of predation (capture, attendance, consumption) were highest as a class, males gave predatory behavior a lower priority than either sexual behavior with receptive females or social behavior with other males.

The Female Pattern

Individual PHG adult females can be characterized as having high, medium, or low interest in predatory behavior, based on their frequency of attendance at consumption episodes and amount of meat eaten. High-interest females were present at kills and obtained meat with a frequency that fell well within the range for adult males (fig. 8.3). Neither rank, sexual

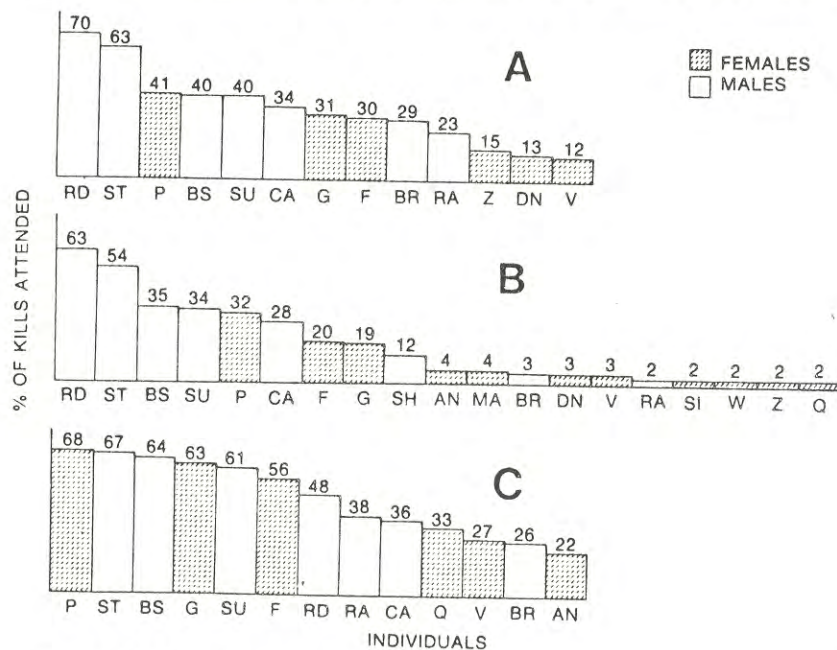


Figure 8.3. Attendance at kills by various members of PHG troop at Gilgil (1973). *A*, percentage of kills attended; *B*, percentage attended at which carcass or scraps were eaten; *C*, percentage attended at which only scraps were obtained. The top graph does not include individuals who attended less than 12% of the kills.

state, family size, nor the number of male or female associates appeared to influence a female's rank in predatory behavior (table 8.6).

For high-interest females, meat-eating took precedence over other behaviors, social or sexual. The interest of these females did not lessen when their own infants or the infants of female associates were born, or when they were in consort; indeed it was often the high-interest female who brought her consort to the kill. These females took advantage of opportunities passed up by their male partners, taking the carcass while the consort male threatened the previous consumer. The contrast between male and female behavior during consortships was exemplified by an incident in which the consort male copulated with and then groomed his female after an agonistic encounter with another male, while the female paid little attention to anything but the meat in her possession.

This suggests that the participation of high-interest females in predatory behavior is more constant than that of adult males. While a female may gain special access to meat through her social or sexual relationships, her interest in meat remains the same in varying social and sexual contexts. Meat ranks highest among incentives for these particular females, and their participation in predatory episodes contrasts markedly with that of males.

Duration of Bouts and Number of Participants

The behavior of the troop played an important role in determining the duration of consumption, the number and type of participants, and the timing of an individual's participation. Adult male PHG baboons were relatively mobile by comparison with adult females or immatures, but even males monitored the troop's behavior when beyond its periphery and responded accordingly. For instance, males who had no difficulty leaving the troop during a hunt showed signs of nervousness and vigilance after consumption had begun and time spent out of contact with the troop increased. Males abandoned a carcass prematurely to rejoin the troop. No captures by adult females and immatures occurred away from the troop, and these animals rarely joined in consumption until the meat was carried close to the periphery of the troop. When the troop moved, adult females and juveniles appeared more nervous than adult males, and attempted to keep the main group within sight. If they could not, then the prey was abandoned and the female or juvenile rejoined the troop.

A subgroup of adult males, adult females, and immatures often formed around the consumer of a carcass. If a sudden troop movement isolated the subgroup, females and immatures remained longer when an adult male was present than they did when one was not involved in consumption. The order of departure from the carcass indicated different distance thresholds for individual baboons and age-sex classes: first to leave were juveniles, then females, and finally males.

Aside from prey species differences (table 8.7), three factors influenced

Table 8.6. Participation of individual females in predation (1973)

	P	F	G	AN	MA	DN	V	SI	W	Z	Q
Consumption rank	1	2	3	4	4	5	5	6	6	6	6
Capture rank	3	3	—	3	3	3	—	—	2	1	—
Dominance rank	1	12	11	16	8	4	7	15	20	6	19
Family size (putative)	4	3	3	3	1	0	2	1	1	2	2
No. of male associates	5	1	0	2	2	0	4	0	0	2	1
No. of female associates	1	3	1	1	2	1	1	2	2	1	1
Sexual state	C/P	P/L	L	P/L	P/L	C	P/L	L/C/P	L/C/P	L/C/P	L/C/P

Note: Only the most interested female participants are listed in this table (11 of 21 adult females in the troop). Their sexual states are listed as C (cycling), P (pregnant), or L (lactating). Associates are defined by individual preference patterns in proximity and grooming. In case of ties in the capture and consumption scores, more than one individual was given the same rank. Dominance position rankings are consecutive and are based on the outcome of agonistic encounters (Strum, 1978).

Table 8.7. Participation in prey consumption (1973)

	Thomson's gazelle	Steenbok	Dikdik	Hare	Bird
Number of baboons attending					
Range	2-24	1-29	2-30	1-30	1-10
Mode	2, 8, 11	11	2, 20	2	3
Median	10	11	20	4	5
Total	312	74	112	252	41
Number of baboons fed					
Range	2-15	1-10	2-8	1-16	1-4
Mode	6	—	2	2	1, 2
Median	6	7	3	2	2
Total	184	34	29	129	16
Number of baboons feeding on carcass					
Range	1-6	1-7	1-4	1-5	1-2
Mode	3, 4	3	1	1	1
Median	4	3	1	1	1
Total	100	20	13	55	13
Time spent feeding on a carcass (min)					
Range	20-96	33-87	17-68	2-60	3-13
Mode	20	—	—	5	5
Median	51	37	33	10	7
Relative access to meat					
No. of episodes	28	6	7	39	9
Average attendance	11.1	12.3	16	6.5	4.6
Average no. fed	6.6	5.7	4.1	3.3	1.8
Average no. fed on carcass	3.6	3.3	1.9	1.4	1.4

Note: Of the 100 kills observed during 1973, 11 were not included because the data were incomplete. Of the 89 kills analyzed here, observations of 26 began after consumption was already under way. A total of 791 baboons attended these kills; 392 (49.6%) were able to feed on either carcass or scraps, and, of these, 201 (25.4%) got access to the carcass of the prey animal.

the duration of consumption: proximity to the troop, the troop's movements, and the number of participating baboons. Long consumptions took place close to the troop, with little troop movement, and with a large number of participants. Although the size of the prey limits the number of meat-eaters more obviously than it does the duration of consumption, the overlapping ranges of different prey species also reflect the influence of these social factors.

Table 8.6. Participation of individual females in predation (1973)

	P	F	G	AN	MA	DN	V	SI	W	Z	Q
Consumption rank	1	2	3	4	4	5	5	6	6	6	6
Capture rank	3	3	—	—	3	3	—	—	2	1	—
Dominance rank	1	12	11	16	8	4	7	15	20	6	19
Family size (putative)	4	3	3	3	1	0	2	1	1	2	2
No. of male associates	5	1	0	2	2	0	4	0	0	2	1
No. of female associates	1	3	1	1	2	1	1	2	2	1	1
Sexual state	C/P	P/L	L	P/L	P/L	C	P/L	L/C/P	L/C/P	L/C/P	L/C/P

Note: Only the most interested female participants are listed in this table (11 of 21 adult females in the troop). Their sexual states are listed as C (cycling), P (pregnant), or L (lactating). Associates are defined by individual preference patterns in proximity and grooming. In case of ties in the capture and consumption scores, more than one individual was given the same rank. Dominance position rankings are consecutive and are based on the outcome of agonistic encounters (Strum, 1978).

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VARIATION IN PREDATORY BEHAVIOR, 1970-1974

Notable changes in the predatory behavior of PHG baboons have occurred over the years, as shown during my 1973 study and by a comparison of my 1973 data with a 1970-1971 study by Harding (1973a, 1975). Further modifications have taken place since 1973. Because some of these occurred either between my study periods or during a break in observation from August 1974 until March 1975, detailed data on the dynamics of change from 1974-1977 are lacking, and I can only describe the results of the later changes.

Changing Capture Techniques

The main type of predation during 1970-1971 was opportunistic capture of concealed prey, but techniques of active searching (simple hunting) were also employed, though infrequently. Harding also observed an unsuccessful sequential chase of an infant Thomson's gazelle by male baboons.

The basically opportunistic nature of predatory behavior was still evident at the beginning of the 1973 study, but simple hunting increased in sophistication and persistence during 1973, culminating in the development of elaborate searching, stalking, and chasing, or what I have termed complex hunting. From December 1972 until July 1973 there was a steady increase in hunting distance, from less than 300 m to 4,000 m ($n = 18$). From August 1973 until January 1974, there was no perceptible change in complex-hunting distance ($n = 23$).²

Complex hunting increased in frequency from January to June of 1973³ and in number of simultaneous hunters (1-5) between January and September of 1973.⁴ At first, single males were responsible for most complex hunting, especially RD, who increased the amount of time he spent in search and scatter, or stalk and chase, behavior from 5 minutes (January, February) to 120 minutes (April, July). At the same time he increased the distance covered during the hunt and distance traveled between the troop and the nearest herd of tommies from 400 m (March) to 4,000 m (July). While RD was the most frequent hunter and most instrumental in the elaboration of complex hunting patterns, other males were also involved in individual fortuitous captures, then in solitary hunting, and finally in multiple efforts.

The sequential chase of Thomson's gazelle observed by Harding was both unsuccessful and probably fortuitous; there was no evidence that the baboons were consciously acting together. Midway in the 1973 study, I observed another instance that succeeded. From that point onward, male baboons changed the orientation of their chases when other hunting baboons were near. Prior to this incident, the prey individual was chased in

any direction, often out onto the open plain. Thereafter, baboon males chased Thomson's gazelles toward other hunters, and several kills resulted from sequential chases. Coordination of hunting activities between several males increased, as evidenced by the rise in the number of simultaneous hunters, from two in April to five in August. However, all incidents that ended with coordination still began with what appeared to me to be individual efforts.

Sometimes several male baboons stalked a herd of gazelles at the same time, often with different prey individuals as their objects. But once one baboon gained on his prey or was near success, others abandoned their individual efforts and converged on the prey. Sometimes this happened after the actual capture, and at other times sequential chases resulted (see "relay chases," Strum, 1975b). If the prey escaped and was not visible, then the assembled group of baboons searched simultaneously.

Whether these behaviors should be considered as "cooperation" (Strum, 1975b) rather than coordination depends both on the definition of the terms and on the degree to which one wishes to ascribe intention to the behavior of the individual baboons. Since social interactions among baboons, and between adult males in particular, are complex (e.g., their ability to ally against specific individuals or against a common threat from outside the group), the basis for strategy, coordination, and cooperation in behavior was already present. Normally these behaviors are used primarily in social situations, but I believe that the elaboration of hunting behavior by PHG males was simply an extension of their basic repertoire to a specific foraging situation.

Discrimination of Prey and Prey Response

Thomson's gazelle herds take three forms: all-male herds; mixed herds containing adult males, females, and young; and female herds with young. Initially the baboons did not distinguish between different types of herds during their complex hunting, and spent much time following, scattering, and searching through herds containing only adult males. As complex hunting developed, the baboons began to look briefly at all-male herds and then ignore them in favor of mixed herds or female herds. During the first 15 complex hunts, from March and May 1973, the baboon did not obviously discriminate between types of gazelle herds. During the sixteenth complex hunt in late May, one male did make this distinction, and at least one baboon hunter did so during the remaining 25 complex hunts observed, between June 1973 and January 1974. During this latter period, if a gazelle herd divided into subunits during a pursuit, the baboon hunter glanced quickly at each but followed only the group containing females and young.

Gazelle herds did not flee from or avoid PHG baboons in 1970-1971 or

for the first 6 months of the 1973 study. But in May 1973, the month with the highest complex-hunting rate, herds that had been hunted most recently or most frequently changed their behavior. They began to show vigilance, and a flight distance of 20–25 m was established. This distance increased during the next few months to 45–275 m, the normal range distance from predators such as lions (Walther, 1969). The change in response of Thomson's gazelle toward baboons was a process of adjustment in which at least certain herds began to recognize baboons as potentially effective predators.

Participants in Capture

Adult male baboons were the main predators in 1970–1971, capturing 44 prey animals. Adult females caught three hares, but male harassment forced two females to relinquish their prey. In 1973 the adult males still captured prey more frequently than did other age-sex classes, and they alone participated in complex hunting. However, females captured prey more often in 1973 than they had during the earlier study, including prey of more varying sizes (see table 8.4).

A change in female response to male harassment was also observed in 1973. Initially, females gave up their prey when approached or chased by males, as they had done in 1970–1971, but during the year they began to avoid adult male pursuers. In 1970–1971, females kept 33% of the prey they captured ($n = 3$), and in 1973 the figure rose to 43% ($n = 14$).⁵ Females lost all antelope prey but kept 60% of the hares and birds they captured.

Juvenile participation in capture began during the 1973 study, and I observed its initial stages. In April 1973 I saw three unsuccessful attempts to capture prey by juveniles, and in May the fourth juvenile seen to try hunting made a successful capture. Two juvenile kills were recorded in June, July, September, and November, three in August and December, and one in October. At first the juveniles were interested only in eating meat, but the successful appropriation of meat appeared to stimulate their interest in capture. Thus juveniles, as a class, started capturing prey after they had been exposed to meat-eating. The same was true of individual juveniles: attendance at consumption episodes consistently preceded attempts by those individuals to capture their own prey. Thus there was a clear sequence of events in individual juvenile participation:

1. Exposure to meat.
2. Obtaining meat fortuitously.
3. Consistent attendance at kills.
4. Attempts to obtain meat against opposition.
5. Opportunistic capture of small prey.
6. Opportunistic capture of larger prey.

Participants in Consumption

Harding noted that males were the major captors and the major consumers in 1970–1971, actively excluding other baboons from their prey (although females gained access to carcasses after males had discarded them). In contrast, by the beginning of the 1973 study, females were frequently present at kills and actively consumed their own prey or that of others. Juveniles and infants began to eat meat during 1973, with infants preceding juveniles. After an initial spurt, infant participation leveled off, while juvenile attendance and meat-eating continued to increase through the 1973 study (fig. 8.4).

Distribution of Meat

Elsewhere in Africa, baboons have not been observed to share food of any kind, either between a mother and her offspring or among adults (e.g., Altmann and Altmann, 1970; DeVore and Hall, 1965; Kummer, 1968; Ransom, 1971; Rowell, 1966; Stolz and Saayman, 1970), although a single piece of food, such as meat, is often consumed in serial fashion by several individuals.

Changes in the pattern of attendance and consumption affected the distribution of meat within the troop. The amount that some individuals obtained during the year was relatively small, but the widespread nature of meat-eating within the troop in 1973 contrasted with the 1970–1971 period.

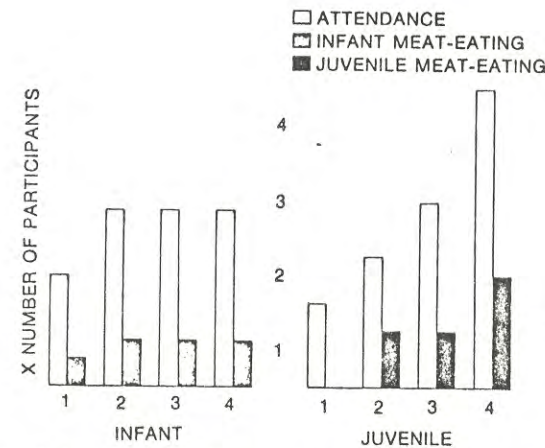


Figure 8.4. Infant and juvenile baboon participation in consumption of meat (1973). The 91 analyzed kills during 1973 are here divided into four groups; the first 22 are placed into quarter I, and the remaining kills are divided into three groups of 23 each.

Two additional changes in behavior were seen midway in the 1973 study: first, individual baboons moved to one side, leaving a significant portion of meat and allowing other individuals (of the opposite sex) to approach and feed in proximity; second, individuals fed from the same carcass simultaneously. Because the distribution of meat between individuals during these episodes differed from the serial distribution of meat seen at other times and was more active in its form, I classify these interactions as "sharing."

A total of 27 instances of sharing were observed in 6 months, beginning with Thomson's gazelle and later including other ungulates and hares. Sharing among adult males and females occurred as frequently in consort situations as outside them. Females shared with males and vice versa; however, sharing between adult males and females occurring outside of consort relationships took place only between adults with a previously established affiliative bond (see Social Factors, below, and table 8.8).

Mechanisms for Change in Predatory Behavior

The PHG baboons offer an unusual opportunity to examine the influence of social, individual, and ecological factors upon predatory behavior in a group-living primate species. Social mechanisms of change are the easiest for me to identify and interpret, since the purpose of my main research project was to describe the troop's social networks. A simple description of ecological variables involved in the changes is possible with the data collected over the years at Kekopey, but since these data are not detailed, they must be interpreted using comparisons with other sites where baboon predation has been observed. Finally, identifying individual factors that influence change is difficult: overt changes in the behavior of individual baboons were easy to observe and record, but motivation or psychological variables can only be inferred.

Social Factors. Among the many affiliative social networks that exist, several have important implications for the social dynamics of the troop and for the dynamics of change in predatory behavior over time. Of particular interest are special relationships between animals known or believed to be related, between adult males and adult females, and between adult males and immatures. Individuals involved in these relationships spent more time together, sought each other's proximity for feeding, resting, and sleeping activities, showed preference for each other as grooming partners, and supported each other during agonistic encounters.

The acquisition of a new behavior requires some type of learning. Investigators have described special requirements for primate learning: the animal must feel safe and secure, it must have a model to imitate, it must be motivated to approach and observe, and it must be motivated to repeat the behavior a number of times (e.g., DeVore, 1963; Hall, 1963a, 1968; Jay, 1962, 1963). The special affiliative relationships which existed in PHG

Table 8.8. Episodes of sharing

Nonsexual		Consort		Mother-offspring		Male-Male		Presumed siblings		Total										
♂	♀	♂	♀	Mo.	Off.	n	n	n	n	n										
1973 (1,200 observation hours)																				
BS	→P	6		BS	→P	4	F	→FO	4	RD	→CA	1								
RD	→F	2		SU	→P	4				ST	→RD	1								
RD	→P	2		CA	→P	2				ST	→PA	1								
1975 (250 observation hours)																				
SU	→P	1					P	→PA	1											
							F	→IA	2											
1976-1977 (792.5 observation hours)																				
GA	→F	1																		
Total		12		10		7				3										
		(35%)		(29%)		(21%)				(9%)										(5%) (100%)

Note: An episode is defined as one example of sharing between partners. There can be more than one sharing episode during a single predatory event if (1) different animals are involved, or (2) time and/or an interaction with other animals intervenes between two episodes. In all cases, *n* = number of episodes.

Male PA was an infant in 1973 and a juvenile in 1975, and the mother-offspring relationship between F and IA (1975) is inferred.

provided appropriate learning contexts and played an important role in the acquisition of certain aspects of predatory behavior by individuals.

Early in 1973 the participation of infants and juveniles in meat-eating was observed. The first infants observed attending kills were the offspring of females with a demonstrated interest in eating meat. These infants were there either because they were still dependent on their mothers or because they were attracted to the kill by their mother's presence, and thus their interest focused on their mother, not on the meat. But observation, investigation, and imitation resulted in meat-eating for infants of all ages.

Special relationships with adult males also influenced infant participation. These were especially important for infants whose mothers were not active participants in meat consumption but whose adult male associates were. An infant might approach when a male associate was attending a kill or when he actually had possession of some meat. Again, the primary attraction for the infant was the male associate, but proximity, observation, investigation, and imitation resulted in meat-eating here also.

A change in adult male possession of the carcass often had a marked effect on infant participation. For example, on one occasion several infants attended a kill with a male with whom they associated regularly. They had no special relationship with the male feeding on the carcass at the time and did not approach it or him. For over 45 minutes they stayed near their male associate, and when the previous consumer finally left and the second male took the carcass, the infants immediately rushed toward him and the meat, investigating the carcass and feeding on scraps that were nearby.

Similar changes occurred in juvenile participation in consumption. In general, juveniles first approached meat because an animal with which they maintained a special relationship was already eating. But juvenile play groups also approached a kill site *en masse*, stumbling across a meat-eating bout while chasing one another in play. They investigated as they would a novel object in the environment, but these investigations seemed to make little impression on a young baboon unless he or she actually obtained some meat. Once this happened, the successful juvenile appeared highly motivated, and meat became a high-priority incentive for juvenile after juvenile.⁶

During 1973, the different effects of adult male-adult female special relationships on female participation were observed. For example, of the two females with the greatest interest in meat, one had no special relationship with the most frequent male captor and consumer. Although she had a number of affiliative relationships with major male predators, her participation appeared relatively independent of them. On the other hand, the second female did have a strong affiliative bond with the major adult male predator, and her success in gaining proximity to meat appeared to be influenced by his presence.

Special relationships were less important in capture than in consumption, although such factors as degree of mobility and social facilitation played a definite role in adult male capture techniques. Male migration occurred frequently within the study population, and males wandered farther from the troop than did females during daily foraging, occasionally detaching themselves to visit distant food sources or another troop, although individuals varied in their day-to-day mobility from the troop. By contrast, females and immatures maintained continuous visual or auditory contact with the troop, and can be characterized as more attached to the troop than adult males, spatially, socially, and probably psychologically as well. The elaboration of hunting behavior during 1973 would not have been possible without this element of male mobility. At first, predatory opportunities were exploited only near the troop, but in time adult males wandered farther and farther. Predatory behavior did not initiate a totally new pattern of ranging for adult males, but existing patterns were modified in response to opportunities for predation.

Capture of prey was primarily a solitary activity, but predatory behavior of one male might stimulate the interest of others. In several cases, the efforts of one male to capture an animal appeared to set off additional attempts by the observing baboons. Overall, the increase in hunting by one male appeared to change the frequency of hunting in other PHG males.

While I could document the interactions through which these changes were accomplished, without controlled experiments I could not pinpoint the exact type of learning that might have been involved. Nevertheless, focusing of attention, communication of intent (predatory or otherwise), and facilitation of behavior were clearly operating within the existing social and motivational system of the adult male baboons. A different social milieu could have prevented or hindered the flow of information and the facilitation of behavior crucial to the elaboration of the baboon's pursuit behavior.

Individual Factors. Physiological and psychological developments occurring within individual animals can rarely be evaluated using field data. Yet our inability to detect these developments through field observations does not negate their importance. A change in primary predatory males that took place in PHG in 1973 provides some suggestion of the nature and role of individual variables in predatory behavior.

In 1970-1971, adult male CA was the most successful predator in PHG, and at the beginning of the 1973 study he maintained this position. RD was also an active predator at this time, but both his success and participation in capture and consumption were less than CA's. In meat-eating, CA appeared to directly limit RD's participation, as CA was able to actively displace RD from kills. Then CA suffered an injury to his hand that was serious enough to hamper his movement; for more than a month he had

difficulty keeping up with the troop, and this curtailed all his activities. CA continued to show interest in predation, but his success was impaired; his chases of prey were too slow and too short. When meat was being eaten, CA waited at a distance, whereas earlier he would have supplanted other animals and obtained the carcass.

After CA's injury, RD was more successful in keeping the meat that he had captured and in obtaining meat that others had captured. Whatever inhibition CA's behavior might have placed on RD was now eliminated, and RD increased his capture and consumption of prey markedly.

The changed relationship between CA and RD had several consequences, the most important of which resulted from RD's predatory behavior and its influence on the predatory behavior of the troop. RD was an integrated member of the troop who formed consortships, had a number of female and immature associates, and had well-defined relationships with other adult males. But he occupied a unique position in the troop, spatially and behaviorally. He was often at the rear (less frequently at the front) of troop movements (cf. Harding, 1977) and at the periphery of the troop when it was stationary. In foraging, he was the widest ranging of the males and readily detached himself from the troop to follow his own route and exploit distant resources. He was out of sight of the troop more frequently than any other individual. Thus RD, while integrated socially into the troop, was at one end of the range of variation in foraging and movement. His predatory behavior also followed this pattern, so that soon he traveled farther and farther from the troop in pursuit of prey, covering more distance than any of the other males had done under similar circumstances. RD also seemed highly motivated in his predatory behavior after CA's change of status, and it probably was his behavior that stimulated complex hunting among PHG males.

RD's effect on PHG baboon predatory behavior resembles the influence exerted on a Japanese macaque troop by specific individuals (Frisch, 1968). CA and RD had the same opportunities for capture, but CA did not respond in the same manner. CA was more attached to the troop, spatially and behaviorally, and even after the initiation of complex hunting, he did not travel as far from the troop to hunt as did most of the other males.⁷ The elaboration of hunting might not have occurred in PHG or might have taken a different form had RD, with his idiosyncratic behavior, not become the principal predatory male.

Ecological Factors. During the preceding 20 years, the study area had been altered for cattle raising by creation of additional grassland through bush-clearing, distribution of water to new areas, and destruction or removal of large predators. Largely as a result of these developments, much of the indigenous wildlife underwent a marked population expansion. For baboons this meant increased opportunities for predation, especially on

Thomson's gazelle. At the same time, baboons were less subject to attack by normal predators (other than man) and were also freer from competition with other predators that might prey on the same species and on the baboons as well.

The primate group, and especially the baboon troop, has been viewed by some as a basic adaptation to problems of defense against predation (A. Jolly, 1972; Simonds, 1974; Washburn and Hamburg, 1965). Animals living in groups are often thought to be in less danger because of the safety-in-numbers principle and because the combined defensive activity of several animals could act to deter a predator. The possibility of attack by large predators is irrelevant to opportunistic baboon hunting that occurs within or near the troop, but it is important in considering activities that take an individual away from and out of contact with the group. (In addition, of course, the presence of researchers reduced the exposure of PHG to attacks by humans.)

A bioenergetic approach to understanding predation, relying on time and energy considerations (e.g., Pianka, 1974; Schoener, 1971), requires that opportunistic predatory behavior be separated from that which involves systematic pursuit, since opportunistic capture costs the predator little in relation to the energy yielded by the prey, while systematic pursuit requires an investment of considerably more time and energy. Data on baboon time and energy budgets during foraging and prey pursuit are not currently available but are needed to determine the costs and benefits of different foraging strategies, a necessary step if baboon predation is ever to be understood in bioenergetic terms.

However, bioenergetic considerations can be applied to PHG baboon predation in another way. Since prolonged or systematic search and pursuit (complex hunting) requires an investment of time and energy, it is reasonable to assume that this effort would be directed toward situations where the likelihood of obtaining the benefits (energy, nutrients, social status, etc.) was increased. Extra effort devoted to hunting solitary animals or secretive animals that live in pairs might not sufficiently increase the chances of finding them to warrant the additional energy expenditure. Group-living prey could change the equation, however, for groups are easily visible and contain more individuals that might be suitable prey. The time and energy cost of hunting a group-living prey would be justified if it increased the chances of obtaining the benefits associated with meat.

PHG baboons take only prey that are smaller than themselves. This implies that baboons cannot easily solve the problems involved in capturing, killing, and consuming larger prey individuals. Since baboons have a generalized primate anatomy, they cannot match the speed of older antelopes, for example, and are limited to younger, less swift individuals. Animals that are small enough for a baboon to hold down do not need to be

killed before being consumed, and immature animals can be dismembered more easily.

Hands are essential to baboon predatory behavior and appear to compensate in part for a lack of predatory specializations. Hands allow a baboon to catch, hold, and consume an animal, but they alone are insufficient to overcome the prey size limitation.

If bioenergetic constraints limit complex hunting to prey living in groups, and if baboons cannot prey on individuals above a certain size because of anatomical restrictions, Thomson's gazelle is the only species at Gilgil that is appropriate for complex hunting.

Why Complex Hunting?

Opportunistic predatory behavior appears to be part of the species repertoire for baboons and may have its origins in protein or nutrient requirements. Thus meat-eating per se does not require explanation, but the development of systematic and extended pursuit by baboon predators does. Complex hunting by baboons, as I have defined it here, has been observed only at Gilgil, although other populations eat meat and take part in simple hunting. A synthesis of the social, individual, and ecological aspects of complex hunting by PHG baboons may help us arrive at an understanding of the changes in predatory patterns from 1970 to 1974. The following assumptions are made:

1. Complex hunting has bioenergetic constraints in which expenditure of time and energy should be offset by an increase in the likelihood of prey capture.
2. Baboons are limited to prey of a certain size by their ability to solve the problems of capture, kill, and consumption with a generalized primate anatomy.
3. In areas with a normal complement of predators, it is hazardous for baboons to engage in behavior that takes them away from the troop.
4. Humans have killed baboons for over 1 million years (Isaac, 1968). In most areas where baboons are found today, possible human intervention must be considered in evaluating baboon safety and behavior.
5. The existence of an abundance of prey and an absence of their usual predators provides new exploitative opportunities for baboons.

Thus the necessary conditions for the development of complex hunting may be the presence of suitably sized, group-living prey in high density, the absence of indigenous natural predators for these prey, and the baboons' relative safety from predation or interference by large feline or human predators.

Usually prey and predator densities go hand in hand; where there is prey in abundance, there are also predators. But at Kekopey there has been a

rare abundance of appropriate prey and absence of normal predators. In addition, the presence of researchers has provided some protection from human predation or interference in the general vicinity of the troop.

Although these may be the necessary conditions for elaboration of baboon hunting, they may not be both necessary *and* sufficient. Not all opportunities are exploited, even when they are obviously advantageous. What is ecologically possible must also mesh with what is socially and psychologically possible. Further conditions for the development of complex hunting behavior might include:

6. Presence of predatory behavior within the species repertoire and that of the group.
7. Individual mobility from the troop within foraging and social contexts.
8. Behavioral variability resulting in individual innovative behavior.
9. Social facilitative mechanisms.
10. Observational learning that allows the transmission of learned behavior from one individual to another.

Most of these conditions exist within any primate group, although the combination and degree of emphasis on each varies. It is apparent in examining PHG baboons that *all* of these conditions were met during 1973, including an especially important one: innovative behavior. The behavior of RD in particular appears to have provided a crucial impetus to the development of complex hunting, and for a time this type of pursuit became a pattern for other adult males as well.

This synthesis suggests that baboons would not practice complex hunting in areas where there are large predators, even when there are group-living prey species of appropriate size. This is the situation at Amboseli, Kenya (Altmann and Altmann, 1970; Hausfater, 1976), where baboons capture prey opportunistically and may pursue them over short distances but do not practice complex hunting [Altmann and Altmann (1970:41) described a male baboon who lagged behind during a predatory pursuit and became another's prey].

Elaboration of baboon hunting behavior could only be expected to occur in areas where group-living prey species the size of Thomson's gazelle or smaller exist in high densities and the usual large predators are absent. These conditions are very limited today in Africa. Group-living animals of appropriate size living in high densities include several species of antelope (Thomson's gazelle, Grant's gazelle, and their faunal equivalents in other parts of Africa), sympatric primate species, and domesticated animals, such as goats and sheep. Human intervention has resulted in widespread faunal destruction; thus the necessary combination of baboons, prey, and an absence of predators seldom occurs.

Appropriate conditions may exist in areas of South Africa where baboons are reported to prey frequently on the young of domesticated stock (Dart, 1963; Marais, 1939; Stoltz and Saayman, 1970), but it is unclear from these reports whether the South African baboons resemble PHG in their hunting behavior. If this pattern of predatory behavior is *not* found in baboon populations living under the appropriate ecological circumstances, some of the other social or individual variables are likely to be absent, especially the kind of innovative behavior reported here. However, PHG data from 1975–1977 also indicate that before predatory behavior can be incorporated into a group's repertoire over the long term, additional requirements must be met.

FURTHER CHANGES IN PREDATORY BEHAVIOR, 1975–1977

Changes that have taken place since 1975 are as marked as those occurring between 1970 and 1974. Unfortunately most of these changes began during a break in observation from August 1974 until March 1975, and therefore discussion of their cause must remain tentative.

Form of Predatory Behavior and Male Participation

Perhaps the most obvious change since 1975 is the cessation of complex hunting and the reduction in amount of simple hunting. Most predatory behavior has become accidental or opportunistic, and systematic searching for prey is rare, although once prey is encountered, pursuit may be systematic. The decline of complex hunting has been accompanied by a markedly decreased participation of adult males as a class in predatory behavior, as well as a striking change in individual male participation. In 1973, adult males were 14% of the troop (excluding infants, who are not potential predators) and accounted for 67% of those captures where the identity of the captor was known. In 1976–1977, adult males composed 20% of the troop, a slight increase, but were responsible for only 31% of all captures (table 8.9).

The participation of each individual male declined as well, particularly those males most involved in complex hunting during 1973. Although RD had been influential in initiating and elaborating complex hunting and was the primary predatory male in 1973, he was not observed to capture any prey during the short 1975 study, or during 1976–1977. The predatory behavior of the other three males (BS, BR, ST) declined similarly (table 8.10).

Although predatory behavior had already changed by the time of the 1975 study, major ecological factors can be excluded as explanations for the change. The drought continued through this period, and there were no

Table 8.9. Trends in prey capture by age-sex class

	1973		1975		1976–77	
	% of troop	% of captors	% of troop	% of captors	% of troop	% of captors
Males	14	67	19	29	20	31
Females	38	15	32	21	28	24
Juveniles	48	18	49	50	52	45
<i>n</i>	50	91	65	14	75	29

Note: Only instances where captors are known have been included here, and subadult males have been included under the "male" category. Since infants were not involved in prey capture, the numbers under "% of troop" refer to the troop size after infants had been subtracted.

Table 8.10. Participation in capture by adult males

	1970-1971 (1,032 hr)	1973 (1,200 hr)	1975 (250 hr)	1976-1977 (792.5 hr)
AL	3	—	—	—
MO	2	—	—	—
CA	18	13	—	—
SU	10	10	1	—
RD	5	18	0	0
BS	0	4	0	1
RA	—	1	—	—
BR	—	3	1	0
ST	—	9	1	2
GA	—	—	1	2
DR	—	—	0	0
MQ	—	—	0	0
RE	—	—	0	—
HD	—	0	0	1
TI	—	0	0	1
BL	—	0	0	1
SN	—	0	0	1

Note: Numbers in parentheses represent observation hours. Where no data appear, the male baboon either had not yet entered the troop or had already left it; a 0 means that the animal was present in the troop but was not observed to capture prey during that year. Male BS was a subadult in 1971 and an adult in 1973; RA entered at the end of 1972; ST and BR entered the troop midway through 1973; GA, DR, and MQ entered between July 1974 and March 1975; RE entered in June 1975; and HD, TI, BL, and SN were juveniles in 1973 and 1975 and subadult males in 1976-1977.

changes in rainfall pattern or in prey availability. Only social and demographic conditions changed, and since these factors were implicated in the previous modification of PHG predatory behavior, it seems reasonable that they influenced this second set of changes as well.

Males gave predatory behavior a low priority when it conflicted with social interactions with males and sexual behavior with receptive females. Major alterations had occurred in the male component of the troop between 1974 and 1975 with the immigration of four males, the emigration of three, and the maturation of seven. The instability caused by such flux and the increase in interactions among males which accompanied these events could account for some of the decline in male predatory interest.

Furthermore, the adult males who left PHG included two major predators: CA, followed shortly afterward by SU. The immigrating males tended to stay close to the troop, a behavior that conflicted with complex hunting. When one of these males had possession of a carcass and the troop departed, the male often abandoned the kill prematurely to keep up with the troop. During this period RD seemed unable to gain or retain

possession of carcasses. He continued to attend consumptions but patiently waited his turn, which might come after some females and juveniles had already eaten. RD's inability to keep his kills may have lowered his motivation to capture prey and especially to expend considerable time and energy in complex hunting. This would be a reverse of the proposed process which stimulated his predatory interest and behavior in 1973. The predatory motivation of ST, the other complex-hunting male remaining in the troop, may have been similarly influenced.

Whatever the correct explanation may be, the behavior of males has changed, both in the type and the amount of predatory behavior they practice. This is more than a simple reversion to the earlier pattern, for the males are now killing less and doing it less systematically than they did during 1970-1971. Thus, while predatory behavior seems established in the troop and independent of any one individual, the *form* that the behavior will take may depend on the motivations and possibly the personalities of the individuals within the troop.

Other Developments in Capture and Consumption

Adult female and juvenile participation in capture seems to have continued the trend identified during 1973, despite the general decline in predatory behavior. Females have increased their participation in capture, although they represent a smaller proportion of the potential captors within the troop (table 8.9). As in 1973, the change in female behavior is less marked than the change in juvenile behavior. Although their proportion in the troop has remained approximately the same, juveniles' participation in capture has more than doubled. The processes identified in the development of juvenile participation (during 1973) continue to apply, and the offspring of high-interest females or the immatures who developed predatory interest early are the highest-scoring individuals in this later period.

Special relationships played an important role in the spread of predatory behavior and in the development of meat-sharing in 1973. Sharing between baboons coincided with already-existing relationships between mothers and infants and between males and females. More sharing was observed in 1973 than in 1975-1977 (table 8.8). The explanation probably involves changes in the nature of existing relationships. In 1973, most sharing took place between four males and two females with whom the males had special relationships, but by 1977 two of these males (CA and SU) had left the troop, one of the males (BS) had a less intense relationship with the same female (P), and the fourth male (RD) no longer got much meat. Males feeding on a carcass in 1977, under circumstances that would have led to sharing in 1973, did not seem inclined to share with females, including the ones with whom special relationships existed. This led one female (P) to try

devious tactics to obtain meat from a new male (DR). First she tried to groom the male into a state of extreme relaxation and obtain some meat while he was not paying attention to her. The male soon realized the effectiveness of this tactic, however, and continued to allow her to groom him, but prevented her from actually seizing any meat. Her next tactic was to direct aggression at a female with whom the male was in association, thus creating for the male a situation of conflict between the meat and his sociosexual interests. The male then abandoned the meat and the female aggressor obtained it. Interested females such as the one described here took advantage of conflicts between males around kills to steal a temporarily neglected carcass.

The development of new special relationships did open opportunities for females whose access to meat had previously depended on other male affiliations that had waned. Thus, the second-highest-interest female (F) gained access to kills in 1973 as a result of her special relationship with RD. Both the decline in RD's predatory behavior and the decline in their special relationship decreased her opportunities for meat-eating, although she still attended kills frequently. However, a developing relationship with a new male (GA) increased her access to meat once more. Sharing between mothers and their offspring still occurred in 1977, and sharing between presumed siblings was documented.

Prey Species

There are differences in prey species profiles between the two periods. If the numbers of successful predations, complex hunts, and Thomson's gazelles captured in 1973 are compared by month, there is a significant correlation between complex hunts and Thomson's gazelles⁸ and between complex hunts and successful predations,⁹ but the correlation between successful predations and Thomson's gazelles captured is not significant. If these correlations were not chance events, then one would predict a decline in the proportion of Thomson's gazelles in the prey profile as complex hunting declined. The decline that occurred between 1975 and 1977 suggests that there is a causal link between complex hunting and Thomson's gazelles captured, and between complex hunting and the amount of successful predation.

If we compare the prey species taken in 1973 and in 1976–1977 (table 8.2), differences in the prey profile are largely due to an increase in the proportion of hares taken and a decrease in the proportion of Thomson's gazelles. Since there is no evidence that prey densities declined between the two periods, and since in 1976–1977 there were repeated examples of situations that would have elicited either simple or complex hunting during 1973 but were now ignored,¹⁰ at least part of the difference in prey profile reflects preferences of different age–sex classes and their differential

participation in capture (table 8.4). However, the type of prey taken by each age–sex class has changed as well. Of the animals caught by males, proportionately fewer were Thomson's gazelles and more were hares, while juveniles began to take more ungulate prey, a continuation of the behavior seen at the end of 1973. Therefore the decline in male participation, the disappearance of complex hunting, the increase in juvenile and female participation in capture, and shifts in prey preference of the various age–sex classes have all affected the PHG prey profile in 1976–1977.

Prey Response

As predatory techniques changed and complex hunting ceased, Thomson's gazelles changed their behavior toward baboon predators. In 1976–1977 herds were less wary of baboons than they were at the end of 1973, no longer fleeing when baboons approached or employing vigilance behavior. It became possible for a baboon to approach within 3–8 m of a gazelle, even a young one, without arousing suspicion. Gazelle mothers stopped herding infants away from the baboons, and the two species often fed peacefully in close proximity.

Scavenging

During a very tense and aggressive interaction between males in 1973, a male baboon briefly ate meat from the carcass of an animal which had not been seen to be captured by the baboons. Although this appeared to be a displacement activity rather than true feeding, it was still the first incident of its kind observed in this population of baboons; on other occasions, including experimental exposure of carcasses (Strum, 1976a), the baboons had investigated but ignored such opportunities when they had not witnessed the prey being captured or consumed by another baboon.

During 1976–1977 six cases were reported of baboons eating animals which they found already dead. Three times they ate a hare (personal observation with D. Manzanillo; J. Stone, D. Harding, personal communications), once they fed on the disarticulated leg of an impala (personal observation), once they ate a bird electrocuted by high-tension wires (M. Demment, personal communication), and once they ate a bird found dead in a trap (personal observation). One of the hares was decapitated and already stiff, and the impala leg and two birds were still warm. In the most recent hare incident, the carcass was treated as if the baboons had captured it themselves.

The PHG baboons have exploited more opportunities to eat dead animals during 1976–1977 than they have in the past: using my data only, in 1973 one case was seen during 1,200 hours of observation that could be classified as scavenging, compared to three cases in 792.5 hours during 1976–1977. Furthermore, opportunities to eat dead animals were ignored

in previous years, whereas no such opportunity was missed in 1976–1977; interestingly, as more chances for predatory behavior have been ignored, scavenging has increased.

Rates of Predation

Predatory behavior and, by extension, rates of predation are obviously influenced by the demographic characteristics of the predatory species, their social behavior, and ecological considerations such as prey density and availability. Table 8.11 shows four different ways in which a rate of predation might be constructed, although each method is inadequate to some degree. Method 1 provides a rate uncorrected for any biases. Method 2 attempts to correct for number of animals in the troop (see Hausfater, 1976) but the rate is distorted to a greater or lesser degree, depending on the demographic structure of the troop, because infants are included in the figures. Method 3 corrects Method 2 by eliminating infants (who are not potential captors) from the calculation, but it does not correct for differential participation of age–sex classes in capture. Method 4, a first attempt at incorporating differential age–sex class participation into the construction of a predatory rate is based on the 1973 PHG baboon data. At that time it seemed appropriate to weight males more heavily as potential predators, the assumption being that the significant male proportion of participation in capture would remain relatively constant. However, the 1976–1977 PHG data contradict this assumption, further illustrating how difficult it is to make comparisons of rates. Whichever method is used, the predatory rate of PHG baboons has declined by one-half or more between

Table 8.11. Methods of estimating predation rates at Gilgil

	1970–1971	1973	1975	1976–1977
Method 1 ^a	22	12	16	17
Method 2 ^b	1076	756	1312	1534
Method 3 ^c	856	600	1016	1265
Method 4 ^d	747	425	739	927

Note: Figures are number of observation hours necessary to log one kill, calculated according to the following formulas:

- $\frac{\text{observation hours}}{\text{number of kills}}$
- $\frac{\text{observation hours} \times \text{troop size}}{\text{number of kills}}$
- $\frac{\text{observation hours} \times \text{troop size (less infants)}}{\text{number of kills}}$
- $\frac{\text{observation hours} \times [M + \frac{2}{3}(N - M)]}{\text{number of kills}}$

where N = troop size less infants, and M = adult and subadult males.

1973 and 1976–1977. The 1975 rate, although from a shorter time period, seems to be intermediate between the two.

It is difficult to attribute the changing rate to demographic changes, because there were more potential captors and also more male captors in the later period, and thus one would expect the predatory rate to increase rather than decrease. The decline in rate is not likely to be the result of reduced prey density, as we know of no reduction in prey populations. Although prey availability may have been different between the study periods because of the complex interaction between prey movements and predator ranging patterns, the baboons ignored too many potential opportunities each month to make that a convincing explanation.

In all probability, the change in rate reflects actual changes in the behavior (and motivation) of the baboon predators. The predatory behavior of adult males has changed, both in overall participation and in complex hunting of Thomson's gazelles, but there also seems to be a general decline in predatory behavior by all age–sex classes which requires explanation. There may be ecological or nutritional factors, in addition to the social ones already identified, that contributed to the decline in PHG predatory behavior; a simple ecological explanation is unlikely, however, as drought conditions persisted throughout this period.

Conclusions from the 1976–1977 Data

Although PHG baboons still captured prey and ate meat frequently, by 1976–1977 the form of this behavior had changed once again. They no longer hunted over long distances or used relatively sophisticated tactics to capture Thomson's gazelle. Gazelle herds were less wary of baboons than in 1973, perhaps because of the decline of complex hunting. Young baboons were still introduced to meat-eating as they had been in 1973, and the social interactions around the consumption of a carcass were similar although there was less sharing of meat. Females and juveniles continued their trend toward greater participation in capture whereas male participation declined significantly. Males took fewer Thomson's gazelle, while juveniles took proportionately more than they ever had. The overall predatory rate decreased by more than half, and opportunities for predatory behavior were routinely ignored. At the same time, scavenging, though still rare, was slightly more frequent than before.

The 1976–1977 data on predatory behavior in PHG may raise more issues than they settle, but they emphasize several important points. Social processes are influential in predatory behavior, and we cannot assume that this behavior will remain unchanged over time. The evolution of behavior cannot be seen in orthogenetic terms, for reversals in behavioral development may be the rule, rather than the exception, in dynamic and complex social systems.

Male predatory behavior may be more flexible and more subject to change than female predatory behavior. This hypothesis fits well with what is known about other aspects of baboon behavior: females appear to be the conservative and stable element while males' relationships are more fluid and dynamic (Hausfater, 1975; Strum, 1978, n.d.).

The 1976–1977 data on predatory behavior demonstrate the sometimes crucial role of individual motivation. Although the baboons had the same opportunities to hunt Thomson's gazelle in 1977, they no longer practiced complex hunting. Complex hunting appeared to be an effective predatory pattern, and it is thus all the more curious that it was so quickly extinguished. Why was there a decline in general predatory behavior, in particular among adult males, who had previously been the major predators? Why should the baboons scavenge more than before, while at the same time ignoring many chances to capture prey for themselves?

Finally, the recent changes in predatory behavior, although not documented as thoroughly as the changes that took place between 1970–1971 and 1973, raise the same important questions. How and why does a new behavior pattern develop, and how and why does the new pattern become incorporated into a group's permanent behavioral repertoire? The 1975–1977 data suggest that innovation, cultural transmission, and success and efficiency of a pattern, as seen in 1973, may be necessary for the initial incorporation of behaviors, but may not be sufficient to maintain them in a group over a longer period of time, even though ecological conditions remain constant.

DISCUSSION

Teleki's discussion of primate subsistence patterns (1975) emphasizes that subsistence behavior within the order Primates, and predatory behavior in particular, exists along a continuum. To interpret the evolution of human subsistence patterns, we must use a variety of information. Studies of baboon and chimpanzee behavior have identified a primate potential for predation. Comparison of this evidence with the behavior of living human hunters should provide insights into the way in which predatory behavior developed during the course of hominid evolution. The time scale of change and the sequence of events can be determined by the fossil evidence of hominid remains, both their bones and their cultural assemblages. Speculations about the mechanisms leading to change during hominid evolution should then derive from the evidence of the predatory behavior of human and nonhuman primates, as well as from the behavior of social carnivores.

As a starting point, I suggest that a crucial difference between nonhuman and human primate predators is that humans can hunt game as large as or

larger than themselves. Given the difficulties faced by a small unspecialized primate in the capture, killing, and consumption of large prey, determining the means by which the early hominids overcame these limitations becomes a vital task if we are to understand the human position on the primate subsistence continuum.

The time when the transition from predation on small animals to hunting of large ones took place is uncertain and depends on interpretations of the fossil evidence. Which (if any) of the known early hominids made this transition is complicated by the number of different hominid species that coexisted during the Plio-Pleistocene (Day, Leakey, and Wood, 1975; Day et al., 1975; F. C. Howell, 1969; Johanson and Coppens, 1976; Johanson, Taieb, and Coppens, 1978; Johanson, White, and Coppens, 1978; R. E. Leakey, 1971, 1972, 1973, 1976), and by questions about the nature of the association between the hominids and the fauna found with them. New data have revived old issues about who were the hunters and who the hunted (e.g., Dart, 1949; Washburn, 1957), about which hominids and which cultural assemblages belong together (e.g., Dart, 1957; L. S. B. Leakey, Tobias, and Napier, 1964; Robinson, 1963), about the relationship between hunting behavior and hominid anatomy (e.g., Bartholomew and Birdsall, 1953; Laughlin, 1968; Dart, 1949; Washburn and Avis, 1958), and about the importance of technology, communication, and brain expansion to predation on large game (e.g., B. Campbell, 1966; Holloway, 1966; Oakley, 1961; Washburn and DeVore, 1961; Washburn and Lancaster, 1968).

If the fauna found in association with the australopithecines was killed and eaten by these hominids, then it is apparent that a small-brained, bipedal hominid with a relatively simple tool assemblage successfully solved the problems of predation on large game. If the newly found hominid forms with their larger brains were hunters and tool-makers, then past arguments about the relationship of increasing brain size and predation on large animals may still be valid. Yet the nonhuman predation data suggest the possibility that early hominids could have practiced a variety of subsistence patterns (e.g., Schaller and Lowther, 1969; Teleki, 1975) with different lineages or different populations possessing unique variations.

There is less controversy about the evolutionary status and behavior of Middle Pleistocene hominids, collectively referred to as *Homo erectus* (Howell, 1966, 1967; Howell and Clark, 1963; Howells, 1967; Isaac, 1968; Mann, 1971; Pilbeam, 1970, 1975). These hominids regularly hunted large game and had larger brains, more advanced toolkits, and knowledge and use of fire. The elaboration of their material culture may have been instrumental in the expansion of their distribution from the tropics to the temperate zones of the Old World. Isaac (1975) has argued that, given the

current archaeological evidence, the contrast between Lower and Middle Pleistocene hominid predatory behavior was not marked, with only a slight increase in large mammalian prey and more remains of individuals of gregarious animal species.

Although there is disagreement over the interpretation of the fossil record, the contrast between hominid and nonhuman primate predator behavior indicates that there was a transition from a collector/predator pattern to a gatherer/hunter one, in which prey individuals larger than the primate predator were successfully captured, killed, dismembered, and consumed.

Study of the predatory behavior of the PHG baboons is useful to the interpretation of human evolution in two ways. First, it serves to establish a baseline for the subsistence behavior of nonhuman primates, and especially for the predatory component of this behavior. From this foundation, intelligent questions about the changes which had to occur during the course of human evolution can be formulated. But beyond that, assuming that the early hominids were at least as complex as the PHG baboons, we can make specific speculations about precursors to later human behaviors and about processes that facilitated or inhibited changes in the general pattern of behaviors.

Perhaps it is the multiplicity of factors contributing to changes in predatory behavior which is the most important new emphasis resulting from the PHG evidence. In particular, the elaboration of predatory pursuit to include complex hunting in PHG in 1973 can be seen as a response to the rare convergence of a number of factors: an abundance of group-living prey of appropriate size, the reduced numbers of natural predators, the innovative behavior of a specific baboon, and the influence of that individual's behavior on other group members.

These data suggest that explanation of adaptive shifts by hominid predators should take into account the importance of ecological, social, and individual variables, since no one of these would be sufficient to explain the exploitation of a new opportunity. Hooton's observation that "a cat does not become a walrus because of an inundation; it either drowns or scuttles away to dry land" (1931) is particularly relevant to those discussions of hominid evolutionary events which primarily emphasize ecological factors. Selective forces in the Plio-Pleistocene period were operating on a primate species which already had certain predispositions, and not on a *tabula rasa*. Obviously there was an interaction between predatory behavior, as performed by a primate, and those adaptations existing at the time the initial adaptive shift to a gatherer/hunter subsistence pattern occurred. It may be important to consider the susceptibility of these basic adaptive patterns to modification, their advantages and disadvantages for a hominid predator, and the compromises

in behavior and social organization necessary and possible once a gatherer/hunter mode of subsistence became important to a group-living primate. Furthermore, as the 1975-1977 PHG data demonstrate, changes in predatory behavior can come without any major change in ecological conditions. This would suggest that predatory behavior, although part of a subsistence pattern, at times might change as a result of social or other stimuli not normally conceptually linked with subsistence.

Changes in predatory behavior among the PHG baboons depended on both elaboration of existing elements in their repertoire and on innovation, the creation of new elements. For example, the mobility of the adult males in general foraging and in group transfer made some aspects of their predatory behavior possible. Strategies and cognitive abilities necessary in nonpredatory contexts may have been preadaptive for more elaborate predation. Adult male baboons cooperate with each other in response to threats from within the group or outside of it, and this cooperative experience may have facilitated the coordination of male predatory behavior seen in 1973.

Innovation in the context of subsistence is not rare in nonhuman primates, and some of the changes in PHG baboon predation between 1970 and 1977 can probably be attributed to this factor alone. Variability in primate behavior and personality can be an important source of innovations (Frisch, 1968; Green, 1975; Itani and Nishimura, 1973). Once an innovation occurs, individuals acquire the new behavior through learning. How and from whom they learn depends on the type of behavior and the nature of communication and affiliation networks within the group (for other primate examples, see Beck, 1975; DeVore, 1963; Hall, 1962, 1963, 1968; Jay, 1963; Kawai, 1965; Kawamura, 1959; Rogers, 1973).

The initial success of the PHG male predators may have reflected the hitherto peaceful relationship between them and their prey. At first, it may have been relatively easy for baboons to get close to a Thomson's gazelle with a minimum of effort, time, and strategy. With increased hunting by baboons, gazelle herds modified their behavior, instituting and increasing flight distance, vigilance, and protective maneuvers. This increased wariness made approaching and stalking more difficult for baboon hunters, and the greater amount of time which baboons spent hunting in 1973 may reflect both their interest in predation and the newer difficulties involved in pursuit. Thus the success of the hunting behavior itself may have provided negative feedback in which initial elaboration of techniques increased prey avoidance and success simultaneously. Baboons then required more time and effort to be as successful as they had been; thus the conditions for further elaboration of hunting techniques were created but additional innovations may have been beyond baboon capabilities.

Although all the members of PHG troop (except infants) are potentially

capable of certain kinds of predatory behavior and most have an interest in meat to motivate them in the performance of these behaviors, there are limits on participation even for very interested individuals. These include the existing group structure, established patterns of interaction, and underlying emotions. "Learning often involves the differential strengthening of existing behavioral tendencies rather than the establishment of entirely new ones" (Bitterman, 1975:699).

The most highly motivated female baboon, with or without a dependent infant, never took part in a complex hunt although she was physically capable of doing so. By contrast, when the potential victim was near the troop, she chased and captured prey animals equal in size to those hunted by the males. Male participation was also controlled by individual differences in mobility. The different priorities that PHG males and females gave to meat-eating suggests that male reproductive strategies may have strongly limited the degree of male involvement in predation while female reproductive strategies did not.

Let us apply the information on PHG baboon predation to make suggestions about human evolutionary events. Here I am not using baboons as a model for hominids but rather as an illustration of how a primate system operates and how behavior might change. The divergence of the hominids from the nonhuman primates in such areas as cooperation, strategy, division of labor, and certain cognitive abilities is widely discussed by authors concerned with human behavior. The PHG baboon data illustrate that these behaviors, which would be critical to a primate predator attempting to capture large game, have precursors among the nonhuman primates. Differences between human and nonhuman primates could have resulted from increasing selection for certain behaviors that differentially strengthened existing tendencies. For example, those writing about the role of hunting in human evolution (e.g., B. Campbell, 1966; Laughlin, 1968; Lee and DeVore, 1968a; Pfeiffer, 1969; Tiger, 1969; Washburn and Lancaster, 1968) have speculated that the origin of human sexual division of labor is to be found in hunting for prey that included large animals. But the PHG data suggest that even among collector/predators a difference in male and female predatory behavior exists that may reflect basic differences in the way male and female primates are integrated into the group, and perhaps differences in reproductive strategies for the two sexes as well. Chimpanzee predation, tool use, and insect exploitation (McGrew, 1974; Teleki, 1974, 1975) also support such a notion. Sexual differences may have originated before the shift from collector/predator to gatherer/hunter took place, while males but not females engaging in certain aspects of predatory behavior. The infant dependency argument which has been advanced as part of the hunting/sexual division of labor position may still be valid, for once hominids had larger brains, more helpless infants,

and longer periods of infant dependency, the problems of infant care could have further contributed to whatever patterns already existed.

Sexual division of labor is intimately tied to reproductive strategies of males and females, for all mammals. For PHG baboons, reproductive strategies may limit a male's ability to participate in predatory behavior and place a ceiling on the development of predation as an important subsistence activity. If a similar system existed among early hominids, a major change in reproductive strategies would have been necessary before males could give predation the priority it needed as a prelude to further division of labor between the sexes. This is not a novel suggestion but is a more plausible one now that there are some data demonstrating the limitations that the nonhuman primate pattern places on elaboration of a subsistence economy based on hunting and gathering.

How did changes occur? As was the case with the PHG baboons, changes in hominid behaviors could have resulted from innovation; the behavior of one hominid could have provided an initial impetus for the group (and population). I am not implying that such a possibility existed only once, in one individual of one group at a particular time. Rather, I suggest that the potential for innovation and exploitation of new opportunities could have existed in many groups, under suitable conditions.

Once an innovation occurs, its development and elaboration may be quite rapid, if the PHG baboon data provide a reasonable model. In the past, theories about human evolution have often assumed that adaptive changes occurred slowly and were irreversible, but the PHG data show that rates of change can be more variable when the behaviors involve learning. Once a new behavior pattern is introduced, its acquisition and elaboration may proceed rapidly, among hominids as well as baboons. Since some behaviors are appropriate only under a complex set of conditions, changes in those conditions will affect such behaviors. As the more recent PHG baboon data illustrate, behaviors can become extinct as rapidly as they are elaborated, and reversals or rapid alternations may have been common in human evolution. As I have speculated was the case with baboon predators, the initial stages of the hominid adaptive shift to predation on large game may have been facilitated by the newness of the predatory behavior and the consequent lack of effective prey response. When predation became successful, prey wariness may have increased as well, producing a situation that required improved hunting techniques to achieve essentially the same results. If the members of a hominid group were not capable of further innovations (as may have been the case with the PHG baboon predators), the development of predatory behavior would not have proceeded any farther.

Burton and Bick discuss the phenomenon of a deme-wide shift in behavior following an innovation by an individual, and label it "tradition

drift." They raise important questions about "when, how, and how frequently do behavioral innovations occur, who are the innovators, what are the conditions for the spread of such innovations within a deme, how rapidly do such innovations spread, how much innovation loss occurs, when can we say that such innovations have become fixed in the behavioral/pool-repertoire, etc.?" (1972:58). These questions are particularly relevant to the development of primate and hominid predatory behavior over both short and long terms. The PHG data show that many conditions are necessary for the initial incorporation of behaviors into a group's repertoire but these same conditions may not be sufficient to maintain the behaviors over a longer period of time.

The PHG baboon data (along with evidence from other baboon and chimpanzee predator populations) suggest that primate predatory habits could have occurred and developed in a variety of habitats, given the appropriate ecological, social, and individual opportunities. But if elaborate hunting behavior has important bioenergetic determinants, then some habitats would be especially suitable for the hominid development of large-game hunting. For example, a forest habitat has few species of large animals and few communal species; prey exist there in low density and wide distribution, and visibility is poor. These conditions would make the development of predation on large animals unlikely. By contrast, the savannah, with its great numbers of large, group-living prey, would provide frequent opportunities for this type of hunting to develop. Thus, if the evolution of predation within the primate order was a graded process, the adaptive shift that included large animals as prey probably occurred in open savannah or open woodland. Once predation on large animals became an established pattern, improved techniques or special ecological conditions could have made hunting the larger forest species feasible, or necessary.

The PHG baboon data also argue against single-origin explanations of hominid hunting behavior (see Teleki, 1975, for chimpanzee evidence). Population variability in predatory behavior appears to be the norm, not only among baboons but also among chimpanzees (J. Goodall, 1963b; Suzuki, 1969; Teleki, 1973a,b; Wrangham, 1975) and social carnivores (Kleiman and Eisenberg, 1973; Kruuk, 1972).

Just where and how scavenging fits into the evolution of human predatory behavior is still debated (Bartholomew and Birdsell, 1953; W. E. L. Clark, 1967; Reynolds, 1966; Schaller and Lowther, 1969). Whether scavenging played an important role cannot be decided by the data now available on nonhuman primates. However, the complexity of the relationship between hunting and scavenging was demonstrated in 1976, when the PHG baboons ignored usual opportunities to capture prey while eating more dead animals than in the previous years. The PHG material does sound a note of

caution—the relationship of scavenging to hunting may not be as simple as often conceived of in discussions of hominid evolution.

The primate potential for predatory behavior is well illustrated by the data on PHG baboons, which add to our understanding of the continuum of predatory behavior within the order Primates and clarify some of the issues in the evolution of human behavior. In particular, they provide an example of how a predatory potential can be elaborated, and how complex the adaptive shifts in primate groups can be. As a result we have a better, albeit only partial, understanding of the multiple factors at work and how these can interact.

The predatory behavior of the earliest hominids may have been similar to that of today's baboons or chimpanzees, and could have originated many times, among groups in different populations living under differing ecological conditions. But there was an additional transition that involved a shift from a "collector/predator" mode of subsistence to a "gatherer/hunter" mode including predation on large animals. The fact that nonhuman primates can be sophisticated and successful hunters of small animals, without elaborate tools or more advanced systems of communication, does not repudiate ideas about the importance of (large-game) hunting in human evolution. Instead, the comparison clarifies the limitations of nonhuman primate predatory behavior and the unique aspects of the human predatory pattern. What baboon and human hunters do is different: to hunt just one large animal requires solutions to specific problems which, based on the current evidence, appear to be outside the reach of nonhuman primates. Artificial barriers in the evolutionary continuum should not be constructed to assure the unique status of hominid behavior, but at the same time we must recognize the crucial difference between similarity and identity.

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NOTES

1. Age-sex classifications used in both text and tables are: infant, 0-12 months; juvenile female, 1-4 years; juvenile male, 1-5 years; subadult male, 5-8 years; subadult female, 4-5 years; adult female, >5 years; adult male, >8 years. Where subadult is not a separate category

in text or tables, these individuals are included in the adult category. Juvenile males and females are usually combined.

2. The best fit line calculated for these data has the characteristics: $y = 0.06x - 0.23$. Regression analysis shows that $F = 11.602$, where rejection at the .005 level takes place at $F = 10.64$.

3. Using a runs test for trend data, analysis of change in complex hunting rate from January through May of 1973 yields a t_s of 3.51, where rejection at the .001 level is 3.29 for departure from a random trend.

4. Using a runs test for trend data, analysis of change in number of simultaneous hunters in complex hunts from March through August of 1973 yields a t_s of 3.51, where rejection at the .001 level is 3.29 for departure from a random trend. The trend is for an increase in the average number of simultaneous hunters (1 to 3) and the greatest number of simultaneous hunters (1 to 5) in hunts per month.

5. A χ^2 test with a Yates correction for continuity comparing the ability of females to retain captured prey in 1973 with that in 1970–1971 shows a significant difference: $\chi^2 = 3.85$, with 1 d.f., $p = .05$.

6. In comparing the monthly attendance of 12 juveniles at predatory episodes before and after they first gained access to meat, the hypothesis that these two sets of data had the same distribution can be rejected using a χ^2 evaluation for goodness of fit: $\chi^2 = 70.63$, with 11 d.f., where rejection at the $p = .001$ level is at 31.2.

7. The average distance traveled from the troop during complex hunts from March 1973 through January 1974 was as follows: RD, 1200 m; ST, 1060 m; SU, 800 m; BS, 800 m; BR, 645 m; RA, 645 m; CA, 530 m.

8. $r = .593$, $\alpha = .01$.

9. $r = .75$, $\alpha = .001$.

10. In 1976–1977, the PHG baboons failed to take advantage of opportunities to prey on Thomson's gazelle at a rate of one case every 21 hours of observation. This contrasts with a rate of one case every 226 hours from May 1973 until January 1974, when the same scan sampling technique was used.

The Omnivorous Diet and Eclectic Feeding Habits of Chimpanzees in Gombe National Park, Tanzania

A century ago, long before accurate information on the dietary patterns and feeding habits of wild primates was available, some naturalists were open-minded enough to speculate that faunal resources, including vertebrate meat, were occasionally exploited by the nonhuman members of the order Primates (e.g., Hartmann, 1886). Between the 1880s and the 1960s (when firm data on primate feeding habits began to accumulate from numerous field studies), many eminent scientists concerned with human evolution adopted the notion that all nonhuman primates are, and always were, plant-eating mammals, that monkeys and apes do not hunt prey or share food (e.g., Spuhler, 1965). Even those professionals who presumably knew of Jane Goodall's preliminary observations (1963b) on chimpanzee hunting behavior had become so locked into viewing primates as vegetarians that they described these predatory apes as "unusual" and "atypical" of the species (e.g., Morris and Morris, 1966) or as "deviant" in their behavior (Thompson, 1975).

How this shift of opinion occurred when no additional evidence was obtained during those years is baffling, for it is widely claimed that scientific thought progresses in tandem with accumulation of reliable information. I would venture, in retrospect, that changing perceptions in the arena of paleoanthropology, especially among those bent on promoting a "man-the-hunter" interpretation of human evolution, played a basic role in establishing belief in the existence of a vegetarian primate prototype. It was vital, given the nature of the hypothesis, to have a plant-eating, tree-living, forest dweller as ancestor to the emergent primate novelty—a meat-eating, ground-living, savannah-dwelling hominid.

Launched in the 1920s, this view continues to lead a robust and healthy life (Wood Jones, 1926; Pfeiffer, 1978). Indeed, the premise that hunting behavior was a unique development—a pivotal adaptation—of the hominid line has become the prevailing doctrine, stated and restated in most of our textbooks (e.g., B. Campbell, 1974; Fagan, 1974) and in popular literature