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Baboon Cues for Eating Meat

Two types of manipulations were performed with a troop of predatory baboons to elucidate the cues which individuals use in eating meat. Gazelle carcasses which had been killed, consumed and abandoned by the baboons were presented to various members of the troop. Live domestic rabbits were also placed among the troop. Gazelle carcasses were eaten by individuals who had eaten from the carcass earlier in the day or who had seen other baboons eating the carcass, and were avoided by individuals who had no prior experience with the carcass. Rabbits were investigated, groomed or rejected although one predation did occur.

These data suggest a complex process of evaluation in baboon meat-eating in which social cues can be an overriding factor. The data also argue for a conservatism in baboon consumption of meat which may have an evolutionary basis. Such a conservatism could provide an inhibition to scavenging among non-human primates and has implications for models of human evolution which posit a scavenging stage. These implications are discussed.

1. Introduction

Predatory behavior is widespread but infrequently practised among non-human primates, and has been extensively described for several wild populations (for review see Teleki, 1975; Strum, 1975, 1976*a*, 1981; see also Hausfater, 1976; Busse, 1977*a*, *b*; McGrew *et al.*, 1978; Hamilton & Busse, 1978; Rose, 1978; Nishida *et al.*, 1979; Kortlandt, 1967, 1972, 1980). There is little agreement on the cause of primate predatory behavior and the causal factors granted greatest legitimacy have shifted in accord with the historical trend in explanations of primate behavior. The candidates can be classified under two broad categories: social hypotheses and foraging hypotheses (see Hamilton & Busse, 1978, for a more extensive discussion of some of these hypotheses).

Social hypotheses of predation have attracted great interest. Ardrey (1961) produced what is perhaps the best known popular view of primate predation suggesting a strong link between social aggression and predation. Other social hypotheses derive primarily from data on chimpanzees. For example, in Kortlandt's view (1972, 1980) predation is a method to control food competition by eliminating the competitor. At the same time, predation can act as a masculine display involving intimidation and the redirection of aggression. Chimpanzee predation in the Gombe Stream population is most comprehensively described by Teleki (1973). He interprets predation to be a means to enhance an individual's social status. Wrangham's data on the same population (1975) suggest an element of social appeasement during meat consumption which prevents feeding interference but other aspects of predatory behavior are not seen as socially induced.

Predation is viewed as a foraging strategy by more researchers than those who advocate social hypotheses. Yet different authors emphasize different aspects, such as the nutritional value of meat in a primate's diet (Dart, 1963; Kortlandt & Kooij, 1963; Jolly, 1972; Hausfater, 1976; DePelham & Burton, 1977) or the energy advantage of eating meat (Gaulin & Kurland, 1976; Hamilton & Busse, 1978). Predation is also seen as part of a

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diversified feeding strategy (Kortlandt & Kooij, 1963; Wrangham, 1975; Busse, 1977*b*, Rose, 1978).

The evidence that some primates are cannibalistic (Suzuki, 1971; Bygott, 1972; Nishida *et al.*, 1979; Goodall *et al.*, 1979) confuses the situation further. Are cannibalistic chimps stimulated to predatory pursuit of their own species by social stress (Kortlandt, 1972; Teleki, 1975) or are they executing a reproductive strategy where infanticide (Hrdy, 1974) is extended to include consumption of the victim (Nishida *et al.*, 1979)?

Observers of primate predation are in all likelihood witnessing the simultaneous effect of several factors and the relative importance of one over another may shift between species, between populations or between groups in the same population. The best primate predation data derive from baboon and chimpanzee populations as do most of the hypothetical explanations. Careful scrutiny of these data suggest that baboon and chimpanzee predation may be quite different in aspects not previously emphasized. As a result, observers of different species would tend to favor one class of explanation over another. For example, when comparing just one aspect of predation, the consumption of the prey, baboons and chimpanzees behave quite differently. By baboon standards, the length of time it takes chimpanzees to eat one baby monkey requires more than a feeding model.

Elsewhere, I have argued that primate predation can be understood (rather than just described) only within a framework that, at a minimum, considers individual, social and ecological factors at both the proximate and ultimate levels and the complex interplay of these (Strum, 1976*a*, *b*, 1981). The deficiencies of any simple, single factor hypothesis becomes obvious when it is applied to existing data on non-human primate predation. For example, Gaulin & Kurland (1976) present a bioenergetic hypothesis to explain baboon predation at Gilgil. Their ideas have been addressed in detail elsewhere (Strum, 1976*b*) with data from the period ending January, 1974. Subsequent data on baboon predation at Gilgil (Strum, 1981 and unpublished data) show no conformity to the predictions of their bioenergetic model, yet aspects of bioenergetics are crucial to an understanding of baboon predation at Gilgil and elsewhere (Strum, 1976*a*, 1981).

Rather than view the various hypotheses that have been proposed as competing and mutually exclusive, it would be more heuristic to attempt models of increasing complexity. This is particularly important because the predatory behavior of non-human primates is often the basis for models of human evolution, especially at its earliest stage (e.g. Schaller & Lowther, 1969; Teleki, 1975; Lancaster, 1975; Leakey & Lewin, 1977). It is unfortunate that data on predatory behavior of any sort is rare, even for those populations with the highest predatory rates (Teleki, 1973; Strum, 1975; Busse, 1977*a*, *b*). Data concerning the dynamics of predatory behavior that might provide insights into origins and variations, are even less abundant although the history of baboon predation at Gilgil provides useful information.

To augment these data, I performed simple manipulations with one troop of predatory baboons. The purpose of the manipulations was to elucidate the characteristics which the baboons used in their choices about eating meat, and to investigate the degree of complexity entailed by such events. Results indicate that the primary cues baboons use can be social. The role of the social element in meat-eating differs from its role in other baboon feeding and also differs from the social processes described in the acquisition of novel vegetable foods among Japanese macaques (Yamada, 1957; Kawamura, 1959; Itani, 1958; Kawai, 1965). These data are useful in discussions of primate predatory patterns, particularly the role played by scavenging.

2. Methods

One troop of live baboons, *Papio anubis*, was observed for 1200 hours between December 1972 and January 1974 , near Gilgil in the central Rift Valley of Kenya. Details of this high altitude savannah habitat are provided elsewhere (Blankenship & Qvortrup, 1974; Harding, 1976). Predatory behavior was recorded *ad libitum*. The Pumphouse baboons have been described by Harding (1973) as the most predatory of any non-human primate group yet studied. During my subsequent observations in 1973, the predatory rate increased significantly (Strum, 1975, 1976*a*, *b*, 1981). In the last month of the study I presented carcasses which had been killed, consumed and abandoned by the baboons to various troup members. Live domestic rabbits were also placed among the troop. These rabbits are similar in size, general appearance and predator defense to Cape hares, *Lepus capensis*, a normal prey for this troop. Rabbits were used instead of hares to test subtleties of prey selection. The reactions and social interactions among nearby members of the troop were recorded after each presentation. I also noted the behavior of the potential prey when live animals were used.

3. Results

Presentation of Abandoned Carcasses

Thomson gazelles represented 33% of the prey items consumed by the baboons during this study (Table 1). Sometimes when consumption of a gazelle ended, the carcass still contained edible portions. Most often this was the brain, since only some baboons knew how to extract it (Strum, 1975, 1981). Frequently flesh still adhered to the long bones which had not yet been cracked for their marrow.

The first presentation was to a male, the primary predator, who knew the techniques of brain extraction; the carcass still contained the brain. The male had been present during the earlier consumption but had not obtained any meat. When the carcass was placed near him, he walked to it and immediately began to eat the brain. Later, another male, the original consumer, and an adult female each fed in turn.

The second presentation, five days later, was to the same male. The brain of this gazelle

Table 1 **Predatory episodes 1973: prey species, rate, captors and consumers**

	Prey caught by				
Species	Males	Females	Juveniles	Unidentified	Total
Thomson's Gazelle	24	1	1	7	33
Hare	22	9	9	1	41
Bird	3	1	6	1	11
Dik Dik	4	3			7
Other Ungulates					8
Steinbok	6				6
Impala	1				1
Klipspringer	1				1
Total Prey	61	14	16	9	100
Predatory Rate	100 kills in 1200 hours of observation One episode per 756 monkey-hours of observation*				

* Hours of observation × number of animals in the troop ÷ number of cases of predation.

had been eaten already but some meat remained on the limb bones. The male had not been involved in the previous predation episode and the troop was sufficiently dispersed to be certain that he had not seen any of the events. In this case, the male avoided the carcass, showing signs of fear. The carcass was then carried to other individuals who had not previously seen it. They responded similarly. Finally the carcass was presented to a male who had fed on it earlier. His acceptance was instantaneous. Other males, females and juveniles also fed sequentially after him, including individuals who had previously rejected the item.

Six Thomson gazelle carcasses were presented in this manner (Table 2). Baboons who had seen the original predation, either capture or consumption, always accepted the carcass upon presentation. A similarly consistent pattern of rejection occurred when an individual had not witnessed the previous predatory sequence. However, if the individuals being tested saw another baboon consume the prey, they would subsequently feed on it themselves. This happened even when an individual had not observed the predation and initially rejected the carcass.

Table 2 **Response of different age–sex classes to carcass presentations**

	Observed original predation			Did not observe original predation						
Age-sex class	Yes	Accept carcass	Reject carcass	Yes	Accept carcass	Reject carcass	Observe baboon consumer	Accept carcass	Reject carcass	Total trials
Adult male	9	9	0	8	0	8	2	2	0	19
Adult female	3	3	0	4	0	4	2	2	0	9
Juvenile male	1	1	0	10	0	10	5	5	0	16
Juvenile female	—			3	0	3	2	2	0	5
Infant male	—	—	—	—	—	—	—	—	—	—
Infant female	—	—	—	4	0	4	—	—	—	4
Totals	13	13	0	29	0	29	11	11	0	53

Presentation of Live Rabbits

On three occasions live domestic rabbits were placed in the vicinity of the baboons. The first instance occurred near a refuse pit that the troop sometimes visited.* The rabbit was placed on the ground near, but not in, the pit. Immediately one male rushed to it, grabbed it and began to eat. The rabbit's vocalizations drew the attention of nearby baboons and these approached and watched the male feed, remaining there for 15 minutes. At his departure another male claimed the scraps but didn't feed. Instead, he investigated it by touching and sniffing the meat, lifting it to his face and dropping it to the ground. In the end, he rubbed the pieces in the dirt while the others watched. Subsequent individuals handled but did not consume the meat.

The retrieved remains were placed near other baboons. Those who had not been present previously showed apprehension, while those who were present earlier, investigated, but did not eat the meat.

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*The baboons were not provisioned or otherwise fed by humans. The only human food they obtained was what they normally found in two refuse accumulations. This food constituted less than 1% of the diet of males, who tried to monopolize the resource, and a much smaller percentage for females and immatures.

A second rabbit was placed near the troop's sleeping cliffs where the baboons investigated it, initiated by the male who was the most frequent predator. The rabbit tried to escape by alternatively moving and freezing just as would a wild Cape hare. Juveniles were the most interested, turning the rabbit on its back and sniffing its underbelly. When it screamed, they would clutch it like a baby baboon and groom it; fur was occasionally pulled out, sniffed and discarded. By contrast, when the troop's dominant female smelled the rabbit she violently recoiled from it.

The rabbit was then positioned equidistant between two males and although both ran to it, the captor quickly abandoned his catch. Other baboons showed some interest but ultimately did not consume the animal. The rabbit was given its freedom after an adult male, the one who consumed the previous rabbit, briefly dragged it through the grass by its ears.

4. Discussion

Kortlandt & Kooij (1963) and later Kortlandt (1967, 1972) discuss the presentations of live and dead prey, other animals, other foods and inanimate objects to forest-dwelling chimpanzees in the Beni Chimpanzee Reserve. Although that population was not observed to prey on vertebrates under normal conditions (fecal examination supported this view) their results provide the only existing comparative data. Kortlandt's chimpanzees avoided inanimate objects and showed an extreme conservatism in response to potential vegetable foods. No presentations of prey items resulted in consumptions including items now known to be eaten by chimpanzees elsewhere. Their reaction to the presentation of an infant monkey was curiosity, investigation, and "maternal solicitude" (Kortlandt, 1967, p. 212). Fear was elicited in response to presentations of dead and seemingly dead animals while no fear was present when snakes were presented.

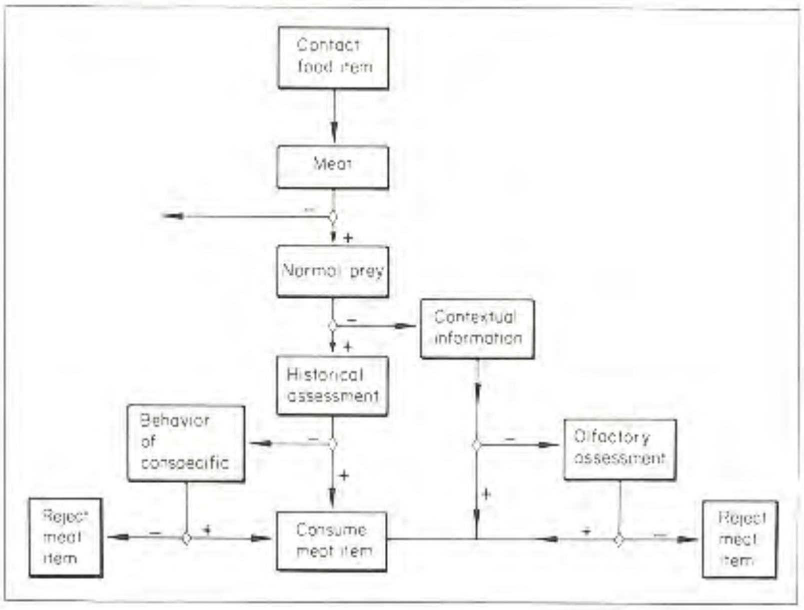
Pumphouse baboons, who are actively predatory, normally only eat meat from animals that they have captured themselves. However, when presented with an abandoned gazelle carcass, the presence of individuals at the previous predatory event, or their awareness of it, determined whether they would eat from the carcass. Yet individuals can also take their cues about the suitability of an item for consumption from other baboons and change their own behavior accordingly. Once a troop member had accepted a gazelle carcass, the participation of others did not depend on their previous experience with the prey.

Context and olfaction contributed to baboon decisions about eating rabbits. Except in one case, the presentation of live rabbits sparked the investigatory but not the predatory interest of the baboons, much like the presentation of a live monkey to the Beni chimpanzees. The most frequent investigation was olfactory and was directed at the animal, bits of fur which were pulled out, or places where the rabbit had been. Predatory interest was more pronounced when the rabbit was active, either when it moved or screamed. Rabbits resemble Cape hares, a normal prey species, in these behaviors.

There was only one predation during the presentations of live rabbits. The context of that episode may have played an important role since the same male did not prey on other rabbits elsewhere. The context was a refuse pit and the predator was the male who most frequently fed at the pit. There, all baboons ate meat when they found it, regardless of whether it was raw, cooked or rotten, beef, pork or fowl. The pit may have signaled to the baboons the consumability of items found there. That the male did not investigate the prey before eating it supports this view. The rabbit must have had a taste similar to normal prey since the male continued to feed. The rabbit's appearance, behavior and taste were seemingly more appropriate than its smell because other baboons olfactorally investigating the carcass, rejected it.

Together the data from both types of manipulations suggest a complex process of evaluation incorporating olfactory, contextual and historical information. However, evaluations based on one or a combination of cues can be changed by other information. Contextual input may override olfactory assessments and for some types of food, the behavior of other baboons can modify an individual's choices based on any or all other factors (Figure 1).

Figure 1. Procedure used in evaluating the suitability of meat for consumption. A minus represents a negative answer to the box and a plus represents a positive answer. For example: Is it meat? If yes go on to the next box; if no, exit the system.



Social factors seem to play a pivotal role in both individual meat-eating choices and in the elaboration and extinction of other aspects of Pumphouse predatory behavior (Strum, 1981). The role of social factors in meat consumption also appears greater than for non-meat items as evidence by the troop's subsequent raiding of crops. In this situation, vegetable foods completely novel to the baboons were quickly incorporated into their diet. Who gets involved in raiding and its exact timing does rely heavily on social factors, however (Strum, in prep.). The lack of conservatism in the baboon's reaction to crops may be a contrast to the chimpanzee attitudes tested by Kortlandt but accords well with the view of baboons as opportunist feeders.

While predatory behavior can originate in previous patterns of vegetable collecting (Rose, 1978), animal food appears to be perceived differently by the baboons. The Pumphouse data hint at a conservatism in baboon meat-eating, one which may inhibit their tendency to scavenge. What might be its evolutionary origins?

Harding (1974) suggests the recent origin of predatory behavior in the Pumphouse troop but the ubiquity of baboon predation, despite different species or subspecies and different habitats (Bartlett & Bartlett, 1961; Dart, 1963; DeVore & Washburn, 1963; Hall, 1966; Rowell, 1966; Kummer, 1968; Altmann & Altmann, 1970; Stoltz & Saayman, 1970; Ransom, 1971; Hausfater, 1976; McGrew *et al.*, 1978; Ray Rhine, pers. comm.; Joe Popp, pers. comm.), argues against this position. We cannot assume, therefore, that the novelty of meat as a food explains the baboons' conservatism.

Disease avoidance may be another factor selecting for conservatism in meat consumption. Hamilton & Busse (1978) present the most recent statement of this position. They argue that the risk of contracting diseases such as anthrax and botulism from carrion is an important adaptive reason to avoid eating meat that is not fresh. They suggest that the best way to guarantee against diseased meat is for the consumer to make the kill or see the kill made. If they are correct, the Pumphouse data imply that taking a cue from the meat-eating behavior of conspecifics is normally also a good tactic. Evidence on baboons and chimpanzees at Gombe Stream intimates that cues from other primate species may work in the same manner (Morris & Goodall, 1977).

At Gilgil, the lack of predators and scavengers which are dangerous to baboons (except for leopards, domestic dogs, and humans) creates a situation atypical for most savannahs. In earlier times at Gilgil and certainly in other areas with a full complement of carnivores, scavenging would put baboons in potential danger (Strum, 1976*a*, 1981). The risks of interactions with other predators over meat are high since some of these also prey on baboons and have the competitive advantage when exploiting the same resource. Given these liabilities, selection against individuals who were attracted to carcasses may have been sufficient to create a predatory conservatism of the type observed in the Pumphouse data.

5. Conclusions

Two findings provide information about the complexity of primate predatory behavior both at a motivational and at an evolutionary level. Pumphouse baboons are among the most predatory of the non-human primates and yet the form and frequency of their behavior has changed over a period that represents only one-third of a baboon's lifetime (Strum, 1981). Given that suitable prey exist, that the members of the troop are already experienced predators, and that there is some advantage to eating meat, the actual decision to eat from a carcass seems to be a system of checks and balances. Cues from all modalities are used but the power of veto or facilitation belongs disproportionately to information coming from the behavior of conspecifics.

Models which do not incorporate this minimum degree of complexity for non-human primate predation have little hope of providing the basis for reconstructions of human evolution. The issue of the role of scavenging is a case in point. Some models of human evolution have argued for the origins of hominid predatory behavior in a scavenging stage (e.g. Leakey, 1967; Schaller & Lowther, 1969; Pfeiffer, 1969; Szalay, 1975; Wolpoff, 1980) which would allow an adaptive shift from infrequent predation, as found in non-human primates, to the human pattern of hunting large game. While the "collector-predator" (Teleki, 1975) origin of hominid predation is supported by the recent non-human primate data, the shift to predation on large game is a significant one (Strum, 1976*a*, 1981; but see Teleki, 1975, for an opposing view). Could scavenging have played a role in this shift? If early humans foraged at all like Pumphouse baboons, at least two major obstacles must have been overcome before a scavenging pattern could develop. The long-recognized dangers of competitive interactions with other predators had to be reduced and the general inhibition about exploiting already dead prey, which I shall assume has an adaptive basis, would need to be modified.

Tool-use and co-operation between hominid predators could have provided a solution to the first problem, as existing models recognize, making early hominids more successful in competition with other predators. The baboon data suggest a mechanism to overcome the second difficulty. Cues which normally prevent an individual from scavenging can be modified by the behavior of conspecifics. It is possible to imagine that if a baboon began to eat consistently from prey not captured by baboons, for whatever idiosyncratic reasons, this individual shift could stimulate a broader adaptive change. Similar cultural innovations have been demonstrated for Japanese macaques as well as for Pumphouse baboons in other aspects of their predatory behavior. "Scavenging" from conspecifics within a group might lead to the possibility of scavenging from outside the group (M. D. Rose, pers. comm.). This has the greatest probability under conditions where meat-eating is relatively frequent but sharing of meat is not widespread.

However, if the disease avoidance hypothesis is correct, there would be a serious adaptive barrier to the development of even a limited scavenging pattern. Two factors may reduce the validity of such an argument. First, hominid scavengers, like other scavenger-predators, should have been able to recognize and avoid dangerously diseased carcasses. And, secondly, even if this was an imperfect ability, the risks of disease are much less than implied because scavenged items are normally confiscated kills rather than isolated carcasses (Kruuk, 1972; Schaller, 1972). Furthermore, during times of drought, when the chances of encountering unclaimed carcasses are greatest, the cause of death is also most likely to be starvation and not disease.

The cues used by baboons in eating meat are multifaceted, suggesting, along with other non-human primate data, that the dynamics of predatory behavior are more complicated than previously proposed. Whether scavenging would facilitate hunting large game (through innovations in tool-use, co-operation, etc.) is a moot point if there was an adaptive conservatism in meat-eating in the ancestral predatory pattern which could not be modified. The Pumphouse baboon data suggest that innovative individuals and the effect of social factors on foraging decisions could have played an important part in an adaptive shift to scavenging. The question left open for consideration is whether it is easier to develop technical and social innovations within a scavenging context, to gain a competitive edge on other predators, or within a hunting context, to allow the exploitation of larger prey. In either case non-human primate predatory behavior once again considerably clarifies the questions we should ask about human evolution and the answers that will be acceptable. It also illustrates a complexity that predates the human experiment.

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References

Altmann, S. & Altmann, J. (1970). *Baboon Ecology: African Field Research*. Chicago: University of Chicago Press.

Ardrey, R. (1961). *African Genesis*. London: Atheneum.

Bartlett, D. & Bartlett, J. (1961). Observations while filming African game. *South African Journal of Science* **57,** 313–321.

Blankenship, L. & Qvortrup, S. (1974). Resource management on a Kenya ranch. *Annals of the South African Wildlife Management Association* **4,** 185–190.

Busse, C. (1977*a*). Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution* **31,** 907–911.

Busse, C. (1977*b*). Do chimpanzees hunt cooperatively? *American Naturalist* **112,** 767–770.

Bygott, D. (1972). Cannibalism among wild chimpanzees. *Nature* **238,** 410–411.

Dart, R. (1963). The carnivorous propensity of baboons. *Symposium of the Zoological Society of London* **10,** 49–56.

DePelham, A. & Burton, F. (1977). Predatory behaviour in nonhuman primates, a reply. *Current Anthropology* **18,** 107–109.

DeVore, I. & Washburn, S. (1983). Baboon ecology and human evolution. In (F. C. Howell & F. Bourliere, Eds) *African Ecology and Human Evolution*. pp. 335–365. Chicago: Aldine.

Gaulin, S. & Kurland, J. (1976). Primate predation and bioenergetics. *Science* **191,** 314–315.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, F., Pierce, A. & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In (D. Hamburg & E. McCown, Eds) *The Great Apes*, pp. 13–54. Menlo Park: Benjamin/Cummings.

Hall, K. (1966). Distribution and adaptation of baboons. *Symposium of the Zoological Society of London* **17,** 49–73.

Hamilton, W. J., Buskirk, R. E. & Buskirk, W. H. (1978). Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *American Naturalist* **112,** 911–924.

Hamilton, W. J. & Busse, C. (1978). Primate carnivory and its significance to human diets. *BioScience* **288,** 761–766.

Harding, R. (1973). Predation by a troop of olive baboons (*Papioanubis*). *American Journal of Physical Anthropology* **38,** 587–592.

Harding, R. (1974). The predatory baboon. *Expedition* **16,** 30–39.

Harding, R. (1976). Ranging patterns of a troop of baboons (*Papioanubis*) in Kenya. *Folia Primatologica* **25,** 143–185.

Hausfater, G. (1976). Predatory behaviour of yellow baboons. *Behaviour* **56,** 44–68.

Hrdy, S. (1974). Male-male competition and infanticide among the langurs of Abu, Rajasthan. *Folia Primatologica* **22,** 10–58.

Itani, J. (1958). On the acquisition and propagation of a new food habit in the troop of Japanese monkeys at Takasakiyama. *Primates* **2,** 84–98.

Jolly, A. (1972). *The Evolution of Primate Behavior*. New York: Macmillan.

Kawai, M. (1965). Newly acquired precultural behaviour of the natural troop of Japanese monkeys on Koshima Islet. *Primates* **6,** 1–30.

Kawamura, S. (1959). The process of subculture propagation among Japanese macaques. *Primates* **2,** 43–60.

Kortlandt, A. (1967). Experimentation with chimpanzees in the wild. In (D. Starck, R. Schneider & H. Kuhn, Eds) *Progress in Primatology*, pp. 208–224. Stuttgart: Fischer.

Kortlandt, A. (1972). *New Perspectives on Ape and Human Evolution*. Amsterdam: Stichting voor Psychobiologie.

Kortlandt, A. (1980). Early man's defense against predators. *Journal of Human Evolution* **9,** 79–112.

Kortlandt, A. & Kooij, M. (1963). Protohominid behaviour in primates. *Symposia of the Zoological Society of London* **10,** 61–88.

Kruuk, H. (1972). *The Spotted Hyena*. Chicago: University of Chicago Press.

Kummer, H. (1968). *Social Organization of Hamadryas Baboons: a Field Study*. Chicago: University of Chicago Press.

Lancaster, J. (1975). *Primate Behaviour and the Emergence of Human Culture*. New York: Holt, Rinehart and Winston.

Leakey, L. S. B. (1967). Development of aggression as a factor in early human and pre-human evolution. In (C. D. Clemente & D. B. Lindsley, Eds) *Aggression and Defense. UCLA Forum of Medical Sciences* **7,** 1–33. Berkeley: University of California Press.

Leakey, R. & Lewin, R. (1977). *Origins*. New York: Dutton.

McGrew, W., Tutin, C., Baldwin, P., Sharman, M. & Whiten, A. (1978). Primates preying upon vertebrates: new records from West Africa. *Carnivore* **1,** 41–45.

Morris, K. & Goodall, J. (1977). Competition for meat between chimpanzee and baboons of the Gombe National Park. *Folia Primatologica* **28,** 109–121.

Nishida, R., Uehara, S. & Nyundo, R. (1979). Predatory behaviour among wild chimpanzees of the Mahale Mountains. *Primates* **20,** 1–20.

Pfeiffer, J. (1969). *The Emergence of Man*. New York: Harper and Row.

Ransom, T. (1971). Ecology and social behaviour of baboons at the Gombe National Park. Ph.D. dissertation. University of California, Berkeley.

Rose, M. D. (1978). The roots of primate predatory behaviour. *Journal of Human Evolution* **7,** 179–189.

Rowell, T. (1966). Forest living baboons in Uganda. *Journal of Zoology, London* **149,** 344–364.

Schaller, G. (1972). *The Serengeti Lion.* Chicago: University of Chicago Press.

Schaller, G. & Lowther, G. (1969). The relevance of carnivore behaviour to the study of early hominids. *Southwestern Journal of Anthropology* **25,** 307–341.

Stoltz, L. & Saayman, G. (1970). Ecology and social organization of chacma baboon troops in the northern Transvaall. *Annals of Transvaal Museum* **26,** 99–143.

Strum, S. (1975). Primate predation: Interim report on the development of a tradition in a troop of olive baboons. *Science* **187,** 755–757.

Strum, S. (1976*a*). Predatory behaviour of olive baboons at Gilgil, Kenya. Ph.D. dissertation. University of California, Berkeley

Strum, S. (1976*b*). Primate predation and bioenergetics. *Science* **191,** 314–317.

Strum, S. (1981). Processes and products of change: Baboon Predatory Behaviour at Gilgil, Kenya. In (G. Teleki & R. Harding, Eds) *Primate Subsistence Patterns,* pp. 255–302. New York: Columbia University Press.

Suzuki, A. (1971). Carnivore and cannibalism observed among forest-living chimpanzees. *Journal of the Anthropoligical Society of Nippon* **79,** 30–48.

Szalay, F. (1975). Hunting-scavenging protohominids: a model for hominid origins. *Man* **10,** 420–429.

Teleki, G. (1973). *The Predatory Behaviour of Wild Chimpanzees.* Lewisburg, Pennsylvania: Bucknell University Press.

Teleki, G. (1975). Primate subsistence patterns: collector-predators and gatherer-hunters. *Journal of Human Evolution* **4,** 125–184.

Wolpoff, M. (1980). *Paleoanthropology.* New York: Knopf.

Wrangham, R. W. (1975). The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation. Cambridge University.

Yamada, M. (1957). A case of acculturation in a subhuman society of Japanese monkeys. *Primates* **1,** 30–46.