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14 Chimpanzee Hunting Behavior

Nicholas E. Newton-Fisher

Abstract

The pursuit, capture and consumption of small- and medium-sized vertebrates, appears to be typical of all chimpanzee (*Pan troglodytes*) populations, although large variation exists. Red colobus monkeys (*Piliocolobus* sp.) appear to be the preferred prey but intensity and frequency of hunting varies from month to month and between populations. Hunting is a predominately male activity and is typically opportunistic, although there is some evidence of searching for prey. The degree of cooperation during hunting, as well as prey selection, varies between East and West African populations and may be related to the way the kill is divided: in West Africa, hunters often collaborate, with kills tending to be shared according to participation, whereas in East Africa, the kill is typically divided tactically by the male in possession of the carcass, trading meat with females in return for sex or with other males to strengthen alliances, and cooperation in hunting is more limited. The adaptive function of chimpanzee hunting is not well understood, although it appears that it may be both a means to acquire a nutritionally valuable commodity that can then be traded and as a means for males to display their prowess and reliability to one another.

14.1 Introduction

The pursuit, capture and consumption of small- and medium-sized vertebrates, appears to be typical of all chimpanzee (*Pan troglodytes*) populations. Such hunting behavior has aroused considerable interest among anthropologists since it was first reported (Goodall 1963). Hunting, the division of the kill, and the consumption of meat all play an important role in the lives of modern hunter-gather societies (Lee 1979; Kaplan and Hill 1985; Hawkes et al. 2001; Hawkes and Bird 2002), and factor in a number of hypotheses concerning human evolution (Washburn and Lancaster 1968; Isaac 1978; Hill 1982; Tooby and DeVore 1987; Stanford 1998; Stanford 2001). While early ideas such as "Man the Hunter" (Washburn and Lancaster 1968) have largely been discredited, hunting as a means to acquire meat remains important in many modern scenarios (Domínguez-Rodrigo 2002; Hawkes and Bird 2002). Animal tissue has high calorific value relative to plant material, is rich in fat and protein, and contains essential amino acids (Milton 1999). It is therefore a valuable resource. The nonrandom sharing of meat has been proposed as an important selective force driving the evolution of intelligence (Stanford 2001), and the consumption of meat has been invoked as an important proximate factor enabling the evolution of larger brains in the *Homo* lineage (Aiello and Wheeler 1995).

Chimpanzees show large variation between populations in the choice of prey species, frequency of hunting, and the techniques employed. Understanding both how and why chimpanzees hunt is important for the framing of evolutionary hypotheses; chimpanzees provide our best evidence for the behavioral capabilities of early hominines (Domínguez-Rodrigo 2002). In this chapter, I will review chimpanzee hunting behavior and attempt to address current hypotheses concerning the reasons why chimpanzees hunt, drawing out both similarities and differences between populations in their hunting behavior.

14.2 Chimpanzee hunting

All populations of chimpanzees that have been studied show some evidence of hunting and consuming vertebrate prey. Such hunting has been systematically documented among the East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Gombe (van Lawick-Goodall 1968; Teleki 1973; Busse 1977; Stanford 1998) and Mahale (Nishida et al. 1979; Takahata et al. 1984; Uehara 1997) National Parks in Tanzania, of the Kibale Forest National Park (Mitani and Watts 1999; Watts and Mitani 2002) in Uganda, and among the West African chimpanzees (*P. t. verus*) of the Taï National Park, Cote D'Ivoire (Boesch and Boesch 1989; Boesch and Boesch-Achermann 2000). Other reports of hunting by chimpanzees come from East African populations in the Budongo Forest, Uganda (Newton-Fisher et al. 2002), Kahuzi-Biega National Park, DRC (Basabose and Yamagiwa 1997), Kasakati, Tanzania (Kawabe 1966), Semliki, Uganda (Hunt and McGrew 2002), from central African populations (*P. t. troglodytes*) of Lopé, Gabon (Tutin and Fernandez 1993), Ndoki, Cameroon (Kuroda et al. 1996; Takenoshita 1996), and from West African populations of Mt. Assirik, Senegal (McGrew 1983; Hunt and McGrew 2002), Bossou, Guinea-Bissau (Sugiyama and Koman 1987), and Tenkere, Sierra Leone (Alp and Kitchener 1993).

14.2.1 Prey diversity

Across populations, prey diversity is high with at least 40 species of vertebrates targeted. Chimpanzees are known to hunt a variety of primate species, as well as ungulates, rodents, birds, lizards, and frogs, and show a clear focus on mammalian prey (➋ *Table 14.1*). Some chimpanzee populations appear to have a diverse range of prey, whereas others are more specialized. The Mahale chimpanzees, for instance, are known to hunt at least 17 species of mammals, while in Taï, chimpanzees hunt only 7 of the 15 sympatric mammal species, all primates (Boesch and Boesch-Achermann 2000; Boesch et al. 2002). Prey are typically small, up to a maximum of around 20 kg, the weight of an adult male black and white colobus monkey (*Colobus guereza*) (Kingdon 1997) or a part-grown bushpig (*Potamochoerus porcus*), but often much smaller (Goodall 1986).

14.2.2 Prey specialization

Monkeys, in particular colobus monkeys, appear to be the main prey of chimpanzees wherever the species are sympatric. Red colobus (*Piliocolobus tephrosceles* in East Africa, *Pilicolobus badius* in West Africa) are the primary prey for many populations of chimpanzees, with black and white colobus (*Colobus guereza* in East Africa, *Colobus polykomos* in West Africa) as a secondary target.

The degree to which chimpanzees specialize on monkeys to the exclusion of other prey species varies between populations. In the Taï Forest, the chimpanzees show a notably strong specialization. Between 1984 and 1995, 93% of all prey were colobus monkeys: 80% black and white colobus (*Colobus polykomos*) and 13% red colobus (*Piliocolobus badius*) (Boesch and Boesch-Achermann 2000). A similar specialization is apparent among the Ngogo chimpanzees of the Kibale Forest, where between 1995 and 2000, 92.5% of all prey were colobus monkeys: 87.8% red colobus (*Piliocolobus tephrosceles*) and 4.7% black and white colobus (*Colobus guereza*). At Gombe, the specialization is less extreme but still noticeable: red colobus (there are no black and white colobus at this site) constituted 59% of the chimpanzees' prey between 1970 and 1975, 66% between 1976 and 1981, and 84.5% between 1990 and 1995 (Goodall 1986; Stanford 1998).

In contrast, red colobus constituted only 53% of all prey for the Mahale chimpanzees (Nishida et al. 1992) and black and white colobus (*Colobus guereza*) were 43.8% of all prey for the Sonso chimpanzees in the Budongo Forest (Newton-Fisher et al. 2002), a location where there are no red colobus. These

Table 14.1

Diversity of mammalian prey hunted by chimpanzees across Africa

	Pan troglodytes schweinfurthii							*P. t. troglodytes*		*P. t. verus*			
	Budongo	*Gombe*	*Kahuzi*	*Kasakati*	*Ngogo*	*Mahale*	*Semliki*	*Lope*	*Ndoki*	*Assirik*	*Bossou*	*Taï*	*Tenkere*
Primates													
Red colobus													
Piliocolobus badius												✓	
Piliocolobus tephrosceles		✓			✓	✓							
Black and white colobus													
Colobus guereza	✓				✓		✓						
Colobus polykomos												✓	✓
Colobus satanus								✓					
Olive colobus													
Procolobus verus												✓	
Gray-cheeked mangabey													
Lophocebus albigena					✓			✓					
Sooty Mangabey													
Cercocebus atys												✓	
Olive baboon													
Papio anubis		✓											
Yellow baboon													
Papio cynocephalus						✓							
Vervet monkey													
Cercopithecus aethiops						✓							
Red tail monkey													
Cercopithecus ascanius	✓	✓		✓									
Campbell's monkey													
Cercopithecus campelli													✓

Diana monkey									
Cercopithecus diana									✓
L'Hoest's monkey									
Cercopithecus l'hoesti			✓						
Blue monkey									
Cercopithecus mitis	✓	✓	✓		✓				
Mona monkey									
Cercopithecus mona								✓	
Lesser spot-nosed monkey									
Cercopithecus petaurista								✓	
Crowned monkey									
Cercopithecus pogonias							✓		
Bushbaby									
Galago sp.					✓				
Potto									
Perodicticus potto								✓	
Chimpanzee									
Pan troglodytes	✓	✓		✓	✓				
Ungulates									
Forest duiker									
Cephalophus sp.	✓			✓			✓		✓
Blue duiker									
Cephalohus moniticola	✓			✓	✓	✓			
Bushbuck									
Tragelophus scriptus		✓			✓				
Suni									
Neotragus moschatus									
Bushpig									
Potamocherus porcus		✓			✓				
Warthog									
Phacochoerus aethiopicusl					✓				

Table 14.1 (continued)

	Pan troglodytes schweinfurthii							*P. t. troglodytes*		*P. t. verus*			
	Budongo	*Gombe*	*Kahuzi*	*Kasakati*	*Ngogo*	*Mahale*	*Semliki*	*Lope*	*Ndoki*	*Assirik*	*Bossou*	*Taï*	*Tenkere*
Others													
Giant elepant shrew													
Rhynchocyon sp.						✓							
Yellow-spotted hyrax													
Heterohyrax brucei													
White-tailed mongoose													
Ichneumia albicauda						✓							
Civit													
Civettictis civetta						✓							
Rodents (various spp.)		✓	✓			✓			✓		✓	✓	
Pangolin									✓	✓			

Populations (study sites) of chimpanzees are arranged by subspecies. A ✓ indicates that the species has been recorded being killed or consumed. Not all species of prey are present at all sites.

two populations appear to differ from the others in that the chimpanzees also prey upon small ungulates, particularly blue duiker (*Cephalophus monticola*), to an appreciable degree: 34% of all prey in Mahale (Nishida et al. 1992) and 25% of all prey in Budongo (Newton-Fisher et al. 2002). Data from Budongo are sparse, but recent observations support the idea that these chimpanzees do not demonstrate the extreme prey specialization seen in Taï and Ngogo (Newton-Fisher unpublished data). Forest ungulates, particularly duiker and bushpig, are in fact hunted by all the East African chimpanzee populations studied (Gombe: Goodall 1986; Mahale: Nishida et al. 1992; Budongo: Newton-Fisher et al. 2002; Kibale: H. Sherrow personal communication), but do not appear to be regarded as prey by West African chimpanzees (Uehara 1997; Boesch and Boesch-Achermann 2000). More research is needed on chimpanzee predation on ungulates.

Chimpanzee populations also appear to differ in their choice of the age and sex of prey. For the Taï chimpanzees, half of their colobus monkey prey were adults, mostly females (Boesch and Boesch-Achermann 2000). This is in contrast to chimpanzees at Mahale and Gombe, where the vast majority of colobus prey were juveniles and infants (Goodall 1986; Uehara 1997) and some chimpanzee hunters target very young colobus monkeys, snatching them from their mothers (Stanford 1998). There is less information on the age and sex of non-colobus prey. Among the ungulates, bushbuck are targeted only as infants (fawns), as typically are bushpig (piglets) (Goodall 1986). Age and sex estimates of duiker kills are more difficult to obtain, given that the prey is rapidly torn apart and consumed entirely by the chimpanzees, however it seems clear that chimpanzees are quite capable of killing adult blue duiker (personal observations).

14.2.3 Sex bias in hunting

Hunting by chimpanzees is a predominately male activity. Among the chimpanzees of the Ngogo community in the Kibale Forest, adult or adolescent males made 98.8% of all kills recorded between 1995 and 2000 (Watts and Mitani 2002). In two decades of data from Gombe, adult males were responsible for 91.5% of all kills (Stanford 1998). Female chimpanzees will and do hunt, however. Data from Gombe for 1977–1979 showed that females joined an average of 26% (median: 25%, range: 0%–67%) of red colobus hunts for which they were present, and those females that were more likely to join males in a hunt were also more likely to hunt when apart from the males (Goodall 1986). One female, Gigi, contributed 4% of the total kills (Stanford 1998). Any kills that females made during a mixed sex hunt were likely to be taken by males (Goodall 1986), which may in part explain female unwillingness to hunt when with males. Females may prey more on ungulates (Uehara 1997), but quantitative data are difficult to collect, in part due to the nature of ungulate hunting.

14.3 Hunting frequency

Detecting hunting in a chimpanzee population can be problematic, particularly, if the chimpanzees are poorly habituated. Typically in this situation, hunting is rarely if ever seen, and studies rely on finding animal remains, skin or bone, in chimpanzee feces (McGrew 1992). Unfortunately, sampling feces does not appear to be a reliable indicator of the occurrence of hunting; while the presence of remains can confirm that consumption does occur, little can be said about the frequency of consumption (cf. Uehara 1997). Long-term observations of habituated chimpanzees in the Taï Forest have revealed a pattern of frequent hunting and consumption that is not mirrored in the pattern of prey remains found in fecal samples (Boesch and Boesch-Achermann 2000). Further, fecal sampling can say nothing about the number of hunting attempts that fail to secure prey, the division of the prey once obtained, or the relative importance of scavenging as a method of acquiring meat. Similar problems may also occur when hunting is actually rare, or when prey species are alerted or scared away by the presence of humans accompanying the chimpanzees, although in some cases chimpanzees may exploit their prey's fear of humans to increase hunting success (Goodall 1986; Boesch 1994).

14.3.1 Predation pressure

While in some populations chimpanzees appear to hunt only rarely, in other populations they are significant predators who may hunt at levels that appear to be unsustainable (Goodall 1986; Wrangham and van Zinnicq Bergmann Riss 1990). Estimates for Gombe suggest anything from 8% to 42% of the colobus population can be killed each year, with the number varying from year to year: 8%–13% (1973–1974: Busse 1977), 41.6% (1972–1975: Wrangham and van Zinnicq Bergmann Riss 1990), 16.8%–32.9% (1982–1991: Stanford et al. 1994), while at Taï during the 1980s, the figure was between 3% and 8% (Boesch and Boesch-Achermann 2000). In contrast, the Mahale chimpanzees were estimated to kill only around 1% of the red colobus population each year during the 1980s (Boesch et al. 2002). Basabose and Yamagiwa (1997) estimate that the chimpanzees of Kahuzi-Biega kill 11%–18% of the *Cercopithecus* monkey population each year (predominately *Cercopithecus mitis* but also *Cercopithecus l'hoesti*). Hunting of ungulates may also impose high levels of mortality. Wrangham and van Zinnicq Bergmann Riss (1990) estimated chimpanzee-imposed mortality on bushbuck at 27% (although this figure includes bushbuck fawns killed by baboons and subsequently stolen by chimpanzees) and on bushpig at 7%, for populations in the Gombe National Park between 1972 and 1975.

These estimates, both for primates and ungulates, are based on comparing the number of kills with the population density of prey within the chimpanzee community's home range. There is potential for error in the estimates of each of these variables. If, for example, home range is overestimated (cf. Newton-Fisher 2004), then predation pressure will be underestimated, while underestimating the number of potential prey will inflate the estimate of predation pressure (Wrangham and van Zinnicq Bergmann Riss 1990).

14.3.2 Variation in hunting frequency

Such estimates of hunting frequency and predation pressure, however, disguise wide variation. Within a single community, the total number of hunts can vary from month to month and year to year. Across populations, chimpanzees appear to have hunting "seasons," during which the number of kills increases either as a result of more hunting or more successful hunting, or both. For the chimpanzees at Gombe, Mahale, and Taï, this hunting season falls toward the end of the year, peaking in September and October. At Gombe, this corresponds to the later part of the dry season (Stanford 1998). At Mahale, the peak is slightly later, reaching into November and appears to coincide with the end of the dry season and the first rains of the wet season (Takahata et al. 1984). Preliminary work at Budongo suggested a dry season (December to February) peak in hunting activity (Newton-Fisher et al. 2002), but subsequent work has failed to confirm this idea (Newton-Fisher unpublished data).

The hunting behavior of the Ngogo chimpanzees does not appear to correspond to timing of rainfall, but hunting seasons instead occur during periods of fruit abundance (Watts and Mitani 2002) that are not correlated with rainfall (Mitani et al. 2002). Similarly, the hunting season at Mahale occurs when more fruit is available (Uehara 1997). At Taï, the hunting season runs from mid-August to mid-November, between periods of low and high fruit abundance and ending when chimpanzees switch to highly calorific *Coula edulis* nuts from which they gain sugar, protein, and fat. The peak in hunting is also in September and October, but this is during the wet season at the time of greatest rainfall (Boesch and Boesch-Achermann 2000).

In addition to these seasonal changes, hunting frequency within a single community varies between years. Such changes might be related to changes in the abundance of prey species or the number of chimpanzees who might hunt. A comparison of hunting success for Mahale chimpanzees between the 1980s and early to mid 1990s showed a threefold increase in the percentage of the red colobus population killed by the chimpanzees, rising from around 1% to at least 3% of the population per year (Boesch et al. 2002). This seemed to accompany an expansion in the red colobus population. Hunting success then fell in the later part of the 1990s, following a drop in the number of chimpanzees in the study community (Boesch et al. 2002). A similar drop in hunting was seen following a decrease in the number of adult males in the study community in the Taï Forest (Boesch and Boesch-Achermann 2000). Chimpanzees may also experience greater hunting success when individuals with a flair for hunting are present. These individuals demonstrate both a high willingness to hunt and a consistently high probability of success (Goodall 1986; Stanford 1998; Boesch and Boesch-Achermann 2000).

14.3.3 Hunting binges

A further source of variation in hunting frequency within a community is the occurrence of hunting "crazes" (van Lawick-Goodall 1968) or "binges" (Stanford 1998). These are periods during which the chimpanzees hunt "almost daily": more than three hunts in a 7-day period, with chimpanzees appearing to hunt on contact with prey (Stanford 1998). In the Kasekela (Gombe) community, 23 binges were recorded between 1990 and 1995. The longest of these lasted 74 days and consisted of 38 observed hunts and at least 76 kills, all red colobus. Correcting the number of kills for observation time suggests that over 100 colobus monkeys were killed during this 74-day period (Stanford 1998). The Ngogo chimpanzees went on a 57-day hunting binge in 1998, during which they hunted 22 times, killing 69 red colobus, 1 mangabey (*Lophocebus albigena*), and 1 red duiker (*Cephalophus* sp.). Only 4 of these 22 hunts were unsuccessful, including two attempts to hunt black and white colobus (*Colobus guereza*). This and other hunting binges at Ngogo coincided with major fruit crops, and most hunting occurred when large parties of males were traveling together (Watts and Mitani 2002). Large parties with high numbers of males also seem to be linked to hunting binges at Gombe (Stanford 1998). Large numbers of chimpanzees traveling together suggests that fruit is particularly abundant, and so hunting binges at Gombe may also be linked to periods of food abundance.

14.4 How do chimpanzees hunt?

Many of chimpanzee hunts are opportunistic, in that chimpanzees appear to decide to hunt after encountering prey during the course of normal foraging activities and travel around the home range. This seems to be the typical pattern at Gombe (Goodall 1986; Stanford 1998) and at Ngogo (Mitani and Watts 2001). In contrast, chimpanzees in Taï appear to search actively for prey, listing for the vocalizations of either colobus monkeys or of Diana monkeys (*Cercopithecus diana*) with whom the colobus are frequently associated (Boesch 1994; Boesch and Boesch-Achermann 2000).

Chimpanzees hunt without the use of tools or weapons, although there are a few reports of rocks or branches being hurled, possibly in an attempt to panic defensive formations of adults (Goodall 1986), and tools (sticks and leaves) are sometimes used to aid in the processing of the carcass (McGrew 1992).

During a hunt, prey are typically chased, seized, and then killed either by a bite, disembowelment or by being torn apart (Goodall 1986). Hunts may yield single or multiple kills. Between 1973 and 1981, Gombe chimpanzees made multiple kills in 37.5% of colobus hunts; most of these were two kills per hunt. A typical colobus hunt at Gombe will produce two (Watts and Mitani 2002) or three (Stanford 1998) kills and at Ngogo, four kills (Mitani and Watts 2001). Single kills seem to be more usual for Taï chimpanzee hunts (Stanford 1998), although these will typically be of adult monkeys (mean number of kills per successful hunt: 1.2; Watts and Mitani 2002).

Chimpanzees will hunt alone and in the company of others. Solitary hunts occur rarely at Taï (16% of hunts: Boesch and Boesch-Achermann 2000) and Mahale (28% of hunts: Takahata et al. 1984; Uehara et al. 1992), while they are more common at Gombe (64% of hunts: Busse 1978; Teleki 1973) where the chimpanzees appear to be highly effective solo hunters. Boesch (Boesch 1994) calculated that Gombe chimpanzees had a success rate of 50% when hunting alone, capturing an average of 1.6 kg of prey within 7 min of hunting. In contrast, his estimate for the success rate of lone hunters at Taï was only 13%, yielding an average of 9.5 kg of prey within 39 min of hunting. The forest canopy is lower and more broken at Gombe than it is at Taï, which may make it easier for lone chimpanzees to isolate colobus monkeys and so allow them to capture and kill their prey more often and more quickly (Boesch 1994). This idea is supported by data from Ngogo, where chimpanzees were more likely to hunt when encountering prey in, or close to, areas with broken or no tree canopy than when in primary forest (Watts and Mitani 2002).

Group hunts are often a case of individual chimpanzees making their own efforts in a collective setting, perhaps exploiting the panic in the prey produced by the presence of multiple hunters, and reacting to the actions of other chimpanzees. Collaborative hunting, where males taking particular roles such as "drivers" and "blockers" (Boesch and Boesch 1989), appears to be the primary form of hunting among the Taï chimpanzees (77%: Boesch and Boesch-Achermann 2000) but is rare among the East African chimpanzees (Boesch 1994; Stanford 1998; Boesch and Boesch-Achermann 2000; Watts and Mitani 2002). A division of roles between those that pursue the prey and those that wait on the ground to capture monkeys that fall from the canopy is, however, fairly common among East African chimpanzees.

14.4.1 Cooperative hunting?

There is little consensus over the extent to which chimpanzee hunting is cooperative. To the extent that chimpanzees take different roles, and are responsive to one another's behavior during a hunt, there is good evidence for social cooperation, but to demonstrate that chimpanzee hunting is functionally cooperative, individuals need to do better when hunting as a group. Thus, if cooperation occurs, hunting attempts should be more successful when more individuals take part, or at least certain number of hunters should be more successful than solitary hunters. At Gombe, Ngogo, and Taï, the probability of killing prey during a red colobus hunt increases with the number of hunters present, but this appears to be a simple effect of more hands grabbing at the monkeys; there does not appear to be an additional effect from males working together (Stanford 1998). At none of these sites does the mass of prey per individual hunting correlate with the number of males hunting (Stanford 1998; Watts and Mitani 2002), although Gombe chimpanzees do gain a higher return (greater mass of prey per hunter) when more than seven are hunting together (Stanford 1998). Many male chimpanzees hunting together may be able to overwhelm the defensive strategies of the red colobus, and reduce the opportunities for panicked monkeys to escape. Among Taï chimpanzees, the number of hunters is strongly correlated with the mass of prey caught because the likelihood of capturing an adult monkey increases but gains per hunter peak at four males (Stanford 1998), presumably because most hunts terminate after the first kill.

The hunting of ungulates is less well described. Bushpigs are probably the most difficult of ungulate prey. Chimpanzees are wary, if not fearful, of the adults and they retreat to the trees in the face of aggression by adult pigs. At Gombe, chimpanzees have been described using stealth to seize piglets before the adults are alerted to their presence, and also of using aggressive displays to panic the adults, capturing piglets either in the confusion or if abandoned by adults that run off (Goodall 1986).

Bushbuck fawns hide in dense cover as an antipredator strategy, while adults typically freeze or flee. Chimpanzees search for hiding fawns when their attention is drawn to particular areas by the presence of adult bushbuck or possibly auditory or olfactory cues. A captured fawn's mother may be aggressive toward chimpanzees, but this is difficult to determine as human presence causes them to flee (Goodall 1986). Duiker captures are typically opportunistic, with chimpanzees seizing them if they come within reach. Chimpanzees sometimes show interest in duiker vocalizations (personal observations) but the extent to which they search for duiker is unclear.

14.4.2 Scavenging

Chimpanzees are reluctant scavengers. Only a handful of reports exist of scavenging, acquiring meat from an abandoned carcass. Most of these observations concern the sizing of fresh kills from other predators, a behavior often labeled piracy (Goodall 1986; Uehara 1997; Stanford 1998), although plundering, the forcible stealing of goods, might be more appropriate term. At Gombe, chimpanzees have been recorded stealing fresh kills from baboons (Morris and Goodall 1977; Goodall 1986), and at Budongo, the body of infant blue monkey (*Cercopithecus mitis*) was stolen from the adult blue monkey who killed it (Newton-Fisher et al. 2002). Boesch and Boesch-Achermann (2000) report three instances of Taï chimpanzees robbing eagles of red colobus captures while the monkeys were still alive, and a further four instances of chimpanzees eating the kills of eagles; presumably these were recently killed monkeys, but this information is not reported. Given that chimpanzees are quite willing, if they can steal or beg part of the carcass, to eat prey that chimpanzees other than themselves have killed, it is not surprising that they are similarly willing to take fresh kills from other species.

True scavenging, however, appears particularly rare. In 36 years of observation at Gombe, fewer than 20 instances have been recorded (Stanford 1998), and at least 9 of these (all red colobus) are likely, or known, to be previous chimpanzee kills (Goodall 1986). Similar low rates have been recorded at Mahale; seven cases in over 25 years of observation: six ungulates and one red-tailed monkey (*Cercopithecus ascanius*) (Hasegawa et al. 1983; Uehara 1997). Scavenging has not been reported from Taï: Boesch and Boesch-Achermann (2000) record ten encounters with fresh carcasses, none of which were eaten by the chimpanzees.

Most encounters with fresh carcasses result in apparent curiosity-type behaviors in the chimpanzees, with no indication that the chimpanzees regard these carcasses as a source of meat. Stanford (1998) reports an observation from Gombe of a juvenile male briefly chewing on 1- or 2-day-old colobus meat that was ignored by the adults, and Muller et al. (1995) record a further observation, from the same community, of a party of chimpanzees encountering a dead bushbuck, presumed to be killed by a leopard. The chimpanzees showed strong curiosity over the carcass, even grooming it, and one female rolled around inside the eviscerated carcass, but they did not feed (Muller et al. 1995). In contrast, chimpanzees at Mahale did feed on the carcasses of two adult bushbuck thought to be the remains of leopard kills (Hasegawa et al. 1983).

14.5 Meat eating

All populations of chimpanzees subsist on a primarily frugivorous diet. Typically, fruit constitutes 60%–80% of the time spent feeding (Gombe: 63%, Wrangham 1977; Kibale: 79%, Wrangham et al. 1996; Budongo: 64.5%, Newton-Fisher 1999a). This is supplemented by leaves, primarily, as well as other plant materials. Even in communities that hunt frequently, such behavior constitutes a very small portion of the time spent foraging. Watts and Mitani (2002) recorded 131 predation episodes in 6 years at Ngogo (1.8 hunts per month) while Boesch and Boesch-Achermann (2000) recorded 413 hunts in a 12-year period at Taï (2.9 hunts per month). Nevertheless, chimpanzees do hunt, kill, and consume meat, and competition over the division of the kill can be high.

14.5.1 The value of meat

A single carcass can represent a sizable resource, despite substantial variation between species. *Colobus guereza* adults weigh up to 23 kg, although Ugandan populations may not reach this size, while the western black and white colobus (*Colobus polykomos*: adult male body weight: 8–12 kg) is smaller and similar in size to the eastern red colobus (*Piliocolobus tephrosceles*: adult male body weight up 13 kg). The western red colobus (*Piliocolobus badius*) are lighter, with an adult body weight of only 5–10 kg (Kingdon 1997).

Commonly, the entire animal is consumed, including bones and skin, and chimpanzees will compete for the smallest scraps. The chimpanzees will therefore be consuming not only the protein-rich flesh, but also fat, notably from the brain, and bone-marrow, together with minerals present in the blood and bones (Stanford 1996; Stanford 1998).

The quantity of meat, including the associated elements of the carcass, consumed by some individuals may be relatively significant. In good hunting years, the total amount of meat consumed may be more than double that consumed in poorer years. The 45 Gombe chimpanzees of the Kasakela community in 1992 consumed over 500 kg of red colobus meat, and their total meat consumption for the year was probably close to 700 kg. The previous year (1991), colobus meat consumption was less than 200 kg, and in 1988, this figure was less than 150 kg (Stanford 1998). Averaged over years, the level of consumption in the 1980s and 1990s seems similar to the estimate of 441 kg of meat per year for the same community in the 1970s (Wrangham and van Zinnicq Bergmann Riss 1990; Stanford 1998).

Boesch and Boesch-Achermann (2000) estimate that, averaged across the year, male Taï chimpanzees consume 186 g per day, while females consume 25 g per day. Their estimates for Gombe chimpanzees, similarly averaged, are 55 g per day for males and 7 g per day for females. These are similar to estimates made by Stanford (1998) of 70 g per day for males during peak hunting season and by Wrangham (1975) of 22 g averaged over males and females.

Meat therefore appears to be a valuable resource to chimpanzees, although there are exceptions. Captured prey may be only partly eaten before being discarded. In the Taï Forest, adult cercopithecine monkeys have been treated in this way (Boesch and Boesch-Achermann 2000). At Gombe, chimpanzees have been observed discarding captured adult red colobus in favor of pursing immature monkeys (Boesch 1994; Stanford 1998) and giving a carcass to another individual in order to hunt again (Goodall 1986). In the Budongo Forest, an adult male chimpanzee captured and killed an elephant shrew (*Rhynchocyon* sp.) but took only a single bite before discarding the carcass (Newton-Fisher unpublished data), and the bodies of infant chimpanzees killed by adults are sometimes only partially eaten before being handed on to another individual or discarded completely (Newton-Fisher 1999b). Furthermore, any kills made during a group hunt are typically divided in some way among some or all of the chimpanzees present.

14.5.2 Begging and food sharing

Following a kill there is commonly a degree of competition for the meat, the intensity of which reinforces the idea that chimpanzees desire and value meat. If the chimpanzee in possession of the carcass has companions, these individuals will attempt to acquire part of the carcass. More dominant individuals may attempt to steal the entire carcass for themselves. Others will sit around the possessor and beg for a share of the meat. Begging individuals seem to exert a lot of pressure both by their presence and by their harassing gestures and vocalizations. Chimpanzees unwilling to share will commonly move away from the crowd of begging individuals, although they are likely to be followed. When harassed by one or two others, a chimpanzee may simply turn its back toward them to avoid them reaching toward the carcass.

Sharing of the carcass can be either an active or passive process. Most sharing is passive and ranges from an individual patiently scrounging the scraps that fall from a carcass as the possessor feeds, through harassment of the owner of carcass by gestures and vocalizations, to an individual who is not in possession of the kill taking a portion of carcass without the use of aggression. Active sharing is less common and involves the individual who possesses the carcass handing part, or all, of the carcass to another chimpanzee. There are a number of theories to explain why food should be shared, and the patterns of sharing observed. These including tolerated theft, reciprocity, kin selection, mutualism, buy-off, and harassment. As they apply to chimpanzees, these theories have been discussed elsewhere (de Waal 1989; Mitani and Watts 2001; Fruth and Hohmann 2002; Stevens 2004; Stevens and Gilby 2004).

Patterns of sharing appear to differ between West and East African chimpanzees. In the Taï Forest, West African chimpanzees tend to divide the kill among the individuals who participated in the hunt. Older and more dominant males gain a greater share of the meat, but hunters tend to receive more than nonhunters, even when socially subordinate. The amount of meat obtained by females is not dependent on participation in the hunt, but females will support hunters over nonhunters when there is competition (Boesch and Boesch-Achermann 2000). In East Africa, at Gombe (Stanford 1998), Mahale (Nishida and Hosaka 1996), Ngogo (Mitani and Watts 2001), and Budongo (Newton-Fisher unpublished data), chimpanzees use a different strategy for the division of the carcass. Males tend to monopolize the carcass and share only with particular adult females and other adult males, biasing their sharing toward alliance partners.

The sharing strategy employed by West African chimpanzees may oblige them to hunt adult monkeys. Collaborative group hunting appears necessary to increase hunting success and to reduce the time spent hunting in a habitat that favors escape by the prey but may only work if males are rewarded for participating in the hunt (Stanford 1998). Colobus monkeys are smaller in West Africa than they are to the East, which might make targeting juveniles unprofitable if the meat has to be shared among all hunters.

For East African chimpanzees, the larger body size of the colobus monkeys may pose a greater hazard and East African chimpanzees show greater fear of adult colobus monkeys than do those in West Africa. Adult colobus monkeys can successfully threaten and rout chimpanzees, chasing them from trees on occasion (Nishida et al. 1979; Goodall 1986; Boesch and Boesch 1989). Given that the strategy adopted by East African chimpanzees of targeting juvenile and infant chimpanzees appears to be profitable (Boesch 1994), the additional costs of targeting adult monkeys together with the more Machiavellian sharing strategy may make hunting adult monkeys a less attractive and unnecessary option.

14.6 Why do chimpanzees hunt?

Meat is a nutritious food and it seems likely that chimpanzees who eat meat, particularly those males who consume relatively large quantities, gain nutritional benefits. Nevertheless, the frequency of consumption varies from individual to individual, month to month, year to year, and between populations. Chimpanzees are omnivores, carnivory does not appear to be critical for survival or reproduction, and various theories have been advanced to explain the occurrence of their hunting behavior.

14.6.1 Hunting for nutrition

Early views of chimpanzee hunting favored the view that hunting was driven by nutritional demands. Teleki (1973) proposed that Gombe chimpanzees may hunt to compensate for nutritional shortfalls, given the strong seasonality at this site. The body weights of Gombe chimpanzees are lower during the dry season (Williams et al. 2002), which may to be the consequence of low-food availability, and hunting at Gombe is more pronounced during the dry season than it is during the wet season (Stanford 1998). A nutritional perspective was also emphasized by Wrangham (1975), with a similar view emerging from research at Mahale (Takahata et al. 1984).

14.6.2 Hunting for trade goods

The nutritional content of meat and associated tissues, together with the fact that it is both divisible and portable, means that each portion has an inherent value and can be either consumed or given to another individual. Meat can thus be considered a commodity that can be traded with other individuals for other goods or services, which for chimpanzees are likely to be biases in future social interactions such as support in agonistic confrontation or increased levels of grooming. Such a “biological markets” (Noe and Hammerstein 1995) perspective is implicit in two further theories concerning chimpanzee hunting, both of which see an adaptation in the nonrandom sharing of kills, with hunting simply the most common behavior that provides access to carcasses.

The first of these, labeled “meat-for-sex” by Mitani and Watts (2001), was also proposed by Teleki (1973). He noted that cycling females with conspicuous ano-genital swellings tended to receive meat from adult males more frequently than did females without these sexual swellings, and suggested that males shared meat with females in exchange for sexual access. Swollen females are attractive to males (Dixson 1998) as the swellings generally indicate approaching ovulation, although females will also show swellings when pregnant (Wallis and Lemmon 1986). Supporting evidence for this hypotheses was provided by Stanford (1998) who found that, at Gombe, the presence of a swollen female in a party of chimpanzees was the best predictor of a hunt occurring when encountering a group of red colobus, and reported five observations of females begging for meat from males, and only being given part of the kill after copulating.

The other theory that involves using prey as a trade good is the “male-social-bonding” hypothesis. Nishida (Nishida et al. 1992; Nishida and Hosaka 1996) provided data to support the idea that males trade meat with other males in order to develop and maintain the alliances that play an important role in male–male competition for status. Mitani and Watts (2001) showed that, at least for the Ngogo chimpanzees, while the presence of a female with a sexual swelling was a significant predictor of the decision to hunt, this was an artifact of the relationship between the presence of such females and the number of adult males, and that it was the number of adult males alone that predicted hunting. They also showed that males shared reciprocally, at least when considering all pairs of males simultaneously, and that there was a positive association between sharing of carcasses and support in agonistic coalitions (Mitani and Watts 2001; Watts and Mitani 2002).

14.6.3 Hunting to assess reliability

Male chimpanzees vary in their hunting ability, as demonstrated by the proportion of hunts that they join, the number of kills that they make, and their success at hunting alone (Stanford et al. 1994; Stanford 1998; Boesch and Boesch-Achermann 2000; Watts and Mitani 2002). Among the Ngogo chimpanzees, and potentially elsewhere, good hunters are also more frequent members of the territorial patrols that monitor and probe boundaries with neighboring communities. Furthermore, males that hunt together patrol together, and the frequency of joint patrolling is correlated with the frequency with which males form coalitions and the amount of grooming between them (Watts and Mitani 2001;

Watts and Mitani 2002). This leads to the hypothesis that hunting itself may have a function that is independent from acquiring meat: it demonstrates risk-taking and allows males to assess the reliability of others when faced with danger (Watts and Mitani 2001). This is essentially a refinement of Kortlandt's (1972) "hunting-to-display-social-prowess" hypothesis. Given the risks associated with patrolling and intercommunity encounters (Goodall et al. 1979; Boesch and Boesch-Achermann 2000; Muller 2002), such assessments may be important for male chimpanzees. This hypothesis may be important in relation to the "showoff" hypothesis proposed to explain hunting behavior in human males (Hawkes 1991; Hawkes and Bird 2002).

14.6.4 So who do chimpanzees hunt?

This question, which addresses the adaptive value of hunting, remains to be answered. It is only recently that quantitative analyses comparing the different hypotheses have been undertaken (Mitani and Watts 2001) and, while there are efforts to draw together results from different populations (Uehara 1997; Boesch et al. 2002), systematic analyses have yet to be applied across populations.

The possibility that chimpanzees achieve nutritional benefits directly from hunting cannot be easily dismissed. The necessary nutritional studies quantifying chimpanzee diet have not been conducted, and for either of the trade-goods hypotheses to operate, there must be a nutritional gain to the individuals who receive and consume parts of the carcass. If there were not, the carcass would hold no value and could not be traded. The particular hypothesis that chimpanzees switch to hunting to compensate for nutritional shortfalls finds little support from the only direct test: Mitani and Watts (2001) found that Ngogo chimpanzees hunted more frequently as fruit became more abundant, suggesting that chimpanzees are more likely to hunt when they have enough surplus energy. This makes sense if hunting is energetically costly, and individuals risk not gaining enough meat following division of the kill to offset such costs.

Whether this relationship between food abundance and frequent hunting applies to all populations of chimpanzees remains to be determined, but hunting seasons do coincide with fruit abundance in Mahale (Takahata et al. 1984; Uehara 1997), although apparently not at Taï (Boesch and Boesch-Achermann 2000) where chimpanzees may gain shares of the kill that depend on their participation in hunting (Boesch 1994). If the Taï chimpanzees capture and kill a sufficiently large prey in each hunt, and if they can rely on this system of dividing the meat, then net nutritional gains would accrue to all participants.

At Gombe, the relationship between seasonal changes in body weight and condition and hunting remains intriguing, although Stanford (1998) concludes that the nutritional shortfall hypothesis is unlikely to explain hunting in this population. Prey are typically small, often immature monkeys, and division of the kill is unequal. As a result, hunters cannot rely on recouping lost energy.

It appears that East African chimpanzees, at least, hunt to gain meat but not to compensate for nutritional shortfalls. This meat is used as a commodity and traded with others. While the “meat-for-sex” and “male-social-bonding” hypotheses are commonly presented as alternatives (Mitani and Watts 2001; Watts and Mitani 2002), they may be alternate, context-dependent, outcomes of the same social strategy. The “meat-as-commodity” hypothesis proposes that chimpanzees hunt to gain possession of a commodity (part or all of an animal carcass) which has economic value within chimpanzee society (Stanford 1998). They can then trade this to further whatever proximate goals are most pressing, providing meat to allies when they have need of them or to females in an effort to coerce their mating behavior.

At Gombe, the presence of a female with a sexual swelling was the best predictor of hunting and this remained true when the effect of number of males in the party (also a predictor of hunting) was removed. Males shared food with swollen females, and in some cases shared only after copulating (Stanford 1998). At Ngogo, by contrast, the number of males was the best predictor of hunting and the presence of swollen females was not a significant predictor once the effect of the number of males was removed. Males of this community did preferentially share meat with swollen females, but did not copulate with those females after sharing at a level above chance, and did not gain a larger share of matings if they shared with a female, comparing female cycles in which the male shared with those in which he did not (Watts and Mitani 2002). It is not clear, however, whether Ngogo males shared before or after copulating; Gombe males were described as withholding meat until the female copulated.

If the “meat-as-commodity” hypothesis holds, then these apparently contradictory findings on the reasons for chimpanzee hunting can be reconciled. If the immediate proximate benefits for the males possessing the meat differed between the two communities, males would be predicted to use their “trade goods” in different ways. Important factors are likely to include the number of males in the community and the intensity of within-community competition for status, which will translate into the opportunities and necessity for alliance formation, respectively. The two communities differ markedly in this respect. The Gombe community in the early 1990s numbered 45 individuals, with 8 adult males (Stanford 1998), whereas the Ngogo community (in the late 1990s) numbered in excess of 140 individuals, including 24 adult males (Mitani and Watts 2001). Other important factors may include the degree to which males can coerce female mating behavior through other means, and differences in female mating strategies. For example, if Gombe females are nutritionally stressed during the dry season, they may be prepared to compromise a promiscuous mating strategy by providing sex in return for even the smallest scraps of food. McGrew (1992) showed that those females who were more successful at getting meat had greater numbers of surviving offspring. Ngogo females may not be under the same pressure, and they may place less value in male-controlled meat. Testing whether "meat-for-sex" and "male-social-bonding" are different proximate outcomes of the same adaptation awaits future research.

Nutritional gain appears to be sufficient to explain hunting in West African chimpanzees (at least at Taï: Stanford 1998) but only if the carcass is divided among the hunters. Given that 47% of individuals sharing in a carcass appear to cheat the system (Boesch and Boesch-Achermann 2000), the possibility that other factors influence hunting needs investigation. The "hunting-as-risk-assessment" hypothesis might apply to the monkey-hunting specialists of the Taï Forest, as is appears to apply to the Ngogo chimpanzees, although it will be necessary to disentangle "hunting-as-risk-assessment" from "meat-for-allies" in testing the relative importance of these two ideas at both sites.

14.7 Conclusions

Chimpanzees are not the only primates that hunt vertebrate prey. Baboons (*Papio* spp.) also hunt opportunistically, targeting small ungulates (Morris and Goodall 1977; Strum 1987). Among New World primates, capuchin monkeys (*Cebus* spp.) prey upon a variety of species with *Cebus capucinus*, perhaps best studied, showing a focus on squirrels, infant coatis, and birds (Rose 1997; Rose et al. 2003), while some squirrel monkeys (*Saimiri* sp.) hunt bats (Boinski and Timm 1985; Souza et al. 1997).

Among the great apes, vertebrate predation appears to be rare or absent among gorillas and orangutans, but bonobos (*Pan paniscus*), the phylogenetic sister species to chimpanzees, do hunt vertebrates. Recorded prey species including black and white colobus (*Colobus angolensis*), red-tailed monkeys (*Cercopithecus ascanius*) (Sabater Pi et al. 1993), flying squirrels (Kano and Mulavwa 1984), and forest duiker (*Cephalophus* spp.) (Hohmann and Fruth 1993; Fruth and Hohmann 2002). Hunting by bonobos typically occurs at a lower rate than in chimpanzees: Fruth and Hohmann (2002) report only 9 kills in 46 months of observation, 7 of which were duiker.

While hunting is thus not unique to chimpanzees among the primates, it does appear to be a ubiquitous aspect of their behavior, occurring in all populations studied thus far. The picture that has emerged from these studies is one of diversity but with some common themes. Across populations, hunting is a predominately male activity. Chimpanzees hunt a variety of vertebrate prey, but there is a common focus on medium-sized mammals, particularly primates, and especially colobus monkeys. Red colobus appear to be the preferred prey, although the species (and body size) of red colobus varies across Africa. Chimpanzees appear to impose significant predation pressure on their main prey species, but the intensity and frequency of hunting varies between populations and from month to month within single communities. Hunting is typically opportunistic on encountering the prey, although there is some evidence of chimpanzees searching for prey. Hunts can be solo or group efforts, and the degree to which individual chimpanzees hunt together varies between East and West African populations. This appears to be related to the way the kill is divided following the hunt. In West Africa, the kill tends to be shared according to participation in the hunt and individual hunters collaborate, taking different roles, whereas in East Africa, the kill is typically divided tactically, with the male in possession of the carcass trading parts of it with females for sex, providing the meat after copulating, or with other males for future coalitional support and group hunts are more akin to individual efforts to secure prey occurring simultaneously.

It is important to recognize that this picture comes from detailed systematic studies of only a handful of communities (Gombe, Mahale, Taï, Ngogo). Comparable systematic studies of hunting by chimpanzees in other populations are lacking, although some data are available from almost every population studied. In addition, much of the research effort has focused on chimpanzees and red colobus monkeys. Far less is known about chimpanzee hunting of other species and the nature and importance of hunting in populations that are not sympatric with red colobus. Certainly, chimpanzees without red colobus to hunt appear to hunt less frequently (Basabose and Yamagiwa 1997; Newton-Fisher et al. 2002), and it is unclear what impact low levels of hunting, providing fewer carcasses to share and consume, have on patterns of chimpanzee behavior. If one goal of studying chimpanzee hunting behavior is to shed light on the behavioral ecology of the hominines then addressing the shortcomings in current data is a priority.

The ubiquitous nature of chimpanzee hunting, the common occurrence of food sharing, and the diversity in the patterns of these behaviors, together with the close phylogenetic relationship between chimpanzees and humans, ensure that consideration of chimpanzee hunting is essential in any discussion of the role played by meat eating and food sharing in the behavioral ecology of early hominine species. The radiation of early hominines encompassed a number of species with different morphologies, and it seems likely that these hominines showed both within and between species variation in habitat and behavioral ecology (Foley 1997). The chimpanzee-red colobus system may be a useful model for some of this variation, but it remains necessary to understand the role of hunting and meat eating across chimpanzee populations, including those with an impoverished resource base. Already it is clear that different populations target different arrays of species, specialize or generalize their choice of prey, and hunt and use meat in different ways. Future studies of new populations are likely to increase this picture of diversity, and systematic tests of the hypotheses for hunting and meat sharing will clarify both why chimpanzees hunt and the importance of this behavior for the study of human evolution.

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