

The Hunting Behavior and Carnivory of Wild Chimpanzees

Abstract

The pursuit, capture, and consumption of small- and medium-sized vertebrates appear 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 vary from month to month and among 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, cooperation in hunting is more limited, and the kill is typically consumed selfishly or divided in response to harassment (begging) by others. In some cases, it may be shared tactically, trading meat with other males to strengthen alliances. The adaptive function of chimpanzee hunting is not well understood, and a variety of hypotheses have been proposed. Ideas that chimpanzees hunt to make up for nutritional shortfalls, or to acquire meat to trade for sex, have failed to find empirical support, while recent work favors nutritional benefits of some kind. Nevertheless, cross-population studies evaluating multiple hypotheses are in their infancy, and there is much to be learned. In particular, very little is known about hunting of nonprimates, particularly ungulates, or the impact that variation in levels of hunting, and of carcasses to share and consume, has on patterns of chimpanzee behavior. If one goal of studying this topic is to shed light on the behavioral ecology of hominins, then efforts to understand the diversity of hunting and carnivory in wild chimpanzees are needed.

Introduction

Hunting - the pursuit, capture, and consumption of small- and medium-sized vertebrates - appears to be typical of all chimpanzee (*Pan troglodytes*) populations. Such 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-gatherer 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 1996, 1998, 2001). While early ideas such as "Man the Hunter" (Washburn and Lancaster 1968) have been largely 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 hominins (Domínguez-Rodrigo 2002). In this chapter, substantially revised and updated from the previous version (Newton-Fisher 2007), I review the data concerning hunting behavior among wild chimpanzees and address current hypotheses concerning the reasons why chimpanzees hunt, drawing out both similarities and differences between populations in their hunting behavior.

Characteristics of Chimpanzee Hunting

All known populations of chimpanzees show some evidence of hunting and consuming vertebrate prey. Such hunting has been documented systematically among the East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Gombe (van Lawick-Goodall 1968; Teleki 1973; Busse 1977; Stanford 1998; Gilby 2006; Gilby et al. 2006, 2010) and Mahale (Nishida et al. 1979; Takahata et al. 1984; Uehara 1997) National Parks in Tanzania and of the Kibale Forest National Park (Mitani and Watts 1999; Watts and Mitani 2002; Teelen 2008; Gilby et al. 2008; Watts and Amsler 2013) in Uganda, as well as 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; Gomes and Boesch 2009). 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), and Semliki, Uganda (Hunt and McGrew 2002); from central African populations (*P. t. troglodytes*) of Lopé, Gabon (Tutin and Fernandez 1993) and Ndoki, Cameroon (Kuroda et al. 1996; Takenoshita 1996); from the Ebo forest, Cameroon (*P. t. ellioti*) (Morgan et al. 2013); 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).

Prey Diversity

Across populations, prey diversity is high with at least 40 species of vertebrates targeted. Chimpanzees show a clear focus on mammalian prey (Table 1) and are known to consume a variety of primate species as well as ungulates and rodents but will also eat birds, lizards, and frogs. Some populations 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 Tai, chimpanzees hunt only 7 (all primates) of the 15 sympatric mammal species (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).

Table 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	Tai	Tenkere
Primates													
Red colobus													
<i>Piliocolobus badius</i>												✓	
<i>Piliocolobus tephrosceles</i>		✓			✓	✓							
Black and white colobus													
<i>Colobus guereza</i>	✓				✓		✓						
<i>Colobus polykomos</i>												✓	✓
<i>Colobus satanas</i>								✓					
Olive colobus													
<i>Procolobus verus</i>												✓	
Gray-cheeked mangabey													
<i>Lophocebus albigena</i>					✓			✓					
Sooty mangabey													
<i>Cercocebus atys</i>												✓	
Olive baboon													
<i>Papio anubis</i>		✓			✓								
Yellow baboon													
<i>Papio cynocephalus</i>						✓							
Vervet monkey													
<i>Chlorocebus pygerythrus</i>						✓							
Red-tailed monkey													
<i>Cercopithecus ascanius</i>	✓	✓		✓	✓								

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												
Cephalophus monticola	✓				✓	✓		✓				
Bushbuck												
Tragelaphus scriptus		✓				✓						
Bushpig												
Potamochoerus porcus		✓				✓						
Warthog												
Phacochoerus aethiopicus						✓						
Others												
Giant elephant shrew												
Rhynchocyon sp.						✓						
Yellow-spotted hyrax						✓						
Heterohyrax brucei												
White-tailed mongoose												
Ichneumia albicauda						✓						
Civet												
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

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, *Piliocolobus 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 Tai Forest, chimpanzees show a notably strong specialization. Between 1984 and 1995, 249 of 267 known kills were of colobus monkeys: 80.5 % red colobus (*Piliocolobus badius*) and 12.7 % black and white colobus (*Colobus polykomos*) (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).

By contrast, red colobus constituted only 53 % of all prey for the Mahale chimpanzees (Nishida et al. 1992), while black and white colobus (*Colobus guereza*) were 43.8 % of all prey for the Sonso chimpanzees of the Budongo Forest, where there are no red colobus (Newton-Fisher et al. 2002). These 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 observations support the idea that these chimpanzees do not demonstrate the extreme prey specialization seen in Tai and Ngogo (Newton-Fisher unpublished data). Forest ungulates, particularly duiker and bushpig, are in fact hunted by all the East African chimpanzee populations that have been 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 regarding chimpanzee predation on ungulates.

Chimpanzee populations also appear to differ in their choice of the age and sex of prey. For the Tai chimpanzees, half of their colobus monkey prey are adult, mostly females (Boesch and Boesch-Achermann 2000). This is in contrast to chimpanzees at Mahale and Gombe, where the vast majority of colobus prey are juveniles and infants (Goodall 1986; Uehara 1997) and some chimpanzee hunters target very young colobus monkeys, snatching them from their mothers (Stanford 1998). Somewhere between 75 % (Stanford et al. 1994) and 86 % (Stanford 1998) of red colobus prey at Gombe are immature individuals. For the Ngogo (Kibale) chimpanzee, the figure is somewhat less: 53-75 % (Mitani and Watts 1999; Watts and Mitani 2002). There is less information on the age and sex of non-colobus prey. Among the ungulates, bushbucks 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 is clear that chimpanzees are quite capable of killing adult blue duiker (personal observations).

Sex Bias in Hunting

The hunting of monkeys is a predominately male activity. Among the chimpanzees of the Ngogo (Kibale) community, 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 who 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 as part of mixed-sex hunting party were likely to be taken by males (Goodall 1986), however, which may in part explain female unwillingness to hunt when males are present.

Females may prey more on ungulates (Uehara 1997), but quantitative data are difficult to collect, in part due to the nature of ungulate hunting. The hunting of lesser bushbabies (*Galago senegalensis*) in Fongoli, Senegal, is rather different to the typical group hunts of monkeys: it is tool assisted, extractive, and individualistic; it also shows a strong female bias, with 14 of 22 observations of female hunters and only one of an adult male hunting in this way (Pruetz and Bertolani 2007).

Hunting Frequency

Detecting hunting in a chimpanzee population can be problematic, particularly if the chimpanzees are poorly habituated to human observers. Typically in this situation, hunting is rarely if ever seen, and studies rely on finding animal remains such as skin or bone in chimpanzee feces (McGrew 1992). Unfortunately, feces do not appear to provide a reliable indicator of hunting: while the presence of remains can confirm that consumption does occur, little can be said about its frequency (cf. Uehara 1997). For example, 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).

Predation Pressure

While in some populations chimpanzees hunt only rarely, in others they are significant predators who hunt at levels that appear to be unsustainable (Goodall 1986; Wrangham and van Zinnicq Bergmann Riss 1990; Teelen 2008; Watts and Amsler 2013). Estimates for Gombe suggest that anything from 8 % to 42 % of the colobus population can be killed annually, with this proportion varying from year to year, 8-13 % (1973-1974: Busse 1977), 41.6 % (1972-1975: Wrangham and van Zinnicq Bergmann Riss 1990), and 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). For Ngogo, Teelen (2008) estimated 15-53 % of the red colobus population is killed by chimpanzees annually, while Watts and Amsler (2013) estimated that almost 2,500 red colobus monkeys were killed in the period 1998-2012, an average of 20.4-24.8 % of the population per year. By 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).

Nevertheless, the level of predation by some chimpanzee communities on red colobus monkeys is extreme. As a reference point, predation by crowned eagles on the total cercopithecoid monkey population at Ngogo is estimated at 2 %: Mitani et al. (2001). There is good evidence that a significant decline in red colobus monkeys in the Ngogo region of the Kibale forest, at least since the mid- to late 1990s and possibly since the 1970s, is the result of chimpanzee predation (Teelan 2007, 2008; Lwanga et al. 2011; Watts and Amsler 2013). Simulations using 3 years (2001-2003) of Ngogo data showed that chimpanzee predation was likely to drive the red colobus population to local extinction within two decades without a dramatic change in the level, or success, of chimpanzee hunting (Teelen 2008). Local extinction is more probable if neighboring communities of chimpanzees also impose significant predation pressure (Watts and Amsler 2013) as this removes any "source" population from which immigrants can be drawn (contra Lwanga et al. 2011). The decline in red colobus in Ngogo has, however, been accompanied by a decline in chimpanzee hunting (encounters, hunts, and prey offtake) which appears to be a consequence of the reduced availability of prey: when these chimpanzees expanded their territory in 2009 (Mitani et al. 2010), they increased rates of both prey encounters and hunting (Watts and Amsler 2013).

Variation in Hunting Frequency

Estimates of hunting frequency and predation pressure typically 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 as a result of either more hunting, more successful hunting, or both. For the chimpanzees at Gombe, Mahale, and Tai, 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; Gilby 2004). 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), and among the Kanyawara chimpanzees of the Kibale forest, hunting rates were higher when preferred species of ripe fruit were abundant (Gilby and Wrangham 2007). At Tai, the hunting season runs from mid-August to mid-November, between periods of low and high fruit abundance, and ends 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, which may 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 decrease in the number of chimpanzees in the study community (Boesch et al. 2002): a similar reduction in the level of hunting was seen following a decrease in the number of adult males in the study community in the Tai Forest (Boesch and Boesch-Achermann 2000).

Impact Hunters

Chimpanzees may also experience greater hunting success when individuals with a flair for hunting are present. These individuals ("impact" hunters) demonstrate both a high willingness to hunt and a consistently high probability of success (Goodall 1986; Stanford 1998; Boesch and Boesch-Achermann 2000). Typically, one or two males in each study populations where monkey hunting is prevalent have been identified as impact hunters (Goodall 1986; Stanford 1998; Boesch and Boesch-Achermann 2000; Gilby et al. 2008), with anecdotal evidence suggesting that these individuals are responsible for initiating hunts, climbing first toward prey. Other male chimpanzees may be spurred into hunting by the actions of these impact hunters. A recent increase in hunting of black and white colobus monkeys by Sonso (Budongo) chimpanzees has been ascribed to the actions of a particular male, while Stanford (1998) found that two males of the Kasekela (Gombe) community were highly successful when hunting alone and that one of these, Frodo, was both a catalyst for hunts and a fearsome predator of red colobus monkeys, killing at least 50 in the period 1990-1992. Gilby et al. (2008) tested the influence of impact hunters among the Kanyawara (Kibale) chimpanzees and found that the likelihood of a hunt occurring was much greater when an impact hunter was present, even when controlling for the number of adult males, and that the chance of other males joining a hunt increased if an impact hunter was hunting.

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, one

mangabey (*Lophocebus albigena*), and one red duiker (*Cephalophus* sp.). Only 4 of the 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 suggest that fruit is particularly abundant, and so hunting binges at Gombe may also be linked to periods of food abundance.

How Do Chimpanzees Hunt?

Many hunts are opportunistic, in that chimpanzees appear to decide to hunt after encountering prey during the course of normal foraging activities or 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). Chimpanzees in Tai, however, show evidence of actively searching for prey, listening for the vocalizations of either colobus monkeys or Diana monkeys (*Cercopithecus diana*) with whom the colobus are frequently associated (Boesch 1994; Boesch and Boesch-Achermann 2000). The likelihood of a hunt when chimpanzees encounter potential prey varies: it is relatively high for the Kasekela (Gombe) community (40 %: Gilby et al. 2006) and the Ngogo (Kibale) community (37 %: Mitani and Watts 2001) but somewhat lower in the Kanyawara (Kibale) community (15 %: Wrangham, cited in Gilby et al. 2006).

Chimpanzees hunt the majority of their prey 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). In Fongoli, Senegal, chimpanzees fashion tools from branches, at times biting the end to create a point, which are forcibly jabbed into tree cavities: observations suggest that this is done to immobilize or kill lesser bushbabies (*Galago senegalensis*) that are then extracted and consumed (Pruetz and Bertolani 2007).

During a monkey hunt, prey are typically chased, seized, and then killed either by a bite, by disembowelment, or by being torn apart (Goodall 1986). Hunts may yield single or multiple kills (or, indeed, may fail completely). 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 Tai chimpanzee hunters (Stanford 1998), although typically such kills are of adult monkeys (mean number of kills per successful hunt: 1.2: Watts and Mitani 2002). Failure rates (i.e., failure to kill any prey during a hunt) vary between communities. For the Tai and Gombe chimpanzees, around 50 % of hunts fail (Boesch and Boesch-Achermann 2000; Gilby et al. 2006), while for Ngogo chimpanzees the rate is lower, at 16 % (Mitani and Watts 2001). In an analysis of hunting by chimpanzees of the Kanyawara community, Gilby et al. (2008) found that an individual hunter had around a 65 % chance of acquiring meat in any hunt that was successful; among the Tai chimpanzees, a male had access to meat in around 48 % of successful hunts (Boesch and Boesch-Achermann 2000).

Analysis of hunting data from both Ngogo (Watts and Mitani 2002) and Gombe (Wrangham 1975; Stanford et al. 1994; Gilby et al. 2010) indicates that hunting is responsive to habitat structure. At Ngogo, chimpanzees were more likely to hunt red colobus when encountering prey in, or close to, areas with broken or no tree canopy than when in primary forest (Watts and Mitani 2002); at Gombe, hunts were more likely and more successful in woodland and semi-deciduous forest than in evergreen forest. These observations suggest that, as with obligate predators, chimpanzees are more likely to hunt in areas where it is harder for prey to escape and hunting costs are lower (Gilby et al. 2010).

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 (personal observations). 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.

Cooperative Hunting?

Chimpanzees will hunt alone as well as 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 (1994) found that Gombe chimpanzees had a success rate of around 50 % when hunting alone, capturing an average of 2.46 kg of prey within 7 min of hunting. In contrast, his estimate for the success rate of lone hunters at Taï was only 13 %. 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).

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 take particular roles such as "drivers" and "blockers" (Boesch and Boesch 1989), appears to be the primary form of hunting among the Taï chimpanzees (77 % of hunts: 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.

There is little consensus over the degree to which such collaborative hunting can be described as cooperative. To the extent that chimpanzees take different roles and are responsive to one another's behavior during a hunt targeting monkeys, there is good evidence for social cooperation. To demonstrate that chimpanzee hunting is functionally cooperative, however, 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; Gilby et al. 2006); at Kanyawara, however, there does appear to a synergistic effect (Gilby et al. 2008).

Many chimpanzees, hunting together, may be able to overwhelm the defensive strategies of the red colobus and reduce the opportunities for panicked monkeys to escape. However, the mass of prey obtained per hunter does not correlate with the number of males hunting at Ngogo (Watts and Mitani 2002), and while Stanford (1998) found that Gombe chimpanzees gained a higher return (greater mass of prey per hunter) when more than seven are hunting together, Gilby et al (2006), using a larger dataset from the same community, found that the mass of prey per hunter actually decreased with the number of adult male chimpanzees present. By contrast, 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.

Scavenging

Chimpanzees are reluctant scavengers: only a handful of reports describe such behavior. Most of these observations concern the seizing 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 plundering 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 plundering red colobus captures from eagles while the monkeys were still alive and a further four instances of chimpanzees eating the kills of eagles: presumably these monkeys were freshly killed, although 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 - acquiring meat from an abandoned carcass - appears particularly rare, however. In 36 years of observation at Gombe, fewer than 20 instances were recorded (Stanford 1998), and at least nine of these (all red colobus) were likely, or known, to have been 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 Tai: 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 apparently curiosity-driven 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 body, even grooming it, and one female rolled around inside the eviscerated carcass, but they did not feed (Muller et al. 1995). By 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).

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, 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 Tai (2.9 hunts per month). Nevertheless, as discussed above, chimpanzees do hunt, kill, and consume meat, while competition over the division of the kill can be high.

The Value of Meat

Animal tissue, including muscle, internal organs, brain, and bone marrow, provides an easily digestible nutritious package (Stanford 1996; Milton 1999). Beyond any particular calorific value, it provides high-quality protein containing all essential amino acids, as well as long-chain polyunsaturated fatty acids, and a range of key micronutrients such as calcium, potassium, magnesium, zinc, B-group vitamins, and vitamin K. Commonly, chimpanzees consume the entire animal, including bones and skin, and will compete for the smallest scraps. A single carcass can, therefore, represent an important resource, despite variation in body size between prey species: adult *Colobus guereza* 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 of 8-12 kg) is smaller and similar in size to the eastern red colobus (*Ptilocolobus tephrosceles*: adult male body weight of 13 kg); the western red colobus (*Ptilocolobus badius*) are lighter, with an adult body weight of only 5-10 kg (Kingdon 1997); and blue duiker (*Cephalophus monticola*) can weigh up to around 9 kg, with duiker (*Cephalophus* sp.) meat providing 20.8 g/100 g of protein and 3.4 g/100 g of fat (Ntiama-Baidu (FAO) 1997).

The quantity of meat, including the associated elements of the carcass, that is 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 chimpanzees of the Kasekela (Gombe) 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) estimated that, averaged across the year, male Tai chimpanzees consumed 186 g per day, while females consumed 25 g per day. Their estimates for Gombe chimpanzees, similarly averaged, were 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. Gilby (2006) estimated that, for adult males of this community in 1999-2002, an individual in possession of a kill consumed between 0.25 and 2.5 kg (mean = 1.16 kg) of meat during each feeding bout. For the Tai chimpanzees between 1987 and 1991, males consumed a mean of 0.48 kg of meat per successful hunt, while females consumed a mean of 0.13 kg (Boesch and Boesch-Achermann 2000).

Thus, meat should be a valued resource for chimpanzees, although there are observations that question this conclusion. In particular, captured prey may be eaten only partly before being discarded. In the Tai 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 pursuing immature monkeys (Boesch 1994; Stanford 1998) and giving a carcass to another individual in order to hunt again (Goodall 1986), while 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). Similarly, 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.

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 this resource. 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 to prevent them reaching toward the carcass.

Sharing of prey 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 the 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 include tolerated theft, reciprocity, kin selection, mutualism, buy-off, and harassment. As they apply to chimpanzees, these theories have been discussed extensively elsewhere (de Waal 1989; Mitani and Watts 2001; Fruth and Hohmann 2002; Stevens 2004; Stevens and Gilby 2004; Gilby 2006).

Patterns of sharing appear to differ between West and East African chimpanzees. In the Tai 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 other adults, both male and female (although it is worth noting that while Gilby (2006) found that Kasekela (Gombe) males, particularly the alpha, controlled carcasses, these males only shared preferentially with adult females with whom they exchanged grooming and did not preferentially share with particular males).

The particular 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 in East Africa, and this 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 a less reliable, more individualistic approach to sharing may make hunting adult monkeys a less attractive option.

Why 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 various hypotheses have been undertaken (Mitani and Watts 2001; Gilby et al. 2006) and, while there are efforts to draw together results from different populations (Uehara 1997; Boesch et al. 2002), systematic analyses across populations are limited (Gilby et al. 2010). Chimpanzees are omnivores, and while those who eat meat,

particularly in large quantities, should gain nutritional benefits, carnivory does not appear to be critical for survival or reproduction, and thus various hypotheses have been advanced to explain the existence of their hunting behavior.

Hunting for Nutrition

Early views of chimpanzee hunting favored the view that it was driven by nutritional demands. Teleki (1973) proposed that Gombe chimpanzees 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 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; Gilby et al. 2006). A nutritional perspective was also emphasized by Wrangham (1975), with a similar view emerging from research at Mahale (Takahata et al. 1984).

Energy Shortfall

The particular hypothesis that chimpanzees switch to hunting to compensate for energy shortfalls finds little support: Gilby et al. (2006) found that once party size and number of swollen (i.e., likely to be ovulating and therefore sexually attractive) females were taken into account, there was no association between diet quality and hunting among the Gombe chimpanzees. Furthermore, Mitani and Watts (2001) and Gilby and Wrangham (2007) found that chimpanzees from the Kibale forest 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, as discussed above, hunting seasons coincide with fruit abundance in Mahale (Takahata et al. 1984; Uehara 1997) although apparently not at Tai (Boesch and Boesch-Achermann 2000) where chimpanzees may gain shares of the kill that depend on their participation in hunting (Boesch 1994). If the Tai 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.

Meat Scraps

Boesch and Boesch-Achermann (2000) suggested that the nutritional value of meat beyond its calorific value might make even small amounts significant for chimpanzees. Gilby et al. (2008) and Tennie et al. (2009) formalized this idea as the "meat-scrap" hypothesis, which assumes that hunting functions as a means of acquiring micronutrients such as vitamins B₁₂ and B₆ and the minerals iron and zinc which are important for primate health and present at relatively high levels in meat but at low levels or virtually absent from primate plant foods. By consuming small amounts of meat ("scraps"), chimpanzees gain these micronutrients without having to consume vast quantities of plant material. This hypothesis assumes a threshold, a minimum amount of meat necessary to accomplish this goal (Tennie et al. 2009).

Both Gilby et al. (2008) and Tennie et al. (2009) provide support for this hypothesis. Among the Kasekela (Gombe) chimpanzees, the probability of an individual acquiring some meat increased by 18 % with each additional hunter, while the total amount of meat per hunter was not correlated to the number of hunters (Tennie et al. 2009) and in fact declined when all adult males present were considered (Gilby et al. 2006). For chimpanzees of the Kanyawara (Kibale) community, males were also more likely to obtain meat as the number of hunters increased, although once there were five or more hunters, males could do as well by begging: accordingly, focal males were less likely to hunt when more than five other males were present (Gilby et al. 2008).

Hunting for Trade Goods

The nutritional content of meat and associated tissue, 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 could therefore be considered to be 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 hypotheses concerning chimpanzee hunting, both of which see an adaptation in the nonrandom sharing of kills. While the "meat-for-sex" and "male-social-bonding" hypotheses are commonly presented as alternatives (Mitani and Watts 2001;

Watts and Mitani 2002), they could be considered to be different, context-dependent outcomes of the same social strategy. This "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 females in an effort to coerce their mating behavior or to allies when they have need of them.

Meat for Sex

The first of these trade-based hypotheses, labeled "meat for sex" by Mitani and Watts (2001), was proposed by Teleki (1973). He noted that cycling females with conspicuous anogenital 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 (Dixon 1998) as the swellings generally indicate approaching ovulation, although females will also show swellings when pregnant (Wallis and Lemmon 1986). Supporting evidence for this hypothesis 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.

However, in detailed analyses of the Gombe data together with data from the Kanyawara community, Gilby et al. (2006, 2010) found no support for the "meat-for-sex" hypothesis: specifically, males did not preferentially share with potentially ovulating females, and males were not more likely to hunt when such females were present. Furthermore, very few copulations occurred in close temporal proximity to meat-sharing events (Gombe: 0.6 %; Kanyawara: 0.1 %: Gilby et al. 2010), and when sharing of meat did occur between a male and a swollen female, mating was equally likely before as after (Gilby et al. 2010). Parous females at Gombe were more successful than nulliparous females at obtaining meat from males, but this was the case whether swollen (72 % vs. 44 % of bouts) or not (60 % vs. 30 % of bouts), and Kanyawara females showed a similar trend (Gilby et al. 2010). This is likely to be due to increased persistence or intensity of begging by parous females, rather than strategic sharing by males.

Similarly, at Ngogo, the presence of swollen females was not a significant predictor of hunting 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 at a level above chance after sharing. Furthermore, they did not gain a larger share of matings if they did share with a female, comparing female cycles in which the male shared with those in which he did not (Watts and Mitani 2002). Among the Tai chimpanzees, Gomes and Boesch (2009) found no evidence of direct exchanges of meat for sex or of a relationship between meat sharing and mating frequency.

There are also theoretical reasons to question this particular hypothesis. Female chimpanzees show a highly promiscuous mating strategy (Nishida 1968; Sugiyama 1968), typically copulating hundreds of times with multiple males during a single ovulatory cycle (Wrangham 2002). As a result, it seems unlikely that they would require meat from males before mating; furthermore, males in possession of meat are typically high ranking: such males may be those most able to coerce female mating behavior through the use of aggression and so the least likely to need to trade anything with females in return for sex. For a more detailed discussion of this topic, see Gilby et al. (2010).

Male Social Bonding

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 are thought to 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).

By contrast, this hypothesis did not account for patterns of sharing between male chimpanzees at Gombe (Gilby et al. 2006). Hunting was more likely in parties with more males, but increasing male party size did not increase the likelihood that an individual focal male would hunt. Furthermore, these males did not share preferentially with those with whom they

groomed or associated frequently (Gilby 2006). Similarly, an analysis of hunting among chimpanzees of the Kanwayara community found no support for this hypothesis, again using grooming and association as proxies for alliance partnerships (Gilby et al. 2008).

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, 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), these kinds of mutual assessments may be important for male chimpanzees. The "hunting-as-risk-assessment" hypothesis might apply to the monkey-hunting specialists of the Tai Forest, as it appears to apply to the Ngogo chimpanzees, although it will be necessary to disentangle "hunting to assess reliability" from "male social bonding" (meat for allies) in testing the relative importance of these two ideas at both sites. This hypothesis may be interesting to consider in relation to the "show-off" hypothesis proposed to explain hunting behavior in human males (Hawkes 1991; Hawkes and Bird 2002).

So Why Do Chimpanzees Hunt?

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.

While it appears that chimpanzees hunt to gain meat, this is not to compensate for nutritional shortfalls. There is also essentially no support for the meat-for-sex trading hypothesis, and this can be largely discounted. That said, Gomes and Boesch (2009) found some evidence for this over a longer term (i.e., not in the immediate sharing context) among the Tai chimpanzees, which remains intriguing. The one context where females refrain from their promiscuous mating strategy is the consortship mating context (Tutin 1979). Does previous meat sharing by males increase the likelihood that females will comply with male efforts to initiate or maintain consortships? This remains to be determined.

While it seems that nutritional (i.e., calorific) gain appears to be sufficient to explain hunting in West African chimpanzees (at least at Tai: Stanford 1998) given the pattern of sharing in relation to participation, evidence that 47% of individuals sharing a carcass appear to cheat the system (Boesch and Boesch-Achermann 2000), as well as the possibility that other factors influence hunting, needs investigation before any firm conclusions can be drawn. For the Ngogo chimpanzees, there is evidence for both the male social bonding and assessing reliability hypotheses. For the Gombe chimpanzees on the other hand, sharing appears to come down to successful harassment of those individuals possessing meat (begging), and there is no support for the male social bonding hypothesis.

The adaptive value - the function - of hunting thus remains unclear. Future work will need to consider variation in both predator and prey demography and perhaps determine more precisely the nutritional gains and energetic costs of hunting. It may also be worth testing hypotheses that address the behavior directly, rather than looking for a function in terms of relationships. It is becoming clear that chimpanzees hunt monkeys more frequently in locations where hunting costs are lower or at least where the prey should find it harder to escape; that hunting typically occurs when other food is abundant, such that hunters can absorb the calorific costs of failure; and that hunters who secure meat can gain substantial quantities in any particular bout. The question that needs to be addressed is whether the additional nutrition gained from meat translates into fitness: is there a direct fitness benefit to hunting?

Marginal Gains

McGrew (1992) showed that female chimpanzees who were more successful at gaining meat had greater numbers of

surviving offspring, but it remains unclear whether males who gain more meat also derive fitness benefits. While it seems unlikely in calorific terms (there is no support for the energy shortfall hypothesis), there may be particular nutrients that are valuable, as suggested by the "meat-scrap" hypothesis. That hypothesis, however, focuses specifically on micronutrients, considering macronutrients such as protein and fat merely as helping to reduce dietary bulk (Tennie et al. 2009), and, with its focus on the minimum threshold, encounters problems explaining the variation in hunting between communities: if obtaining these micronutrients is critical, why are chimpanzees from communities where meat eating is rare able to maintain health and fertility? If the threshold is so low that these chimpanzees can reach it, why do then chimpanzees hunt substantially more frequently elsewhere?

The route out of this conundrum is to recognize that fitness is relative and that for male chimpanzees their primary reproductive competitors are the other males of their community. Thus, any benefits of meat eating need to be evaluated against these rivals, rather than in absolute terms. Here, I propose a new hypothesis that broadens the "meat-scrap" hypothesis as well as recognizes this relative nature of fitness. This new "marginal gains" hypothesis assumes (1) that meat is valuable specifically for both macro- and micronutrients, rather than its calorific value, and (2) that individuals benefit through marginal gains over their competitors. For instance, small amounts of high-quality protein may provide an edge in sustaining muscle mass and thereby improving success in competing for high social rank. This "marginal gains" hypothesis predicts that individuals should value even the smallest scraps, as there is no threshold, and should attempt to gain more than rivals.

"Marginal gains" is therefore consistent with patterns of begging and food sharing seen in East African chimpanzees: individuals without meat are strongly motivated to acquire whatever they can, yet males gain over their rivals by not sharing and so need to suffer harassment costs before sharing. In communities where males willingly share with alliance partners, the need for allies may also outweigh any marginal gains from consumption: it may be no accident that the strongest evidence for sharing with allies comes from the community (Ngogo) with the largest number of adult males. If marginal gains show diminishing returns, this would account for individuals relinquishing possession of kills after feeding and diminishing motivation to acquire and consume meat with the quantity ingested.

Parenting Effort

As a final note, even if there are no nutritional benefits to be gained by males, simply by virtue of hunting they create a resource supply (converting live prey into food) for females that would be otherwise unavailable. If, on average, the most successful hunters are also, for whatever reason, the most successful at fathering offspring, then hunting will function as a form of parenting effort (as has been suggested for male chimpanzee territoriality: Watts and Mitani 2001) without any need for active sharing or provisioning by males. The natural variation in hunting and meat eating within and across chimpanzee communities should provide the opportunity to test such ideas, and more detailed, cross-site studies are needed.

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), while red-tailed monkeys (*Cercopithecus ascanius*) stalk green pigeons (*Treron calva*) (Furuichi 2006). 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 in both gorillas and orangutans, although bonobos (*Pan paniscus*), the phylogenetic sister species to chimpanzees, do hunt vertebrates. Recorded prey species include black and white colobus (*Colobus angolensis*), red-tailed monkeys (*Cercopithecus ascanius*) (Sabater Pi et al. 1993), bushbabies (*Galago demidovii*) (Hohmann and Fruth 2008), flying squirrels (Kano and Mulavva 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 nine kills in 46 months of observation, seven of which were duiker, although data from the Lui Kotale site shows higher rates of predation: 18 kills in 60 months of observation (Hohmann and Fruth 2008).

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 vary between populations and from month to month within single communities. Hunting is typically opportunistic on encountering potential prey, although there is some evidence of searching. 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 often consumed selfishly or shared under pressure and may be shared with other males in the hope of future coalitional support; group hunts are more akin to multiple, simultaneous individual efforts to secure prey. In both East and West African populations, the presence of particularly skilled or motivated "impact" hunters increases hunting frequency and success.

It is important to recognize that this picture comes largely from detailed systematic studies of only a handful of communities (Gombe, Mahale, Tai, Ngogo, Kanyawara). 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.

Addressing these shortcomings is essential if we are to use an understanding of chimpanzee hunting behavior to shed light on the behavioral ecology of the hominins. 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 hominin species. The radiation of early hominins encompassed a number of species with different morphologies, and it seems likely that these hominins 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 that 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.

Cross-References

Dental Adaptations of African Apes
Great Ape Social Systems
Hominin Paleodiets: The Contribution of Stable Isotopes
Modeling the Past: The Primatological Approach
The Biology and Evolution of Ape and Monkey Feeding
The Species and Diversity of Australopiths

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