

Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology

David P. Watts

Dept. of Anthropology, Yale University, P.O. Box 208277, New Haven, CT 06511-8277, USA

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Abstract

Chimpanzees regularly hunt a variety of prey species. However, they rarely scavenge, which distinguishes chimpanzee carnivory from that of some modern hunter-gatherers and, presumably, at least some Plio-Pleistocene hominins. I use observations made over an 11-year period to document all known opportunities for scavenging encountered by chimpanzees at Ngogo, Kibale National Park, Uganda, and describe all cases of scavenging. I also review data on scavenging from other chimpanzee research sites. Chimpanzees at Ngogo encountered scavenging opportunities only about once per 100 days and ate meat from scavenged carcasses only four times. Scavenging opportunities are also rare at other sites, even where leopards are present (Mahale, Tai, Gombe), and scavenging of leopard kills is known only from Mahale. Feeding on prey that chimpanzees had hunted but then abandoned is the most common form of scavenging reported across study sites. For example, several individuals at Ngogo ate meat from a partially consumed red colobus carcass abandoned after a hunt the previous day. Such behavior probably was not common among Oldowan hominins. Ngogo data and those from other sites also show that chimpanzees sometimes eat meat from carcasses of prey that they did not see killed and that were not killed by chimpanzees, and that scavenging allows access to carcasses larger than those of any prey items. However, chimpanzees ignore relatively many opportunities to obtain meat from such carcasses. Scavenging may be rare because fresh carcasses are rare, because the risk of bacterial infections and zoonoses is high, and because chimpanzees may not recognize certain species as potential prey or certain size classes of prey species as food sources. Its minimal nutritional importance, along with the absence of technology to facilitate confrontational scavenging and rapid carcass processing, apparently distinguishes chimpanzee foraging strategies from those of at least some Oldowan hominins.

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Introduction

Wild chimpanzees regularly hunt and consume a variety of vertebrate prey, and they eat more meat than do most or all other nonhuman primates. Detailed data on hunting and meat consumption have been collected at multiple sites, especially at Gombe (Goodall, 1986; Stanford, 1998), Tai (Boesch and Boesch, 1989; Boesch and Boesch-Achermann, 2000), Mahale (Hosaka et al., 2001), and Ngogo (Mitani and Watts, 1999, 2001; Watts and Mitani, 2002). Chimpanzees sometimes opportunistically pursue solitary prey, but more often conduct

group hunts of gregarious prey in which they may deploy complex, cooperative prey-capture tactics (Boesch and Boesch, 1989; Boesch and Boesch-Achermann, 2000). They also commonly share meat after successful hunts. Comparative data on chimpanzee hunting and meat consumption are valuable for investigations of the importance of hunting and meat eating in human evolution (e.g., Moore, 1996; Stanford, 1996, 2001; Kaplan et al., 2001) and the evolutionary ecology of food sharing by humans (e.g., Winterhalder, 2001).

In contrast, reports of scavenging by chimpanzees are rare. In this paper, I summarize published data on scavenging by chimpanzees and present new data from Ngogo, Kibale National Park, Uganda. I discuss these data with reference to the debate over the relative importance of hunting and

E-mail address: david.watts@yale.edu

scavenging in the subsistence strategies of Plio-Pleistocene hominins. Chimpanzees at Ngogo hunt frequently and are unusually successful predators of red colobus monkeys (Mitani and Watts, 1999, 2001; Watts and Mitani, 2002), but they ignore most of their rare opportunities to scavenge, although they have been observed to eat parts of four carcasses. This seems typical of chimpanzees in forest habitats, and the contribution of scavenging to chimpanzee subsistence is minimal.

Scavenging by modern humans and Plio-Pleistocene hominins

The subsistence strategies of some modern human hunter-gatherers include scavenging. The best-studied example is the Hadza, who monitor large carnivores and vultures to learn of scavenging opportunities that they exploit either passively or by confronting the carnivores, including lions, and stealing their kills (O'Connell et al., 1988a; Bunn, 2001). Of all the medium-to-large-sized animal carcasses that a group of Hadza foragers acquired during 14 months in 1985–1986, 20% were scavenged (O'Connell et al., 1988a). Confrontational scavenging led to acquisition of carcasses that were over 75% complete in five of 11 scavenging cases and occasionally provided large amounts of meat. However, seasonal variation in carcass-encounter rates and variation in the size and completeness of carcasses led to high variance in returns from scavenging and made scavenged animal tissue only a “windfall resource.” In addition, passive scavenging yielded little meat (O'Connell et al., 1988a).

Extensive debate surrounds the questions of (1) how important scavenging was, compared to hunting, in Plio-Pleistocene hominin subsistence strategies and (2) when in the course of human evolution meat became a critical dietary component (reviewed by Dominguez-Rodrigo, 2002; O'Connell et al., 2002; Dominguez-Rodrigo and Pickering, 2003; Plummer, 2004). This debate largely involves contrasting interpretations of results from analyses of faunal assemblages from Oldowan sites that show hominin-induced modification. It also involves disagreement about the relative contributions of foods of animal or plant origin to the diets of modern human hunter-gatherers and, concomitantly, (1) the relative importance of men's and women's contributions to hunter-gatherer subsistence; (2) the role of hunting and meat sharing in male reproductive strategies; and (3) the relevance of ethnographic examples to reconstructions of early hominin behavioral ecology. I will only briefly review some aspects of this debate to which chimpanzee data are potentially relevant. If any Oldowan hominins frequently scavenged, and scavenging contributed substantially to their diet, then this would have been a major difference in behavioral ecology from that of extant chimpanzees. In addition, if scavenging had only minor nutritional importance, but confrontational scavenging of carnivore kills was important as a male mating tactic (O'Connell et al., 2002), then this would raise the issue of whether, and if so, how, meat sharing enters into the reproductive strategies of male chimpanzees.

Determining the timing of access to carcasses and how much meat they could have provided is crucial to assessing

how Oldowan hominins assembled modified animal bones. Many kinds of data are relevant to such determinations, including those on the frequency and location of stone-tool cut marks and carnivore tooth marks, on bone-fracture patterns, on skeletal-part profiles, and on how extant carnivores and contemporary human foragers (e.g., the Hadza: O'Connell et al., 1988b; Bunn, 2001) modify carcasses. Extensive analyses of ungulate remains from several Bed I sites (especially FLK I *Zinjanthropus*) at Olduvai Gorge, Tanzania, most of which are from prey of size classes 2 or 3 (adult body weight 40–300 kg) and which date to about 1.75 million years ago (Ma), have led to contrasting interpretations: (1) hominins had only late access to carcasses and probably only extracted marrow from bones mostly defleshed first by carnivores (Blumenshine, 1991), or (2) they regularly had early access to carcasses, consistent with either hunting or theft of carcasses from large carnivores (Bunn and Kroll, 1998; Dominguez-Rodrigo, 1997, 1999; Bunn, 2001; O'Connell et al., 2002; Bunn, 2006). Data from several other Pliocene sites are consistent with early access to carcasses. In particular, high frequencies of cut marks on long-bone midshafts and other meaty skeletal elements, combined with low frequencies of carnivore tooth marks on these elements, point to early access at Olduvai site FxJj 50 (Dominguez-Rodrigo, 2002), Peninj (Dominguez-Rodrigo, 2002), and perhaps at Gona (Dominguez-Rodrigo et al., 2005). In a recent reanalysis of data from FLK-*Zinjanthropus* and critique of earlier analyses, Dominguez-Rodrigo and Barba (2006) concluded that hominins also had early access to the carcasses of medium-sized bovids accumulated at this site.

Early carcass access did not necessarily entail hunting. O'Connell et al. (2002) agreed that bone-modification data and actualistic patterns show early access to many carcasses, but contended that lack of projectile technology prevented Plio-Pleistocene hominins from hunting large game, and that they gained early access by aggressively confronting predators at relatively fresh kills. Likewise, Stiner (2002: 6) argued that, while some hunting of smaller prey probably occurred, large mammals “would have been difficult to kill with Oldowan or early Acheulean technology,” although she also noted that the initial occupation of parts of Eurasia by hominins that possessed such technology depended on foraging strategies that included carnivory. However, Dominguez-Rodrigo et al.'s (2001) plant-residue analysis of Acheulean tools from Peninj provided evidence for woodworking at 1.5 Ma, from which they concluded that *Homo ergaster* had the ability to produce spears that could have been used for hunting. O'Connell et al. (2002) also argued that high carnivore tooth-mark counts on bones from Oldowan sites indicate aggressive scavenging of carcasses already defleshed to varying degrees, not hunting. Dominguez-Rodrigo (2002, 2003; cf. Dominguez-Rodrigo and Pickering, 2003) countered by noting that the high frequency of cut marks on bones where carnivores start defleshing (e.g., upper-limb long bones, pelvis), and especially the high frequency of cut marks on upper-limb long-bone shafts, resembles the pattern that results when humans initiate the defleshing, as happens when they have hunted the animals.

Several researchers have argued that meat obtained from confrontational scavenging was not a major component of Oldowan hominin diets, for a variety of reasons. For example, Blumenschine (1991) argued that the risks of trying to steal fresh carcasses from large carnivores would have been extremely high (with the exception of cached leopard kills) and that the occurrence of scavenging opportunities would have varied greatly on a seasonal basis. Others have argued that confrontational scavenging would have occurred only if the hominins had considerable numerical superiority over their carnivore competitors and/or if they could reduce the risks sufficiently by using weapons (Shipman, 1986; O'Connell et al., 1988a,b; Van Valkenburgh, 2001). Based on their study of Hadza scavenging, Hawkes et al. (1988a) asserted that high variance in the timing of opportunities and in possible returns would have made confrontational scavenging at best a source of occasional windfalls for Oldowan hominins, not a regular activity. As their example of Hadza scavenging of a nearly intact giraffe carcass indicated, however, returns might sometimes have been extremely high. Again relying on Hadza data, O'Connell et al. (2002) argued that confrontational scavenging by males served mainly as costly signaling that gave females accurate information about mate quality, rather than as an important source of nutrients. In their view, meat was an unreliable food source and its dietary importance secondary to that of plant foods, particularly underground storage organs.

However, others have cautioned against taking the Hadza either as general representatives of modern hunter-gatherers or as analogies for Oldowan hominins (e.g., Kaplan et al., 2001; Dominguez-Rodrigo, 2002, personal communication). A review of the ethnographic record supports the claim that most modern hunter-gatherers gained most of their calories from meat, and thus from hunting, a mostly male activity (Kaplan et al., 2001). Dominguez-Rodrigo (2002; c.f. Dominguez-Rodrigo and Pickering, 2003) attributed major importance to meat in Oldowan hominin subsistence, but argued that most of it came from hunting, not confrontational

scavenging. Plummer's (2004) preliminary analysis of prey-size distribution and evidence for butchery and carnivore activity at the 2-million-year-old site of Kanjera helps to shift the debate away from a longstanding focus on large game. Among other lines of evidence, high frequencies of stone-tool cut marks, low frequencies of carnivore tooth marks on limb-bone shafts, and high representation of juveniles (usually completely destroyed by carnivores) indicate that hominins regularly hunted small (<72 kg) bovids there. Hunting is also a more likely explanation than scavenging for small bovids at FLK Zinj, given that lions and hyenas can completely eat these within minutes (Bunn, 2006).

Scavenging by chimpanzees

Regardless of how questions about carcass acquisition by Oldowan hominins and the importance of meat in Oldowan diets are resolved, ethnographic evidence that some modern human hunter-gatherers exploited all scavenging opportunities (O'Connell et al., 1988a) and zooarchaeological evidence consistent with at least occasional scavenging contrast with the paucity of observations of scavenging by chimpanzees at long-term research sites (Table 1). Goodall (1986) reported only ten cases of passive scavenging at Gombe from 1960 to the mid-1980s. At least five of these, and perhaps nine, involved feeding on incompletely consumed carcasses of monkeys killed by chimpanzees earlier the same day ($n \geq 4$) or one day earlier ($n \geq 1$). In the tenth case, a chimpanzee took a monkey carcass that humans had brought back to camp. Chimpanzees also sometimes stole carcasses from baboons, but this occurred in the provisioning area, where aggression between these two species and chimpanzee predation on baboons were atypically high (Wrangham and van Zinnicq Bergmann-Riss, 1990). Gombe chimpanzees have ignored carcasses of prey species killed by baboons and humans, suspected to have been killed by leopards, or found dead of unknown causes (Goodall, 1986; Muller et al., 1995). Few new

Table 1
Scavenging opportunities and characteristics of scavenging in four well-documented chimpanzee populations

	Gombe	Tai	Mahale	Ngogo
Carcass-encounter frequency	Rare	Rare	Rare	1/98 days
Scavenging opportunities	>10 ^a	17	≥11	8
Scavenging cases	10 ^b	7 ^c	7 ^b	4
Cases from earlier red colobus hunts	5–9 ^d	3	0–1 ^d	
Scavenge nonprey species?	No	No	Yes (bushbuck)	No
Extend prey size range?	No	No	Yes	Yes
Ignore large prey?	Yes (bushpig, bushbuck)	? (duiker?) ^e	Yes (bushpig)	Yes
Steal kills by other predators?	Baboon	Crowned eagle	Leopard	Crowned eagle?
Confrontational carcass theft?	Yes	Yes	No	No
Feed on carcasses when predation unseen?	No	No?	Yes	Yes

Sources: Gombe: Goodall (1986), Muller et al. (1995), W. Wallauer (personal communication); Tai: Boesch and Boesch-Achermann (2000); Mahale: Hasegawa et al. (1983), Nishida (1994); Ngogo: this study.

^a Not including carcass thefts from baboons or encounters with baboons eating meat (Goodall, 1986; number of cases not reported).

^b Chimpanzees obtained one carcass from humans at Gombe (Goodall, 1986) and two from humans at Mahale (Hasegawa et al., 1983).

^c Does not include three cases in which chimpanzees stole living prey from crowned eagles.

^d Five definite and four probable Gombe cases; information not provided for one case at Mahale.

^e Chimpanzees at Tai ignore duiker killed by leopards, but also do not hunt duiker.

cases of scavenging have been observed at Gombe since Goodall's (1986) review (W. Wallauer, personal communication). Hasegawa et al. (1983) reported four cases of scavenging at Mahale, two of adult bushback (*Tragelephus scriptus*) probably killed by leopards (one nearly intact, the second fresh but mostly eaten) and two of blue duiker (*Cephalophus callipyga*) carcasses that researchers had handled. Nishida (1994) later reported three more cases: one blue duiker, one red-tailed monkey (*Cercopithecus ascanius*), and one red colobus (*Ptilocolobus tephrosceles*). Based on observations over nearly two decades, Boesch and Boesch-Achermann (2000) reported only seven cases at Tai, including three of feeding on remains of monkeys killed by chimpanzees one or two days previously and four of feeding on monkeys killed by crowned eagles (*Stephanoaetus coronatus*). Chimpanzees also stole wounded red colobus from eagles three times and encountered, but ignored, ten fresh carcasses of several mammalian species, although only one of these (sooty mangabeys, *Cercocebus atys*) was a known prey species. Reynolds (2005) reported one case from Budongo, in which chimpanzees fed on the carcass of an infant blue monkey (*Cercopithecus mitis*) that had been killed and partially consumed by an adult male blue monkey; chimpanzees occasionally prey on blue monkeys at this site.

Scavenging by chimpanzees at Ngogo

Methods: study site and subjects

Ngogo is in the center of Kibale National Park, in western Uganda. The study area, at an altitude of about 1400 m, receives 1700–1800 mm of rain annually, mostly from March through May and mid-August through December. It covers about 30 km² of mixed, mature, and regenerating forest that is transitional between lowland and montane evergreen forest and includes other, minor, vegetation types (Butynski, 1990; Struhsaker, 1997; Lwanga et al., 2003). Three small-to-medium-sized ungulates are common (Struhsaker, 1997): red duiker (*Cephalophus monticola*), blue duiker, and bushpig (*Potamochoerus porcus*). Bushbuck are also present, but are less common. Seven other diurnal primate species are present, with red-tailed monkeys and grey-cheeked mangabeys (*Lophocebus albigena*) being the most common (Mitani et al., 2000).

The chimpanzee community has been continuously observed since mid-1995 and is the largest known; its 140–150 members have included 22–28 adult males and 14–16 adolescent males (Watts, 1998; Mitani and Watts, 2005). The chimpanzees prey on at least 11 vertebrate species, including six diurnal primates and the three common ungulates (although they do not hunt adult bushpigs or adult red duiker). The predation database includes over 650 kills during more than 270 hunts (Watts and Mitani, 2002, unpublished data). Red colobus monkeys are by far the most common prey; about 80% of red colobus hunts result in kills, and chimpanzees make multiple kills of red colobus in most hunts.

I observed chimpanzees at Ngogo for over 10,000 hours between 1995 and 2006. I recorded all hunts and prey captures, collected data on meat sharing, and noted all encounters with fresh prey-species carcasses not killed by chimpanzees and all cases of scavenging.

Results

Chimpanzees encountered only eight recently dead, nondecomposed carcasses of prey species and found one individual of a prey species dying from unknown causes. Thus, the encounter rate with scavengeable carcasses was only once per ca. 98 days, assuming a 13-hour activity period. This includes two cases in which adult male baboons were eating red duiker that they had just killed; the chimpanzees showed no interest in trying to steal these carcasses. In two other cases, chimpanzees encountered dead adult red duiker that they did not consume. In the first of these cases, three male chimpanzees ignored the carcass, and in the second, an adult female with an infant and an adolescent female briefly inspected the carcass, but did not touch it. The four scavenging episodes, and one interaction between an adult male chimpanzee and a dying black-and-white colobus monkey (*Colobus guereza*), are detailed below.

Case 1: adult female red duiker

At 0920 h on September 26, 2002, adolescent males RA and WA and adolescent female BI found a dead adult female red duiker. Its abdomen had a narrow 6-cm opening and some viscera had been removed; no other wounds were visible and the carcass was otherwise intact. The limbs were slightly flexible, but many flies were swarming around the carcass. WA and BI inspected it closely and sniffed it, but did not touch it. RA approached it, sniffed and visually inspected it and poked at its ventrum. He pulled and twisted one of the duiker's legs with both arms for four minutes as if trying to disarticulate it, poked at the opening in the abdomen again and sniffed his finger, then dragged the carcass 3 m and pulled and twisted the leg for another five minutes. Finally he bit into the leg several times, piercing the skin just above the knee and removing a small amount of meat, which he ate; he did not bite into the meatier hip region. He sat next to the carcass for several more minutes and then left the site. WA followed him, but BI then briefly pulled and twisted one leg, bit into it, and removed a small amount of meat, which she ate. She then followed the males. So far as I was aware, no other chimpanzees encountered the carcass.

Case 2: adult female red colobus

At 1645 h on December 10, 2002, 15 adult male chimpanzees, five adolescent males, 12 adult females (seven with infants), two adolescent females, and nine juveniles encountered a red colobus group. They started to hunt the monkeys at 1710 h and made five kills (one adult female, two subadults, and two infants) between then and 1755 h. One more adult

male chimpanzee and one adolescent male arrived during the subsequent meat-eating session.

At 1820 h, chimpanzee screams were audible from the north; the callers belonged to a neighboring community. The Ngogo males became highly excited and rushed in that direction. At least two males were carrying meat (the two largest carcasses), but dropped it as they approached the callers. At 1842 h, the males stopped and listened on the southern edge of a small valley; chimpanzees called from the north side of the valley at 1845 h. The Ngogo males excitedly but silently approached, and at 1858 h they charged the other chimpanzees, who screamed and fled north. Males continued to display until 1915 h, then moved south and nested in the area of the hunt.

On the next morning, 11 of the adult males, three adolescent males, one orphaned juvenile male, and several females, some with dependent offspring, returned to the southern edge of the valley where the males had attacked the neighbors the previous evening. At 1303 h, all the males plus one old female started a patrol to the north and east, during which they traveled several kilometers without encountering neighbors.

At 1205 h, before the patrol started, adult male OR found most of an adult red colobus carcass, presumably the female killed the previous afternoon by HA, on the ground. He picked it up, carried it 20 m, then climbed a tree and started to eat meat. Meanwhile, adult male AY found part of a limb, apparently from the same monkey, and started to eat meat. OR shared meat with two adolescent males. One (DX) briefly retrieved the carcass and ate more meat when OR dropped it at 1240 to follow other males across the valley. These four males treated the carcass like a fresh kill: none hesitated to eat meat, although they did not eat all of it. No other chimpanzees showed interest in obtaining meat.

Case 3: subadult red-tailed monkey

On the morning of July 12, 2005, 14 adult males, 6 adolescent males, an estrous female and her adolescent and juvenile daughters, and at least seven other adult females with five juveniles and four infants were eating *Chrysophyllum warwickii* fruit in several trees. At 1310 h, young adult male GTZ found a dead subadult male red-tailed monkey on the ground beneath one of these trees. It appeared fresh—its limbs were flexible—and had no obvious wounds (although those inflicted by crowned eagles may be visible only on close inspection; T. Struhsaker, personal communication). GTZ grasped its tail and dragged it 10 m as adolescent male MU watched, then stopped and bit into one of its hip joints. After several minutes of biting and pulling at the joint, he tore off one leg and the tail, carried these up a tree, and started to eat meat. No one joined him or begged for meat. Adult male LO, who arrived while GTZ was disarticulating the leg and tail, dragged the rest of the carcass 20 m along the ground, then sat and looked at it for 3 min, but ate no meat. No other chimpanzees investigated the carcass.

GTZ was still eating meat at 1400 h, when four adult males and several females and their dependent offspring moved

south and encountered a red colobus group about 1 km from the scavenging site. One male climbed toward the red colobus, but the monkeys fled. GTZ, still carrying part of the red-tailed monkey carcass, arrived with several other males at 1510 h. He climbed about 12 m up a *Pseudospondias microcarpa* tree and resumed eating meat. An adolescent female joined him and begged unsuccessfully for meat.

At 1605, the chimpanzees hunted black-and-white colobus in the same area and adult male MO killed a juvenile, half of which another adult male stole. GTZ did not participate in the hunt or join begging/meat-sharing clusters that formed around the two meat possessors. He dropped the remains of the red-tailed monkey sometime between then and 1700 h.

Case 4: subadult red duiker

At 1215 h on April 4, 2006, a large party of chimpanzees encountered the carcass of a subadult red duiker lying on the ground in a swampy valley. The duiker appeared to be freshly dead and might have been killed by a crowned eagle. Six adult males plus several young adolescent males and many females, juveniles, and infants crowded around the carcass and looked at it. None of the adults touched it at first, but several juveniles touched, sniffed, and hit it. Juvenile male BN started to drag it away; this prompted alpha male BT to charge through the middle of the assembled group. Most of the chimpanzees fled, and many others also charged at or otherwise engaged in aggressive interactions. During this melee, BN let go of the carcass and a young adolescent female dragged it into thick vegetation, but then also let go of it. At some point, adult male PA seized the carcass and carried it up a *Pseudospondias macrocarpa* tree, where he started to eat it. Six other adult males, one adolescent male, and one juvenile male followed and started to beg for meat. PA was reluctant to share and managed to prevent all but alpha male BT from obtaining meat while he fed on the duiker for over an hour. BT left during this time, but the other males became increasingly agitated, and finally, adult LO charged at PA and precipitated another melee, during which he stole the carcass from PA. Adult male MOR then stole it from him. MOR shared meat with three other adult males and an adolescent female, and refused begging attempts by a fourth adult male. One other adult male and a young adolescent male obtained scraps of meat from the ground. The entire meat-eating session lasted almost four hours and the chimpanzees consumed the entire carcass.

Case 5: subadult male black-and-white colobus

At 1600 h on July 1, 2002, alpha male BT left eight other adult males, two adolescent males, and one female with a juvenile and infant to forage alone. At 1610 h, he heard alarm calls from a group of black-and-white colobus monkeys; he looked towards the monkeys, then rushed over and sat below them. Suddenly he spotted a large subadult male monkey on the ground, alive but not moving. It was not obviously wounded, and might have fallen because of an accident, because of aggression, because it was ill, or because of a crowned eagle

attack. BT dragged the monkey 30 m by its tail, thrashing it against the ground several times; it resisted ineffectively by grabbing at plant stems. After stopping to sit and look at it (without releasing his grip), he dragged it another 10 m, thrashed it against the ground again, and carried it up a *Pseudospondias microcarpa* tree, where he placed it on a large bough and sat next to it. He hit the monkey against the bough several times, sniffed it and inspected it visually, and put his mouth on its head, but did not bite it. He then carried it to a second bough, put it down, and sat looking closely at it. The monkey was no longer moving and appeared dead. Ten minutes after he first climbed the tree, BT descended and moved off without having eaten any meat; he left the monkey in the tree.

Discussion

These observations add to the small body of data showing that wild chimpanzees in lowland evergreen moist forests (Taï), mid-altitude evergreen moist forest (Kibale, Budongo), and dryer, more seasonal forests (Mahale) and woodland (Gombe) scavenge various vertebrate species on which they also prey. However, scavenging is rare, especially compared to rates of predation on some of the same species, and chimpanzees decline a large proportion, and maybe the majority, of scavenging opportunities (Table 1).

One obvious reason for the rarity of scavenging is the rarity of opportunities. The estimate of one encounter per 98 days at Ngogo is considerably lower than seasonal rates of between once per 7.8–36.0 days that O'Connell et al. (1988a) reported for the Hadza. Published data from other chimpanzee research sites do not allow calculation of daily carcass-encounter rates, but the small number of scavenging cases implies that rates are probably similar to that at Ngogo. The density, biomass, and species diversity of grazing and browsing ungulates is lower in the humid forests that constitute most chimpanzee habitats and in woodlands such as Gombe than in the dryer, more seasonal habitat of the Hadza and, presumably, in the apparently wide range of habitats used by Oldowan hominins (O'Connell et al., 1988a; McGrew, 1992; Stanford, 1996; Schoeninger et al., 2001; Plummer, 2004). Concomitantly, predator guilds are less diverse in chimpanzee habitats, and humans have eliminated large mammalian carnivores from some. Additionally, decomposition is faster in humid forests than in dryer woodland and savanna habitats (Moore, 1996; Boesch and Boesch-Achermann, 2000; Roquet et al., 2005). Edible carcasses should thus be less common and have shorter persistence in currently typical chimpanzee habitats than in woodlands and savannas.

These differences in carcass abundance were probably greater in the past, given that the higher diversity of both ungulates and large carnivores in Plio-Pleistocene faunas than in recent faunas in African savanna habitats presumably led to correspondingly higher densities of predators and medium-to-large-sized carcasses (Van Valkenburgh, 2001). Opportunities for confrontational scavenging might thus have been generally more common, although temporally variable, for any hominins

able to exploit them (Blumenschine, 1991; O'Connell et al., 1988a).

Chimpanzees sometimes ignore large, scavengeable meat packages, even when they do not have to confront predators; this distinguishes them from Hadza foragers, who tried to exploit every potentially profitable scavenging opportunity during O'Connell et al.'s (1988a) study. We cannot know how often Oldowan hominins passed up opportunities for confrontational scavenging, but they might have done so relatively more often than Hadza hunters do because of greater technological constraints on their ability to displace large carnivores from kills (O'Connell et al., 1988a; O'Connell et al., 2002). Chimpanzees have been observed to scavenge confrontationally, but only against smaller species that do not prey on them (although adult male baboons are potentially dangerous to adult male chimpanzees). Observed cases of scavenging kills made by leopards, which are known predators of chimpanzees (Boesch and Boesch-Achermann, 2000), did not involve confrontations.

Boesch and Boesch-Achermann, (2000) noted that chimpanzees at Taï do not hunt duiker and seem not to recognize them as potential food, despite their abundance at the site and their inclusion in chimpanzee prey sets at other sites. It is possible that most chimpanzees recognize animal carcasses as food only if they have killed the animals, seen other chimpanzee kill them, or seen other chimpanzees eating them during or after hunts. Chimpanzees at all well-documented sites have ignored at least some scavenging opportunities that do not fall into these categories (Table 1); this reluctance distinguishes them from mammalian carnivores in African savanna ecosystems (Plummer, 2004). In at least four cases at Gombe in which chimpanzees scavenged partially eaten red colobus carcasses, the scavengers had been at the hunts and had either caught the prey, saw it caught, fed from it, or saw other chimpanzees eating it (Goodall, 1986). Relevant information for other cases and for Mahale and Taï is not available. However, Ngogo Cases 3 and 4 and cases of scavenging leopard kills at Mahale (Hasegawa et al., 1983) confirm that chimpanzees sometimes feed on animals not killed in their presence and not killed by other chimpanzees, including animals larger than any they can kill, although they may eat little from these carcasses (e.g., chimpanzees at Ngogo completely consumed the carcass in Case 4, but ate almost no meat in Case 1) and individual variation in perceptions of what is edible may exist.

A large proportion of scavenging cases have occurred when chimpanzees returned to sites of recent monkey hunts to eat meat left there (Table 1). Even this is rare, probably because chimpanzees completely consume most prey immediately after hunts. At Ngogo, individuals may keep meat overnight after hunts late in the day, but rarely leave large amounts of meat at or near kill sites. Case 2 was the only case of scavenging from their own kills, and the many potential consumers at the meat-eating session would almost certainly have eaten everything edible if not for the distraction by neighbors. OR's discovery of a carcass far from the hunt site the following morning was fortuitous. Given that Oldowan hominins faced competition for fresh carcasses with multiple large and

dangerous carnivore species (Van Valkenburgh, 2001; Plummer, 2004), their foraging tactics presumably did not include retrieval of unconsumed meat from previous kill sites.

Chimpanzees may also be less inclined to exploit scavenging opportunities than are carnivorous mammals because they lack comparable physiological barriers to infectious agents in carrion (Hamilton and Busse, 1978; cf. Plummer and Stanford, 2000; Plummer, 2004). In particular, they may face high risks of contracting zoonoses from dead or dying heterospecifics that they have not seen predators attack. For example, both duiker and chimpanzees are susceptible to Ebola (Roquet et al., 2005), and anthrax, botulism, and other diseases are directly transmissible from carcasses (Hamilton and Busse, 1978).

Use of leopard kills at Mahale suggests that scavenging might previously have been more common in habitats from which leopards have been eliminated (e.g., Kibale). However, Mahale chimpanzees responded fearfully to the fresh carcass of an adult bushpig killed by a leopard and thus ignored a meat package far larger than their typical prey (Nishida, 1994). Additionally, researchers have not observed chimpanzees scavenging on leopard kills at Tai (where leopards prey on chimpanzees; Boesch, 1991), although this may be partly because Tai chimpanzees do not hunt duiker, which are the major prey of leopards (Boesch and Boesch-Achermann, 2000; Zuhnerbuhler and Jenny, 2002).

Do social factors contribute to the rarity of scavenging by chimpanzees? Hunting and especially meat eating have social importance. Allowing others to have meat may not be costly to hunters when they capture prey too large for a single individual to eat (e.g., an adult male red colobus monkey) or to others who obtain large shares of such kills, and costs of harassment by beggars may sometimes outweigh the costs of allowing them to have some meat (Gilby, 2006). Still, delayed reciprocity in meat sharing, active sharing, and preferential sharing between male allies (Mitani and Watts, 2001, unpublished data) point towards meat sharing as a means to maintain and strengthen social bonds between males and to develop and maintain alliances. Yet insofar as meat sharing has this function, its effects should not depend on whether initial meat possessors obtain meat via hunting or scavenging.

Hunting by male chimpanzees may involve costly signaling (Hawkes and Bliege Bird, 2002). While meat sharing does not increase male mating success (Mitani and Watts, 2001; Gilby, 2006), hunting monkeys is risky, and motivation to hunt and skill at prey capture may display male quality (Hawkes and Bliege Bird, 2002) and signal willingness to take risks and to provide fitness benefits to other males. Such signals could influence decisions about when to seek opportunities to engage in intergroup aggression (Watts and Mitani, 2001) and could influence alliance strategies (Mitani and Watts, 2001). Acquiring meat through scavenging would not provide comparable signals. Costly-signaling theory may indeed explain certain aspects of hunting and food sharing by human hunter-gatherers, such as Hadza men's specialization on hunting large prey that become public goods (Hawkes and Bliege Bird, 2002) and turtle hunting by Meriam men who

invest considerable time and energy in risky hunts but donate their catch to others (Bliege Bird et al., 2001; Smith et al., 2003). However, the ultimate explanation for hunting by chimpanzees is presumably that meat is an extremely valuable nutritional resource (Mitani and Watts, 2001); this remains true regardless of its source, so long as eating it does not impose fitness costs (e.g., because of disease transmission). Likewise, costly signaling is relevant to hunting by humans precisely because meat has such high nutritional value. Hadza men specialize in hunting large game despite the absence of disproportionate nutritional benefits to themselves and their families when they succeed, but they also typically exploit scavenging opportunities. Confrontational scavenging may provide some scope for costly signaling, but its main importance is presumably nutritional. It seems unlikely that chimpanzees would fail to pursue similar nutritional benefits simply because passive scavenging lacks potential for costly signaling.

At Ngogo, chimpanzees capture only infant and juvenile red duiker and the largest prey (adult male red colobus and black-and-white colobus) are far smaller than the modal size of ungulate species used by Bed 1 Olduvai hominins (Plummer, 2004). Scavenging can increase the size range of carcasses from which chimpanzees gain meat (Table 1): the adult red duiker in Case 1 was larger than all prey items (although RA and BI ate almost none of it), as were the adult bushbuck scavenged at Mahale (Hasegawa et al., 1983). However, it is too rare to provide real nutritional benefit. In contrast, scavenging carcasses of medium-sized bovids and larger mammals probably afforded a nutritionally significant amount of meat to Oldowan hominins (Plummer and Stanford, 2000; Bunn, 2001; Dominguez-Rodrigo and Pickering, 2003; Plummer, 2004).

Scavenging might have been more common in miombo woodland habitats at the extreme of chimpanzee ecological tolerances (e.g., Ugalla) than in rainforests and more humid woodlands, but recent human-induced changes in predator guilds make investigating this possibility difficult (McGrew, 1992; Moore, 1996). Late Pliocene and early Pleistocene hominin habitats experienced a gradual trend towards greater openness, with increased grassland after about 2 Ma, although variation was apparently extensive, with open grasslands, bushlands, locally forested areas, and shrublands with wetlands all reconstructed for localities at which fossils of *Homo* and/or *Paranthropus* have been found (Reed and Reator, 2006). Such variation, plus variation in the local densities, foraging strategies, morphology, and gregariousness of large carnivores, would have led to wide variation in the frequency of scavenging opportunities for Oldowan hominins (Plummer, 2004), but opportunities should have been more common than for chimpanzees in forest habitats. The recent discovery of middle Pleistocene chimpanzee fossils, dated to between 545 ± 3 ka and 284 ± 12 ka, in the Kapthurin Formation of the Tugen Hills, Kenya (McBrearty and Jablonski, 2005), casts doubt on the notion that chimpanzee evolutionary history has been devoid of opportunities to scavenge similar to those available to early *Homo* and of exposure to the same predator guilds. These fossils show that the geographic range of

chimpanzees previously extended into the East African Rift Valley where they were potentially sympatric with *Homo* in semiarid, but largely wooded, habitats (McBrearty and Jablonksi, 2005). Nevertheless, scavenging would probably not have been a major component of chimpanzee foraging strategies in such a context for several reasons. Contemporaneous hominins probably could drive large carnivores from kills by throwing rocks forcefully and accurately (Van Valkenburgh, 2001); chimpanzees lack this ability, and they do not use tools to hunt. Additionally, wild chimpanzees have never been seen producing sharp-edged stone flakes of the sort that would have allowed early hominins to remove meat from carcasses quickly, then leave acquisition sites and thereby reduce their own risk of predation (Foley, 1987; Van Valkenburgh, 2001); ancestral chimpanzees presumably also lacked this ability. Chimpanzees can open the long bones of colobus-sized prey with their molars to extract marrow (Teleki, 1975; personal observation), but have never been seen using hammerstones to open bones; without this ability, they could not have extracted marrow from larger carcasses to the same extent as did Oldowan hominins. Chimpanzees in semiarid, locally wooded habitat in the Mt. Assirik region of Senegal are at risk of predation by lions and hyenas and are not known to scavenge from either of these carnivores; the same might generally have been true of “savanna” chimpanzees in comparable, relatively open habitats (Moore, 1996; Hunt and McGrew, 2002).

Stanford (2001:129) stated that “meat eating patterns by wild chimpanzees lend little support for hypotheses for scavenging as a major component of the early human diet.” This observation might be rephrased to state that data on chimpanzee carnivory have little relevance to hypotheses about the importance of scavenging once hominins started to include meat from medium-to-large mammals in their diets, other than to highlight questions about differences in habitat preferences and other aspects of behavioral ecology, morphology, and cognition. Passive scavenging might have offered little reward to Oldowan hominins (Blumenschine, 1991; Tappen, 2001), and deliberate search for confrontational scavenging opportunities might have been energetically inefficient and risky (Tappen, 2001). Nevertheless, if the foraging strategies of some Pliocene hominins included enough scavenging to yield important nutritional gains, and if they commonly engaged in confrontational scavenging from large carnivores, then these behaviors would have distinguished their behavioral ecology from that of chimpanzees (Plummer and Stanford, 2000; Bunn, 2001; Schoeninger et al., 2001; Plummer, 2004).

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