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From *Pan* to Man the Hunter

Hunting and Meat Sharing by Chimpanzees, Humans, and Our Common Ancestor

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Humans eat more meat than any other anthropoid primate, attesting to a major shift in the diet of our hominin ancestors. Hunting and meat sharing are central to hypotheses explaining the evolution of several derived human traits, including large brains, long childhoods, small guts and teeth, complex cooperation, the sexual division of labor, cooperative breeding, and the expansion of *Homo* spp. around the world (Read 1914; Dart and Salmons 1925; Dart 1926, 1949, 1953; Washburn and Lancaster 1968; Laughlin 1968; Isaac 1978; Hill 1982; McGrew 1992b; Bickerton 2009; Gurven and Hill 2009; Isler and van Schaik 2014). Empirical tests of these hypotheses are challenging, however, as they require reconstruction of the behavior and diet of extinct species. Together with the fossil and archaeological records, studies of living apes and human foraging societies are essential for understanding how hominin behavior has changed since our lineage split from that of the great apes. Here we use the behavior of chimpanzees and human hunter-gatherers to make inferences about hunting and meat sharing by the last common ancestor (LCA), and to inform our understanding of the causes and consequences of increased meat consumption in the human lineage.

Chimpanzees hunt vertebrates at all research sites across Africa (reviewed in Uehara 1997; Newton-Fisher 2014). Given the relative rarity of predation, however, data regarding frequency, seasonal patterns, hunting strategies, and meat sharing have primarily come from six long-term sites (Table 10.1). By contrast, the worldwide sample of human forager societies available for comparison is *much* larger. We focus on six African groups (Table 10.2), three of which (Aka, Efe, and Mbuti) hunt in forested habitats similar to those occupied by the chimpanzee populations in our sample. Our human societies also include those that occupy drier, more open habitats, including the Hadza, Ju/'hoansi, and Central Kalahari foragers (/Gui and //Gana, which we also refer to as /Gui-//Gana, following Tanaka 2014). While small, our human sample represents considerable environmental, genetic, and cultural diversity.

In both species, hunting behavior varies considerably by individual, population, and season. For example, among chimpanzees, the presence or absence of "impact hunters," who catalyze group hunting (Gilby et al. 2008, 2015), may lead to long-term variation in hunting frequency both within and among social groups. Absence of red colobus monkeys (*Procolobus* spp., chimpanzees' most frequent prey) at a particular site will make hunting relatively rare (e.g., Budongo forest, Uganda; Newton-Fisher et al. 2002). Elsewhere, high densities of fruiting trees can support very large communities and foraging parties (e.g., Ngogo; Potts et al. 2011), which facilitate hunting (Mitani and Watts 2001, 2005). Finally, depending on local ecology, hunting frequency may undergo short-term variation, either regularly (e.g., more hunting during the dry season at Gombe; Stanford et al. 1994a) or unpredictably (e.g., during periods when preferred fruit is abundant at Kanyawara; Gilby and Wrangham 2007).

Similarly, researchers describe large disparities in individual hunting skill in the Ju/'hoansi, /Gui-//Gana, Hadza, Efe, and Mbuti (Lee 1979; Ichikawa 1983; Bailey and Aunger 1989; Tanaka 2014; Wood and Marlowe 2013). Hunting success and the proportion of meat in the diet can vary widely, depending on the presence of certain hunters, the length of the observation period, and the occurrence of low-probability but high-yield large game kills (Hill and Kintigh 2009). As with chimpanzees, hunting may be seasonal, but because humans also hunt migratory birds and mammals, variation is likely to be more pronounced. Finally, reliance on tools and the potential for rapid changes in hunting technology provide further sources of variation within

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and among human groups. With these caveats in mind, we now explore broad species-level similarities and differences.

Similarities in Hunting and Sharing by Chimpanzees and Humans

Most Prey Weigh Less Than 10 kg

Since the first report of meat eating by chimpanzees at Gombe (Goodall 1963), predation has been observed or inferred in all known chimpanzee populations (Table 10.1; Newton-Fisher 2014). Summing across all field sites, chimpanzees have been documented to hunt at least forty vertebrate prey species, but the most frequent by far is the red colobus monkey (Struhsaker 2010), which accounts for 53 percent (Mahale: Nishida et al. 1992) to 88 percent (Ngogo: Watts and Mitani 2002b) of all kills at sites where the two species coexist (Uehara 1997; Mitani 2009; Newton-Fisher 2014). East African chimpanzees selectively prey upon immature red colobus (Takahata et al. 1984; Stanford et al. 1994a; Stanford 1998; Mitani and Watts 1999), so while adults *(Procolobus tephrosceles)* may weigh up to 13 kg (Kingdon 1997), most victims are much smaller (Figure 10.1). At Gombe, between August 1970 and April 1975, the median estimated weight of red colobus prey was 4 kg (calculated from Wrangham and Bergmann-Riss 1990). In thirty-five successful red colobus hunts between 1999 and 2002 at Gombe, median estimated carcass mass was 3 kg (calculated from Gilby 2004). Even at Taï, where almost half of the red colobus captured were adults (Boesch and Boesch-Achermann 2000), mean carcass size must have been less than 10 kg, as this is the maximum adult mass of the red colobus species found there (*Procolobus badius;* Kingdon 1997).

After arboreal monkeys, the next most frequent chimpanzee prey species are duiker, bushbuck, and bushpig. Bushbuck prey at Gombe are invariably young fawns (Goodall 1986), which are at most the size of adult blue duikers (~3.5–9 kg; Kingdon 1997). All five bushpigs killed by chimpanzees at Mahale between 1979 and 1982 were juveniles (Takahata et al. 1984), and of thirty-two bushpig kills observed at Gombe between 1972 and 1981, all but three victims were "small, still in their striped natal coats" (Goodall 1986: 276), which weigh approximately 1.5 kg (Wrangham and Bergmann-Riss 1990). Notably,

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TABLE 10.1. Key chimpanzee study sites that have contributed to our understanding of long-term predation patterns.

Population (Study Group)	Location	Subspecies	Habitat	Start of Continuous Study	Mammalian Prey Species	Hunting Frequency Highest during:	% of Prey Red Colobus	Amount of Meat in Diet	Key Hunting and Meat Sharing Studies
Gombe National Park (Kasekela)	Tanzania, East Africa	P. t. schweinfurthii	Evergreen, semideciduous forest; woodland[1]	1960	11[2]	Dry season[3,4]	53%[5]–85%[6]	<5% of feeding time[2,7]; 22 g/day[4]	3–6, 8–17
Mahale National Park (M-Group)	Tanzania, East Africa	P. t. schweinfurthii	Semideciduous forest, woodland[18]	1966	17[19]	Dry season[20]	53%[21]		18–24
Kibale National Park (Kanyawara)	Uganda, East Africa	P. t. schweinfurthii	Moist deciduous forest, swamp, grassland, colonizing forest[25]	1989	5[26]	Periods of high preferred fruit abundance[27]	83%[26]		14, 16–17, 27–28
Taï Forest	Côte d'Ivoire, West Africa	P. t. verus	Evergreen, semideciduous forest[29]	1979	7[29–30]	Wet season[29]	81%[29]	25–180 g/day[29]	29–33

Kibale National Park (Ngogo)	Uganda, East Africa	*P. t. schweinfurthii*	Evergreen rainforest, grassland, colonizing forest[34]	1995	12[35]	Periods of high ripe fruit abundance[36,37]	88%[38]	35–43
Fongoli	Senegal, West Africa	*P. t. verus*	Woodland, grassland, bamboo, gallery forest[44]	2005	6[45]	Wet season (tool-assisted)[45]	0% (not present)[45]	44–45

1. Clutton-Brock and Gillett 1979; 2. McGrew 1992a; 3. Stanford et al. 1994a; 4. Gilby 2004; 5. Goodall 1986; 6. Stanford 1998; 7. Gombe Stream Research Centre, unpublished data; 8. Wrangham 1975; 9. Goodall 1963; 10. Teleki 1973; 11. Stanford et al. 1994b; 12. Gilby 2006; 13. Gilby et al. 2006; 14. Gilby et al. 2010; 15. Gilby et al. 2013; 16. Gilby et al. 2015; 17. Gilby et al. in revision; 18. Nishida et al. 1979; 19. Uehara 1997; 20. Hosaka et al. 2001; 21. Nishida et al. 1992; 22. Kawanaka 1982; 23. Takahata et al. 1984; 24. Uehara et al. 1992; 25. Chapman and Wrangham 1993; 26. Kibale Chimpanzee Project, unpublished data; 27. Gilby and Wrangham 2007; 28. Gilby et al. 2008; 29. Boesch and Boesch-Achermann 2000; 30. Boesch and Boesch 1989; 31. Boesch 1994b; 32. Boesch 1994b; 33. Gomes and Boesch 2009; 34. Struhsaker 1997; 35. Watts and Mitani 2005; 36. Mitani and Watts 2001; 37. Mitani and Watts 2005; 38. Watts and Mitani 2002b; 39. Langergraber et al. 2007; 40. Mitani and Watts 1999; 41. Watts and Mitani 2002a; 42. Mitani 2006; 43. Sobolewski et al. 2012; 44. Pruetz and Bertolani 2007; 45. Pruetz et al. 2015.

TABLE 10.2. African foragers with detailed studies of hunting and meat sharing.

Population	Study Location	Subsistence	Habitat, Average Yearly Rainfall	Key Hunting Technologies	Study Period(s)	Estimated Dietary Contribution of Hunted Meat (% daily kcal)	Key Sources
Efe	Ituri forest, Democratic Republic of Congo (DRC)	Bow hunting, honey collecting, fishing, plant gathering, trade with Lese farmers, wage labor	Primary evergreen lowland rainforest, secondary forest, and cultivated areas ~1,800 mm	Bow, arrow, axe, knife, poison, fire, spear, tree perch, dogs, beating stick, noisemaker, clothing	1980–1982[1,2]	~9%	1–2
Mbuti	Ituri forest, DRC	Hunting, honey collecting, fishing, plant gathering, trade with Bira, Nande, and Lese farmers, wage labor	Primary evergreen lowland rainforest, secondary forest, and cultivated areas ~1,800 mm	Net, bow, spear, arrow, trap, axe, knife, poison, fire, quiver, tree perch, dogs, beating stick, noise makers, clothing	1972–1975 1980–1985	Hunting yields are high, but diet not estimated owing to the trade and selling of meat	3–7
Aka	Southern Central African Republic, northeast Congo, western DRC	Hunting, gathering plants and insects, honey collecting, fishing, bushmeat trading, wage labor and trade with neighboring farmers, some manioc and plantain cultivation	Primary evergreen and deciduous forest, swamp forest, secondary forest, cultivated areas ~1,600 mm	Spears, nets, traps, crossbows, knives, poisoned arrows, guns, fire, clothing	1980–2000	In forest with limited trade: 20–40%; in village setting: 10–20%[8]	9–15

Group	Location	Subsistence	Habitat	Tool kit	Study period	Meat %	Refs
Hadza	Lake Eyasi area, northern Tanzania	Hunting, scavenging, honey collecting, gathering, occasional trade with neighboring pastoralists and farmers	Acacia-Commiphora-Baobab woodland and savanna ~650 mm	Bow, arrow, axe, knife, fire, fire drill, hunting blind, slings, rope, poison, clothing, weaverbird hook	1985–1989; 1996–ongoing	>50% (1985–1989) ~33% (1996–2007)	16–22
Ju/'hoansi	Northern Kalahari desert, northeast Namibia	Hunting, scavenging, trapping, gathering plants, laboring for and exchange with pastoralists, ranchers, and traders	Sandy desert dunes and flats, open scrub-savanna ~400 mm	Bow, arrow, quiver, hunting blind, spear, knife, axe, springhare probe, poison, rope snare, digging stick, fire, fire making kit, hunting bag, carrying skin, carrying net, rope, dogs, club	1960s–1970s	~29–40%[244,271,243]	23–26
/Gui and //Gana	Central Kalahari desert, Botswana	Hunting, trapping, gathering plants, occasional wage labor, exchange with pastoralists, ranchers, and traders	Sandy desert dunes and flats, open scrub-savanna ~400 mm	Bow, arrow, spear, club, quiver, poison, hunting blind, knife, springhare hook, snare, traps, digging stick, fire, hunting bag, carrying skin, carrying net, rope, dogs, horses	1958–1966; 1966–1974; 1982–1983	~20%	27–30

1. Bailey and Aunger 1989; 2. Bailey 1991; 3. Harako 1981; 4. Harako 1976; 5. Tanno 1976; 6. Ichikawa 1983; 7. Hart and Hart 1986; 8. Hewlett, personal communication; 9. Bahuchet 1985; 10. Bahuchet 1990; 11. Kitanishi 1995; 12. Kitanishi 1996; 13. Noss and Hewlett 2001; 14. Lewis 2002; 15. Balinga et al. 2006; 16. Hawkes et al. 2001b; 17. Hawkes et al. 2001a; 18. Hawkes et al. 2001b; 19. Marlowe 2010; 20. Wood and Marlowe 2013; 21. Marlowe et al. 2014; 22. Wood and Marlowe 2014; 23. Yellen 1977; 24. Lee 1979; 25. Biesele and Barclay 2001; 26. Lee 2003; 27. Tanaka 1980; 28. Silberbauer 1981; 29. Osaki 1984 30 Tanaka 2014.

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FIGURE 10.1. A chim-
panzee at Gombe
National Park captures a
juvenile red colobus
monkey. Photo by Ian
Gilby.

one of the exceptions in Goodall's (1986) sample was "estimated at just over
half adult size," suggesting it weighed at least 25 kg (Kingdon 1997).

In the 1960s at Gombe, chimpanzees regularly killed baboons at a chim-
panzee provisioning station that brought the two species together at unusu-
ally high rates. In 1968–1969, the eight baboon victims of known age averaged
twenty-seven weeks old (Teleki 1973), probably weighing between 2.0 and
3.1 kg (based on known weights of two male baboons of eighteen and forty-
one weeks of age; Gombe Stream Research Centre, unpublished data). Two
others were listed as "juvenile" and one as "infant." After provisioning was
reduced and eventually discontinued, chimpanzees preyed upon baboons
at much lower rates, but continued to target infants and juveniles exclusively
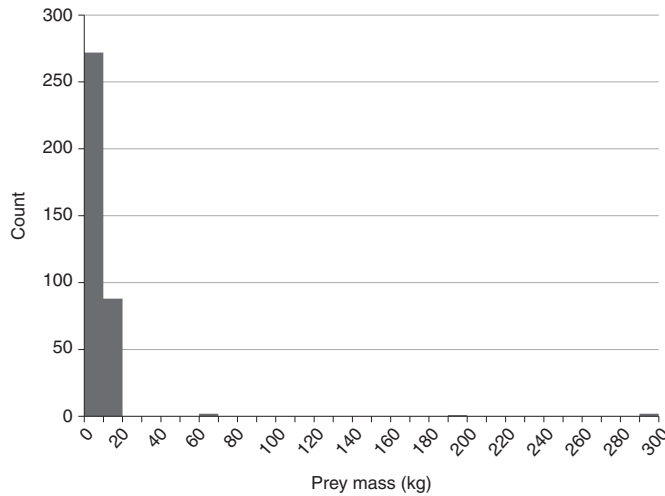(Gombe Stream Research Centre, unpublished data). Finally, other chim-

FIGURE 10.2. Body mass of prey killed by Mbuti. Data are from Tanno (1976), Harako (1981), and Ichikawa (1983). Body mass include total mass of carcasses brought into camp, including edible and inedible parts.

panzee prey include eggs, nestlings, rodents, and nocturnal primates (reviewed by Uehara 1997; Newton-Fisher 2014), all of which weigh less than one kilogram.

African foragers also typically capture prey weighing less than 10 kg, although they do occasionally obtain much larger prey (see below). Figure 10.2 shows the estimated body mass of 365 animals acquired by Mbuti foragers using nets ($n = 320$), bows and arrows ($n = 39$), spears ($n = 4$), and via scavenging ($n = 2$). The median body mass in this sample is 4.5 kg, and 70 percent of animals killed weighed less than 10 kg. Like chimpanzees, Mbuti hunters selectively target red colobus monkeys, partly because they live in large, easily located groups (Harako 1981). Among the Aka foragers, Noss and Hewlett (2001) report that 75 percent of the animals killed in net hunts were blue duikers. The average weight of all animals killed by the Efe was 4.6 kg (Bailey 1991).

Among the Hadza, between 2005 and 2009, 79 percent of the animals killed and brought to camp weighed less than 10 kg (Wood and Marlowe 2013). More small game were killed but consumed outside of camp (Wood and Marlowe 2014). In Lee's twenty-eight-day work diary of the Dobe Ju/'hoansi in 1964, 78 percent of the carcasses brought to camp were animals weighing less

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than 10 kg, and the median body mass of all recorded prey was 5.4 kg. Similarly, we calculated the median weight of prey killed by the Ju/'hoansi in Yellen's 1968 sample to be approximately 4 kg, with 56 percent weighing less than 10 kg Yellen (1977). Using data from Silberbauer (1981), we estimate that 83 percent of prey killed by the/Gui-//Gana over the course of a year weighed less than 10 kg. In sum, the median body mass of prey killed by forest foragers and those in more open habitats seem to be rather similar, all within the 4–6 kg range.

Hunting Is Male-Biased

Among all primates that regularly hunt vertebrates, including chimpanzees, baboons (Harding 1975), and capuchins (Fedigan 1990), males hunt more frequently than females. Boesch and Boesch-Achermann (2000) estimate that male chimpanzees at Taï consume almost seven times more meat than adult females, a difference that can be detected in nitrogen and carbon isotopes extracted from hair and bone collagen (Fahy et al. 2013). This male bias is largely driven by predation upon red colobus monkeys, typically performed by adult males, which made the majority of kills at Taï (81.6 percent; calculated from Boesch and Boesch 1989), Ngogo (93 percent; Watts and Mitani 2002a) and Gombe (89.4 percent: Stanford et al. 1994a). Although females at Kasekela (Gombe) and Kanyawara encountered red colobus less often than males did, when present at a hunt, females were significantly less likely to participate (Gilby et al. in revision). At Kasekela, this may be because female hunters often immediately lose their kill to males (Gilby et al. in revision). Instead of focusing on red colobus, which are active and aggressive, females appear to follow a risk-averse hunting strategy, specializing in relatively low-cost prey. Females at Gombe captured approximately 60 percent of the sedentary prey items (e.g., bushbuck), and a killer was significantly more likely to be female if the prey was sedentary than if it was a red colobus monkey (Gilby et al. in revision). At Kanyawara, females were more likely to capture black and white colobus (Gilby et al. in revision), which are typically less active and aggressive than red colobus. At Mahale, nine of thirteen hunts by females targeted duiker or bushbuck (Takahata et al. 1984), and at Fongoli, females were significantly more likely to engage in tool-assisted capture of cavity-dwelling galagos than males were (Pruetz et al. 2015).

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As with chimpanzees, adult males in African foraging societies are responsible for the majority of the hunting. For example, in Lee's (1979) work diary of the Dobe Ju/'hoansi, every kill was made by men and their dogs. However, women do hunt in some contexts. Further analysis of foods brought to seven Hadza camps studied by Wood and Marlowe (2013) shows that females acquired 3.2 percent of the total mass of animals that were brought to camp. The animals that Hadza females killed were small and relatively immobile: tortoises, infant bushpigs, hyrax, and nesting birds. Similar to the Hadza,/Gui and //Gana women occasionally kill birds, small mammals, and tortoises using their hands, clubs, or digging sticks (Tanaka 1980). More female hunting is apparent among Pygmy foragers. Aka and Mbuti women frequently participate in cooperative net hunts, helping drive game into linked nets stretching 500–800 m through the forest. While participating in such hunts, women typically take on less dangerous roles such as driving the animals, rather than capturing and killing them. Noss and Hewlett (2001) report that Aka women net-hunted on 18.1 percent of observation days, significantly more often than men did (11.6 percent). Including all types of hunts, Kitanishi (1995) reports that 0–20 percent of Aka women hunted per observation day, compared to 40–70 percent of men.

Beyond their actual participation in hunts, women provide various kinds of help that aids men's hunting. Hadza and Ju/'hoansi women help men track wounded animals (Biesele and Barclay 2001), and in all groups in our sample, women help carry meat from kill or scavenging sites. However, there appear to be bounds on the kinds of hunting practiced by African forager women—to our knowledge there are no reports of women hunting solitarily, hunting with projectiles, or killing large game.

Hunting Is Often Communal

When chimpanzees encounter a troop of red colobus, reactions range from indifference to immediate hunting by all present (Goodall 1986; Stanford et al. 1994a). A ubiquitous predictor of hunting probability is the number of adult male chimpanzees present at an encounter with red colobus monkeys—parties containing many males are more likely to hunt than those with fewer males (Boesch and Boesch-Achermann 2000; Hosaka et al. 2001; Mitani and Watts 2001; Gilby et al. 2008, 2015). By contrast, little is known about the relationship between chimpanzee party size and opportunistic hunts of solitary

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or cryptic prey (e.g., duiker, bushbuck, etc.), although we suspect that such hunts may be more likely to occur when parties are small and thus harder for the prey to detect. Indeed, at Kasekela, chimpanzee party size was smaller at kills of terrestrial or concealed prey than at kills of red colobus (Gilby et al. in revision).

In all African forager groups, there are cases in which hunters act alone, and others in which they work together in coordinated groups. Harako (1976) describes hunts in which members of multiple Mbuti residential bands (~30–60 people) join together to track, stalk, and spear elephants. Group hunts in which some individuals drive game toward others waiting with bows and arrows or nets are common among forest-living hunters (Aka, Mbuti, Efe), but rare in more open country foragers (Hadza, Ju/'hoansi,/Gui, and //Gana). Ichikawa (1983) argues that game drives are more common in forests because it is more difficult in such habitats to visually spot and then stalk animals, as hunters often do in more open country./Gui men often hunt in pairs (Silberbauer 1981), as do Hadza men hunting at night (Marlowe 2010). During the day, Hadza men usually forage alone, and men in all other groups occa-

FIGURE 10.3. A group of Hadza men cooperatively hunting zebra. Photo by Brian Wood.

sionally do so, armed with spears or bows. Yellen (1977: 73) notes that Dobe Ju/'hoansi usually hunt alone or with a single partner, but that "all men in camp may cooperate to follow a wounded animal, help butcher it, and carry the meat back to camp."

Meat Is Shared Strategically

Significant human-chimpanzee differences in life history, cultural and technological sophistication, and social organization correspond with major species differences in the characteristics of social relationships, and particularly the role of meat sharing. Nevertheless, we can see in rough outline that within each species, meat is shared preferentially with species-specific "key social partners."

There are several lines of evidence that chimpanzees share meat strategically among allies. The strongest support comes from Ngogo, where rates of giving and receiving meat were positively correlated among partners, and there were positive associations between dyadic meat sharing rates and rates of grooming and coalitionary support (Mitani and Watts 2001; Mitani 2006). At Mahale, one alpha male (Ntologi) shared preferentially with frequent grooming partners, and supported these males in aggressive conflicts (Nishida et al. 1992). Similar correlations were found at the Yerkes Regional Primate Center (de Waal 1989), but not at Gombe, where sharing among males was correlated with neither grooming frequency nor time spent in close proximity (Gilby 2006). At Taï, Boesch (1994b) describes a "social mechanism limiting access to meat by non-hunters," proposing that sharing decisions are based on an individual's past contributions to collective action. The evidence for this conclusion is weak, however (see "Human Hunting Is More Collaborative," below), and more research is needed to rule out the alternative explanation that active hunters get more meat simply because they are more motivated to do so.

While correlational studies are consistent with the hypothesis that chimpanzees use meat in a system of generalized reciprocal exchange, few studies have directly tested whether sharing decisions are directly based on previous exchanges. High fission-fusion dynamics, the relative rarity of meat eating, and uncertainty over the appropriate time frame of exchange make observational studies of contingent reciprocity particularly challenging in the wild. In one captive study, de Waal (1997) found that food sharing was

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FIGURE 10.4. Chimpanzees sharing meat. Photo by Ian Gilby.

more likely to occur if the recipient had groomed the donor within the pre-
ceding ninety minutes than if no grooming had occurred. Although the ef-
fect was rather small, these exchanges were partner-specific, and there was
some evidence of turn-taking.

Among African foragers, the most fundamental way that hunters influ-
ence who will receive meat is by deciding with whom they live. Unlike chim-
panzees, in which all males stay in their natal groups for their entire lives
and members of neighboring communities are generally hostile to one an-
other, African foragers form much more permeable residential groups. They
move their residences within large territories and maintain contact with
hundreds of individuals through temporary visits and the fission, fusion, and
formation of new residential camps (Woodburn 1968b; Yellen 1977; Hill et al.
2014). As such, humans have more flexibility to choose with whom to associate,
exchange information, and share food. Inter-camp movement is a critical
means by which foragers regulate their social environments (Turnbull 1968;
Woodburn 1968b; Lee 1979).

The meat sharing that occurs in African forager camps varies according
to prey type, method of capture, and many other factors. When two or more

individuals collaborate in a hunt, they are generally assured privileged access to the resulting meat. For example, among the Mbuti, individuals who lend their nets to others receive larger shares than do others in camp, including those who actually used the nets to capture the animals (Harako 1981). Among the Ju/'hoansi and the Hadza, two men often travel and work together when hunting, but usually only one man's arrow actually strikes and kills the animal. Nevertheless, both men subsequently enjoy privileged access to the carcass at the kill site, where they often eat raw liver and bone marrow, and cooked rib meat and parts of the head before carrying the animal back to camp (Yellen 1977). Meat sharing among the Efe is also dependent upon an individual's relative contribution to the kill (Bailey 1991). During cooperative hunts of duiker, the man whose arrow first hit the animal receives the largest share (hind quarters and liver), followed by others whose arrows struck the animal (front leg), and then any owner of a hunting dog (front leg and head). Finally, the older men receive first claims to organs and axial parts.

Studies of correlations between dyadic meat sharing totals show strong evidence for reciprocity in meat sharing among the Hadza and the Aka (Gurven 2004; Gurven and Hill 2009, Crittenden and Zes 2015). No such studies of reciprocity in meat transfers have been conducted among other African foragers. Among the Hadza, Ju/'hoansi, and Aka, husbands are expected to share meat with the parents of their wives; this bride-service determines men's residential choices, especially early in marriages (Hames and Draper 2004; Wood and Marlowe 2011). Among the set of people living in one camp, Hadza men have been shown to bias distributions of all the foods they acquire in ways that benefit their key social partners and dependents, including their wives, children, kin living in other households, and the kin of their wives (Wood and Marlowe 2013).

Differences among Chimpanzees and Humans

Humans Kill More Species

Among all study sites and in all years of observation, chimpanzees have been observed to prey upon only forty vertebrate species (reviewed in Newton-Fisher 2014). There is, however, considerable variation in prey diversity

among sites. For example, seventeen prey species have been recorded at Mahale (Uehara 1997), compared to seven at Taï (Boesch and Boesch 1989; Boesch and Boesch-Achermann 2000), even though the availability of potential prey and observation efforts are similar at the two sites. The mean number of mammalian species consumed at each long-term site listed in Table 10.1 is less than ten (although at some sites, certain taxa are listed as one species, e.g., "rodents"). Additionally, prey profiles may change over time. For example, at Mahale, seven species were captured between 1966 and 1981, compared to twelve between 1983 and 1989 (Hosaka et al. 2001).

While chimpanzees specialize on only a few small arboreal and terrestrial species, mainly mammals, human foragers regularly hunt aquatic, terrestrial, subterranean, arboreal, and flying prey, including fish, reptiles, birds, and mammals. Hadza foragers alone kill more vertebrate species than all chimpanzee populations combined: in 242 observation days between 2005 and 2009, they killed forty-one different species (Wood and Marlowe 2013) and recognize several hundred species as potential prey (Marlowe 2010). The Mbuti and Ju/'hoansi hunt and kill at least fifty-three (Harako 1976) and eighty species (Lee 1979), respectively.

Humans Acquire Much More Meat via Scavenging

In general, chimpanzees appear reluctant to scavenge. The bacteria that accumulate rapidly in carcasses pose a greater hazard to chimps than to human foragers, who kill such bacteria by cooking (Smith et al. 2015). Over an eleven-year period, the Ngogo chimpanzees were observed to scavenge only four times, even though they had the opportunity to do so every one hundred days (Watts 2008). Over about twenty years, there were only seven, ten, and two scavenging events at Taï (Boesch and Boesch-Achermann 2000), Gombe (Goodall 1986), and Kanyawara (Gilby et al. in revision), respectively. Chimpanzees at Mahale scavenged twice on fresh adult bushbuck, probably killed by leopards (Hasegawa et al. 1983). The first was, "not large for a normal adult bushbuck," and the second, an adult male, had already been defleshed. With a mass of at least 24 kg (adult females weigh 24–60 kg, males 30–80 kg; Kingdon 1997), these are the largest carcasses that chimpanzees have been reported to eat at any site (with the possible exception of the Gombe bushpig described earlier). However, the chimpanzees consumed only a small portion of the carcasses, perhaps because a leopard lurked nearby.

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More often, chimpanzees "power scavenge"; that is, they seize carcasses directly from other predators (reviewed in Watts 2008). At Gombe, over fifty-three community-years of research in Kasekela and Mitumba, there were forty-eight cases in which chimpanzees seized prey (forty-seven bushbuck and one bushpig) from baboons. In one case described by Goodall (1986), adult female Melissa and her daughter Gremlin displayed together at a male baboon, throwing branches and waving their arms before taking the carcass. To our knowledge, baboons have never been observed to seize meat from chimpanzees.

/Gui-//Gana (Silberbauer 1981), Ju/'hoansi (Yellen 1977), and Hadza (Bunn et al. 1988; O'Connell et al. 1988; Hawkes et al. 1991) drive lions, leopards, caracals, cheetahs, and wild dogs off their kills. Among the Ju/'hoansi, scavenging contributed around 9 percent of the total prey mass acquired. Hadza data from the 1980s show that about 20 percent of all animal flesh was acquired through scavenging (Bunn et al. 1988; O'Connell et al. 1988). Hadza men acquired on average 1.3 kg/day through scavenging, compared to 4.9 kg/day from ambush and intercept hunting (Hawkes et al. 1991). Hyenas and other scavengers often locate animals that have died from Hadza and Ju/'hoansi poisoned arrows, and foragers subsequently drive such scavengers off the carcasses. There are far fewer reports of passive or power scavenging by African forest foragers, probably due to lower visibility and faster rates of decomposition. Harako (1981) describes an Mbuti forager appropriating a red colobus from a crowned eagle, and another case of hunters finding and scavenging a buffalo that died for unknown reasons. Lupo and Schmitt (2005) report that only 0.3 percent of the animals that Aka and Bofi foragers acquired were scavenged. Wrangham (personal communication) observed Efe scavenge a rotten red colobus monkey that was subsequently cooked and eaten.

Human Foragers Occasionally Kill Relatively Large Prey

By targeting prey considerably smaller than themselves, chimpanzees follow a pattern common among predators (Cohen et al. 1993). At Gombe, median adult male body mass is 39 kg (Pusey et al. 2005), and the largest recorded prey item captured there was a young bushpig estimated at 25 kg (Goodall 1986). At other sites, chimpanzees occasionally capture adult male black and white colobus, which may weigh >20 kg (Kingdon 1997, although Watts and

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Mitani [2015] estimate that adult male black and white colobus at Kibale weigh only 9.9 kg). There are many larger animals in some chimpanzee habitats that they do not hunt, including buffalos, hippos, elephants, okapis, adult forest hogs, and adult bushpigs. The largest animals that chimpanzees kill are other adult chimpanzees (Wilson et al. 2014), although these are almost never eaten (but see Pruetz et al. 2017). Nevertheless, we believe that intraspecific killing among chimpanzees has important implications for the evolution of human hunting (see below).

By contrast, even though humans typically kill animals weighing less than 10 kg (see "Most Prey Weigh Less Than 10 kg," above), they can (and do) kill animals much larger than themselves. Okiek (Huntingford 1929), Aka (Kitanishi 1996), Mbuti (Harako 1976), and /Gui-//Gana (Silberbauer 1981) foragers killed African elephants. Hadza, Ju/'hoansi, and /Gui-//Gana have been observed to kill adult male giraffes, which average 1,865 kg (Kingdon 1997). Early twentieth-century accounts by Kohl-Larsen and Cooper (cited in Marlowe 2010) indicate that the Hadza once hunted hippopotamus and rhinoceros, which are no longer found in their area. Mbuti foragers also kill forest buffalos (up to 320 kg), okapis (210–250 kg), giant forest hogs (100–275 kg), and bushpigs (45–150 kg) (adult masses, Kingdon 1997). Such large animals are rare, and therefore opportunities are infrequent, but they result in enormous amounts of meat, which has important implications for food sharing.

Humans Acquire Much More Meat

Meat is a valuable source of protein, fat, iron, vitamin B_{12}, and other micronutrients (Tennie et al. 2009, 2014); however, its contribution to chimpanzee diets is still poorly understood. Nevertheless, by any measure, meat constitutes a small proportion of any individual's diet (e.g., less than 5 percent of feeding time at Gombe: Goodall 1986; McGrew 1992a). At Taï, males and females consume an average of 180 and 25 grams of meat per day, respectively (Boesch and Boesch-Achermann 2000), although there is considerable variation by season and individual.

By contrast, in terms of total calories, hunted meat is estimated to make up between 9 percent and more than 50 percent of the yearly diet of African foragers (Table 10.2). Marlowe (2005) estimates that among all warm-climate

nonequestrian foragers, the average contribution is 25 percent. Each nuclear family of Mbuti net hunters acquired 5.3 kg of game per day (Tanno 1976). As is common among Central African foragers, the Mbuti traded a great deal of this meat with their agricultural neighbors, and were able to receive 12,000 calories of cassava in exchange for only 2,500–4,000 calories of meat. These data attest to the high potential yields from cooperative net hunting in rainforests, and illustrate that meat is usually prized over plant foods on a calorie-for-calorie basis (Hill 1988). Among the Hadza in the 1980s, Hawkes et al. (1991) report that men acquired 4.9 kg / hunter-day. Assuming that camps contained three nonhunters per hunter, this yielded 1.2 kg (~1,830 kcal) per hunter-day, clearly a very large fraction of their diet. Hadza data from 1995–2009 indicate a lower fraction, between 25–35 percent, depending on the season and camp location (Marlowe 2010). Tanaka (1980) estimates that / Gui and // Gana foragers acquired 0.3 kg of meat per person-day, lower than other African foragers, but more than chimpanzees.

Human Foragers Spend More Time Hunting

At Gombe, the average hunt (including failures) of red colobus lasts twenty-eight minutes (Stanford 1998). Using this value with raw data from Gilby et al. (2013), we calculate that between 1976 and 2007, focal male chimpanzees at Gombe spent an average of thirty-five minutes hunting per one hundred hours of observation, or 3.5 minutes per ten-hour day. By contrast, focal males in the same sample spent almost 4.9 hours feeding on plant matter during the average ten-hour day (Gombe Stream Research Centre, unpublished data). Chimpanzees have never been observed (or suspected) to hunt at night.

On average, while living in hunting camps, Mbuti men and women spend between 6.8 (Ichikawa 1983) and 7.5 hours / day (Tanno 1976) net hunting. In Bailey's (1991) study, Efe men spent an average of 2.7 hours / day in the forest searching for, pursuing, butchering, and carrying game. Hadza men spend 4.1 hours out of camp on average (Hawkes et al. 1991), but not all that time is spent hunting. Wood and Marlowe (2014) show that Hadza men spent 62.8 percent of their time out of camp in generalized search (for game, fruit, honey, etc.), and 9 percent following animal tracks, pursuing visually encountered animals, processing carcasses, or atop rock outcrops scanning the

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landscape for animals. Lee (1979) estimates that Ju/'hoansi men spent 29.1 hours per week in subsistence, tool making, and tool repair, and that 83 percent of this work effort (i.e., 3.4 hours/day) was hunting-related. Clearly, African foragers spend much more time hunting than do chimpanzees, although measures of chimpanzee hunting do not include travel time. In addition, humans hunt both during daylight hours and at night (Lee 1979; Hawkes et al. 2001b).

Human Foragers Use Many Complex Tools When Hunting

Some chimpanzees use tools while *consuming* meat. In twenty-six of twenty-eight kills at Taï, chimpanzees modified small sticks to extract bone marrow (Boesch and Boesch 1989). Sticks and leaves are also sometimes used to extract brain matter from monkey crania at Taï (Boesch and Boesch 1989) and Gombe (Teleki 1973). Critically, however, there is no evidence that chimpanzees have ever used tools to cut meat or break open bones, even at sites where they routinely use stone anvils to break open nuts. For a review of chimpanzee tool use, including discussion of the morphological constraints on tool manufacture, see Rolian and Carvalho (this volume).

Chimpanzees rarely use tools while hunting, with one notable exception. At Fongoli, chimpanzees forcibly probe tree cavities with sharpened sticks to flush out, disable, or kill galagos (Pruetz and Bertolani 2007; Pruetz et al. 2015). Over a ten-year period, thirty-five (of a possible forty-four) individuals in this community made 308 attempts to capture galagos in this manner (Pruetz et al. 2015). When infants and juveniles (which never succeeded) were excluded from the analyses, a kill was made in 10.3 percent of attempts. One case of similar behavior was reported at Mahale, when an adolescent female used a stick to flush a squirrel from a hollow tree cavity (Huffman and Kalunde 1993). Goodall (1986: 541) describes cases in which a Gombe chimpanzee "broke off a branch, pushed it into an opening, and moved it rapidly backward and forward." However, apart from ants, termites, and bees, nothing emerged. The high proportion of tool-assisted predation at Fongoli may be due to in part to the absence of red colobus monkeys, but it is unclear why it is so rare at other sites (Pruetz et al. 2015). One possibility is that galago density is greater in the savanna habitat where the Fongoli community ranges, or they might not occupy tree holes at other sites (e.g.,

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Kanyawara; R. Wrangham, personal communication). Pruetz et al. (2015: 9) propose that tool-assisted predation "enables individuals who would be less likely to chase down larger vertebrate prey access to an energetically and nutritionally valuable food resource in a patchy savannah environment," a claim that has important implications for hunting by early hominins.

In sharp contrast to chimpanzees, humans use numerous types of multi-part tools when hunting (Table 10.2). These tools are used to kill prey outright or slowly via blood loss, poisoning, or sepsis. Among the Hadza, hunting tools are more technologically complex than are tools used for gathering (Marlowe 2010). This trend in tool complexity seems likely to apply to other African foragers. All African foragers occasionally capture small game by hand, without the use of deadly weapons, but even on such occasions, hunters are wearing clothing, carrying tools, and benefiting from technological aids to their foraging. Through the use of tools, humans can kill arboreal, terrestrial, subterranean, and aquatic prey, exploiting more predatory niches than any other predator on earth.

Language Facilitates Hunting and Sharing among Humans

Apart from pant-hoots, anticipatory food grunts, and specific "hunting calls" (Mitani and Watts 1999), which simply seem to advertise that a hunt is underway, there is no indication that chimpanzees deliberately communicate during a hunt. Even at Taï, where complex collaboration has been reported (Boesch 1994b, 2002; Boesch and Boesch-Achermann 2000), hunters do not appear to intentionally signal to one another.

By contrast, language is an enormously powerful tool that allows humans to accumulate, maintain, and use complex bodies of knowledge. Using language and mimicry, hunters can recall and represent past hunts, and imagine and plan future hunting scenarios. While hunting, African foragers use sophisticated repertoires of hunting calls, whistles, words, body language, and hand signals to communicate intent and coordinate actions. Language allows for the retention and pooling of collective memories, and the effective teaching of hunting skills. Language permits more effective planning of cooperative hunts, the management of meat distribution, and the resolution of problems associated with collective action and coordination (Bowles et al. 2010; Smith 2010).

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Humans Travel Greater Distances in Search of Meat

It is difficult to ascertain the extent to which chimpanzee ranging patterns are affected by hunting. While the Gombe chimpanzees are more likely to encounter red colobus monkeys on days when they travel greater distances (Gilby et al. 2013), they do not seem to deliberately seek prey. Instead, encounters appear to occur by chance. In contrast, 41 percent of encounters with red colobus at Ngogo occurred on "hunting patrols," during which chimpanzees traveled quickly and quietly, apparently searching for monkeys (Mitani and Watts 1999). Similar behavior occurs at Taï, where there were "clear signs of hunting intention before any prey was seen or heard" in 50 percent of hunts (Boesch and Boesch 1989). Using published data from Gombe, Kanyawara, Taï, and Fongoli (males only), Pontzer (this volume) calculated a mean day range of 3.6 km / day for adult males and 3.0 km / day for adult females. Chimpanzees at Fongoli, which occupy a woodland-savanna habitat, travel much further in the dry season (J. Pruetz, personal communication), which was not included in this sample. However, there is no evidence that hunting dictates ranging patterns in this or other chimpanzee populations.

Humans spend more time traveling, and they do so faster than chimpanzees (Pontzer, this volume). As a result, human daily path lengths are longer. For example, Efe men are reported to have traveled on average 9.4 km per day (Bailey 1991), while Pontzer et al. (2012) found that on average, Hadza men traveled 11.4 km and women 5.8 km per day. Marlowe (2005) reports that among warm-climate nonequestrian foragers, males and females traveled on average 14.1 and 9.5 km per day, respectively. The larger day range of forager males is undoubtedly due to men's hunting, and the fact that men pursue foods that are more mobile, unpredictable, and scarce than female-acquired foods.

Silberbauer (1981) estimates that / Gui- // Gana hunters living together at one camp made use of a maximal foraging area that was 800 km² in size, which is more than nine times larger than the largest chimpanzee home range (85 km² at Fongoli: Wilson et al. 2014). / Gui- // Gana foragers also moved camps several times a year, and thus made use of an even larger total foraging area. Like chimpanzees, human foragers living in more productive environments use smaller ranges. The Mbuti studied by Harako (1981) used 100–200 km² territories in one year, while those studied by Tanno (1976) made use of 120–150 km².

Human Hunting Is Most Productive during the Dry Season; Chimpanzee Hunting Seasonality Varies by Site

At Ngogo, chimpanzee hunting frequency is correlated not with rainfall, but instead with ripe fruit availability (Mitani and Watts 2001), which enables the formation of large hunting parties (Mitani and Watts 2005). Similarly, at Kanyawara, hunting increases when preferred fruits are particularly abundant (providing surplus energy), and there is no regular, seasonal pattern (Gilby and Wrangham 2007). At Mahale and Gombe, however, hunting is strongly seasonal, peaking during the dry season (Hosaka et al. 2001; Stanford et al. 1994a), when large chimpanzee parties form (Takahata et al. 1984; Gilby et al. 2006). Hunting at Taï is also seasonal, reaching its maximum during the wettest months (Boesch and Boesch-Achermann 2000). Boesch and Boesch-Achermann (2000) attribute this increase to reduced alternative food sources, increased ease of capture (due to slippery branches) and the red colobus birth season. At Fongoli, 95.1 percent of tool-assisted predation occurred during the wet season (Pruetz et al. 2015).

In contrast to the variation observed among chimpanzee populations, all African foragers experience an increase in hunting productivity during the dry season. Among the Hadza, this appears to be because the movement of game is predictably restricted to fewer sources of water and forage during the dry season (Hawkes et al. 2001b; Wood and Marlowe 2013), making nighttime ambush hunting particularly effective. Hunting in general, and especially large game hunting, is more frequent and more successful for the Ju/'hoansi in the dry and late dry seasons (Lee 1979: 104). The Mbuti hunt during the dry season, while during the rainy seasons they reside in villages where they depend almost entirely upon farm products (Tanno 1976). Regarding the Mbuti, Tanno (1976: 115) notes that "the hours per day spent in net hunting are determined mainly by the rainfall . . . if it begins to rain while the hunting is in progress, they cease hunting and return to the camp." The Efe's hunting season is also the driest part of the year (Bailey 1991: 65–67).

Human Males in Their Forties and Fifties Acquire Significant Amounts of Meat

Among the Taï chimpanzees, learning to hunt is a long process, with the necessary skills acquired over at least twenty years, starting at the age of nine

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or ten (Boesch and Boesch-Achermann 2000). At both Gombe (Kasekela) and Kanyawara, male hunting probability follows an inverted U-shaped distribution, with males in the twenty-one to twenty-five year age category exhibiting the highest rates (Gilby et al. 2015). There was a significant decline in hunting rates after ages thirty and forty at Kasekela and Kanyawara, respectively. Similarly, success rates peaked between ages twenty-one and twenty-five at Kasekela before falling. However, at Kanyawara, hunting success rates continued to increase with age—though males older than thirty-six rarely hunted, when they did so they were more likely to succeed than their younger counterparts were. Importantly, there is considerable individual variation in both hunting propensity and skill—at Gombe, Frodo had made at least forty-two kills by the time he was fifteen years old (Stanford et al. 1994a), in contrast to the next most successful young hunter, Ferdinand, with twenty kills (data from Gilby et al. 2015). Over the course of the whole Gombe study, all other males made ten or fewer kills by age fifteen. Frodo continued to exhibit high participation and kill rates for his whole life (Gilby et al. 2015).

Because humans experience lower adult mortality than chimpanzees, groups of human foragers contain more males over the age of forty than do chimpanzee communities. Chimpanzees at Kanyawara have only a 14 percent chance of reaching age forty, and a 9 percent chance of reaching age fifty (Muller and Wrangham 2014). Among the Hadza, 40 percent of males reach age forty and 35 percent reach age fifty; if they survive to age forty, they can expect to live another twenty-three years (Blurton Jones 2016).

There are few quantitative records of men's hunting success by age among African foragers. Silberbauer (1981) notes that/Gui-//Gana hunters begin to kill large game around the age of eighteen, and are most effective and active between their late twenties and the age of thirty-five. At around age forty, men start to shift their efforts away from bow-and-arrow hunting and toward trapping and digging for springhares. Lee (1979) notes that Ju/'hoansi men's peak hunting success occurs between the ages of thirty and forty-five. Mbuti men appear to have peak success as spear hunters between ages thirty and fifty (Harako 1981). The most detailed data on hunting rates by age among African foragers come from the Hadza. In Table 10.3, we provide additional analysis of Wood and Marlowe's (2013) food returns data.

Hadza men aged forty and over contributed only 20 percent of the observation days in this sample but acquired 40 percent of the total meat brought to camp. The highest hunting returns (kg brought to camp per observation

TABLE 10.3. Rates of Hadza men acquiring and bringing meat to camp by age.

Age	n Individuals	Person Days Observed	n Small Game	n Large Game	Total kg Game	kg Game/Person Day
0–9	32	1,072 (27%)	9	0	0.85	0.00
10–19	14	737 (18%)	62	0	31.05	0.04
20–29	17	631 (16%)	63	7	1,060.12	1.68
30–39	19	744 (18%)	52	18	1,459.16	1.96
40–49	11	378 (9%)	22	8	521.26	1.38
50–59	8	292 (7%)	28	12	1,144.60	3.92
60–69	3	59 (1%)	3	1	43.60	0.74
70+	2	84 (2%)	3	0	0.33	0.00

Note: These data are derived from the sample described in Wood and Marlowe (2013), which includes seven camps observed between 2005 and 2009. Weights include all parts of animals brought into camp, including edible and inedible parts.

day) were among men age fifty to fifty-nine. Surely, if Hadza had an age structure more similar to chimpanzees, there would be much less meat in their diets. Given cross-cultural patterns in the age dependency of economic productivity, this is also likely to be the case among other African foragers. Gurven and Gomes (this volume) provide a discussion of the importance of intergenerational cooperation and food sharing in traditional human populations, and the role it might have played in the evolution of the human life span.

Human Hunters Ambush Prey

With the exception of searching for red colobus at Ngogo and Taï, chimpanzees appear to encounter prey by chance during routine travel. While it is possible that they may alter their travel routes to pass through prey-rich areas, there are no reports of any chimpanzees waiting for prey to arrive. By contrast, Mbuti (Harako 1976), Hadza (Hawkes et al. 1991), and Efe (Bailey 1991) hunters often search for fresh signs of prey, and then, based on such signs, select a location where the animal is likely to pass in the near future—often water sources, fruiting trees, game paths, or salt licks. Hunters then conceal themselves, either by using naturally occurring vegetation or by constructing a blind, stand, or pit, and wait quietly for animals to arrive. This requires foresight, calculation, and patience, and is commonly used for killing the largest game. Mbuti hunters use this technique to spear buffalo,

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FIGURE 10.5. A Hadza couple cooperatively hunting a hyrax—the wife blocking possible points of escape while her husband spears the animal. Photo by Brian Wood.

okapi, giant forest hog, and bushpig (Harako 1981). Hadza men use it to shoot zebra, eland, buffalo, impala, and smaller game. This is a very effective strategy for the Hadza in the late dry season, when animal movements are more predictable, and while hunting at night (Hawkes et al. 2001b). Ju / 'hoansi men also occasionally hunt at night from blinds (Lee 1979).

Human Hunting Is More Collaborative

There has been considerable interest in the degree to which chimpanzees "work together" during communal hunts of arboreal monkeys. Boesch (2002) argues that increasingly sophisticated cognitive ability is required for species to move along a continuum of cooperation from "similarity," when hunters simultaneously target the same prey without coordination, to "collaboration," in which they "perform different complementary actions" (Boesch and Boesch 1989). True collaboration involves observation, anticipation, and reaction to the actions of the prey and other predators in space and time. It has also been proposed that particular psychological traits, in-

cluding impulse control (Stevens and Hauser 2004), have evolved to facilitate collaboration. Boesch (1994b) has argued that truly collaborative species have also evolved the ability to selectively form bonds with "trusted partners," which allows individuals to more reliably predict the outcome of collaborative actions, such as meat sharing after a kill. However, chimpanzees at most sites rarely hunt in a manner that is consistent with true collaboration (Mitani and Watts 2001; Gilby et al. 2006, 2015). The exception is Taï, where Boesch and Boesch-Achermann describe the frequent occurrence of hunts in which "drivers" funnel colobus monkeys past "blockers" (who restrain themselves from chasing) toward "ambushers" and "chasers" who ultimately make the kill (Boesch and Boesch 1989; Boesch 1994b, 2002; Boesch and Boesch-Achermann 2000). However, with the data presented, one cannot rule out the more parsimonious alternative that this apparent coordination is a by-product of the selfish efforts of several hunters, each attempting to make his own kill and reacting to the actions of others (Gilby and Connor 2010; Tomasello and Moll 2010; Gilby et al. 2015).

African foragers work together, share knowledge, tools, and food, and perform complementary actions that far exceed the complexity and effectiveness of the limited coordination observed among chimpanzees. Foragers collaborate in all their subsistence pursuits. The range of collaborative hunting activities is quite broad—multiple camps of Mbuti work together to track and spear elephants, with individuals playing different roles based on age and skill (Harako 1976); /Gui-//Gana men travel together and coordinate shots of arrows at their prey (Silberbauer 1981); Efe and Mbuti women drive duikers toward their husbands, who tend nets, with all the individually owned nets tied together as one unit for the group's collaborative hunt (Tanno 1976).

Human hunters are never quite alone—their behavior is structured by the fact that they can expect to find information, food, water, warmth, and shelter when they return home. Solitary human hunters also draw on coordinated assistance from others as needs arise. When solitary Ju/'hoansi, /Gui-//Gana, Hadza, and Mbuti men shoot animals with arrows, they return to their camps and recruit help from others to track wounded prey, butcher carcasses, and carry the meat back to their camp (Woodburn 1968a; Harako 1976; Yellen 1977; Lee 1979; Biesele and Barclay 2001).

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Social Norms and Kinship Regulate Hunting and Sharing
among Humans, While Chimpanzees Are Primarily Motivated
by Immediate Self-Interest

Hunting in groups increases the probability that a given chimpanzee imme-
diately obtains meat (Boesch 1994b; Gilby et al. 2008, 2010; Tennie et al.
2009). While subsequent sharing may secure reciprocated (delayed) benefits
in the form of more meat, coalitionary support, grooming, or sex (de Waal
1989, 1997; Mitani 2006; Gomes and Boesch 2009), chimpanzees do not ap-
pear to base their hunting decisions on the potential for delayed exchanges—
neither the presence of a preferred male social partner at Kanyawara (Gilby
et al. 2008) nor sexually receptive females at Ngogo, Kanyawara, or Gombe
(Mitani and Watts 2001; Gilby et al. 2006, 2008, 2015) improved the chances
of a hunt occurring. Instead, the primary motivation for a chimpanzee to ini-
tiate or join a hunt seems to be to obtain meat for itself.

Most meat sharing by chimpanzees (e.g., 76.4 percent of 529 sharing events
at Gombe; Gilby, unpublished data) is "passive," in which a possessor neither
facilitates nor resists others' attempts to take pieces or feed from the same
carcass. While there is growing evidence of preferential sharing with
frequent grooming and coalition partners, the "sharing under pressure"
(Wrangham 1975) or "harassment" (Stevens 2004) hypothesis also explains
a significant proportion of chimpanzee meat-sharing events. Similar to the
tolerated theft model proposed for humans (Blurton Jones 1984), the sharing
under pressure hypothesis states that in the face of persistent begging, it is
immediately beneficial for a possessor to share if doing so reduces the nega-
tive effects of harassment. It is critical to note that harassment does not equal
"aggression"; instead, harassment need only impose a cost for the possessor
to immediately benefit by sharing. Gilby (2006) found that (1) meat possessors
at Gombe consumed meat less efficiently when faced with many beggars, (2)
sharing with beggars encouraged their departure, and (3) sharing probability
increased with the level of harassment. We emphasize that while there are
many reasons why chimpanzees share meat, most of these transfers would
not occur in the absence of harassment.

Like chimpanzees, African foragers face pressure to share. However,
physical harassment and theft are rare. Instead, meat sharing is governed
by social norms that establish guidelines for distribution, and which re-
duce chances of outright conflict or freeloading. First, the hunter who made

the kill typically benefits the most. Hadza men keep heavier and more valuable shares of their kills than they give to others (Wood and Marlowe 2013, 2014). Among the /Gui- //Gana, the hunter who kills a large animal receives the back meat, including the sinew, which is used for a variety of tools. He also retains the skin, which is extremely valuable for clothing, carrying devices, sleeping surfaces, and working surfaces (Tanaka 1980). The same norm of hunters keeping the valuable skins from their kills is found among the Hadza (Wood and Marlowe 2013). Second, in all groups, hunters share preferentially with their wives (e.g., Hadza: Wood and Marlowe 2013). The institution of marriage is one means by which, relative to chimpanzees, human females come to play a more active role in managing the sharing of meat. In reference to the Aka, Noss and Hewlett (2001) note that women "control the division and distribution of game acquired captured on net hunts." Hadza men deliver small animals, fruit, and honey directly to their households, and their wives largely control the subsequent sharing that occurs within the family and with neighbors. By contrast, although male chimpanzees preferentially share meat with maternal brothers when there is the opportunity to do so, most meat-sharing events occur between unrelated males (Langergraber et al. 2007). Third, sharing of tools or contribution of labor to a kill obliges the owner to share. Fourth, meat-sharing norms that benefit older males are reported for the Efe, the Ju/'hoansi, the /Gui- //Gana, and the Hadza.

The Evolution of Human Hunting

While it is possible that some similarities in hunting and meat sharing arose independently in the human and chimpanzee lineages via convergent evolution, the most parsimonious explanation is that these are homologies; it is therefore likely that the LCA (1) hunted mostly small prey, (2) exhibited male-biased hunting, (3) often hunted in groups, (4) occasionally appropriated carcasses from other predators, and (5) shared meat with key social partners but also under pressure. In their reconstructions of ancestral states in hominoid evolution, Pickering and Domínguez-Rodrigo (2010) and Duda and Zrzavý (2013) similarly propose that the LCA already engaged in more hunting than is typical for a primate. Environmental changes affecting the availability of prey likely provided selective pressures resulting in early

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differences in hunting behavior within the hominin lineage. As the climate became cooler and drier, African woodland and savanna habitats expanded (Reed 1997; Bobe and Behrensmeyer 2004). To exploit these more open habitats, early hominins would have needed to increase their day range (Foley 1987), encountering more terrestrial prey species, particularly grazing herbivores. This would have lowered the frequency of encountering arboreal monkeys. However, since chimpanzees have been shown to respond to reduced numbers of preferred prey by switching to alternative species (Watts and Mitani 2015), early hominins surely did the same, incorporating easily acquired terrestrial prey such as infant antelopes and bovids, fledgling birds, and hyrax. Additionally, in woodland and savanna habitats, large herbivores tend to congregate near sources of water, consequently attracting large carnivores (Valeix et al. 2010). In order to exploit the expanding savanna, early hominins would have also needed to visit waterholes, presenting them with more frequent opportunities to capture prey and scavenge fresh kills, although they would also have experienced increased predation risk. The fact that chimpanzees engage in coalitionary killing of adult conspecifics (Wilson and Glowacki, this volume) suggests that even without the use of weapons, the LCA likely had the capacity to kill large-bodied, dangerous animals.

While paleoclimatic data provide hints about what life could have been like for early hominins between 7.9 Ma and 3.3 Ma, the archaeological record itself is silent, and therefore our ability to make inferences about their behavior is limited. It is possible that rates of hominin carnivory and scavenging increased during this period, but without supportive data, the most we can say is that meat comprised at least 1–5 percent of their total diet (comparable to that of chimpanzees).

The earliest stone tools appear at 3.3 Ma at the site of Lomekwi, Kenya (Harmand et al. 2015). It seems safe to assume that the hominins that manufactured such stone tools would also have fashioned simple wooden implements of a complexity similar to those used by chimpanzees today. We therefore suggest that by 3 Ma, hominins were using minimally modified sticks as clubs or short spears in various contexts including predator defense, power scavenging, hunting, and digging for animal or plant foods.

The site of Kanjera South, Kenya, has produced well-preserved stone tools and cut-marked bones that are approximately 2.0 million years old. These attest to hominin occupation of a grassland environment adjacent to Lake

Victoria (Ferraro et al. 2013). The counts and distributions of stone tool cut-marks and carnivore tooth marks on the faunal material indicate that by this point hominins regularly engaged in hunting and / or power scavenging, giving them access to large, fleshed carcasses. The species responsible for these early assemblages is not known, but an early member of our genus, either *Homo habilis* or *Homo ergaster,* is the most likely candidate. While it is not possible to estimate the median body mass of prey items killed by these hominins, the Kanjera South assemblage contains numerous wildebeest-sized prey, and a few even larger. Spatial and taphonomic analyses at this site indicate that hominins returned with fleshed carcasses to a central place, representing a notable change in social organization relative to that of chimpanzees and our reconstructed LCA. As discussed by Blumenschine et al. (1991), transporting food back to a central place can serve several functions: providing refuge from risks of predation (Isaac 1983), accessing cached stone tools to aid butchering (Potts 1984), and provisioning others.

These archaeological materials reflect several of the derived features of modern human hunting: technological sophistication, the occupation of a wider range of habitats, and the (at least occasional) incorporation of large prey. The power scavenging and / or hunting involved in acquiring these larger-bodied prey almost certainly involved cooperation, although the degree of collaboration is unknown. However, we can assume that at the very least, they exhibited the kind of loosely coordinated group action typical of chimpanzee hunts of red colobus.

While some have argued that only large carcasses provide sufficient evidence for food sharing (e.g., Binford 1981), studies of chimpanzees and human foragers illustrate that even very small game are regularly shared. Most likely, the meat derived from the kills at Kanjera South and Olduvai was being shared, but the specific details of such transfers and the nature of in-group social relationships involved remain a mystery. Given the technological sophistication and foraging capabilities of these hominins, we estimate that meat would have contributed a significant fraction of their diet, perhaps 5–20 percent of their total calories. Similarly, these hominins were probably acquiring other high-quality extracted foods (e.g., honey, tubers, nuts), leading to an overall increase in dietary quality and diversity relative to the LCA.

Given that the changes in social organization and foraging strategies suggested by the archeological record correspond closely to a marked increase in brain size in the genus *Homo,* several researchers have proposed that dietary

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shifts (including increased carnivory) led to, resulted from, or coevolved with larger brains and increased intelligence (Foley 2001; Foley and Lee 1991; Kaplan et al. 2000). In principle, more fossil and archaeological data could help resolve the timing of these shifts. At present, the fact that increased meat eating and early brain size expansion coincide relatively closely in time lends support to ideas that changes in diet and social structure coevolved with larger brains.

Nearly coincident in time with these examples of increased meat eating and encephalization of early *Homo* in Africa, there is evidence for the rapid dispersal of *Homo erectus* outside of Africa, north to the Republic of Georgia by 1.8 Ma (Gabunia et al. 2000), and east to the island of Java by 1.7 Ma. This range expansion is not likely to be a consequence of population growth, but rather was due to a fundamental shift in ranging and foraging capabilities (Anton et al. 2002). Comparative analyses show that primates with larger brains are better able to buffer themselves against highly seasonal environments (van Woerden et al. 2012), and among mammals, larger brains are correlated with greater chances of survival in novel habitats (Sol et al. 2008). In particular, hunting would have facilitated the expansion of hominins into and through colder habitats, where gathering would have been less productive.

The control of fire undoubtedly had several important impacts on hunting, meat eating, and many other features of hominin diet and socioecology (Wrangham 2009; Carmody, this volume). Considerable debate surrounds the identification of the first controlled fire (Gowlett and Wrangham 2013), but the earliest irrefutable evidence appears at Wonderwerk Cave in South Africa, approximately 1.0 Ma (Berna et al. 2012). A hominin (probably *Homo ergaster*) that could roast meat could kill the harmful bacteria that rapidly accumulate in carcasses postmortem (Smith et al. 2015). A fire-controlling hominin could thus increase its meat consumption without any change in the rate of killing prey or encountering carcasses killed by other predators. Cooking and tool-aided pounding and tenderizing of meat increase its digestibility (Carmody et al. 2011), and reducing the costs of digestion could free up time and energy for other pursuits. Beyond cooking, fire has myriad adaptive functions among living foragers, and the cross-cultural investigation by Scherjon et al. (2015) show that fire is frequently used to drive and kill game, to make landscapes more attractive to game animals, and to clear vegetation so as to facilitate travel, including pursuit of prey. The antiquity of such behaviors is unknown, but hopefully future archaeological research will shed light on this important topic.

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At least three significant characteristics of hunting among modern human foragers require language-based cumulative culture: (1) complex weapon manufacture, (2) extensive collaboration, and (3) sharing norms. If the LCA already hunted in groups, as we assume it did, then the advent of language would permit more effective information sharing among hunters. This would have increased prey encounter rates and reduced handling costs, ultimately leading to greater foraging efficiency. Archaeological materials from the last 500 Ka are suggestive of language-aided cultural innovations. Hafted spear points appear in South Africa (Kathu Pan) dated to 500 Ka (Wilkins et al. 2012). During the Middle Stone Age, spear points exhibit regional differences in style across Africa (McBrearty and Brooks 2000). In the Levant region, butchery marks found on the bones of large mammals become increasingly standardized after 190 Ka, perhaps indicating task specialization in the realm of butchery and meat sharing (Stiner et al. 2009).

Summary

In *The Descent of Man,* Darwin (1871) speculated that men who could "best defend and hunt for their families . . . would succeed in rearing a greater average number of offspring." Data from modern human foraging populations show that better hunters do indeed have higher reproductive success (Smith 2004). Therefore, any genetic traits that underlie hunting ability remain under positive selection (in some populations), although of course not all such traits are genetic, and all require development, practice, and learning. Since success in hunting is known to lead to both higher reproductive success and prestige, Darwin's inference remains reasonable, and we can assume that over an extraordinarily long period of time, genetic and cultural adaptations have arisen owing to their fitness consequences in the hunting context.

The use of deadly weapons, extensive collaboration, and social norms are key components of hunting and sharing among modern African foragers, but the cultural and genetic factors underlying these traits would not have arisen *only* vis-à-vis their role in hunting. Adaptations that arose in other domains would have been co-opted and applied in hunting, and vice versa. A simple wooden hunting spear, for example, is but a lengthened digging stick, and traits underlying the efficient manufacture and use of either tool would influence its use in other domains. Likewise, new means of effectively

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defending against predators or enemies—concealment, detection, mobbing, or the use of weapons, could all be usefully employed in confrontational scavenging or in hunting. Traits that facilitate success in hunting are functionally linked to other important domains of behavior and social organization. Both humans and chimpanzees engage in coalitionary killing of adult conspecifics, and this suggests that even without the use of weapons, the human-chimpanzee LCA likely had the capacity to kill large and dangerous animals. The same neural architecture that gives humans the ability to symbolically represent, communicate, and reason about the behavior of other people is likely to also be useful for predicting the behavior of nonhuman predators and hunted prey.

The meat-sharing norms that humans exhibit today only make sense given a host of derived changes in the structure of human social life: the development of pair-bonds, increased dependence of juveniles on maternal, paternal, and grandparental investment, larger networks of social interaction, and longer lives (Hooper et al., this volume). Several researchers have argued that these traits coevolved with or depended on more human-like hunting (Kaplan et al. 2000; van Schaik and Burkart 2010). These ideas remain viable, but significant obstacles remain in our ability to conclusively test them owing to the difficulties of reconstructing past hunting, food sharing, or social organization. Regardless of the original function(s) of our species' technological skills, cognitive traits, and collaborative subsistence systems, surely one consequence of them is that all humans—not just hunter-gatherers—today exploit a more meat-centric dietary niche that remains relatively unexploited by chimpanzees or any other hominoid.

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