



Hunting Behavior of Chimpanzees at Ngogo, Kibale National Park, Uganda

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Received May 17, 2000; accepted September 12, 2000

Chimpanzees (Pan troglodytes) prey on a variety of vertebrates, mostly on red colobus (Procolobus spp.) where the two species are sympatric. Variation across population occurs in hunting frequency and success, in whether hunting is cooperative, i.e., payoffs to individual hunters increase with group size, and in the extent to which hunters coordinate their actions in space and time, and in the impact of hunting on red colobus populations. Also, hunting frequency varies over time within populations, for reasons that are unclear. We present new data on hunting by chimpanzees at Ngogo, Kibale National Park, Uganda, and combine them with earlier data (Mitani and Watts, 1999, Am. J. Phys. Anthropol. 109: 439–454) to examine hunting frequency and success, seasonality, and cooperation. The Ngogo community is the largest and has the most males of any known community. Chimpanzees there mostly hunt red colobus and are much more successful and make many more kills per hunt than at other sites; they kill 6–12% of the red colobus population annually. The number of kills and the offtake of meat per hunt increase with the number of hunters, but per capita meat intake is independent of hunting party size; this suggests that cheating occurs in large parties. Some behavioral cooperation occurs. Hunting success and estimated meat intake vary greatly among males, partly due to dominance rank effects. The high overall success rate leads to relatively high average per capita meat intake despite the large number of consumers. The frequency of hunts and of hunting patrols varies positively with the availability of ripe fruit; this is the first quantitative demonstration of a relationship between hunting frequency and the availability of other food, and implies that the chimpanzees hunt most when they can easily meet energy

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needs from other sources. We provide the first quantitative support for the argument that variation in canopy structure influences decisions to hunt red colobus because hunts are easier where the canopy is broken.

KEY WORDS: chimpanzees; predation; red colobus; cooperation; meat eating.

INTRODUCTION

Chimpanzees (*Pan troglodytes*) in all well-studied populations prey on a variety of vertebrates (reviews: Wrangham and Bergman-Riss, 1990; Uehara, 1997). They prey most heavily on red colobus (*Procolobus (Piliocolobus)* spp.) where the two species are sympatric (Boesch and Boesch, 1989, 2000; Goodall, 1986; Hosaka *et al.*, in press; Mitani and Watts, 1999; Uehara, 1997). Ultimately, the fact that meat and bone marrow are rich sources of energy, protein, and other nutrients presumably explains why chimpanzees hunt (Boesch, 1994a,b; Mitani and Watts, 2001; Stanford, 1996a,b; Takahata *et al.*, 1984; Teleki, 1973, 1981). However, hunting also has social importance, and the role of meat procurement and sharing in maintaining cooperative social relationships between males (Nishida *et al.*, 1992; Stanford, 1998; Stanford *et al.*, 1994b) may supersede the nutritional importance of hunting. Hunting frequency and success rates, predator pursuit tactics, meat intake, and other aspects of hunting and meat eating vary considerably across and within populations, and often vary over time within communities (Boesch and Boesch, 1989, 2000; Goodall, 1986; Stanford *et al.*, 1994a; Uehara, 1997; Wrangham and Bergmann-Riss, 1990). This variation is partly due to ecological factors. For example, the taller, more continuous canopy at Taï than at Gombe and the larger size of red colobus at Taï help to explain why Taï chimpanzees rarely hunt by themselves and why they cooperate in pursuing prey more often than Gombe chimpanzees do (Boesch, 1994b; Stanford *et al.*, 1994a).

However, many questions about variation in chimpanzee hunting behavior are unresolved. For example, disagreement exists about the extent to which chimpanzees hunt cooperatively, partly because definitions of cooperation have varied. Most red colobus hunts are group activities (Boesch, 1994a,b; Boesch and Boesch, 1989, 2000; Mitani and Watts, 1999; Stanford, 1996, 1998; Uehara, 1997). Individuals can benefit by hunting in groups if hunting success increases with the number of hunters and this leads to greater per capita meat intake or net energy gain (Boesch, 1994b; Boesch and Boesch, 2000; Packer and Ruttan, 1988; Scheel and Scheel, 1995). Such payoffs could occur because hunters coordinate their actions in ways that improve their capture success (Boesch and Boesch, 1989). However, group members that pursue prey risk exploitation by others that refrain from

pursuits but try to gain shares of captures (Packer and Rutman, 1988). Packer and Rutman (1988) concluded from early Gombe data that the chimpanzees hunted cooperatively because the percentage of hunts that led to captures increased with the number of males present at hunts. However, success rates were lower than predicted by a model of pure cooperation, which they took as evidence of cheating. Some later data from Gombe (Stanford, 1996) also showed that hunting success increased with increases in the number of adult males present at hunts, and success increased with the number of hunters at Tai (ibid.; Boesch and Boesch, 2000). However, Stanford (1996) argued that Gombe chimpanzees did not hunt red colobus cooperatively because per capita meat intake did not also increase with hunting party size. Positive correlations between the number of males at hunts and hunting success were not evident in other Gombe data (Busse, 1978), nor did success increase with the number of hunters in Boesch's (1994b) Gombe sample. A better criterion for cooperation is that net per capita energy gain increases with group size, at least up to some optimum, and is higher for groups than for solo hunters (Boesch, 1994b; Scheel and Scheel, 1995). In the only study of chimpanzees that included estimates of its net energy returns, Boesch (1994b) found that it met this criterion at Tai, but not at Gombe. As defined by the extent to which individual hunters coordinate their behavior in space and time, cooperation is also common at Tai, but not at Gombe (Boesch, 1994b; Boesch and Boesch, 1989, 2000; Stanford, 1996).

Rates of predation by chimpanzees commonly vary over time (Boesch and Boesch, 1989, 2000; Goodall, 1986; Mitani and Watts, 1999; Stanford, 1998; Stanford *et al.*, 1994; Takahata *et al.*, 1984; Uehara, 1997; Wrangham and Bergman-Riss, 1990), and researchers have invoked both ecological and social factors as explanatory variables. At Tai and Mahale, hunting is more common during rainy seasons. These may be times of high fruit abundance at Mahale (Takahata *et al.*, 1984; Uehara, 1997). During the season of hunting at Tai, fruit abundance may initially be low, but subsequently increases (Boesch, 1994a, 1996; Boesch and Boesch, 2000), and this also tends to be a birth season for red colobus (Boesch and Boesch, 2000). In contrast, predation on red colobus at Gombe is more intense during dry seasons (Stanford *et al.*, 1994a). Stanford (1996) raised the possibility that Gombe chimpanzees hunted more during the dry season because they needed energy, but noted that the large mean size of parties was inconsistent with the assumption that dry season fruit availability was low. He argued instead that variation in the number of cycling females was probably more important (Stanford, 1996a,b; Stanford *et al.*, 1994a). However, quantitative data on fruit availability are not available for these sites.

We present new data on hunting by chimpanzees at Ngogo, in Kibale National Park, Uganda, collected during 11 months in 1998–1999, and add

them to data published by Mitani and Watts (1999). The Ngogo community is unusually large, and the chimpanzees are more successful at hunting red colobus and make more kills per hunt than chimpanzees elsewhere (Mitani and Watts, 1999). We use our larger data set to update information on hunting frequency, prey choice, and hunt durations, to reexamine demographic influences on hunting success, to examine the hypothesis that hunting is cooperative in ecological terms, and to describe social cooperation. We also examine individual variation in hunting, estimate total red colobus offtake in numbers and in biomass, and update our estimates of the impact of predation on the red colobus population. We provide quantitative data on how forest structure influences decisions to hunt red colobus and hunting success. Finally, we analyze the relationships of hunting frequency and prey offtake to variation in the availability of ripe fruit and provide quantitative evidence that hunting frequency varies positively with the abundance of ripe fruit.

METHODS

The Ngogo study area covers about 30 km² of mixed mature and regenerating forest transitional between lowland and montane evergreen forest and other, minor vegetation types (Butynski, 1990; Struhsaker, 1997). Most chimpanzees in the Ngogo community, including all males, are well habituated, but its exact composition is still uncertain. However, it is the largest one to be documented (Mitani *et al.*, 1999, in press; Mitani and Watts, 1999; Pepper *et al.*, 1999; Watts, 1998, 2000a,b; Watts and Mitani, 2000): by mid-1999, we had firmly identified 24 adult males and 15 adolescent males, and estimated 47 adult and 9 adolescent females, 15 juveniles, and 34 infants, for a total of 146 members.

We have opportunistically collected data on three kinds of predation episodes (Table I; cf. Mitani and Watts, 1999). Occasionally we found chimpanzees eating meat just after a successful hunt that we had not seen (meat-eating episodes) or found individuals carrying carcasses (carcass-carrying episodes). Hunts, during which we saw chimpanzees rush at prey, accounted for most episodes (Table I). We define hunts as successful when the chimpanzees captured ≥ 1 prey. For hunts, we recorded the prey species, the number of kills, and the age–sex class of the prey. We also recorded the time whence the first chimpanzee climbed toward the prey until the first kill (hunt duration) for hunts of monkeys. We identified all chimpanzees present, noted the identities of all that captured prey and that obtained some meat, and noted all instances of meat sharing and theft (cf. Mitani and Watts, 1999).

The large size and spread of hunting parties, combined with constraints on visibility in the canopy, precluded collection of systematic data on whether

Table I. Frequency of predation episodes at Ngogo, listed by prey species

Species	H	#S	ME	CC	Total	Kills	% Kills
Pennant's red colobus, <i>Procolobus (Piliocolobus) pennantii</i>	82	67	6	3	91	258	88.4
Black-and-white colobus, <i>Colobus guereza</i>	14	7			14	11	3.8
Red-tailed guenons, <i>Cercopithecus ascanius</i>	8	4	1	1	10	10	3.4
Mangabeys, <i>Lophocebus albigena</i>	3	1			3	1	0.3
Blue monkeys, <i>Cercopithecus mitis</i>	1	1			1	1	0.3
Red duiker, <i>Cephalophus monticola</i>	2	2	5		7	7	2.4
Blue duiker, <i>Cephalophus callipyga</i>			2		2	2	0.7
Bushpig, <i>Potamochoerus porcus</i>	1	0	1		1	1	0.3
Guinea fowl, <i>Guttera pucherani</i>			1		1	1	0.3
Total	111	80	16	4	131	292	

Note. H: hunts; ME: meat-eating; CC: carcass-carrying; #S: number of successful hunts; Kills: total number of observed kills.

all chimpanzees present pursued prey, on how much time individuals devoted to pursuits, and on whether individuals typically took certain roles during hunts. The same problems prevented us from systematically collecting data regarding behavioral coordination, though we did so opportunistically, and on recording precise observations on how much meat all individuals obtained. These uncertainties mean that our analyses of cooperation are preliminary. Because of the observational constraints, we followed the convention established by other students and used the number of adult males present as our estimate of hunting party size (Stanford, 1996, 1998; Gombe: Stanford *et al.*, 1994a; Mahale: Hosaka *et al.*, in press). The counts may overestimate the number of hunters because not all males necessarily pursue prey, and we hope to get more precise counts of the number of pursuers in the future.

There are two reasons why the total number of adult males present is a reasonable estimate of hunting party size. First, bystanders that watch the progress of hunts from positions on the ground can quickly become pursuers when they see good opportunities to capture monkeys in the canopy or when monkeys fall or are knocked to the ground (cf. Hosaka *et al.*, 2000; Watts and Mitani, in press). We suspect that certain males routinely stay on the ground and use the wait-for-monkey-to-fall tactic also seen at Mahale by Hosaka *et al.* (in press). Thus, absolute distinctions between bystanders and hunters often do not exist. Second, whether cheaters exploit the efforts of pursuers is a crucial issue with regard to whether individuals do better by hunting in groups than by hunting alone, or by hunting in larger groups rather than smaller ones (Packer and Ruttan, 1988). Using the total number of males as the independent variable provides conservative tests of the hypotheses that hunting success and prey offtake increase with the size of hunting parties.

Success and offtake should not be positively related to total party size if large parties contain relatively many cheaters (Packer and Ruttan, 1988).

For successful hunts of red colobus, we estimated the biomass of prey harvested per hunt by multiplying the number of kills for a given age–sex class by the estimated body mass of a member of that class, and then summing across classes. Body masses were 11 kg for adult males, 6 kg for adult females and for subadults, 3 kg for juveniles, and 1 kg for infants (Stanford, 1996; Struhsaker, 1975; Struhsaker and Leland, 1987). Per capita meat availability for adult male chimpanzees is the total biomass of prey killed divided by the number of males present. We used Struhsaker and Leakey's values for the proportional representation of different age–sex classes in the red colobus population to test the hypothesis that the chimpanzees preyed on classes nonselectively (Struhsaker and Leakey, 1990). We used values of 2.04 red colobus groups per km² (Mitani *et al.*, 2000b) and 42 individuals per group (T. Struhsaker, pers. comm.) to estimate the annual impact of chimpanzee predation on the red colobus population.

During fieldwork in 1998–1999, we noted all visual encounters between chimpanzees and red colobus; this yielded a total of 164 encounters, in 59 of which the chimpanzees hunted. We assigned the forest structure at encounter sites to one of three categories: (1) primary forest with a tall, continuous canopy; (2) regenerating forest or swamp forest with a broken, mostly low, canopy; and (3) forest with a tall canopy, but within about 100 m of regenerating forest, open swamp forest, or grassland or bush with no tall trees. Forest in the second and third categories offered the monkeys fewer escape routes than tall primary forest did. We then used logistic regression to examine the effect of forest structure on decisions to hunt, represented by the categorical variable hunt/no hunt. We conducted a similar analysis for the total sample of hunts ($n = 82$) to examine the effects of forest structure on hunting success, represented by the categorical variable success/no success. We pooled data from forest structure categories 2 and 3 in the analysis of hunting success because few hunts in these areas were unsuccessful.

We used data on phenology, tree size, and tree densities of the top 20 fruit species in the chimpanzees' diet, as measured in 263 plots, each 5 × 50 m, to compute an index of ripe fruit availability (ripe fruit score; RFS) each month:

$$\text{RFS} = \sum_{i=1}^{20} p_i \cdot d_i \cdot s_i$$

Where in p_i = percentage of the i th tree species possessing ripe fruit

d_i = density of the i th tree species (trees/ha)

s_i = mean size of the i th tree species in cm DBH.

We collected phenological data on the first 5 days of a month and centered months around the midpoint of each sample for analytical purposes, under the assumption that RFS values represent mean fruit availability during the resulting interval. For example, the RFS value for April, 1999, applied to behavioral data from March 19 through April 18.

We measured monthly frequencies of hunts and of hunting patrols as the number of hunts or patrols per day per month, with months defined as in the phenology sample. We included only days when we observed the chimpanzees for ≥ 6 h, so that we could be reasonably sure we did not miss hunts (cf. Boesch and Boesch, 2000). We then regressed the number of red colobus hunts, the number of hunting patrols, and the number of kills per month on RFS values to examine the relationship between hunting and fruit availability. Data on hunting and phenology is available for 16 months in 1998–1999.

RESULTS

Prey Species and Pursuit Frequencies

The total sample is 131 predation episodes, 85% of which (111/131) were hunts, involving 9 prey species (Table I), including 59 hunts, 43 of which were successful, added during the 11-month 1998–1999 sample (Period 2). Most hunts and kills were of red colobus (Table I). Black-and-white colobus (*Colobus guereza*) were the secondmost frequently targeted primate prey, followed by red-tailed guenons (*Cercopithecus ascanius*), mangabeys (*Lophocebus albigena*), and blue monkeys (*Cercopithecus mitis*; Table I). We saw two red duiker (*Cephalophus monticola*) hunts and 3 meat-eating episodes in Period 2; combined with two earlier meat-eating episodes there have been 7 predation episodes involving red duiker. We saw one unsuccessful hunt of a juvenile bushpig (*Potamochoerus porcus*) in Period 2, to add to an earlier meat-eating episode (Mitani and Watts, 1999). A successful mangabey hunt and the guinea fowl (*Guttera pucherani*) meat-eating episode in Period 2 (Table I) are the first records of predation on these species at Ngogo.

We have probably underestimated the frequency of red-tailed guenon hunts, which are opportunistic and quick. For example, T. Windfelder (pers. comm.) saw a solitary adult male chimpanzee grab a red-tailed guenon that had descended close to the forest floor in response to an attack on its group by a crowned eagle (*Stephanoetus coronatus*). We once found a solitary male chimpanzee eating a juvenile red-tailed guenon that he had presumably just caught from a group foraging nearby. In contrast, all red colobus hunts

were by groups of males (cf. Mitani and Watts, 1999). We may also have undercounted hunts of black-and-white colobus, which also are brief and sometimes are solo hunts.

As at Gombe (Goodall, 1986) and Mahale (Uehara, 1997), duiker hunts are opportunistic. Observed captures were by single individuals, though others quickly joined them to beg for or to steal meat. We became aware of duiker meat-eating episodes by following chimpanzees attracted to capture sites. They were noisy events, but we are less likely to know of captures made by isolated individuals, especially by adult females.

Hunting Success and Kills Per Red Colobus Hunt

Eighty-two percent of red colobus hunts were successful (Table I), including 33 of 39 hunts (85%) in Period 2. This is far more than hunting success at Tai, Mahale, and Gombe (Fig. 1; cf. Mitani and Watts, 1999). Success rates for hunts of black-and-white colobus and of red-tailed guenons, though lower, were still 50% (Table I) and comparable to values for red colobus hunts elsewhere. We have seen too few hunts of other species to

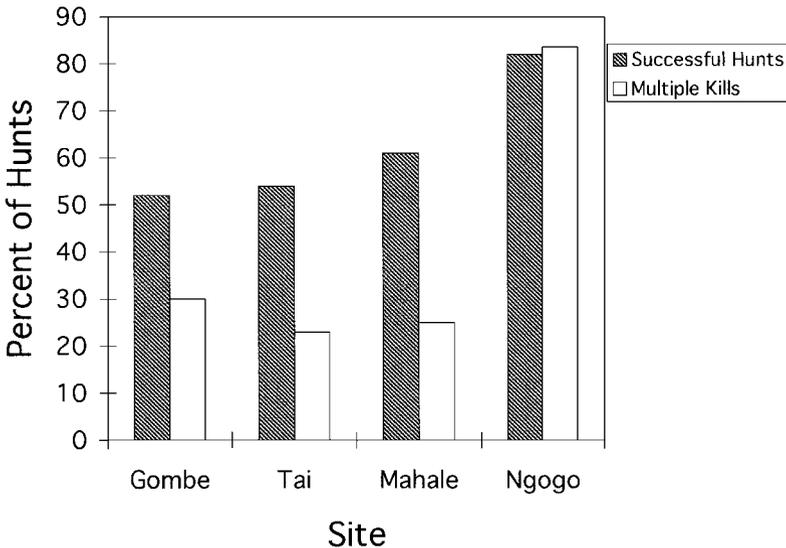


Fig. 1. The percentage of red colobus hunts that were successful at Ngogo and at three other research sites (successful), and the percentage of successful red colobus hunts at which chimpanzees made multiple kills at Ngogo and at three other sites (multiple kills).

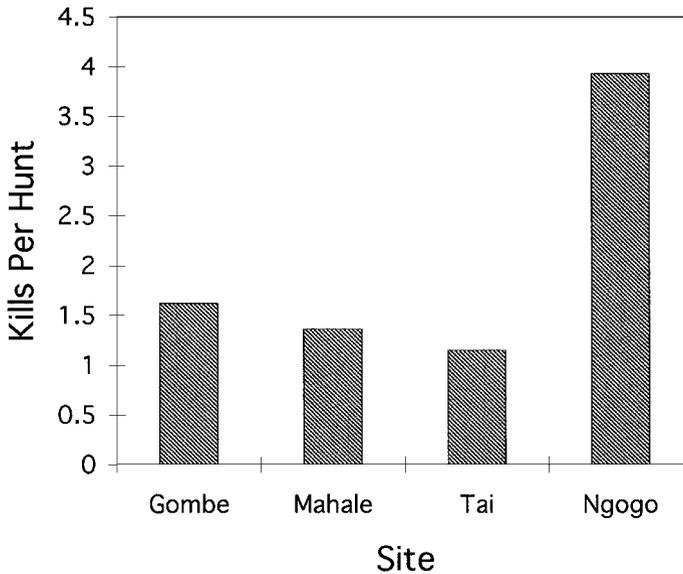


Fig. 2. The mean number of kills per successful red colobus hunt at Ngogo and at three other sites.

estimate success rates. The chimpanzees made multiple kills in $\geq 87\%$ (58/67) of red colobus hunts (Fig. 1), including 90% (30/33) in Period 2. The mean number of kills per hunt in Period 2 is 4.67 (SD = 2.57, range = 1–13), and the overall mean is 3.93 (SD = 2.33, range = 1–13), which also is far higher than at other sites (Fig. 2; cf. Mitani and Watts, 1999).

Hunt Durations

Red colobus hunts had a shorter mean duration in Period 2 than in the earlier sample (13.4 vs. 21.4 min). The overall mean is 17.7 min (SD = 17.1 min, range = 1–91 min; $n = 57$ hunts), with a median of 15 min and a mode at 6–10 min (Fig. 3). Nine completely observed hunts of other monkey species had a mean duration of only 4.5 min (SD = 2.0, range = 1–7 min; Fig. 3). It is significantly shorter than hunts of red colobus (Mann-Whitney test: $z = -3.61$, $n, m = 9, 57$, $p < 0.001$), which reflects the fact that red colobus usually did not flee from hunting chimpanzees, whereas other species did. The chimpanzees often sat under red colobus groups for long periods and repeatedly rushed at them. In 6 hunts, the chimpanzees made successful initial attacks, ate meat for ≥ 20 min, then made ≥ 1 subsequent attacks in

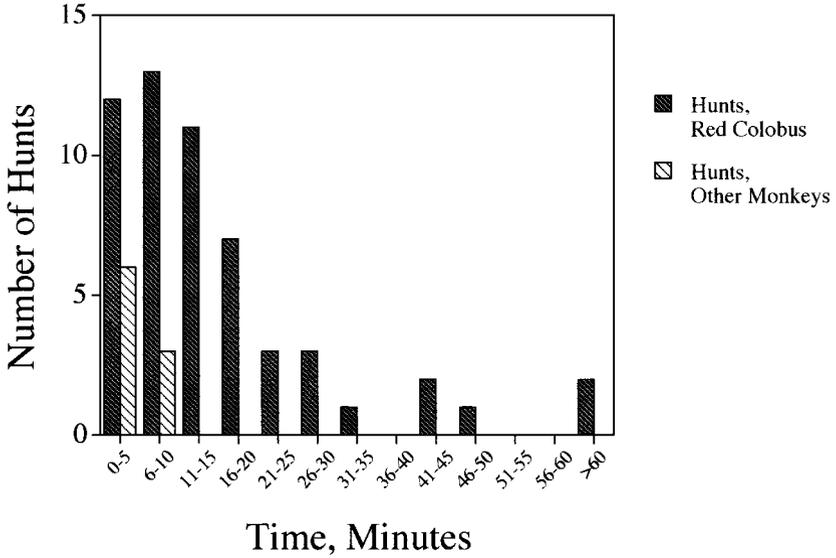


Fig. 3. Frequency distribution of the duration of monkey hunts at Ngogo.

which they killed more monkeys. In no case did the red colobus leave the site after the first attack. In the 3 longest hunts of Period 2 (43, 45, and 63 min), the red colobus were initially isolated in one or two tall trees that the chimpanzees could enter only at a single point, where male red colobus could attack them. After long hesitation, one or two male chimpanzees entered the trees and drove the monkeys toward the crown edges. More males then entered the trees, and the chimpanzees started to catch monkeys either there, in the canopies of neighboring trees into which the monkeys leapt, or on the ground after the monkeys fell. In contrast, the chimpanzees pursued other species only briefly and made kills quickly or not at all.

Hunting Success, Kills Per Hunt, and Hunting Party Size

The likelihood that the chimpanzees would make a kill during red colobus hunts increased with the number of adult males present. We have not seen single males hunt red colobus. Parties with ≤ 5 males hunted red colobus only 3 times and captured prey in only one of them, while all hunts at which ≥ 20 were present were successful (Fig. 4). Both the number of kills per hunt and estimated offtake also increased significantly in association with the number of adult males present (kills: $F(1, 80) = 69.49$, $r^2 = 0.68$, $p < 0.001$; Fig. 5; offtake: $F(1, 65) = 17.23$, $r^2 = 0.21$, $n = 67$ hunts, $p < 0.001$; Fig. 6).

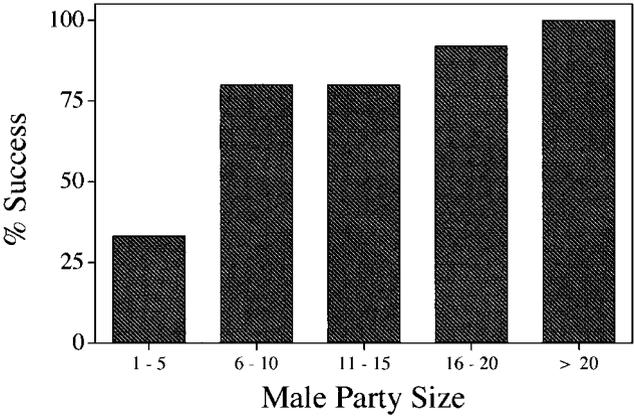


Fig. 4. The percentage of successful red colobus hunts by parties that contained different numbers of adult male chimpanzees.

Males that joined large hunting parties had good chances to obtain some meat: the number of males that obtained meat increased with the number of males present ($F(1, 65) = 36.85, r^2 = 0.36, n = 67$ hunts, $p < 0.001$) and with estimated meat offtake ($F(1, 65) = 77.75, r^2 = 0.55, p < 0.001$; Fig. 7). Also,

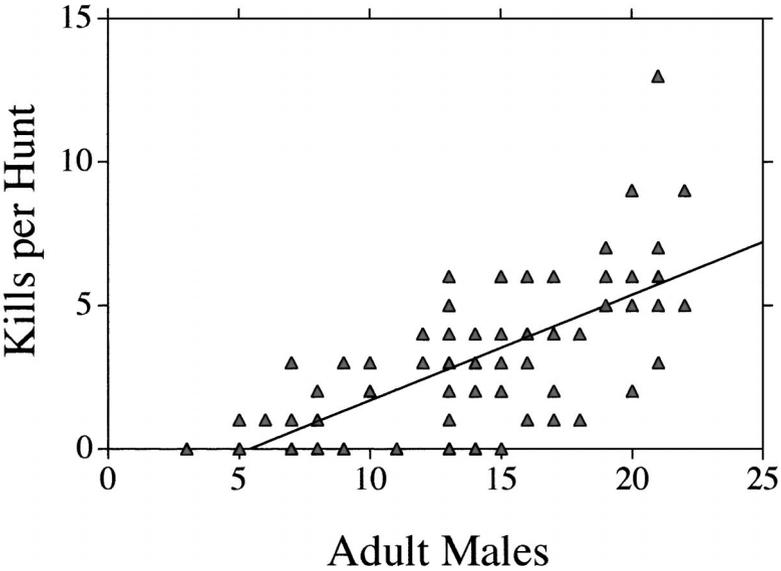


Fig. 5. Relationship between the number of kills per red colobus hunt and the number of adult male chimpanzees in the hunting party.

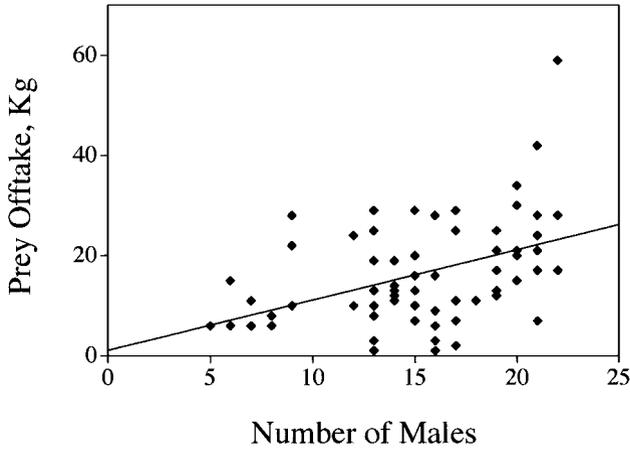


Fig. 6. The relationship between estimated total prey offtake, in kg, and the number of adult male chimpanzees in the hunting party, for red colobus hunts.

the percentage of males that obtained meat is higher in large hunting parties than in smaller ones ($F(1, 65) = 4.52$, $r^2 = 0.05$, $p < 0.05$). However, the relationship between per capita meat availability and the number of males present, though positive, is nonsignificant ($F(1, 65) = 0.50$, $n = 67$ hunts, $p = 0.48$; Fig. 8). Our data do not permit adequate estimates of individual

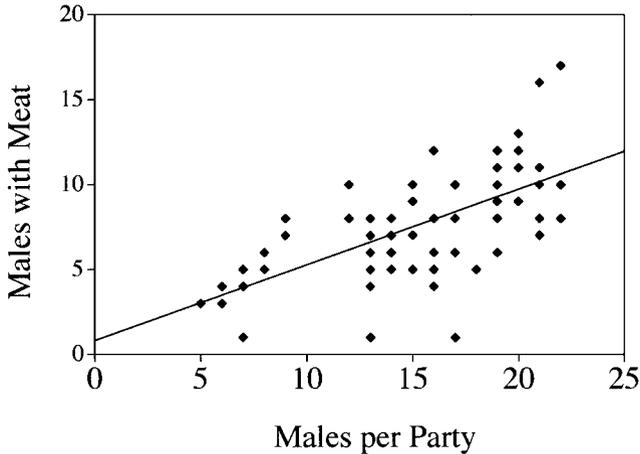


Fig. 7. Relationship between the number of adult male chimpanzees that obtained meat per hunt and the number present in the hunting party.

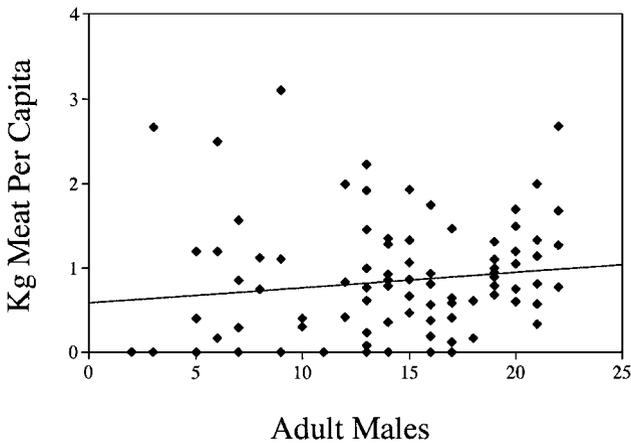


Fig. 8. Estimated mean per capita meat availability per hunt, in kg, in relation to the number of adult males in the hunting party.

energy expenditure and intake during hunts, but this result makes it seem unlikely that, on average, males had higher net energy gains in large hunting parties than in smaller ones. It also suggests that some males in large parties cheated.

Social Cooperation During Red Colobus Hunts

Males often took positions in trees surrounding those where red colobus had taken refuge. This left them well placed to capture monkeys that leaped into them as they fled attacks by other males. It also allowed pursuit from several directions, and sometimes ≥ 2 males simultaneously pursued a single prey. For example, CO chased a subadult red colobus that fled along a large bough during one hunt, then leaped to a smaller branch. While CO lunged at the monkey, PI ran along the bough from the opposite direction and grabbed it. PI and CO then divided the carcass. Chimpanzees on the ground often rushed ahead when red colobus fled through the canopy and climbed to advantageous position along the monkeys' route. They sometimes caused monkeys to fall by hitting them, pulling their tails, or shaking branches to which they were clinging. Other males often sought terrestrial positions that afforded opportunities to capture them, and certain males seemed especially likely to do so. We saw 19 red colobus kills on the ground, including ≥ 16 of 19 adult males in the prey sample. Whether this tactic pays off depends on the behavior of other chimpanzees in the canopy.

Age–Sex Classes of Successful Hunters

Period 2 data reinforce the earlier conclusion (Mitani and Watts, 1999) that hunting is overwhelmingly an adult male activity. Of kills for which we identified the killer, adult males accounted for 90% (235/261) and adolescent males 8% (22/261). Adult females definitely killed two red colobus, and we once saw several that were with their dependent offspring, but not with adult males, eating a freshly killed red colobus. One adolescent female killed a juvenile red colobus. An adult female also killed a blue duiker, though she quickly lost it to adult males. One adult and one adolescent male captured red duikers. Adult males were the first observed possessors and probable captors of other red duiker carcasses, but we could not rule out theft.

Variation in Hunting Success Among Individual Males

The 24 males observed throughout all study periods were present at a mean of 59 hunts of monkeys ($SD = 13.1$, range = 29–78), of which 49 ± 11.3 were red colobus hunts (range = 22–68). On average, each male killed a total of 9.8 monkeys ($SD = 6.7$, range = 1–22), including 9.4 ± 6.5 red colobus (range = 1–22). Individual males killed a mean of 0.18 ± 0.11 red colobus per hunt in which they participated (range = 0.02–0.35; Table II). The wide ranges show that the most successful males had success rates more than an order of magnitude greater than the least successful.

Male dominance rank and age influenced this variation. Presence at red colobus hunts ($F(1, 22) = 4.44$, $r^2 = 0.13$, $p < 0.05$) and hunting success ($F(1, 22) = 14.03$, $r^2 = 0.36$, $p < 0.001$) both increased significantly with rank. The most successful hunter, EL, that made many kills on the ground, occupied ranks 2–4, and some other high-ranking males also had high success ratios (e.g., LO, that became alpha male in 1999; Table II). However, the 4 males, besides EL, that killed >0.30 red colobus per hunt covered a wide range of ranks (Table II). Long-time alpha male MW had only the 15th highest success ratio, though he regularly obtained meat from others and ate meat at 77% of hunts and meat-eating episodes at which he was present, the highest proportion among males. The 3 lowest-ranking adults had the lowest hunting success (Table II). Among them, ST and DZ were the smallest adults, and ST had a deformed hand that impeded arboreal locomotion and might have made pursuing red colobus particularly risky. The third, MZ, was apparently the oldest male in the community and rarely pursued prey, though he was highly successful at begging from others and obtained meat in 55% of hunts he attended. Another noticeably old male, AY, had a low number of kills per hunt, but a third (RU) was one of the most successful hunters (Table II).

Table II. Hunting success of individual adult males

Male	Hunts	Success	RC	Success	% Meat	Availability	
						1	2
MW	66	0.09	54	0.11	77.0	16.0	45.3
LO	59	0.24	48	0.29	60.0	35.3	26.8
BA	80	0.21	67	0.24	58.0	40.3	44.6
EL	63	0.29	52	0.35	67.7	48.6	43.2
CO	55	0.22	44	0.25	42.6	27.1	28.8
HA	66	0.20	55	0.20	55.7	29.8	37.4
BF	68	0.29	58	0.33	48.4	48.6	37.9
HO	72	0.14	60	0.18	38.7	24.3	33.7
PA	76	0.17	61	0.20	32.8	32.6	34.7
RU	58	0.26	49	0.31	60.7	43.1	30.8
MG	75	0.23	61	0.25	44.3	37.5	32.4
PI	57	0.30	50	0.34	42.1	45.8	29.1
DO	73	0.25	61	0.28	67.7	43.1	41.3
TY	48	0.08	38	0.11	24.2	11.0	14.2
AY	67	0.09	54	0.11	49.2	13.2	30.0
MO	78	0.30	70	0.33	39.2	59.6	37.0
OR	56	0.09	46	0.09	18.8	11.0	12.8
MI	43	0.14	36	0.14	14.6	11.0	6.8
BE	71	0.10	56	0.13	11.3	13.8	12.0
BS	31	0.10	24	0.13	40.0	12.5	16.8
GA	46	0.04	39	0.05	13.5	5.5	6.9
MZ	34	0.03	30	0.03	51.4	3.0	18.7
ST	55	0.02	45	0.02	4.0	2.8	4.1
DZ	60	0.05	40	0.04	4.7	5.5	3.0

Note. Males are listed in approximate order of dominance rank during Period 2 (some males were tied, and several rank reversals occurred). Hunts = number of hunts of all species at which a male was present; RC: number of red colobus hunts at which he was present; Success: number of kills per hunt; % Meat: hunts and, for duiker, meat-eating episodes at which a male obtained meat, as a percent of those at which he was present. Availability, 1: estimated annual meat availability in kg, Version 1; Availability, 2: estimated annual meat availability, Version 2 (see text for explanation).

Age–Sex Classes of Red Colobus Prey

The chimpanzees preyed disproportionately on red colobus age–sex classes ($\chi^2 = 208$, $DF = 4$, $p < 0.001$). Adult males are underrepresented, and immatures overrepresented, relative to proportions in the population (Table III). We saw proportionately more infant kills in Period 2 than earlier (Mitani and Watts, 1999). We probably miss some infant kills, because sometimes captors run off with infants to avoid pressure to share meat, and our records might have been more complete for Period 2. However, the chimpanzees killed many infants during several hunts of large groups in Period 2, and the greater representation of infants is probably real. For example, the maximum number of kills in one hunt is 13, of which 8 were infants.

Table III. Age–sex class distribution of red colobus prey

	Adult males	Adult females	Subadults	Juveniles	Infants	Total
Period 2	17 (11.3)	29 (19.2)	24 (15.9)	29 (19.2)	52 (34.3)	151
All	20 (7.8)	48 (18.6)	38 (14.7)	74 (28.7)	78 (30.2)	258
Expected	35	86	16	99	22	

Note. Period 2: data from October, 1998, through August, 1999; All: data from all observation periods. Values in parentheses are percentages of totals. Expected values are based on demographic data in Struhsaker and Leakey (1990).

The increased representation of adult males in the Period 2 sample (11 vs. 2% in earlier data; Mitani and Watts, 1999) is striking. Chimpanzee hunters seemed to confront male red colobus directly and tried to dislodge them from trees more often during Period 2.

Impact on the Red Colobus Population

Our estimate of the red colobus population in the 30 km² study area is 2570, or 2150 for the 25 km² where the chimpanzees spend most of their time. We saw one successful hunt per 6.6 observation days, or 55.2 per year, in Period 2. At 4.67 kills per hunt, this yields 258 kills per year, or 10–12% of the population killed per year. Combined data from all study periods gives an estimated 45.1 successful hunts per year. At 3.93 kills per hunt, this yields 167 kills per year, or 6–8% of the population. Both estimates are higher than the 3% we reported earlier, because the hunting rate and number of kills per hunt were higher during Period 2 than earlier and because the estimated density of red colobus groups was revised downward (Mitani *et al.*, 2000b).

Amount of Meat Eaten by Chimpanzees

Given the age–sex distribution of kills, the weighted mean prey body mass is 4 kg. We estimated the total biomass of red colobus captured by first multiplying this value by 3.93 kills per hunt to give 15.7 kg captured per hunt. Given 55 hunts per year and 82% success, the chimpanzees obtained about 708 kg annually. Similar assumptions give estimates of 11 successful hunts of other monkey species and 7 of red duiker per year, plus occasional kills of blue duiker and bushpig. The total annual biomass of prey may be about 850 kg. Adult males made 90% of red colobus kills; if this was 90% of prey biomass (637 kg), they accounted for 26.6 kg per capita.

We also used two other methods to estimate per capita availability of red colobus meat for males more directly. First, we multiplied each adult male's hunting success rate by the mean prey biomass and by the number of hunts at which he was present per year, then averaged across males (Version 1 in Table II). This gives a mean of 25.5 kg (SD = 17.6 kg) captured per male annually. Males shared some meat and lost some to theft, but most also obtained some meat from others. Variation in hunting frequency and success meant that individual males captured as much as about 60 kg and as little as about 1 kg per year (Table III). Good hunters thus had a substantial annual meat intake, even though they shared some of their meat.

In the second method (Version 2 in Table II), we first noted that means of 15.2 adult males and 12.5 other adults and adolescents were present per hunt, but only 8.7 adult males and 12.1 individuals ate meat, excluding ones that ate only dropped scraps. This gives 1.8 kg per male or 1.3 kg per consumer. With 45 successful hunts per year, mean annual meat available per male is

$$M = \left(\sum_{i=1}^{24} p(H) \cdot S \cdot 45 \cdot 1.8 \text{ kg} \right) / 24 = 26.2 \text{ kg (SD = 13.6 kg)},$$

Where in $p(H)$ = the proportion of hunts at which a male was present, and S = the proportion of hunts at which he obtained meat.

This is quite close to the estimate based on individual hunting success, though estimates diverged for some individuals, e.g., MW and MZ (Table II). The assumption that all meat-eaters got equal portions is unrealistic; males that controlled carcasses would often have obtained more than was available per capita. However, this method takes into account the fact that some males were particularly successful at getting others to share with them, e.g., MW and MZ (Table II).

The estimate of annual prey availability yields only about 6.3 kg of red colobus and perhaps 7.7 kg total per individual in the community, excluding infants, not all of which is edible. Adult males controlled most carcasses and undoubtedly ate more than members of other age-sex classes did. Despite uncertainty in our estimates, we can reasonably conclude that they obtained a mean of 15–20 kg annually and that individuals got anywhere from 2 to 40 kg. Adolescent males generally gained little meat from adults and, except when they made kills, got meat mostly by finding scraps under trees where adults were feeding. Adult females were more successful at begging, but most ate meat less often than most adult males did. On average, about 3 females ate meat per red colobus hunt; if each obtained 1.3 kg of meat (almost certainly an overestimate), then the average female obtained only about 3.7 kg annually. Those we saw most often at red colobus hunts might have obtained closer to 10 kg.

Influence of Forest Structure on Hunting Decisions and Success

The chimpanzees were significantly less likely to hunt red colobus on encounters when they were in primary forest, far from areas with broken canopies, than when they were in or near areas where the canopy was broken and mostly low ($\chi^2 = 42.80$, $DF = 2$, $p < 0.0001$). They hunted in 64% of encounters (27/42) in regenerating or swamp forest and 56% (19/34) of ones near such forest or near grassland, but in only 15% of encounters (13/88) in primary forest. Variation in the number of male chimpanzees present also significantly influenced hunting decisions (Mitani and Watts, in press). However, a multivariate logistic regression shows that canopy structure had effects independently of those of male number (Wald statistic = 21.91, $DF = 2$, $p < 0.0001$).

Correspondingly, hunters were less likely to succeed in primary forest ($\chi^2 = 14.90$, $DF = 1$, $p < 0.001$). Only 55% of hunts (12/22) in primary forest were successful, whereas 92% (55/60) of hunts in or near regenerating forest, swamp forest, grassland, or bush were successful. The chimpanzees had difficulty catching red colobus when the monkeys fled, especially where the canopy was high and continuous. All six unsuccessful hunts in Period 2 occurred in mature forest, and the monkeys fled in 5 of them. The 3 hunts with the highest kill totals ($n = 13$, 9, and 9) started when the red colobus were in narrow strips of tall forest, on shallow slopes, bounded by open swamp forest at the foot of the slope and grassland or low regenerating forest at the top. The chimpanzees isolated the monkeys in several tall trees or, in one case, chased them up and down the slope several times while cutting off escapes to the sides.

Hunting Frequency, Hunting Patrols, and Variation in Fruit Availability

The number of hunts per day increased significantly as the amount of ripe fruit, as measured by RFS, increased ($F(1, 14) = 9.22$, $r^2 = 0.38$, $p < 0.01$; Fig. 9(A)). The number of kills per month also showed a significant positive relationship to RFS values ($F(1, 14) = 7.30$, $r^2 = 0.30$, $p = 0.05$; Fig. 9(B)).

In earlier data (Mitani and Watts, 1999), 41% of 49 hunts occurred during patrols, on which the chimpanzees moved quietly and in single file, sometimes for hours, while deliberately searching the canopy for monkeys. Little or no other foraging occurred during the patrols. Patrols were even more common in Period 2. Most (27/39) red colobus hunts happened during patrols. The chimpanzees hunted black-and-white colobus, and killed 2, during a patrol on which they later hunted red colobus and made 13 kills. On

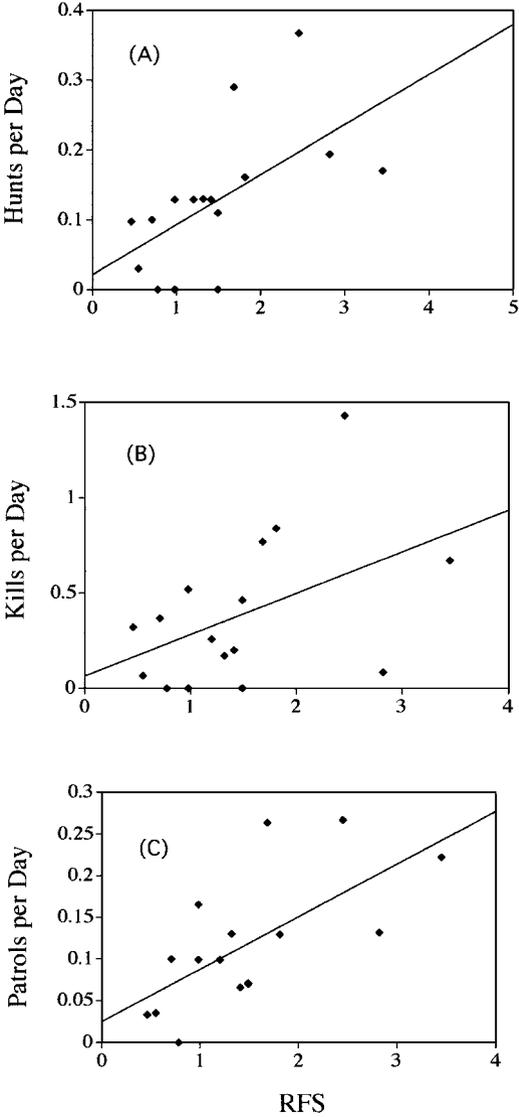


Fig. 9. (A) The number of monkey hunts per day, in relation to ripe fruit availability as estimated by the ripe fruit score (RFS); (B) the number of kills per day in relation to the RFS; (C) the number of hunting patrols per day, in relation to the RFS.

another, they unsuccessfully hunted black-and-white colobus and mangabeys. They also patrolled 5 times without finding monkeys. In all, 46% (50/108) of hunts of monkeys involved patrols. The number of patrols per observation day also increased significantly with the RFS ($F(1, 14) = 11.07$, $r^2 = 0.40$, $p = 0.005$; Fig. 9(C)).

The chimpanzees went on a 57-day binge from October until December, 1998, during which they hunted red colobus 17 times (15 of which were successful), mangabeys twice, and black-and-white colobus twice and killed 69 red colobus, one mangabey, and one red duiker. Fifteen of the hunts occurred during hunting patrols, and they made 3 other patrols without encountering monkeys. This binge coincided with a major fruit crop of *Uvariopsis congensis*, which had fruited earlier in 1998, during which fruiting peak there also was a hunting binge (Mitani and Watts, 1999). Binges in 1995 and 1996 had also coincided with major fruit crops and with periods when the chimpanzees formed large parties on most days (ibid.).

DISCUSSION

General Results

Our results corroborate earlier Ngogo data (Mitani and Watts, 1999). The chimpanzees hunt ≥ 9 vertebrate species, but overwhelmingly focus on red colobus. Hunting frequency at Ngogo is higher than at Kanyawara, also in Kibale (R. Wrangham, pers. comm.), but lower than reported for Gombe (Stanford *et al.*, 1994a,b) and Tai during some periods (Boesch and Boesch (1989, 2000) give a lower value for an earlier period). However, the success rate for red colobus hunts at Ngogo and the proportion of hunts with multiple kills far exceed values from other sites, and the mean number of kills per hunt is more than twice the highest value reported elsewhere. The main reason for these differences is presumably the extraordinarily large number of males and the large size of hunting parties at Ngogo (Watts and Mitani, 1999). Hunts of black-and-white colobus and of red-tailed guenons are much less common, but success rates are comparable to those for red colobus hunts at Tai (Boesch and Boesch, 1989), Gombe (Stanford *et al.*, 1994a,b), and Mahale (Uehara, 1997; Hosaka *et al.*, in press).

Cooperative Hunting

The probability that the chimpanzees captured prey during red colobus hunts, the number of kills, the amount of meat obtained, and the number of males that got meat all increased with the number of males present.

Hunting party size and the probability of success were also positively related at Gombe (Packer and Ruttan, 1986; Stanford, 1996, 1998), and success increased with the number of active hunters at Tai (Boesch and Boesch, 2000; Stanford, 1996). Large hunting parties at Gombe were also more likely to make multiple kills (Stanford *et al.*, 1994a), and the amount of meat obtained increased with hunting party size (Stanford, 1996). Mahale data have not been analyzed in the same way, but successful hunting parties there a significantly larger than unsuccessful ones (Hosaka *et al.*, 1995).

Nevertheless, individuals did not necessarily gain by hunting red colobus in large groups. The absence of solitary hunts suggests that hunting in groups is a better tactic, though it prevents us from making direct comparisons. However, per capita meat availability was independent of the number of males per party and of the number that obtained meat, as Stanford (1996) found at Gombe. We cannot rule out the possibility that net energy capture is positively related to the number of hunters without more detailed data on the behavior of individuals during hunts. Still, if the number of males present at hunts is a valid estimate of the number of hunters—and we reiterate that no clear distinction between bystanders and hunters exists at most hunts—Ngogo data concur with those from Gombe (Boesch, 1994b), which show that hunting in groups does not invariably pay for individuals. Males may be more inclined to cheat when in large hunting parties than when in small ones (cf. Packer and Ruttan, 1988).

However, per capita meat availability is independent of the number of males per party and of the number that obtained meat. Data on the number of captures and on meat offtake only measure gains from hunting, and we need better data on costs and on the activities of individuals during hunts to assess the relationship of net payoffs to hunting group size (Boesch, 1994b; Creel and Creel, 1995). Even so, if the number of males present is a valid estimator of hunting group size, Ngogo data are initially consistent with others (Boesch, 1994b) showing that hunting in groups does not invariably pay for individual chimpanzees.

Males may be more inclined to cheat when in large hunting parties than in small ones (cf. Packer and Ruttan, 1988); we plan to focus on this issue in the future. Certainly some cheating occurs, as witnessed by the high frequency with which MZ obtained meat. In this case and others, social factors might have influenced success at obtaining meat independently of participation in hunts. For example, rank influenced how successful males that had not made captures were at getting meat, and long-time alpha male MW, which could easily steal meat and often begged successfully, had the best access to meat despite its low hunting success (Table II). However, begging for meat was not necessarily cheating. Males often pursued prey and begged in the same hunt, and abandoned their own efforts to catch

monkeys to try to get meat from others that had caught some. The surviving monkeys did not always take the resulting opportunity to escape. Hunts in which the chimpanzees made 7, 9, or even 13 kills involved multiple attacks, and males that did not succeed in gaining much meat from others after the first attack were likely to initiate the second.

As the example of CO and PI shows, males sometimes showed coordination (Boesch and Boesch, 1989), i.e., concentrated similar actions on the same prey and related their actions in space and time. Cases in which males drove red colobus into trees where other chimpanzees were waiting looked like collaboration (hunters direct complementary actions at the same prey; Boesch and Boesch, 1989). The large number of captures of monkeys that fell or were knocked to the ground also raise the issue of collaboration, especially given that certain males seemed likely to be either on the ground or engaged in arboreal pursuits. However, distinguishing consistent role-taking and other forms of collaboration from the simultaneous pursuit of individual tactics by multiple males (Goodall, 1986) is difficult and requires more detailed data on individual behavior than we have.

Individual Variation in Hunting Behavior

New data corroborate the earlier finding that male hunting success varied considerably (Mitani and Watts, 1999), as at other sites (Gombe: Goodall, 1986; Stanford, 1996; Tai: Boesch and Boesch, 2000). Some males, e.g., MG and BF, seemed especially motivated to pursue monkeys (Table II). Variation in motivation and success must depend partly on variation in characteristics like age and body size. The significant relationship between dominance rank and hunting success may have arisen because both covaried with features like size, agility, willingness to take risks and skill at assessing when to do so, and ability to coordinate the effects of one's own behavior with those of the behavior of others de Waal (1982) and Nishida (1983) have noted similar characteristics of successful alpha males. But some highly motivated and skilled males were not high-ranking; a few, e.g., MO and DO (Table II), probably had not been so previously, nor will they become so.

Males were not equally able to gain meat from others. For example, long-time alpha male MW, which could easily steal meat and often begged successfully, had the best access to meat despite his low hunting success.

Meat Intake and Impact on the Red Colobus Population

Our estimates of annual per capita meat intake by males are lower than those from Gombe (Stanford, 1996; Stanford *et al.*, 1994a; Wrangham and

Bergmann-Riss, 1990), but the difference is small despite the much higher frequency of hunting at Gombe. This reflects the large size of hunting parties at Ngogo, their high success rates, and the large number of monkeys they kill per successful hunt, and it shows the important influence that demographic variation can have on chimpanzee hunting behavior (Mitani and Watts, 1999). Also, Stanford and colleagues (Stanford, 1996; Stanford *et al.*, 1994a) used higher prey body mass values, notably 9 kg for adult females and subadults (which seems high for Kibale; Struhsaker, 1975). However, estimated average meat intake by males at Taï was much higher, over a 4-year period, than estimated intake at Ngogo (Boesch and Boesch, 2000). Proportionately more captures at Taï were of adults, especially adult males, which accounts for some of this difference. More importantly, hunts were almost 5 times more frequent at Taï during this period than at Ngogo (Boesch and Boesch, 2000). The population density of red colobus is higher at Taï (Holenweg *et al.*, 1996; Mitani *et al.*, 2000b), and chimpanzees encounter red colobus far more often there than at Ngogo (Boesch, 1994a; Boesch and Boesch, 2000; Watts and Mitani, unpublished data).

The estimate of 6.5–12% of the red colobus population killed annually is much lower than values of 16–40% reported for Gombe (Stanford, 1996, 1998; Wrangham and Bergmann-Riss, 1990). However, it is higher than estimates of 3.2–7.6% for Taï (Boesch and Boesch, 2000) and 3% at Mahale, the estimated annual potential growth rate of the red colobus population there (Ihobe and Uehara, 1999). Comparison of Ngogo census results from different time periods show a long-term decline in the density of red colobus groups in the study area, possibly because of predation by chimpanzees (Mitani *et al.*, 2000). Population density should also have declined, unless average group size has increased considerably; future research on red colobus will address this issue.

Forest Structure and Hunting

Many observers at Gombe, starting with Wrangham (1975) and Teleki (1975), have proposed that chimpanzees preferentially hunt red colobus in areas with a broken canopy (Boesch, 1994b; Stanford, 1998; Stanford *et al.*, 1994b). Boesch (1994b) noted that the forest at Gombe is lower and more open, with a more broken canopy, than at Taï and argued that capturing red colobus is consequently more difficult at Taï unless the chimpanzees cooperate. Ours are the first quantitative data to show that variation in forest structure influences hunting decisions and to corroborate the impression that capturing red colobus is more difficult in tall forest with a continuous canopy, independently of other factors.

The large disparity in hunting success between areas where the canopy is broken and those where it is not introduces a nuance into our earlier argument about the impact of demographic variation on variation in hunting success. On the one hand, the percentages of hunts in primary forest in which the chimpanzees captured prey were about equal for Taï (Boesch and Boesch, 1989, 2000) and Ngogo, despite the far larger number of males at Ngogo. This highlights the importance of cooperation (in the sense of coordination of activities among individuals; Boesch and Boesch, 1989) at Taï. On the other, larger mean hunting party size at Ngogo meant that the mean number of captures per successful hunt was almost 3 times that at Taï. This fact, plus the strong positive relationships between hunting party size and the number of kills per hunt at Ngogo, highlights the impact of variation in the number of males per community on overall hunting success.

Hunting Seasonality

Ngogo data are also the first to establish a quantitative relationship between fruit availability and variation in hunting frequency and in the intensity of predation on red colobus. Hunting frequency should vary inversely with fruit abundance if meat is an alternative source of energy during fruit-poor months. Conversely, if hunting is energetically expensive, but most important for other nutritional reasons or for social reasons, it should be more common when fruit is abundant. Wrangham and Bergmann-Riss (1990) found no significant temporal variation in hunting frequency at Gombe between 1972 and 1975. Subsequent Gombe data (Stanford, 1996, 1998; Stanford *et al.*, 1994a,b) and data from other sites where researchers have stated that hunting frequency or predation pressure or both vary seasonally (Taï: Boesch and Boesch, 1989; Mahale: Takahata *et al.*, 1984; Hosaka, 1995; Uehara, 1997) have not been accompanied by contemporaneous data on variation in fruit availability. For example, in discussing Gombe data from 1982 through 1991, Stanford and colleagues (Stanford, 1996, 1998; Stanford *et al.*, 1994a,b) argued that fruit was scarce during dry seasons, as was the case in 1972 and 1973 (Wrangham, 1977). Dry seasons are predictably fruit-poor at Lopé, Gabon (Tutin *et al.*, 1991) and offer less fruit than rainy seasons at Ndoki (Kuroda *et al.*, 1996), which may be true at Gombe. However, fruit production in Kibale varies unpredictably at Kanyawara (Wrangham *et al.*, 1996) and independently of rainfall at Ngogo (Mitani and Watts, in press); thus rainfall is not a universal proxy for fruit availability. Even at Lopé, fruit production is not significantly related to rainfall, and production varies greatly from year to year (Tutin *et al.*, 1991). Kibale data also show that some tree species fruit asynchronously in different parts of the forest and that

different chimpanzee communities in the same population can experience quite different patterns of variation in food availability (Chapman *et al.*, 1997). We need similar quantitative data from other sites to determine if hunting frequency and fruit availability are consistently related.

We do not know whether red colobus groups become more vulnerable to attack during periods of peak fruit availability at Ngogo, e.g., because they are predictably attracted to certain areas to feed or spend more time in areas with broken canopy. Future research on red colobus behavior and ecology should answer this question. Two lines of evidence suggest that the chimpanzees do not hunt more frequently at these times simply because the monkeys are more conspicuous. First, the increased frequency of hunting patrols accounts for much of the increase in hunts. Second, the percent of encounters that result in hunts also increases significantly with increases in the availability of ripe fruit (Mitani and Watts, in press).

Rather than showing significant variation in hunting frequency, Gombe data from 1982 to 1991 actually show that the mean number of red colobus kills per month and per hunt and the proportion of encounters in which the chimpanzees hunted were higher during the dry season (Stanford *et al.*, 1994a). Also, parties were larger, on average, during dry season months, and hunting success increased with party size. Thus the chimpanzees did not hunt more often during the dry season (except for a binge in 1990, when 47 hunts occurred within 68 days), but hunted more successfully and killed more monkeys then. As Stanford (1996, 1998) notes, party size data were inconsistent with the idea that meat is a fallback energy source when fruit is scarce (Stanford *et al.*, 1994a), given that party size varied inversely with fruit availability in Wrangham's (1977) Gombe sample, which is also the case in Kibale (Wrangham *et al.*, 1996; Chapman *et al.*, 1997; Mitani *et al.*, in press).

As Stanford *et al.* (1994b; Stanford, 1996, 1998) stressed, multiple factors explain why chimpanzees hunt and why they decide to hunt at some encounters with red colobus, but not others (cf. Mitani and Watts, in press). These almost certainly include nutritional factors, given the nutritional value of meat, but energy may not be prominent among them. Hunting is energetically expensive (Boesch, 1994b). Energy gains hunts can outweigh costs (Boesch, 1994b), but this may often not be the case, at least for many participants. Hunting may be nutritionally important because meat, marrow, and bones provide nutrients other than energy (Stanford, 1996, 1998; Stanford *et al.*, 1994a; Takahata *et al.*, 1984). Suitable alternative sources of such nutrients may be sufficiently common, though. For example, leaves are a major source of protein (Wrangham *et al.*, 1991), and oil palm fruit, which are high in energy and lipids, are abundant during the dry season at Gombe (Stanford, 1996). Hunting patrols, during which the chimpanzees may walk

for hours without feeding, add to the energetic cost of many hunts at Ngogo. Hunting there seems to be most likely when the chimpanzees can easily meet their daily energy needs because they have large fruit crops available. Hunting patrols were most common at such times and typically started in the afternoon, after the chimpanzees had eaten meals of fruit. Except for any individuals still eating meat at dusk, they also had large fruit meals again after patrols and hunts. They may hunt on encounter at any time, particularly if they are in large parties (Mitani and Watts, in press.). But hunting and hunting patrols are more likely when no risk of energy shortfalls exists. We suspect that this is true for some other habitats, but only data on diet and phenology can properly address the question.

ACKNOWLEDGMENTS

We thank The Uganda Wildlife Authority, Makerere University, and Drs. John Kasenene and Gilbert Isibiryé-Basuta for permission to work at the Makerere University Biological Field Station. We thank Dr. Jeremiah Lwanga for his expert management of field assistants at Ngogo and his many contributions to research there. We are indebted to Godfrey Mbabazi, Adolph Magoba, Lawrence Ndagezi, and Alfred Tumusiime for invaluable assistance in the field and, in particular, for helping us to keep track of what happens during hunts. C. Boesch provided valuable discussion of some of the material presented here. J. Mitani was supported by NSF Presidential Faculty Fellowship Award SBR-9253590 and by the L.S.B. Leakey Foundation, and D. Watts was supported by the L.S.B. Leakey Foundation, Primate Conservation, Inc., and Yale University. C. Boesch and one anonymous reviewer provided constructive criticism of an earlier version of this paper, and we also thank C. Boesch for stimulating discussions of some of our results and their comparative implications.

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