Demographic Influences on the Hunting Behavior of Chimpanzees

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ABSTRACT   We investigated hunting in an unusually large community of wild chimpanzees at Ngogo in the Kibale National Park, Uganda. Aspects of predation were recorded with respect to the prey, the predators, and hunting episodes. During 23 months of observation, the Ngogo chimpanzees caught 128 prey items from four primate and three ungulate species. Chimpanzees preyed selectively on immature red colobus primarily during group hunts, with adult males making the majority of kills. Party size and composition were significant predictors of the probability that chimpanzees would hunt and of their success during attempts. Chimpanzees were more likely to hunt red colobus if party size and the number of male hunters were large; party size and the number of male hunters were also significantly larger in successful compared with unsuccessful hunts. The Ngogo chimpanzees did not appear to hunt cooperatively, but reciprocal meat-sharing typically took place after kills. Hunts occurred throughout the year, though there was some seasonality as displayed by periodic hunting binges. The extremely high success rate and large number of kills made per successful hunt are the two most striking aspects of predation by the Ngogo chimpanzees. We compare currently available observations of chimpanzee hunting behavior across study sites and conclude that the large size of the Ngogo community contributes to their extraordinary hunting success. Demographic differences between groups are likely to contribute to other patterns of interpopulation variation in chimpanzee predation. Am J Phys Anthropol 109:439–454, 1999.   © 1999 Wiley-Liss, Inc.

Hunting and meat-eating have long been held as two hallmarks of the Hominidae, with hunting in particular figuring significantly in reconstructions of early hominid behavior (Dart, 1953; Washburn and Lancaster, 1968; Tiger and Fox, 1971; Isaac, 1978; Hill, 1982; Tooby and DeVore, 1987; Stanford, 1996). Placed within the context of human evolution, observations of hunting and carnivory in our closest living relatives, the chimpanzee, take on considerable interest. Goodall (1963) was the first to document wild chimpanzees hunting and eating meat during her pioneering field work in the Gombe National Park, Tanzania. Since the initial observations of Goodall (1963), chimpanzees have been the subjects of numerous field studies, and wherever studied in any detail, they have been recorded to hunt and engage in carnivorous behavior (Uehara, 1997).

Despite the ubiquity of chimpanzee carnivory, hunting patterns vary considerably

among populations. For example, differences appear to exist in prey choice and in hunting frequency, tactics, duration, and success (Uehara, 1997). Boesch and Boesch (1989) proposed that forest-dwelling chimpanzees in Tai National Park, Ivory Coast, hunt more often and choose prey more selectively than chimpanzees living in the more open and wooded environments of Gombe and the Mahale Mountains (Nishida, 1990). Further observations suggest that the Tai chimpanzees hunt more in groups, more cooperatively, and with greater success than those at Gombe and Mahale (Boesch and Boesch, 1989; Boesch, 1994a–c). Ecological differences may account for several of these variations in chimpanzee hunting behavior. Special attention has been drawn to the more spatially complex and heterogeneous food supply in forests compared with woodlands and to the possibility that tall trees found in forests make capturing arboreal prey difficult for chimpanzees (Boesch and Boesch, 1989; Boesch, 1994a,c). Contrasts between forest and woodland ecology are hypothesized to affect the degree of cooperation in group hunts, which in turn leads to other differences in chimpanzee predatory behavior (Boesch and Boesch, 1989; Boesch, 1994a,c).

While previous studies focused on potential ecological causes of variation in chimpanzee hunting behavior, other factors have recently been implicated as key determinants. Stanford et al. (1994a) emphasized demography and group structure in attempting to explain changes in chimpanzee predation at Gombe. Male chimpanzees are the primary hunters in all populations studied to date (Uehara, 1997), and a doubling of the number of male hunters over time at Gombe may have led to an increase in observed hunting frequency at that site. Furthermore, hunting success is positively correlated with chimpanzee party size, and seasonal patterns of variation in party size influence hunting frequency and success (Boesch and Boesch, 1989; Stanford et al., 1994a; Stanford, 1998a).

Ngogo in Kibale National Park, Uganda, was the site of one of the first studies of unprovisioned chimpanzees in a forest habitat over 20 years ago (Ghiglieri, 1984). Recent observations of the Ngogo chimpanzee community indicate that it is unusually large, with over 100 individuals and 20 adult males (Watts, 1998; Mitani et al., 1999; Pepper et al., 1999). The unique structure of the Ngogo chimpanzee community makes it particularly suitable to assess demographic effects on hunting behavior, and here we report observations of the predatory behavior of these animals for the first time. Our observations and comparisons with results from previous studies confirm that demographic factors exert an important influence on chimpanzee hunting behavior and highlight several unresolved problems in our current understanding.

METHODS

We observed chimpanzees at Ngogo in the Kibale National Park, Uganda. Ngogo has been the site of behavioral research on primates since 1974 (Struhsaker, 1997), including studies of chimpanzees by M. Ghiglieri (1976–1981; Ghiglieri, 1984), R. Wrangham et al. (1988–1995; Wrangham et al., 1992), B. Grieser-Johns and field assistants (1992–1993), and D. Watts (June–August 1993). The Ngogo chimpanzee community is the largest ever described in the wild. As of June 1998, we identified 117 individuals, including 26 adult males, 40 adult females, 16 adolescent males, 5 adolescent females, and 30 infants and juveniles. Three adult males (Ar, Bl, and Jr), identified in 1995, disappeared during the course of study and are excluded from some of the analyses presented below.

The Ngogo study area comprises moist evergreen rain forest interspersed between blocks of *Pennisetum purpureum* grassland and secondary forest regenerating from past agriculture (Struhsaker, 1997). A grid of trails of more than 130 km covers approximately 12 km^2 at Ngogo. Chimpanzees travel across the entire trail grid and move off in each direction to range over an area of about 25 km^2. Ngogo is home to seven other species of diurnal anthropoid primates, all of whom are known to be preyed upon by chimpanzees (Uehara, 1997). One species, L'Hoest's monkey (*Cercopithecus l'hoesti*), is seen rarely at Ngogo and is not included in this study. Population densities of the six

TABLE 1. Common anthropoid primate species at Ngogo, Kibale National Park

Species	Density (groups/km^2)
Baboon (*Papio anubis*)	0.63
Black and white colobus (*Colobus guereza*)	0.55
Blue monkey (*Cercopithecus mitis*)	0.08
Mangabey (*Lophocebus albigena*)	2.76
Red colobus (*Procolobus badius*)	2.92
Redtail monkey (*Cercopithecus ascanius*)	6.23

commonest primate prey species were calculated based on 36 censuses conducted over 18 months between January 1997–June 1998 and range from 0.08–6.23 groups/km^2 (Mitani, Struhsaker, and Lwanga, unpublished data; Table 1). Censuses were conducted twice each month over a 4.4-km route that passed through the middle of the Ngogo chimpanzee's home range. We employed line transect census methods to obtain density estimates following standard protocols (National Research Council, 1981).

Chimpanzees were observed during four periods between June–December 1995, June–December 1996, June–August 1997, and January–June 1998. One author (D.P.W.) conducted field observations between June–August 1996 and the 1995 and 1997 study periods. The other author (J.C.M.) observed chimpanzees between June–August 1995 and the 1996, 1997, and 1998 field seasons. Chimpanzees at Ngogo were not provisioned in this or previous studies, and at the beginning of our observations in 1995, they were only semihabituated to human presence. Animals initially tolerated human observers while feeding arboreally in large parties, but they fled quickly when alone or in small parties. During all four study periods, we made near-daily contact with chimpanzees, and as a result, they habituated rapidly to our presence. By the end of our last observation period in 1998, we could approach all of the males to within a few meters on the ground.

We made observations of chimpanzee predation opportunistically during the course of our studies on other aspects of their behavior (Watts, 1998; Mitani et al., 1999; Pepper et al., 1999). During the initial 4 months of this study, it was not possible to follow individuals reliably, and as a result, a record

of a single hunt was obtained while following chimpanzees collectively in a group. All subsequent observations of chimpanzee hunting behavior were derived while following individual subjects, whether alone or in groups. We obtained three types of data regarding predation, and we refer to these collectively as "hunting episodes" (cf. Uehara et al., 1992). Most of our records were made of complete hunts (36/49 = 73%). Here we observed chimpanzees who encountered prey, pursued them, and subsequently made captures. We initiated approximately one fifth of all observations shortly after a suspected hunt and while chimpanzees were already in the process of eating meat (9/49 = 18%). A few times we observed animals carrying carcasses of kills made previously (4/49 = 8%). Hunting success was scored only in those situations where hunts were observed in their entirety and in which chimpanzees made kills (n = 36). We excluded meat-eating and carcass-carrying episodes from these calculations, since chimpanzees are known to scavenge occasionally (e.g., Uehara et al., 1992). We scored failed hunting attempts (n = 13) whenever chimpanzees were observed to climb into trees with monkeys, pursue them actively in a manner similar to that witnessed during successful predatory episodes, and fail to capture a prey item.

Aspects of chimpanzee predation were recorded with respect to the prey, the predators, and hunting episodes. During each successful hunt we noted the prey species and the numbers and identities of prey items. For successful and unsuccessful hunts, we recorded the locations, chimpanzee party sizes, the numbers and identities of adult male and estrous female chimpanzees, and the identities of individuals who captured, acquired, and consumed prey items. Estrous females were identified operationally by their sexual receptivity and the fact that they mated with males. These females were typically at maximal or near-maximal tumescence (cf. Stanford et al., 1994b). We scored captures by individuals whenever we observed animals seizing prey or making kills. In some cases we relied on indirect but strongly circumstantial evidence to record captures. These instances involved chimpan-

zees who were witnessed with fresh carcasses moments after fights, struggles, or chases with prey. Meat acquisition and consumption were scored when we observed individuals carrying or eating prey items, respectively. To evaluate the effects of party size and the numbers of males and estrous females on the outcome of hunting, we considered all chimpanzees present as potential hunters (sensu Stanford, 1998a). The large number of participants and the wide area over which hunting activities took place made it impossible to monitor all individuals and differentiate those who actively pursued prey from those who acted merely as "bystanders" (sensu Boesch and Boesch, 1989).

We also collected party size and composition data at other times when we observed chimpanzees during the course of fieldwork (n = 789 parties), and in 1998, during a small number of encounters with red colobus in which chimpanzees did not pursue prey (n = 12). In the former case, we defined parties as all individuals present when we first contacted chimpanzees (cf. Tutin et al., 1983). We tallied the total number of hunting episodes observed and divided this by the number of days we followed chimpanzees in the field to estimate hunting frequency. For each successful hunt, we counted the minimum number of prey items killed and recorded the identities of chimpanzees who shared or stole meat. Sharing was recorded whenever two animals exchanged meat in an apparent voluntary fashion. Sharing involved both the active or passive transfer of meat (sensu Boesch and Boesch, 1989). Theft was scored if one animal used aggression or force to seize meat from another individual. We measured the duration of successful predatory episodes from the time chimpanzees initiated a hunt to the time of first capture (cf. Busse, 1977; Boesch and Boesch, 1989; Uehara et al., 1992). Additional aspects of the behavior of monkey prey, such as mobbing, were recorded ad libitum.

Analyses

We examined variations in party size, male group size, and the number of estrous females per party to investigate the effects of party size and composition on hunting outcomes. We analyzed the effect of male rank on interindividual variation in meat acquisition by conducting Spearman rank correlations between rank and the number of times males either killed prey, received meat from others, or stole meat. Assignments of male rank were based on previous observations made in 1995 and 1996 (Watts, 1998). We computed monthly averages of observed party sizes, male group size, and the number of estrous females per party and conducted Spearman rank correlation tests to investigate the effects of each of these three variables on monthly hunting frequency. We employed parametric analyses of variance (ANOVAs) or Student's t-tests to examine differences between observations measured on interval scales. Analyses involving estrous females did not satisfy the assumptions of parametric ANOVAs, and in these cases, we report results of equivalent Mann-Whitney U nonparametric tests. We used chi-square tests for comparisons involving categorical data and implemented the K_r test of Hemelrijk (1990) to examine reciprocity of meat-sharing between male chimpanzees. The K_r test is a variant of the test of Mantel (1967) for matrix correlation and controls for interindividual variation in behavior.

We used the number of kills per km² per year and red colobus population density to estimate red colobus offtake through chimpanzee predation. The number of successful hunting episodes per month of observation, the mean number of kills per successful hunt, and the approximate home range size of the Ngogo chimpanzees provided a means to estimate the number of kills made per km² per year. We estimated the population density of red colobus at Ngogo by multiplying mean group size and group density. Information on red colobus group size was provided from long-term observations of six social groups living in unlogged forest throughout the Kibale National Park (Struhsaker, personal communication), while current group densities were estimated using our own census data (Mitani, Struhsaker, and Lwanga, unpublished data; Table 1). We divided our figure of the number of red

TABLE 2. Mammalian prey species eaten by chimpanzees at Ngogo, 1995–1998[1]

Prey species	No. of observed prey items (% of total)	No. of expected primate prey
Primates		
Cercopithecus ascanius	2 (2%)	59
Cercopithecus mitis	1 (1%)	1
Colobus guereza	4 (3%)	5
Lophocebus albigena	0 (0%)	26
Papio anubis	0 (0%)	6
Procolobus badius	117 (91%)	28
Ungulates		
Cephalophus monticola	2 (2%)	
Cephalophus callipygus	1 (1%)	
Potamochoerus porcus	1 (1%)	
Total	128	

[1] Numbers of expected primate prey items are calculated on the basis of their proportional representations in the forest derived from 36 censuses conducted over 18 months (see Table 1).

TABLE 3. Age-sex classes of red colobus prey items[1]

Age-sex class	Observed kills	Expected kills
Adult male	2	13
Adult female	18	32
Subadult	11	6
Juvenile	45	37
Infant	20	8
Total	96	

[1] Numbers of expected prey items are calculated on the basis of each age-sex class's proportional representation in the forest (Struhsaker and Leakey, 1990).

colobus kills by red colobus population density to derive an estimate of chimpanzee predation rate.

All statistical tests are two-tailed with the criterion of significance set at 0.05. Some of the following analyses involve multiple comparisons. To correct for the increased probability of committing type I errors when making these comparisons, we adjusted our criteria of significance downward, using the sequential Bonferroni technique (Holm 1979). For k multiple tests, our adjusted alpha levels, α', were set at:

$$\alpha'_i = \alpha/(1 + k - i)$$

where $\alpha = 0.05 = $ the overall experiment-wise error rate, and i = the i'th sequential test, from smallest to largest.

RESULTS

The prey

Prey species. Table 2 provides a list of mammalian species preyed upon by the Ngogo chimpanzees. During 23 months of observation, 128 prey items were caught in 49 successful hunting episodes. Four species of primates were eaten along with three species of ungulates (Table 2). Red colobus monkeys were the most common prey item, constituting over 90% of all kills. The high rate of predation on red colobus produced a clear pattern of nonrandom selection of primate prey, with the observed numbers of prey differing significantly from those ex-

pected on the basis of chance ($\chi^2 = 370$, 5 df, $P < 0.001$; Table 2).

Age-sex classes of red colobus prey. The Ngogo chimpanzees preyed on young animals selectively. Among red colobus prey, immature animals were killed more often than expected on the basis of their proportional representations in the forest ($\chi^2 = 26.14$, 1 df, $P < 0.001$; Table 3).

Behavior of red colobus during hunts. Red colobus prey were typically quiet prior to an encounter with chimpanzees. Following detection, red colobus frequently moved higher into the treetops and gave alarm calls repeatedly. Adult male red colobus monkeys mobbed and chased chimpanzees during some hunts and occasionally engaged in arm-to-arm fights with them. Defensive behavior was generally shown only after chimpanzee predators began to pursue red colobus prey, although a few times, adult male monkeys launched unprovoked attacks on chimpanzees before they initiated a hunt. Chimpanzee hunting success is extremely high (see below), and red colobus were largely ineffective in deterring predation through mobbing.

Red colobus at Ngogo are often found with other monkeys in mixed-species associations (Struhsaker, 1981), but it is doubtful that they gain any advantage in reducing chimpanzee predation through such associations (cf. Noe and Bshary, 1997). Chimpanzees pursue rather than stalk their prey and show a clear preference for red colobus. As noted above, mobbing is largely ineffective. Accordingly, it is not clear whether red colobus gain any of the commonly invoked benefits of reducing predation through mixed-species associations, such as increased detection, dilution, or deterrence (Cords, 1987).

TABLE 4. *Effects of chimpanzee party size and composition on hunting*[1]

	Party size	No. of adult males	No. of estrous females
Hunting parties	24.1 ± 9.1 (49)	13.3 ± 5.1 (49)	0.8 ± 0.8 (49)
Nonhunting parties	7.8 ± 8.6 (789)*	4.0 ± 4.7 (789)*	0.3 ± 0.6 (789)*
Hunts	25.0 ± 7.5 (21)	13.6 ± 4.4 (21)	0.9 ± 0.9 (21)
Encounters	17.0 ± 10.5 (12)*	9.9 ± 5.1 (12)*	0.4 ± 0.7 (12)
Successful hunts	26.3 ± 7.9 (36)	14.3 ± 4.6 (36)	
Unsuccessful hunts	18.2 ± 10.1 (13)*	10.6 ± 10.1 (13)*	

[1] Means ± one SD are shown with samples sizes in parentheses. Observations of hunts and encounters were collected at Ngogo during 1998.
* $P <$ sequential Bonferroni criterion for comparisons between hunting and nonhunting parties, hunts and encounters, and successful and unsuccessful hunts.

The predators

Hunting parties. Chimpanzees at Ngogo hunted monkeys exclusively in groups. We did not observe solitary chimpanzees hunting monkeys, although circumstantial evidence suggests that single individuals at Ngogo hunt ungulates opportunistically, as reported for chimpanzees at Gombe and Mahale (Nishida et al., 1979; Takahata et al., 1984; Goodall, 1986; Uehara et al., 1992). Hunting parties were significantly larger than those that formed during other times ($\alpha' = 0.02$, $F_{1,837} = 166$, $P < 0.001$; Table 4). Similarly, the average numbers of adult males and estrous females in hunting parties exceeded those found in nonhunting parties (males: $\alpha' = 0.03$, $F_{1,837} = 178$, $P < 0.001$; females: $\alpha' = 0.05$, Mann-Whitney U test, $Z = 6.62$, $n_1 = 49$, $n_2 = 789$, $P < 0.001$; Table 4).

Party size and composition appeared to influence whether chimpanzees would hunt and their success during subsequent attempts. Party size and the number of adult males in hunting parties were significantly greater when chimpanzees hunted red colobus compared with times they encountered monkeys and did not pursue them (parties: $\alpha' = 0.02$, $F_{1,31} = 6.46$, $P < 0.02$; males: $\alpha' = 0.03$, $F_{1,31} = 4.82$, $P = 0.03$; Table 4). In contrast, the number of estrous females did not affect the tendency of chimpanzees to hunt ($\alpha' = 0.05$, Mann-Whitney U test, $Z = 1.55$, $n_1 = 12$, $n_2 = 21$, $P > 0.10$; Table 4). Party size and adult male numbers in hunting groups were also larger during successful hunts than those during unsuccessful hunts (parties: $\alpha' = 0.03$, $F_{1,47} = 8.53$, $P < 0.03$; males: $\alpha' = 0.05$, $F_{1,47} = 5.23$, $P < 0.03$; Table 4).

Identity of hunters and participation in hunts. Adult male chimpanzees at Ngogo were the predominant and most successful hunters, accounting for 86% of all kills (n = 90 captures). Adolescent males were the second most successful age-sex class of hunters (12% of kills), while adult and adolescent females caught prey infrequently (3% of kills). There was considerable variability in the number of times adult males hunted, with individuals participating in hunts 6–34 times (Table 5).

Meat-sharing and theft. Males frequently shared meat with each other. The overall frequency of sharing (n = 113) exceeded the number of times chimpanzees stole meat from each other (n = 26), and individuals shared more often than they stole (sharing $\overline{X} = 4.9$ episodes/individual, SD = 6.1; theft $\overline{X} = 1.1$ times/individual, SD = 2.0, n = 23 males; paired t-test, t = 3.84, 22 df, $P < 0.001$). While these data suggest an apparent imbalance between levels of cooperation and competition during hunts, it is important to note that meat theft occurred quickly and either high in the trees or as animals rushed rapidly along the ground. For these reasons, we likely missed making observations of theft more often than sharing, which frequently took place during protracted bouts after kills were made. Despite this caveat, males shared meat reciprocally; there was a significant association between the tendency to give meat to specific individuals and the tendency to receive meat from those same individuals (K_r test, $K_r = 167$, 10,000 iterations, $P < 0.001$).

TABLE 5. *Meat acquisition and hunting participation, success, sharing, and theft by adult male chimpanzees of varying ranks*

Male	Male rank	No. of hunting episodes	Meat acquisition (times/hunt)	No. of kills	Meat reception (times/hunt)	Meat theft (times/hunt)
Ar	19	6	0.00	0	0.00	0.00
Ay	15	26	0.54	5	0.27	0.00
Bf	12	22	0.36	6	0.09	0.00
Bg	22	22	0.00	0	0.00	0.00
Bl	17	8	0.50	1	0.25	0.13
Bt	2	32	0.59	7	0.25	0.16
Co	3	15	0.20	1	0.00	0.07
Di	24	30	0.03	0	0.00	0.00
Do	10	32	0.66	8	0.38	0.00
El	4	30	0.73	8	0.30	0.10
Ga	26	13	0.15	1	0.00	0.00
Hr	11	34	0.50	5	0.26	0.09
Ho	6	22	0.23	1	0.18	0.05
Jr	14	15	0.13	1	0.00	0.00
Lo	7	23	0.61	4	0.48	0.04
Mg	8	33	0.39	3	0.27	0.00
Mi	23	14	0.07	1	0.00	0.00
Mo	18	33	0.27	6	0.03	0.03
Mw	1	27	0.81	3	0.56	0.30
Mz	16	17	0.47	1	0.71	0.00
Or	20	16	0.06	0	0.00	0.00
Pk	13	31	0.16	2	0.06	0.00
Pi	9	26	0.35	8	0.15	0.00
Ru	5	27	0.70	6	0.26	0.11
St	21	21	0.00	0	0.00	0.00
Ty	25	11	0.09	0	0.09	0.00

Interindividual variation in meat acquisition. Rates of meat acquisition varied substantially among males, ranging from 0–0.80 times per hunt (Table 5). Meat acquisition by males was affected by three factors: hunting skill, meat-sharing, and theft. Twenty of the 26 adult males in the study group killed prey (Table 5). Most males received meat from others at least once during hunts (17/26 males), while less than one half of all males stole meat (10/26 males; Table 5). Male rank affected the number of times individuals obtained meat during hunts (Spearman r = 0.76, $P < 0.001$) and was positively correlated with all three factors that affected meat acquisition. High-ranking males killed prey ($\alpha' = 0.02$, Spearman r = 0.57, $P < 0.01$), received meat from others ($\alpha' = 0.03$, Spearman r = 0.61, $P < 0.01$), and stole meat more often ($\alpha' = 0.02$, Spearman r = 0.68, $P < 0.001$) than low-ranking males.

Estrous females were observed during 24 of the 49 hunting episodes and obtained meat only about one third of the time they were present (7/24 hunts = 29%).

Chimpanzee behavior during hunts. Chimpanzees at Ngogo hunted both opportunistically and in a manner that appeared intentional. Most hunts were initiated after chimpanzees encountered prey during their normal course of movements (29/49 hunts = 59%). In striking contrast, several other hunts followed "searches" or "patrols" (20/49 hunts = 41%). These hunting patrols were characterized by a suite of behaviors similar to those displayed by chimpanzees during territorial boundary patrols (Goodall et al., 1979) and closely resembled the behaviors described as "searches" by chimpanzees in the Tai National Park (Boesch and Boesch, 1989). During hunting patrols, the Ngogo chimpanzees became unusually silent, moving together in directed fashion in single file. The chimpanzees would stop, look up into the trees, scan, and change directions several times without calling. Chimpanzees were extremely attentive to any arboreal movements and would stop and search whenever motion was detected. If monkeys, particularly red colobus, were spotted, a hunting attempt would ensue. If prey were not

encountered, the chimpanzees would continue patrolling, sometimes for several hours. Single-file movements and the silent nature of hunting patrols are two of their most salient features and differ sharply from the behavior displayed by chimpanzees most other times. Chimpanzees are highly vocal and use loud calls to coordinate movements between individuals who are typically widely separated (Mitani and Nishida, 1993). Hunting patrols took place far from home-range boundaries and were thus easily distinguished from territorial patrols. Hunting patrol party sizes ($\overline{X}$ = 25.7, SD = 8.4, n = 20) did not differ from those displayed by hunting parties formed in the absence of a patrol ($\overline{X}$ = 23. 0, SD = 9.6, n = 29; $F_{1, 48}$ = 1.01, $P > 0.30$).

The Ngogo chimpanzees hunted monkeys in "groups" as defined by Boesch and Boesch (1989, p. 550): "... at least two hunters acting together against the same prey or group of prey." Red colobus hunts typically involved the simultaneous pursuit of several individual prey by different chimpanzees. Observation conditions precluded determining the number of times pursuits involved two or more chimpanzees simultaneously trying to capture the same monkey, but this appeared to occur occasionally. Similarly, it was difficult to ascertain the degree to which chimpanzees cooperated during hunts with any precision. Boesch and Boesch (1989, p. 550) operationally defined cooperation as "... the behavior of two or more individuals acting together to achieve a common goal." They explicitly distinguished this definition from one based on fitness effects, although Boesch (1994b) later defined chimpanzee hunting as cooperative if hunting success increased with party size (cf. Busse, 1977). Boesch and Boesch (1989) also distinguished four forms of cooperation during hunts. Of these four, the Ngogo chimpanzees sometimes "collaborated" by encircling red colobus groups, blocking potential escape routes, or "driving" prey down hill slopes from taller to shorter trees. The other forms of cooperation involve similar action towards a single prey by all hunters, with or without attempts by individual hunters to relate their actions to those of others in time and space. Such "similarity," "synchrony," and "coordination" are common
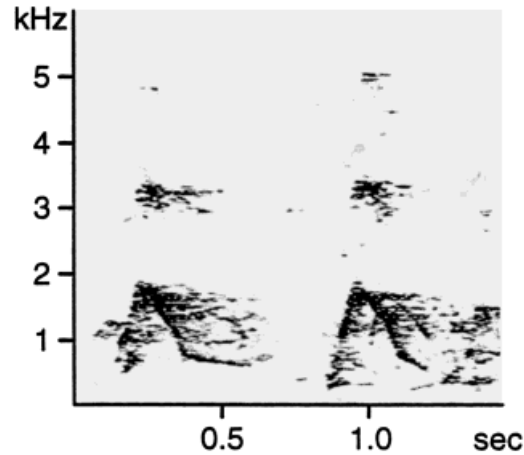

Fig. 1. Chimpanzee hunting calls. Audiospectrograms of two calls given by an adult male are shown. Calls were sampled at 12,000 kHz with 16-bit precision, using Avisoft sound analysis software. Frequency resolution = 23 Hz.

at Tai (Boesch and Boesch, 1989), but were not obviously evident at Ngogo, although individual hunters clearly adjusted their actions relative to the effects other hunters had on potential prey.

Chimpanzees occasionally gave a specific call, the "hunting call" (Fig. 1), at the start of some hunts. This call appeared to mobilize potential hunters, who might be sitting underneath red colobus, into action. Alternatively, isolated chimpanzees who had encountered red colobus prey occasionally gave this call to distant conspecifics; these latter animals would in turn rush to the site and begin to hunt.

Predatory episodes

Hunting frequency, seasonality, and attempts. We witnessed 62 hunting episodes and attempts in 471 days of observations of chimpanzess, or about 4 episodes per month. We recorded hunts during the majority of all months of observation (18/23 months = 78%); this figure rises to 89% (17/19 months) if we exclude the first 4 months of observation in 1995 during which the chimpanzees were relatively intolerant of humans and the presence of observers might have inhibited hunting. Despite their regular occurrence, hunts were not equally distributed across time. Two distinct hunting "binges" or "crazes" took place (Fig. 2).
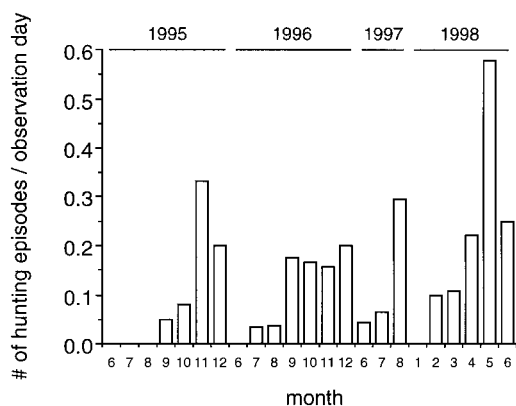
Fig. 2. Temporal variation in the occurrence of hunts by the Ngogo chimpanzees.

The first occurred at the end of the first observation session in November 1995, while the second was recorded during the last field season reported here in May 1998 (Fig. 2).

Figure 3 shows the relationships between monthly hunting frequency and the 1) mean party size per month, 2) mean number of adult males per party per month, and 3) mean number of estrous females per party per month. Results indicate that both party size and the numbers of males per party were significantly correlated with hunting frequency ($\alpha' = 0.02$, males: Spearman r = 0.55, $P < 0.01$; party size: $\alpha' = 0.03$, Spearman r = 0.47, $P < 0.03$). In contrast, the presence of estrous females did not affect hunting frequency ($\alpha' = 0.05$, Spearman r = 0.32, $P > 0.10$). Figure 3 reveals that none of the three demographic variables predicted hunting frequency particularly well, and that the relationships may have been unduly influenced by two outliers representing the months during which binges occurred. Removing these two outliers rendered a marginally significant relationship only between hunting frequency and the number of males per party ($\alpha' = 0.02$, Spearman r = 0.48, $P < 0.03$).

We systematically recorded the number of times chimpanzees encountered red colobus only during the 1998 field season. Based on these observations, the Ngogo chimpanzees hunted red colobus during 64% of all encounters with them (21 attempts/33 encounters).
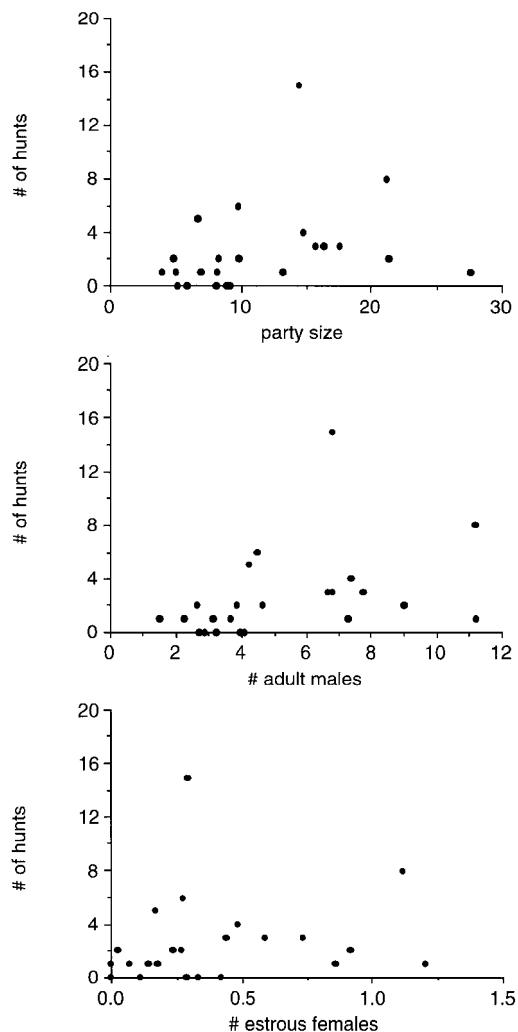

Fig. 3. Effects of demographic variables on chimpanzee hunting frequency. **Top:** Number of hunts per month vs. average monthly party size. **Middle:** Number of hunts per month vs. average number of adult males per party per month. **Bottom:** Number of hunts per month vs. average number of estrous females per party per month.

Duration of hunts. The duration of successful hunts, measured from the initiation of hunting to the time of first capture, varied substantially. The average duration was 19 min (SD = 20 min; range, 2–91 min; n = 29 hunts).

Hunting success. Most hunts undertaken by the Ngogo chimpanzees were successful and resulted in at least one prey item

TABLE 6. Comparative aspects of chimpanzee prey choice

Prey	Gombe	Mahale	Tai	Ngogo
Prey selection				
% red colobus	82%	55%	78%	91%
n (kills)	(429)	(100)	(81)	(128)
Age-sex class of prey				
% immature red colobus	84%[1]	70%	47%	66%
n (kills)	(241)	(40)	(58)	(98)
Reference	Stanford et al., 1994	Uehara et al., 1992	Boesch and Boesch, 1989	This study

[1] Stanford, personal communication.

killed (36/49 hunts = 73%). Hunting success of red colobus prey was slightly higher at 78% (32/41 hunts). These success rates are considerably higher than those reported for some well-studied African carnivores, such as lions (26%, Table 60 in Schaller, 1972), hyenas (34%, Kruuk, 1972, p. 148–197), and cheetahs (30%, Appendices 8 and 11 in Caro, 1994).

Number of kills per hunt. The majority of successful hunts of red colobus that we observed from start to finish resulted in multiple prey items killed (26/32 hunts = 81%). On average, over three red colobus were killed during each successful hunt ($\overline{X}$ = 3.4, SD = 1.8, n = 32 hunts). In contrast, a much smaller sample suggested that hunts involving prey species other than red colobus typically resulted in single kills (3/4 hunts = 75%).

Ecological consequences of predation: red colobus offtake

We observed 39 successful predation episodes on red colobus during the course of this study, or about 30 episodes per year. Using the mean number of kills per successful hunt yields an estimate of 102 kills/year. With an estimated home range of 25 km², the Ngogo chimpanzees make approximately 4 kills/year/km². In the Kibale National Park, red colobus groups average 42 individuals (Struhsaker, personal communication), resulting in an estimated population density of 123 animals/km² at Ngogo. Combined, these observations indicate that about 3% of the red colobus population succumbed to chimpanzee predation each year. This estimate represents a minimum, since we were not able to follow all of the Ngogo chimpanzees at all times, and as a result, did not record some predation episodes.

Comparisons with other studies

Table 6 shows comparative aspects of chimpanzee prey selection at four long-term study sites. Red colobus monkeys constitute the primary prey item at all four sites, though there is significant heterogeneity in the frequency of prey selection among areas, with the Ngogo chimpanzees displaying the highest levels of specialization (χ^2 = 48.14, 3 df, $P < 0.001$; Table 6). At both Gombe and Mahale, the frequency of red colobus predation has increased over time (reviewed in Uehara, 1997), and the most recently reported observations from Mahale indicate a 27% increase in red colobus predation (Hosaka, 1995 and personal communication). Using these data in place of the earlier Mahale observations does not alter the conclusion that chimpanzees prey upon red colobus differentially among study sites (χ^2 = 8.66, 3 df, $P < 0.05$). Chimpanzees also display a preference for immature red colobus prey across populations. Again, heterogeneity exists among groups, with higher levels of predation on adults shown by the West African Tai chimpanzees (χ^2 = 27.51, 3 df, $P < 0.001$; Table 6).

Additional comparisons reveal considerable variation in other aspects of hunting behavior across groups (Table 7). Chimpanzees from different communities do not pursue red colobus equally often. Hunting attempts following encounters with colobus display significant heterogeneity among sites (χ^2 = 220, 3 df, $P < 0.001$; Table 7). Tai chimpanzees appear to hunt red colobus less frequently than do chimpanzees at other sites (but see Boesch, 1994a; Stanford et al., 1994a; Uehara, 1997). Hunting success varies significantly across study sites (χ^2 = 10.57, 3 df, $P < 0.02$; Table 7). The Ngogo chimpanzees are considerably more success-

TABLE 7. Comparative aspects of chimpanzee hunting episodes

Hunting episodes	Gombe	Mahale	Tai	Ngogo
Hunters				
% of captures by males	89%	79%	82%	98%
n (kills)	(350)	(41)	(38)	(66)
Group hunts				
% of all hunts	70%[1]	83%	93%	100%
n (hunts)	(64)	(42)	(80)	(50)
Hunting frequency				
No. of hunts/month	≈8[2]	No data	10	4
n (observation days)			(299)	(471)
Hunting attempts				
% of encounters	72%	63%	17%[4]	64%
n (attempts/encounter)	(414/563)	(74/117)	(39/233)	(21/33)
Hunting duration				
Mean ± range (min)	21 (5–82)[2]	15 (2–43)	18 (1–120)	20 (2–91)
n (hunts)		(19)	(82)	(29)
Hunting success				
% of all red colobus hunts	52%	61%[3]	54%	78%
n (hunts)	(414)	(74)	(83)	(41)
Multiple kills				
% of all hunts	30%	23%	25%	81%
n (red colobus hunts)	(215)	(40)	(55)	(32)
Kills/successful hunt				
Mean ± SD	1.62 ± 1.17	1.36 ± 0.73	1.15	3.41 ± 1.79
n (red colobus hunts)	(215)	(42)	(63 kills in 55 hunts)	(32)
Reference	Stanford et al., 1994a	Uehara et al., 1992	Boesch and Boesch, 1989	This study

[1] Busse, 1978.
[2] Stanford, 1998a; personal communication.
[3] Hosaka, personal communication.
[4] Boesch, 1994a.

ful in capturing red colobus prey than are chimpanzees in other areas. In addition, Ngogo chimpanzees kill significantly more colobus in each successful hunt than do chimpanzees at Gombe and Mahale (overall: $F_{2,286} = 33.92$; $P < 0.001$; Ngogo-Gombe: Tukey-honestly significant difference (HSD) post hoc test, $P < 0.05$; Ngogo-Mahale: Tukey-HSD post hoc test, $P < 0.05$; Table 7). Currently published data do not permit a similar comparison between Ngogo and Tai, though the reported number of kills made per successful hunt at Tai is considerably lower than that at Ngogo (Table 7).

Similarities as well as differences appear to exist in the hunting behavior of chimpanzee populations. Chimpanzees hunted primarily in groups at all four study sites, with the animals at Ngogo showing an extreme proclivity to hunt socially. Levels of group hunting are difficult to compare across sites, since these data are subject to sampling bias; human observers tend to target groups of chimpanzees as subjects, in part to maximize the number of observations of hunting behavior (e.g., Boesch 1994a; Stanford, 1998a; this study). Adult and adolescent

males were the principal hunters in all four chimpanzee populations; predatory success by males was particularly high at Ngogo. Here too, sampling biases intervene to create problems in interpretation. In our study, observations of successful hunters could reflect an artifact of a greater level of habituation of males and our concentration on males as focal subjects (cf. Goodall, 1986; Stanford et al., 1994a). Nonetheless, recent data collected by Stanford (1998a) at Gombe indicate that biased sampling does not affect the finding that adult male chimpanzees are the primary hunters there.

Hunting durations were similar across groups. Boesch and Boesch (1989) indicated that Tai chimpanzees take an average of 19 min to capture red colobus (range, 5–91 min). They cited observations made by Busse (1977) to claim that hunting durations were generally shorter at Gombe and that the Tai chimpanzees were more persistent hunters. However, Busse (1977) did not present data on hunting durations. Boesch (1994b) subsequently reanalyzed observations from Gombe and showed that most hunts there were relatively short. More recent data from

Gombe indicate that kills are made after 21 min (range, 5–82 min; Stanford, personal communication); this figure is strikingly similar to those reported from Tai, Mahale, and Ngogo (Table 7). While previous discussion focused attention on the average lengths of hunts, the wide variation in the range of observed hunting durations may be of greater biological significance. Chimpanzees often capture prey quickly, but sometimes persist for an hour or more (Table 7). The factors that influence this within-site variation in hunting duration are not presently clear and represent an important and unresolved problem.

Previous studies compared hunting frequencies across study sites (Boesch and Boesch, 1989; Stanford et al., 1994a), and controversy continues regarding whether chimpanzees from one site hunt more avidly than those from other areas (Boesch, 1994a; Stanford et al., 1994a; Uehara, 1997). Such comparisons are difficult to perform and render inconclusive results, since equivalent data do not always exist (Table 7).

DISCUSSION

The results presented here indicate that chimpanzees at Ngogo hunt often and prey on several species, but specialize in group hunts of young red colobus. Hunting occurs at all times of the year and is primarily a male activity. Males frequently share meat and do so reciprocally. Overall party size and the number of adult males per party are significant correlates of hunting frequency and success. The extremely high success rate and the large number of kills made per successful hunt are the two most striking aspects of predation by the Ngogo chimpanzees.

Our observations contrast with those of Ghiglieri (1984), who observed only one meat-eating episode and did not witness hunts during 23 months of prior fieldwork at Ngogo during the 1970s. Wherever chimpanzees have been studied, records of hunting typically increase as a function of their habituation (Boesch and Boesch, 1989; Goodall, 1986; Uehara et al., 1992), and as noted by Boesch and Boesch (1989) and Stanford (1996), the paucity of hunts previously reported at Ngogo was almost certainly an artifact of poor habituation. Our observations of frequent hunting complement those made at Gombe, Mahale, and Tai (Uehara, 1997), and demonstrate that hunting behavior is a widespread, species-typical behavior.

Our results bear on two additional topics of current debate and interest regarding chimpanzee predation. First, these data are consistent with the hypothesis that a chimpanzee's decision to hunt is largely dictated by the number of available hunters, particularly the number of adult males. Party size in turn fluctuates with food availability (e.g., Wrangham et al., 1992; Chapman et al., 1995). Additional social factors, such as the presence of estrous females, do not appear to influence whether chimpanzees hunt at Ngogo; estrous females obtain meat less than half the time they attend hunts (cf. Stanford et al., 1994b). Second, our preliminary estimates of prey offtake suggest that despite the success with which chimpanzees prey upon them, the Ngogo red colobus do not appear to be under extreme predation pressure. The minimum estimated loss of 3% of the population per year differs considerably from the much higher 18–42% predation rates reported at Gombe (Wrangham and Bergmann-Riss, 1990; Stanford, 1998a). The relatively low offtake at Ngogo is due in part to the high red colobus population density there. We currently estimate that approximately 2,500–3,700 red colobus live within the range of the Ngogo chimpanzees (Mitani, Struhsaker, and Lwanga, unpublished data). In contrast, Stanford (1995) estimated only about 450–550 red colobus within the hunting range of the Gombe chimpanzees. Aside from these between-site differences in prey densities, our long-term census data indicate that a decline in the red colobus population may have occurred over time at Ngogo (Mitani, Struhsaker, and Lwanga, unpublished data). The extent to which this decrease in numbers has been due to chronic chimpanzee predation bears further investigation.

Ecological and demographic constraints on behavior

Ecological differences have been well-known to affect patterns of variation in primate behavior since the first field studies

over 30 years ago (Jay, 1968), and there is a rich tradition of subsequent research that has interpreted the behavior of primates within an ecological context (Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977; Wrangham, 1980; van Schaik, 1983; Terborgh and Janson, 1986). Recent studies of the hunting behavior of chimpanzees have followed the socioecological tradition by attempting to explain population variation in terms of gross differences in habitat and tree size (Boesch and Boesch, 1989; Boesch, 1994a,c). In contrast to ecology, demography has been generally less well-appreciated as a determinant and constraint on the behavior of primates (Altmann and Altmann, 1979). Nevertheless, demographic variables are now widely regarded as key to the understanding of several aspects of primate behavior, ranging from mating systems to dispersal patterns (Goldizen, 1987; Clutton-Brock, 1989).

The observations reported here suggest that demographic variables are likely to affect population differences in chimpanzee hunting patterns. The high hunting success rate and multiple kills made in each hunt documented here differ strikingly from the patterns shown by other groups. Both of these results can be considered logical outcomes of the unusual demographic structure and composition of the Ngogo community. Hunting success in this and other studies increases as a function of chimpanzee party size and the number of male hunters (Boesch and Boesch, 1989; Stanford et al., 1994a; Stanford, 1998a). Successful hunting parties at Ngogo included an average of 26 individuals and 14 adult males (Table 4); hunting parties of similar size and composition cannot form at other chimpanzee study sites because the communities there are generally smaller than at Ngogo and contain less than 10 males (reviewed in McGrew et al., 1996). Viewed within this context, high hunting success is a near inevitable consequence of the large number of males and community size at Ngogo.

Demographic factors are likely to affect other aspects of chimpanzee hunting behavior. For instance, chimpanzees do not appear to hunt red colobus often in situations where the probability of success is low. Such cases

apply to communities characterized by chronically small male parties. Only 3–6 adult males lived in the now extinct K group at Mahale (Nishida et al., 1985); the current Mitumba community at Gombe contains only 3 adult males. Both of these groups hunted red colobus rarely (Nishida et al., 1979; Stanford, 1998a). The demographic structure and composition of the prey species may also affect chimpanzee hunting patterns. East African chimpanzees prefer to prey on young red colobus monkeys, and Stanford (1998a) recently reported that the Gombe chimpanzees selectively targeted groups containing large numbers of young. In similar fashion, the Ngogo chimpanzees appear to "harvest" individuals within groups of red colobus. During the hunting binge of late April–early June 1998, the Ngogo chimpanzees preyed on a minimum of 12 different groups of red colobus over 44 days. In 6 of 14 patrols observed during this period, the chimpanzees failed to hunt when they encountered groups of red colobus from whom they had recently eaten young; patrols either dissolved in the absence of another encounter with red colobus or continued until the chimpanzees met another group that had not been preyed upon recently.

Comparisons with other studies

Hunting by the Ngogo chimpanzees displays a combination of features that are both similar to and different from those shown by animals living in other East and West African populations. All East African chimpanzee groups studied to date appear to prey selectively on immature red colobus prey (Uehara et al., 1992; Stanford et al., 1994a; this study). This is in contrast to the pattern of selection by the Tai West African chimpanzees, who prey upon adults and immatures in roughly equal proportion (Boesch and Boesch, 1989). Red colobus prey mob chimpanzee predators, and cooperation among chimpanzees is generally lacking during hunts at all East African study sites (Busse, 1978; Stanford et al., 1994a; this study; Mitani, personal observations). In contrast, red colobus do not typically mob chimpanzees, and cooperative hunting appears to occur regularly at Tai (Boesch and Boesch, 1989; Boesch, 1994a,b). Patrolling behavior

is one behavioral similarity the Ngogo chimpanzees share with the Tai chimpanzees that is not commonly displayed by the Gombe and Mahale populations, where chimpanzees frequently hunt opportunistically (Busse, 1978; Uehara et al., 1992; Stanford et al., 1994a). What factors account for these similarities and differences in hunting patterns across sites?

Boesch and Boesch (1989; cf. Boesch, 1994a–c), contrasting Tai with Gombe and, to a lesser extent, Mahale, identified variation in habitat structure as the driving force behind differences in prey selection, hunting success, cooperation, and colobus defensive tactics. In this view, the difficulty of capturing arboreal monkeys in the high, continuous tree canopy at Tai (height ≈20–30 m; Boesch, 1994c) leads to cooperative hunting; otherwise, success rates would be too low to make hunting energetically profitable (Boesch, 1994b). Cooperation also allows the Tai chimpanzees to overcome the defenses of adult male red colobus and to capture adult males relatively easily. Conversely, the lower and broken canopy at Gombe (height ≈10–15 m; Boesch, 1994c) forces red colobus there to be "much more aggressive" (Boesch, 1994a, p. 1140) than those at Tai; the same presumably also applies to Mahale, where red colobus typically mob chimpanzees (Mitani, personal observations). Gombe chimpanzees can still prey on red colobus with high success without extensive cooperation (cf. Stanford et al., 1994a; Stanford, 1996, 1998a), but do not pursue adult males because this would be too risky.

Our observations reinforce only part of this scenario. Highly successful predation on red colobus by mostly noncooperative chimpanzees at Ngogo, a forest habitat with a high, continuous canopy (height ≈25–30 m; Butynski, 1990), shows that cooperation is not a prerequisite for success in such habitats. Proposed explanations for the intersite variation in red colobus defensive behavior are incomplete, and the issue deserves further study. Boesch and Boesch (1989), using data then available from Tai and Gombe, found that Tai red colobus mobbed chimpanzees more often, but less effectively, than those at Gombe. Boesch (1994b) subsequently used different observations to argue

that mobbing was more common at Gombe, and noted that mobbing frequency might have increased over time there. Stanford (1996) gave independent data from Gombe supporting the argument that red colobus mob more often there. Stanford (1998a,b) also found that the effectiveness of mobbing increased directly with the number of males per red colobus group. This effect only held for chimpanzee hunting parties with five or fewer members; when more than five adult males hunted, cooperative defense by the colobus was ineffective. These observations can be combined with the explanation by Boesch (1994a) and Boesch and Boesch (1989) for differential predation on red colobus males. The finding of a plateau in defense effectiveness at Gombe, and the repeated observation that hunting success increases with hunting group size, reinforce what we view as our principal contribution to the ongoing discussion. Specifically, we need to incorporate demographic variation explicitly into any explanation of variation in chimpanzee hunting behavior. Boesch and Boesch (1989, p. 566) anticipated this argument when they indicated that their data "… show that duration of the hunt, hunting success, and organization of group hunts are all related to the number of hunters," but the implications of this statement were not developed adequately. Ngogo chimpanzees overwhelm red colobus defenses by massing large numbers of hunters, whose largely opportunistic pursuit tactics make their hunts highly successful and often result in multiple kills. Chimpanzees at Gombe achieve a similar effect, although less often, when they hunt in relatively large parties. This demographic effect is the missing element in the comment by Boesch (1994a) that Gombe chimpanzees do not need to hunt cooperatively in order to equal or surpass the success of those at Tai.

We conclude from this general review that robust differences exist in the predatory behavior of chimpanzees across sites. These involve prey selection, hunting success, cooperation among chimpanzee predators, and defensive behavior by red colobus prey during hunts. Additional research will be necessary to uncover with certainty the causal factors underlying these differences, but the

demographic compositions of both predators and prey promise to be critical components in any proposed explanations.

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