Why do chimpanzees hunt and share meat?

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Wild chimpanzees, *Pan troglodytes*, frequently hunt and share meat. Despite widespread interest and considerable study, continued controversy exists regarding the factors that influence chimpanzee hunting decisions and meat sharing. Three hypotheses invoke the importance of ecological, reproductive and social factors. A nutritional shortfall hypothesis suggests that chimpanzees hunt to compensate for seasonal shortages in food availability. A second hypothesis argues that male chimpanzees hunt to obtain meat that they swap for matings. A third hypothesis proposes that males use meat as a social tool to develop and maintain alliances with other males. We tested these hypotheses using observations of an unusually large community of chimpanzees at Ngogo in Kibale National Park, Uganda. Results did not support the nutritional shortfall or meat-for-sex hypotheses. The Ngogo chimpanzees hunted primarily during times of food abundance rather than scarcity. The presence of oestrous females did not predict the tendency of chimpanzees to hunt. Furthermore, meat-for-sex exchanges occurred infrequently, and males did not gain a mating advantage through sharing meat. Additional observations were consistent with the male social bonding hypothesis. At Ngogo, male chimpanzees were likely to hunt when accompanied by other males. Males shared meat nonrandomly and reciprocally among themselves, and males exchanged meat for agonistic support. Although several factors are likely to affect chimpanzee hunting decisions and meat sharing, these results indicate that primary causes will not be found through invoking simple energetic or reproductive considerations.

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Considerable attention has been devoted to the study of wild chimpanzee, *Pan troglodytes*, hunting behaviour ever since Goodall's (1963) pioneering observations of the phenomenon. Hunting and meat eating by chimpanzees have important implications for several ecological, ethological and evolutionary problems. For instance, studies of chimpanzee hunting behaviour have increased our understanding of ecological relationships between predators and their prey and of how primate population sizes are regulated (Boesch 1994a; Stanford 1995a, 1998). Field research on chimpanzee hunting has also furnished insights into issues of traditional ethological concern, such as the evolution of cooperation in animals (Busse 1978; Boesch & Boesch 1989; Boesch 1994b). Finally, observations of carnivory in our closest living relations have featured significantly in attempts to reconstruct early human behaviour (Ghiglieri 1987; Wrangham 1987; Boesch & Boesch 1994; Stanford 1995b, 1996, 1999).

As a result of widespread interest in chimpanzee hunting behaviour, a wealth of information regarding what,

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when and how chimpanzees hunt now exists, with considerable data on prey choice as well as hunting success, frequency and tactics (reviews in Uehara 1997; Stanford 1998; Mitani & Watts 1999). Wild chimpanzees preferentially prey on red colobus monkeys, *Colobus badius*, whenever they are sympatric, hunting them between 4–10 times each month. Chimpanzees are unusually successful predators, with hunting success rates typically averaging over 50%. Red colobus hunts often occur opportunistically, as is the case when, during the course of their normal foraging activities, chimpanzees encounter monkeys and begin to pursue them. Alternatively, other hunts appear to be 'planned' in the sense that chimpanzees will first assemble and then actively patrol their territory in search of red colobus (Boesch & Boesch 1989; Mitani & Watts 1999). That chimpanzees search long distances for red colobus prey is not surprising because meat represents a compact, readily assimilated package high in protein and fat that is clearly valued by all individuals (Stanford 1998). Chimpanzees, however, frequently ignore potential red colobus prey upon encountering them and will voluntarily relinquish this highly prized resource to other individuals, two observations that are not easily explained (e.g. Stanford et al.

1994). Thus despite an impressive amount of data on chimpanzee hunting behaviour, we still lack clear answers to two fundamental questions: what factors influence a chimpanzee's decision to hunt and why do individuals share meat?

Three hypotheses have been proposed to answer these questions. The first and simplest hypothesis invokes energetic and other nutritional factors. Chimpanzees are frugivores, which feed principally on sugar-rich fruits (Wrangham 1977; Tutin et al. 1991; Wrangham et al. 1996, 1998). Fruit availability varies both in time and space and results in seasonal and sometimes unpredictable shortfalls in food (Wrangham et al. 1992, 1996, 1998; Chapman et al. 1995). Teleki (1973) originally speculated that chimpanzees in the Gombe National Park hunt to compensate for seasonal food shortages. This view was echoed by Takahata et al. (1984), who observed a nearby population of chimpanzees in the Mahale Mountains National Park, as well as by Stanford (1996, 1998) during subsequent research at Gombe. Tentative support for this hypothesis is provided by analyses that show measures of predation intensity are negatively correlated with a proxy variable for food availability. The number of kills per month, the mean number of kills per hunt, and the proportion of encounters in which chimpanzees hunted red colobus at Gombe were all higher during dry season months, the purported time of food scarcity, than during the rainy season (Stanford et al. 1994; Stanford 1996, 1998). Nevertheless, hunting frequency, the variable of interest, did not vary significantly with rainfall, nor has it been shown that rainfall correlates positively with fruit abundance. The uncertainty arising from these analyses calls for a simpler and more direct test of the nutritional shortfall hypothesis. This hypothesis makes the straightforward prediction that chimpanzees should hunt more frequently during fruit-poor times. Observations necessary to evaluate this proposal, however, have not been available.

Although some studies have focused on the potential nutritional significance of hunting, additional research suggests that hunting confers direct reproductive benefits. In the first systematic study of chimpanzee hunting, Teleki (1973) used limited observations of meat sharing to suggest that oestrous females obtain meat more often than anoestrous females. This led him to propose a second hypothesis that males might increase their mating opportunities by first acquiring and then subsequently sharing meat. Stanford (Stanford 1996, 1998; Stanford et al. 1994) renewed interest into the relationships between hunting, meat-sharing and mating behaviour through an analysis of more recent observations of the Gombe chimpanzees. His results revealed that the mean number of oestrous females in foraging parties was the single best predictor of the proportion of times chimpanzees pursued red colobus after encountering them (Stanford et al. 1994). Stanford (Stanford 1996, 1998; Stanford et al. 1994) combined this result with additional, although scant, observations of (1) meat sharing between males and oestrous females and (2) matings that ensued between sharers and recipients, to argue that male chimpanzees hunt to procure meat that they swap for matings.

Four predictions follow from this provocative 'meat-for-sex' hypothesis. First, this hypothesis predicts that decisions to hunt should be proximately affected by the presence of oestrous females. The meat-for-sex hypothesis also predicts that sharing between males and oestrous females should occur more frequently than between males and anoestrous females. Third, the hypothesis leads to the expectation that meat will be commonly exchanged for matings. A fourth prediction is that males that share meat will obtain more matings than they would otherwise.

While acknowledging the potential direct reproductive benefits that males may gain through meat acquisition and sharing, other researchers have suggested that additional social factors motivate chimpanzees to hunt. For example, Nishida et al. (1992; cf. Nishida & Hosaka 1996) provided data consistent with the idea that the alpha male at Mahale used meat as a social tool to develop and maintain alliances with other adult males. Since males are the primary hunters in chimpanzee society, a third hypothesis stemming from these observations suggests that hunting serves an intrasexual social function. Three specific predictions can be derived from the male social bonding hypothesis. First, this hypothesis predicts that the tendency to hunt will be proximately affected by the presence of adult males. A second prediction suggests that meat sharing will take place nonrandomly and reciprocally among males. A final prediction made by this hypothesis is that the tendency to share meat will be associated with significant aid, such as coalitionary support.

During prior research, we have shown that chimpanzees living within the Ngogo study area of Kibale National Park, Uganda, hunt frequently and with an unusual degree of success (Mitani & Watts 1999; Watts & Mitani, in press). The frequency with which the Ngogo chimpanzees hunt creates an ideal venue to test the three hypotheses outlined above concerning the ecological, reproductive and social factors that affect chimpanzee hunting decisions and meat sharing. In this paper we provide such tests by analysing observations of chimpanzee hunting behaviour in relation to food availability and party composition. Additional observations of meat sharing, mating and coalition formation permit us to evaluate the proposed inter- and intrasexual functions of hunting behaviour.

METHODS

Study Site and Animals

We observed chimpanzees at the Ngogo study site in Kibale National Park, Uganda. Observations were conducted over 16 months between two periods, January–June 1998 and October 1998–August 1999. Ngogo lies at an interface between lowland and montane rainforest and is covered primarily with moist, evergreen forest interspersed between large blocks of *Pennisetum purpureum* grassland. Ghiglieri (1984), Butynski (1990) and Struhsaker (1997) provide more detailed descriptions of the Ngogo study area.

The Ngogo chimpanzee community comprises the largest number of animals heretofore described in the wild. Approximately 140–150 individuals reside within the Ngogo community, including 24 adult males, 15 adolescent males, and more than 45 adult females during the period considered here. We have maintained observations of chimpanzees at Ngogo continuously since 1995, and as a result, subjects were well habituated to our presence.

Behavioural Observations

We collected data on chimpanzee hunting behaviour opportunistically while studying other aspects of their behavioural ecology (e.g. Watts 1998; Mitani et al. 2000). We distinguished two types of interactions involving chimpanzee predators and their red colobus prey. Hunts, both successful and unsuccessful, were scored if chimpanzees actively pursued red colobus. We recorded interactions as 'encounters' when chimpanzees came within visual range of red colobus, as assessed by human observers, and did not hunt them. For both hunts of, and encounters with, red colobus, we noted the number of chimpanzees in each party and the numbers and identities of adult males and oestrous females present. We identified oestrous females by the fact that they were sexually receptive to and mated with male chimpanzees. These females typically possessed oestrous swellings at maximal tumescence (cf. Stanford et al. 1994).

Chimpanzees are pursuit hunters, and hunts of red colobus typically occur quickly with several chimpanzees chasing prey over large areas simultaneously, both on the ground and in the trees. At Ngogo, successful hunts include an average of 26 chimpanzees (Mitani & Watts 1999). These factors render it impossible to record the actions of all individuals present at hunts precisely. Some prior studies differentiate active hunters from 'bystanders', the latter representing individuals that may be present at hunts but nevertheless fail to participate (e.g. Boesch & Boesch 1989; Boesch 1994b). Such an empirical distinction is difficult to make for hunts at Ngogo. Differentiating active hunters from passive bystanders is problematic here since individual chimpanzees frequently alternate between these different roles during the same hunt. Given the prevailing observation conditions and nature of hunts, we followed the convention adopted by most field investigators and considered all chimpanzees present at hunts as potential hunters (Stanford et al. 1994; Hosaka et al., in press).

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 monthly hunting frequency. For this computation, we included only days on which we observed chimpanzees for at least 6 h, a procedure that allowed us to be reasonably sure that we did not miss hunts (cf. Boesch & Boesch 2000). Other aspects of chimpanzee behaviour, such as meat sharing and coalitions, were noted ad libitum. Meat sharing was scored whenever two individuals exchanged meat in an apparently voluntary fashion. Sharing involved both the active and passive transfer of meat (sensu Boesch &

Table 1. Fruit trees used by the Ngogo chimpanzees

Species	Density (trees/ha)	Size (mean DBH cm)
Aningeria altissima	0.01	185
Celtis durandii	39.70	40
Chrysophyllum albidum	39.54	56
Cordia millenii	0.46	110
Ficus brachylepis	1.37	184 (*N*=26)
Ficus cyathistupula	0.15	65 (*N*=22)
Ficus dawei	0.15	207
Ficus exasperata	0.01	135
Ficus mucuso	0.15	245
Ficus natalensis	0.76	150 (*N*=26)
Mimusops bagshawei	4.11	78
Monodora myristica	4.56	66
Morus lactea	0.30	84
Pseudospondias microcarpa	2.59	121
Pterygota mildbraedii	13.84	139
Teclea nobilis	2.28	24
Treculia africana	0.46	83 (*N*=23)
Uvariopsis congensis	64.64	19
Warburgia ugandensis	0.76	99 (*N*=28)
Zanha golungensis	0.61	82

Densities and average tree sizes are shown for the top 20 tree species fed upon at Ngogo. Densities of each tree species were computed based on counts from 263 5×50-m plots. Thirty trees of each species were measured to calculate mean diameter at breast height (DBH) tree sizes, except where noted in parentheses.

Boesch 1989). We recorded coalitions between two males whenever they directed aggression together towards a third individual (e.g. Watts 1998; Mitani et al. 2000).

We calculated UPGMA cluster analysis dendrograms to display graphically patterns of meat sharing and coalition formation between adult males. We computed distance metrics between individuals by dividing each pairwise value by the largest score in the matrix and subtracting these from 1. All trees were thus standardized to unit length with the highest and lowest levels of meat sharing and coalition formation assigned distances of 0 and 1, respectively.

Food Availability and Rainfall

To test the nutritional shortfall hypothesis, we monitored the phenological stages of fruit trees composing the top 20 species in the diet of the Ngogo chimpanzees throughout the 16-month study period (Table 1). We noted the presence or absence of ripe fruit for 20 trees of each species each month. Phenological observations were made during the first 5 days in each calendar month. We selected tree species to monitor on the basis of previous observations of the feeding behaviour of chimpanzees both at Ngogo and at the nearby Kanyawara study site (Ghiglieri 1984; Wrangham et al. 1992; R. Wrangham, personal communication; D. P. Watts, J. C. Mitani & J. S. Lwanga, unpublished data). Preliminary analyses indicate that these 20 species compose over 75% of the diet of the Ngogo chimpanzees (D. P. Watts & J. C. Mitani, unpublished data). Individual trees selected for sampling were

randomly scattered across the Ngogo chimpanzee community range. We used phenological data along with the sizes of each tree species and their densities recorded in 263 plots (5 × 50 m) to compute an index of food availability each month:

$$\sum_{i=1}^{20} p_i \star d_i \star s_i$$

where: p_i=percentage of the ith tree species possessing ripe fruit; d_i=density of the ith tree species (trees/ha); and s_i=mean size of the ith species (diameter at breast height, DBH, cm).

We used DBH as an estimate of tree size. Previous research has shown that tree DBH is a good proxy variable for the overall size of fruit crops in trees used by chimpanzees and other primates (e.g. Leighton & Leighton 1982; Chapman et al. 1992). For 15 tree species, we measured DBH of the 20 trees included in our phenological samples plus an additional 10 randomly selected individuals to calculate average tree sizes. For five tree species we could not locate a sufficient number of individuals, and in these cases, DBH samples ranged from 22 to 28 individuals (Table 1).

We collected daily records of rainfall during the 16-month study period. Observations were made each morning at our base camp, with total amounts of rainfall measured to the nearest 0.1 mm.

Analyses

We examined the relationship between monthly hunting frequency and fruit availability to test the hypothesis that meat is an alternative source of energy during fruit-poor months. We examined the effects of rainfall on fruit availability and hunting frequency by regressing the 16 summed monthly rainfall scores against measures of mean monthly fruit availability and monthly hunting frequency. For these analyses, we constructed monthly scores of behavioural observations centred around the times we recorded phenological observations. For example, our records of hunting for March 1999 included observations from 19 February to 18 March 1999.

We assessed whether males shared meat with each other nonrandomly by comparing observed levels of sharing with those expected by chance. For this analysis, we began by computing the average number of times males shared with each other across all 276 possible dyads. We then calculated the absolute value of each dyad's deviation from the overall mean. We used the sum of these absolute values as our test statistic. To generate an expected distribution of deviations, we employed a resampling technique based on our original observations (Good 1999). We began by assigning each possible dyad a unique number between 1 and 276. We then used a random number generator to select values between 1 and 276, allocating a sharing event to each dyad whose unique number was selected. We repeated this selection process 284 times until the 24 × 24 resampled matrix contained as many sharing events as our original data matrix. After randomly allocating sharing events to these resampled matrices, we computed the test statistic, using it as a single data point to generate an expected distribution. We iterated this process 10 000 times to calculate the expected distribution of deviations, and then compared our observed test statistic to the 5% right-hand tail of the expected distribution to assess the null hypothesis that males shared meat with each other randomly.

We evaluated the frequency of meat sharing between males and oestrous and anoestrous females by comparing the observed number of sharing episodes against those expected by chance. Here we compared the observed number of times meat sharing occurred between males and each class of female against a theoretical distribution generated on the assumption that sharing occurs randomly between individuals. We computed expected frequencies of sharing by assuming that male chimpanzees that possessed kills would share their carcasses with females in direct proportion to the numbers of females in the hunting party. For our test statistic, we used the percentage of times males shared with oestrous females relative to the total number of sharing episodes between males and all females. We calculated an expected distribution for this test statistic using a resampling procedure. We began this process by employing a random number generator to select numbers between 0 and 1. If the random number generator assigned a value equal to or less than the expected percentage of times males shared with oestrous females, we scored a sharing episode for that assignment. Values greater than expected were assigned as sharing events between males and anoestrous females since the probabilities of males sharing with oestrous and anoestrous females summed to unity. For each hunting party, we iterated this assignment procedure N times, where N equalled the observed number of sharing episodes in each hunt. We repeated this procedure for each hunt where we observed sharing with females, or 24 times. At the end of these 24 simulations, we summed the number of times the random number generator assigned a sharing episode between males and oestrous females and between males and anoestrous females. We used these summations as single data points to calculate the expected number of sharing episodes predicted to occur between the sexes over all hunting episodes. Expected distributions were produced after iterating the assignment procedure 10 000 times. Comparing our observed number of sharing episodes to the 2.5% tails of the expected distributions for each class of female provided a two-tailed statistical test of the null hypothesis that the observed number of sharing events between males and oestrous females and between males and anoestrous females did not exceed those predicted by chance.

We used logistic regression to test the hypothesis that the presence of oestrous females predicted the Ngogo chimpanzees' tendency to hunt after encountering red colobus monkeys. Here the dependent variable took a categorical form of to hunt or not to hunt, while the predictor variable was the presence or absence of at least one oestrous female in each chimpanzee party that encountered red colobus monkeys. We also employed logistic regression to investigate whether the number of

adult males present in chimpanzee parties predicted their decisions to hunt. In a final analysis, we used both the presence of oestrous females and the number of adult males as independent variables to predict whether chimpanzees hunted after encountering red colobus prey. To evaluate the effects of the numbers of males on the tendency to hunt, we considered all chimpanzees present as potential hunters (see above). The large number of participants and the wide area over which hunting activities took place made it impossible to monitor all males and differentiate those that actively pursued prey from those that acted merely as 'bystanders' (sensu Boesch & Boesch 1989; Boesch 1994b).

We recorded the number of times matings followed meat-sharing episodes between males and females to assess the degree to which males exchanged meat for sex. Here we reasoned that if males gain a mating advantage through sharing, then mating should follow sharing events frequently. We used a binomial test to evaluate this possibility, setting chance expectation to one-half. A few males shared meat with oestrous females during some of the females' oestrous cycles but not others. We used this variation to test the hypothesis that meat sharing increased male mating success. For this analysis, we compared the percentage of all matings males achieved with females during oestrous cycles in which sharing took place with those that occurred during other cycles without sharing. We employed a Wilcoxon matched-pairs signed-ranks test to analyse differences in male mating success as a function of sharing.

We employed Hemelrijk's (1990) K_r test to examine the relationship between meat sharing and coalition formation. In this analysis we specifically asked whether males exchanged meat for agonistic support. The K_r test also provided a means to investigate whether males shared meat reciprocally. The K_r test is a matrix permutation procedure and variant of the Mantel (1967) test for matrix correlation. We employed the K_r test rather than the Mantel procedure since the former takes inter-individual variation in behaviour into account. We used 10 000 permutations to generate expected levels of association between variables in both tests.

RESULTS

Hunting Frequency

During the 16 months of study, chimpanzees encountered red colobus monkeys 164 times, or about 10 times per month. Hunts ensued in 61 encounters (37%), with 51 (84%) resulting in kills. A total of 213 red colobus monkeys succumbed to chimpanzee predation in the 51 successful hunts or about four kills per hunt.

There was considerable temporal variation in the number of times chimpanzees encountered red colobus and hunting frequency (Table 2). Chimpanzees encountered red colobus 1–33 times per month, with hunts occurring 0–11 times per month. After controlling for observation time, seasonal peaks of hunting correlated in a simple manner with the number of times chimpanzees encountered red colobus ($F_{1,14}=5.56$, $r^2=0.28$, $P<0.04$).

Table 2. Temporal variation in encounters between chimpanzee predators and red colobus prey and hunting frequency

Month	Encounters per day per month	Hunts per day per month
February 1998	0.06	0.04
March 1998	0.08	0.07
April 1998	0.14	0.13
May 1998	0.46	0.29
June 1998	0.82	0.17
October 1998	0.09	0.03
November 1998	0.79	0.37
December 1998	0.40	0.19
January 1999	0.14	0.00
February 1999	0.41	0.11
March 1999	0.42	0.16
April 1999	0.11	0.00
May 1999	0.23	0.13
June 1999	0.35	0.13
July 1999	1.14	0.13
August 1999	1.00	0.13

Ecological Correlates of Hunting Frequency

Hunting frequency should vary inversely with fruit abundance if meat is an alternative source of energy during fruit-poor months. In contrast to this expectation, the number of hunts per month increased significantly as the amount of ripe fruit increased ($F_{1,14}=8.28$, $r^2=0.37$, $P=0.02$; Fig. 1a). There was no relationship between fruit availability and rainfall ($F_{1,14}=0.61$, $r^2=0.04$, NS; Fig. 2), and as a result, hunting frequency did not increase during dry periods ($F_{1,14}=1.38$, $r^2=0.09$, NS; Fig. 1b).

Social Influences on Hunting Decisions

Oestrous females were present approximately a quarter of the times chimpanzee parties encountered red colobus prey (43/164=26%). A logistic regression analysis indicated that the presence of oestrous females in chimpanzee parties was a significant predictor of whether chimpanzees hunted red colobus monkeys after encounter (Wald $\chi_1^2=17.88$, $r=0.27$, $P<0.001$). While this result is consistent with the hypothesis that male chimpanzees hunt in order to procure meat that they later can swap for matings, the relationship between oestrous female presence and the decision to hunt may be spurious if the former is correlated with a hidden third variable that is itself a better predictor of hunting. In fact, the number of oestrous females and adult male hunters were positively correlated with each other ($F_{1,162}=64$, $P<0.001$), and the number of adult male hunters was also a significant predictor of the tendency to hunt (Wald $\chi_1^2=49.76$, $r=0.47$, $P<0.001$). When both the presence of oestrous females and the number of adult male hunters were used as independent variables in a logistic regression model, only the number of males was a good predictor of a chimpanzee's decision to hunt (Wald $\chi_1^2=42.69$, partial $r=0.43$, $P<0.001$). After partialling out the effects of adult males, the presence of oestrous females did little to
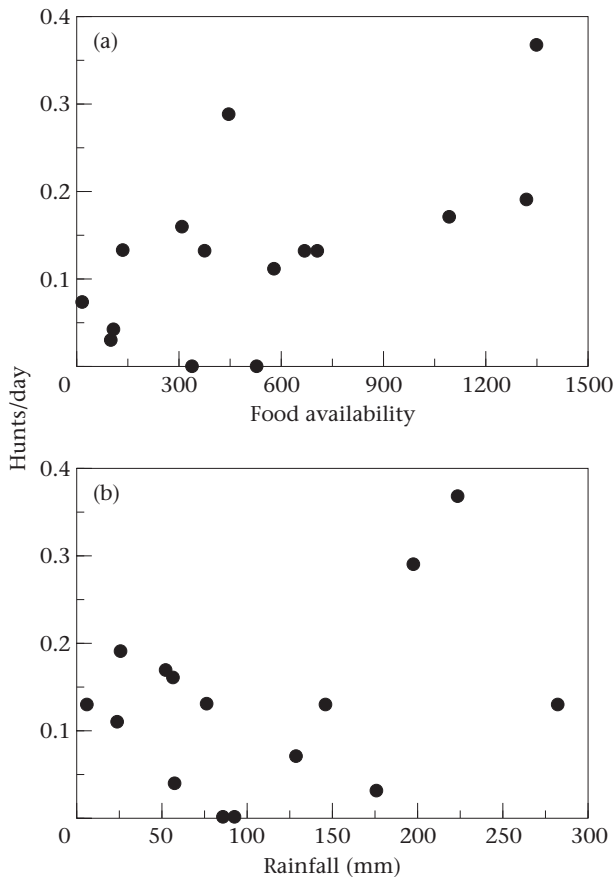
Figure 1. Relationships between hunting frequency and (a) fruit availability and (b) rainfall. Each data point represents a monthly average (N=16 months).
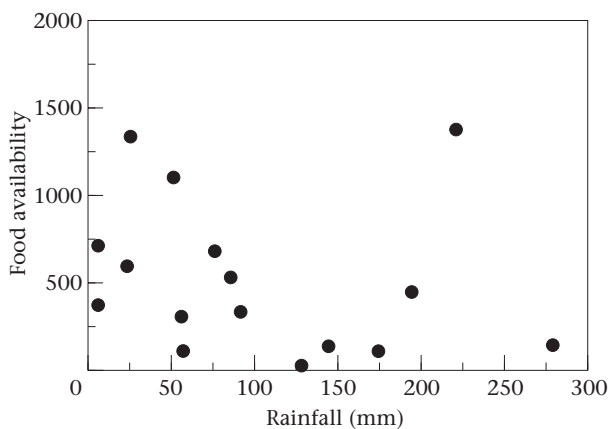

Figure 2. Relationship between fruit availability and rainfall. Each data point represents a monthly average (N=16 months).

explain why chimpanzees hunt (Wald χ_1^2=0.48, partial r=0, NS).

Factors Affecting Meat Sharing

Twenty oestrous and 107 anoestrous females were present at 24 hunts during which males shared meat with females. We observed sharing between 23 pairs of males

and oestrous females. In contrast, males shared with anoestrous females twice as often in 56 pairs. Despite this disparity, males shared with oestrous females more frequently than one would expect given their proportional representation in hunting parties (P<0.001). Alternatively, males shared with anoestrous females less often than expected by chance (P<0.01).

Males shared meat with each other on average one time ($\bar{X}$=1.03, N=276 dyads), but there was considerable variability in the degree to which different males shared (SD=1.79, range 0–11). Consequently, there was a nonrandom pattern of meat sharing among males (P<0.001).

We observed 284 meat-sharing episodes between adult male chimpanzees or about 1.3 episodes per colobus kill. We recorded 350 coalitions between males during the 16 months of study. Figure 3 illustrates patterns of meat sharing and coalition formation between the 24 male subjects through UPGMA cluster analysis dendrograms. Several pairs of males that shared meat with each other often, also formed coalitions frequently (e.g. BT–MW, EL–HR, AY–MG). A matrix permutation test revealed that there was a significant association between the number of times males shared meat with each other and the number of times males received coalitionary support (K_r=954, N=22, P=0.0002). Meat was also shared reciprocally; males that shared meat with others were likely to receive meat from those same individuals in return (K_r=1619, N=22, P=0.0001).

Meat Sharing and Mating Behaviour

We observed oestrous females at about half of all successful hunts (25/51=49%). Oestrous females were not particularly successful in obtaining meat from males through their begging efforts. Females begged 68 times and were successful on 30 occasions (44%). Seven successful begging episodes involved females that obtained meat more than once from a single male at the same hunt. Excluding these exchanges, we recorded 23 meat-sharing episodes between males and oestrous females. Mating ensued only 14 of the 23 times males shared with females, a proportion that did not deviate from a chance expectation of 0.5 (binomial test: NS).

We recorded 12 cases in which a male shared meat with a female during one of her oestrous cycles but not another. Males did not achieve more matings with females during cycles they shared compared with cycles in which they did not share (Fig. 4; Wilcoxon matched-pairs signed-ranks test: T=47, N=12, NS).

DISCUSSION

Results of the preceding analyses are consistent with the hypothesis that male chimpanzees hunt to obtain meat that they later share with other males for social purposes. Adult male chimpanzees at Ngogo share meat non-randomly and reciprocally among themselves and are likely to hunt when accompanied by other males. In addition, there was a strong association between meat sharing and coalitionary support. Males that shared meat
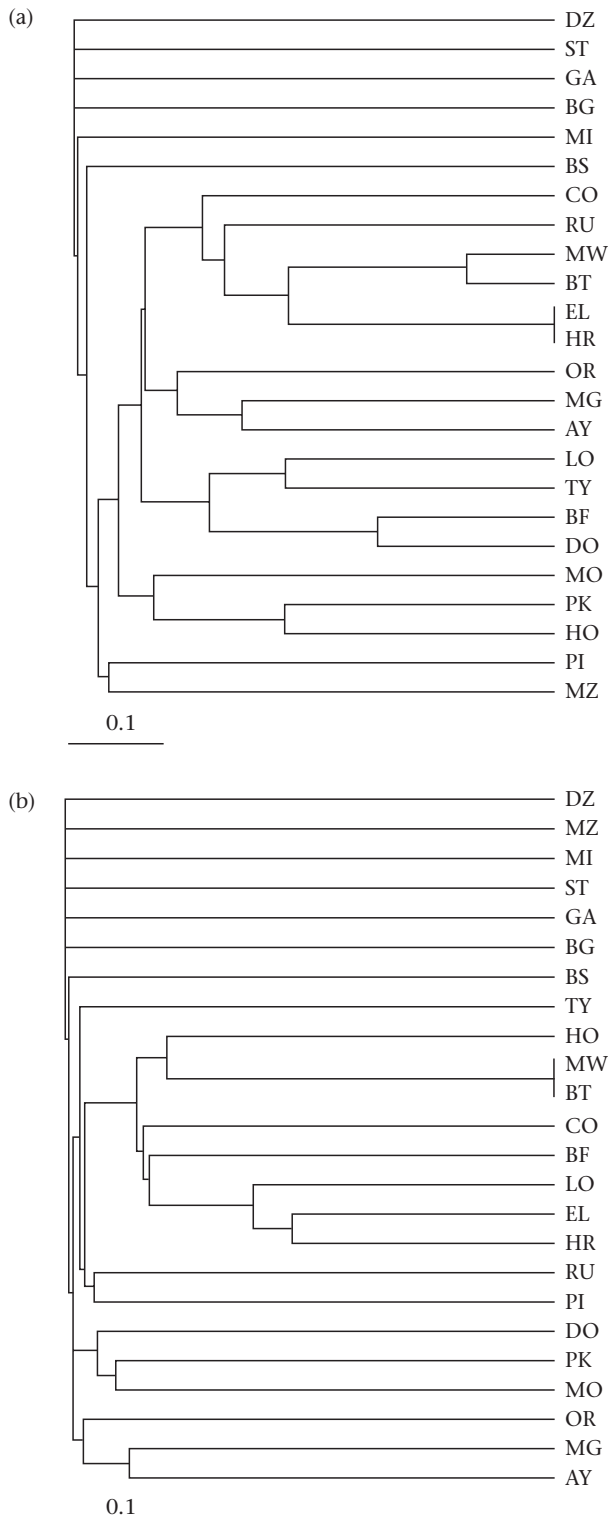
(a)

(b)

Figure 3. UPGMA cluster analysis dendrograms of (a) meat sharing and (b) coalitions between adult male chimpanzees.
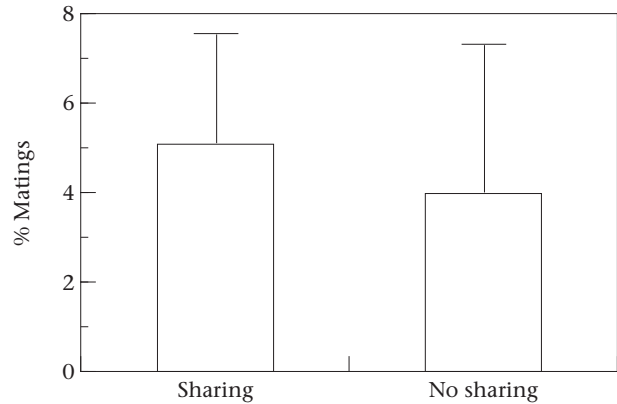

Figure 4. Mating success as a function of meat sharing. The percentage of matings that males achieved during oestrous cycles in which they shared meat versus those in which they did not share meat. Data for 12 male–female dyads are shown. Means+1 SD are displayed.

commonly received agonistic aid. Our results do not support alternate hypotheses that posit hunting compensates for nutritional shortfalls or males use meat to increase mating opportunities. The Ngogo chimpanzees hunt predominantly when food is abundant. After controlling for male participation in hunting parties, the presence of oestrous females does not predict the tendency to hunt. Although male chimpanzees share meat more often with oestrous females compared with anoestrous females, three additional observations are not easily reconciled with the hypothesis that an intersexual function underlies the motivation to hunt. First, meat is shared infrequently with oestrous females. Second, meat-for-sex exchanges are not common. Third, males do not gain a mating advantage by sharing meat. In the following, we explore some general implications of these findings.

Teleki (1973) was the first to hypothesize explicitly that chimpanzees hunt to compensate for nutritional short-falls. Early observations at Gombe did not support the suggestion that changes in food availability alone accounted for the tendency of chimpanzees to hunt. Between 1970 and 1975 there was little evidence of seasonal variation in hunting nor was there a correlation between seasonal changes in chimpanzee body weight and predation frequency (Wrangham 1975; Wrangham & Bergmann-Riss 1990). Stanford (1996, 1998; Stanford et al. 1994) revived inquiry into the nutritional basis of chimpanzee hunting decisions through an examination of more recent observations from Gombe. His analysis indicated that between 1982 and 1991 chimpanzee pre-dation frequency increased in the dry seasons, the hypothesized periods of food shortage. Until now a lack of precise information regarding food availability has precluded a direct test of the nutritional shortfall hypothesis. While dry seasons appear to correlate with fruit-poor times at some chimpanzee research sites (e.g. Ndoki, Kuroda et al. 1996), no data have been presented to ascertain whether this is also true at Gombe. In fact, fruit abundance does not correlate with rainfall at the Lope Reserve, Gabon (Tutin et al. 1991). In addition, fruit production varies 'unpredictably' at Kanyawara in Kibale (Wrangham et al. 1996), and our own observations show that there is no relationship between rainfall and the abundance of ripe fruit at Ngogo.

The results presented here disprove the hypothesis that chimpanzee hunting takes place to compensate for nutritional shortfalls. At Ngogo, we have established for the first time a positive relationship between hunting frequency and fruit availability. But why do chimpanzees hunt when there is an abundance of food? Two factors are likely to play a role here. First, hunting is an energetically expensive activity (Boesch 1994b). Energy gains from successful hunts will sometimes outweigh the costs (Boesch 1994b), but this may not always be the case, at least for many participants. Hunting patrols, during which chimpanzees may walk for hours without feeding (Mitani & Watts 1999), add to the energetic cost of hunts at Ngogo. Hunting here occurs most often when the chimpanzees can easily meet their daily energy needs because they have large fruit crops available. Thus, hunting and patrols are to some extent luxury activities that occur when no risk of energy shortfalls exists. We suspect that this is true at other sites also, but only observations that incorporate direct measures of food availability and feeding behaviour can properly address this question. Second, party size and the number of adult males in each party are known to vary positively with fruit availability at the only two sites for which quantitative observations exist, Kanyawara (Chapman et al. 1995; Wrangham 2000) and Ngogo (J. C. Mitani, D. P. Watts & J. S. Lwanga, unpublished data). Party size and the number of adult males in turn affect hunting success. Success at Ngogo and elsewhere increases as a function of both hunting group size and the number of male hunters (Boesch & Boesch 1989; Stanford 1998; Mitani & Watts 1999). These relationships suggest that chimpanzees base their hunting decisions in part on an assessment of whether they will be successful. Chimpanzees hunt when ecological conditions permit the formation of parties containing a large number of adult male hunters that are likely to succeed in capturing prey. In contrast, chimpanzees that associate in small parties during food-poor times generally forego hunting attempts (references above).

Teleki (1973) was also the first to propose that male chimpanzees might hunt to increase their mating opportunities, a view that has been subsequently advocated by Stanford (Stanford 1996, 1998; Stanford et al. 1994). Despite widespread interest and publicity garnered by the meat-for-sex hypothesis, only scant data exist to support it. The paucity of behavioural observations that show meat is reliably exchanged for matings is difficult to resolve with this hypothesis, as is the fact that oestrous females do not consistently obtain meat through their begging efforts at hunts. Instead of bartering meat for sexual favours, our observations support an alternate hypothesis that hunts ensue to facilitate social exchanges between males (Nishida et al. 1992; Nishida & Hosaka 1996). The results presented here reveal that: (1) the presence of males is the best predictor of a chimpanzee's decision to hunt; (2) meat sharing takes place nonrandomly and reciprocally between males; and (3) males exchange meat for significant social aid.

Cooperative hunting appears to occur regularly among chimpanzees in the Taï National Park, Ivory Coast (Boesch & Boesch 1989; Boesch 1994b). Observations of the Taï chimpanzees have led Boesch (1994b) to propose an additional hypothesis that links meat sharing with cooperative hunting: male chimpanzees selectively share meat with others that have cooperated with them to make kills (Boesch 1994b). According to this hypothesis, a selective pattern of meat sharing ensures that 'bystanders', individuals that are present but fail to participate in hunts, do not obtain meat and are thus unable to exploit the hunting efforts of cooperators. We cannot address this hypothesis given the rarity with which the Ngogo chimpanzees cooperate to capture prey. Chimpanzees at Ngogo, like those elsewhere in East Africa, do not generally coordinate their actions nor cooperate during hunts of red colobus (Uehara et al. 1992; Stanford 1998; Mitani & Watts 1999; Watts & Mitani, in press). Instead, the Ngogo chimpanzees typically pursue red colobus prey individually, while simultaneously exploiting the actions of other hunters. Although we recognize the theoretical importance of distinguishing cooperators from 'cheaters', making this distinction is problematic methodologically and empirically. Methodologically, prevailing observation conditions do not permit us to record in detail the behaviour of all chimpanzees during hunts. The empirical justification for such a distinction is questionable since individual chimpanzees frequently alternate between active hunters and passive bystanders at the same hunt.

Our observation that the number of males in a hunting party is the best predictor of whether a hunt will occur contrasts with an earlier finding from Gombe that showed the tendency to hunt is affected primarily by the presence of oestrous females (Stanford et al. 1994). We propose that this apparent discrepancy results from an important methodological difference between these studies. The Gombe analysis examined the relationship between the propensity to hunt and the number of oestrous females by lumping data over an 11-year period and subsequently using mean monthly values in a standard regression analysis. Pooling data in this fashion is likely to obscure much of the variation that might exist between the two variables of interest. In contrast, the logistic regression technique employed here maintains the inherent variability in the data set by treating each encounter with prey species as an independent data point. It remains to be seen whether reanalysis of the Gombe data in the manner done here will yield significantly different results.

In summary, current evidence is consistent with the hypothesis that male chimpanzees hunt to obtain meat, a high-quality food item that is used to develop and maintain social relationships with other males. As recognized by Stanford (1998), multiple factors are likely to affect why chimpanzees hunt. In this context it is important to stress that we do not suggest that male chimpanzees will forego using meat to achieve matings with females. On the basis of the analyses presented here, we simply dispute the hypothesis that meat-for-sex exchanges provide the primary motivation for male chimpanzees to hunt (cf. Stanford et al. 1994). In similar fashion, although our results do not support the hypothesis that chimpanzees hunt to compensate for nutritional shortfalls, the meat

provided through hunting may satisfy specific nutritional requirements, such as fat, protein, or trace nutrients (Stanford 1996, 1998). Additional research will be required to evaluate this hypothesis and to clarify how various ecological, reproductive and social factors interact to affect chimpanzee hunting decisions and meat sharing.

Acknowledgments

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