Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation

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Social predation (hunting in groups) presents a collective action problem. If nonhunters can obtain meat following a kill, it is unclear why an individual would choose to incur hunting costs. We explored this question using long-term data on chimpanzees from Kanyawara (Kibale National Park, Uganda) to test why hunting probability increases with chimpanzee party size. Social predation was not simply a function of the additive probability of intrinsic individual hunting rates. The potential for sharing meat with preferred social partners or sexually receptive females did not increase hunting probability, and there was no evidence of collaboration. Instead, individual variation in hunting motivation was critical for predicting hunting. Two 'impact' males had persistently high hunting rates, and hunts rarely occurred in their absence. When present, these males acted as hunting 'catalysts'. We argue that the profitability of social predation for chimpanzees differs from social carnivores, for which energy maximization is the expected goal. Since meat contains valuable micronutrients that complement a predominantly plant-based diet, obtaining even a small amount of meat is likely to be beneficial to a chimpanzee. We found that the probability that a male obtained meat increased with the number of hunters, and thus social predation was economically profitable. However, in the largest parties, hunters and nonhunters were equally likely to obtain meat, suggesting that there was incentive to refrain from hunting. Together, our results show that the catalytic action of impact males promotes cooperative hunting to a degree, but the collective action problem persists in large parties.

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Keywords: by-product mutualism; chimpanzee; cooperative hunting; individual variation; payoff currency; predation

Social predation (hunting in groups) presents a collective action paradox. Hunting is energetically expensive and dangerous, and after a kill, nonhunters are often able to obtain meat (African lions, *Panthera leo*: Packer & Pusey 1985; grey wolves, *Canis lupus*: L. D. Mech, personal communication; orcas, *Orcinus orca*: Hoelzel 1991; spotted hyaenas, *Crocuta crocuta*: Holekamp et al. 1997; chimpanzees, *Pan troglodytes*: Boesch 1994b). It would therefore seem detrimental to an individual's fitness to risk hunting when instead one could reap the benefits of others' behaviour without paying the costs.

Nevertheless, social predation is taxonomically widespread and is commonly cooperative (for reviews, see Packer & Ruttan 1988; Creel & Creel 2002), meaning that an individual's net payoff is higher when hunting with others than when hunting solitarily (Packer & Ruttan 1988; Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995). Therefore, many species have evidently solved the collective action problem. However, evidence of economic profitability does not explain why specific individuals initiate or join the cooperative effort. One possibility is that all individuals have the same intrinsic motivation to hunt. Alternatively, hunting propensity could vary among individuals or by context. For example, willingness to cooperate could vary according to which individuals are present, similar to the finding in captivity that a chimpanzee's decision to cooperate is affected by its social relationship with a potential collaborator (Melis et al. 2006). Such ideas have different implications for the evolution and maintenance of social predation, but cannot be evaluated currently because little is known about the behaviour of specific individuals during group

hunts. Our aim in this study, therefore, is to understand the contribution of individual hunting motivation to social predation.

Chimpanzees commonly prey upon red colobus monkeys (*Procolobus* spp.; Goodall 1986; Boesch & Boesch 1989; Uehara 1997; Mitani & Watts 1999; Hosaka et al. 2001), an arboreal primate that lives in troops of nine to more than 130 individuals (Struhsaker & Leland 1987, T. Snaith, personal communication). The costs associated with hunting red colobus monkeys are considerable. Chasing agile, arboreal prey is energetically expensive (Boesch 1994b), and adult male red colobus monkeys attack and mob hunters (Busse 1977; Boesch & Boesch 1989; Stanford 1995). Adult male chimpanzees are responsible for more than 95% of kills, although females sometimes participate (Boesch & Boesch 1989; Uehara et al. 1992; Stanford et al. 1994a; Mitani & Watts 1999). Chimpanzee predation upon red colobus monkeys can be classified as social predation because hunting frequency increases with party size. Specifically, at four study sites where the two species are sympatric, there is a strong positive association between adult male party size (the number of adult male chimpanzees in a party that encounters red colobus monkeys) and the probability of hunting by at least one male (Gombe National Park, Tanzania: Gilby et al. 2006; Mahale Mountains National Park, Tanzania: Hosaka et al. 2001; Ngogo, Kibale National Park, Uganda: Mitani & Watts 2001; Kanyawara, Kibale National Park: Gilby & Wrangham 2007).

Here we used long-term data from the Kanyawara chimpanzee community to test why hunting probability (defined as the probability of hunting by at least one male) increases with party size. In all, we tested five hypotheses. Together, they allowed us to evaluate (1) how individual variation might affect group-level behaviour and (2) how individuals benefit from social predation.

Additive Probability

The most parsimonious explanation for why hunting probability increases with party size is the 'additive probability' hypothesis (Gilby et al. 2006), which proposes that by simple probability, large parties will be more likely to contain at least one male that will hunt. This leads to the assumption that males have similar intrinsic hunting rates that are unaffected by male party size. It predicts that the probability of hunting by at least one male will be statistically similar to $[1 - (1 - H)^N]$, where H is the intrinsic (lone) individual hunting rate and N is the number of adult males present. The additive probability hypothesis is mutually exclusive with respect to the remaining hypotheses, which hinge upon variation in individual hunting rates within and between individuals and contexts.

Impact Hunters

The second hypothesis is based on evidence of variation in intrinsic hunting rates among individual males. Chimpanzee communities in different study sites often contain at least one male informally described as having a particularly high hunting rate (Gombe: Frodo: Stanford 1998; Gilby 2004; Ngogo: Monk: Watts & Mitani 2002b; Taï: Snoopy: Boesch & Boesch 1989; Brutus: Boesch & Boesch-Achermann 2000). We label such males as 'impact hunters'. The impact hunter hypothesis proposes that the probability of hunting (by at least one male) increases with party size because large parties are more likely to contain an impact hunter. It predicts that at a given party size, a hunt will be more likely to occur if an impact hunter is present.

The actions of an impact hunter might also serve as a 'catalyst' for others. Anecdotal observations suggest that impact hunters may initiate hunts, thus bearing the brunt of red colobus defence, which includes mobbing and physical attacks (Busse 1977; Boesch & Boesch 1989; Stanford 1995). For example, at Kanyawara, Imoso and Johnny commonly climb higher than other males and are the first to be confronted by adult male colobus (R. W. Wrangham, personal observation). At Gombe, males often remain on the ground until Frodo hunts, at which point they start hunting (I. C. Gilby, personal observation). At Ngogo, Monk is usually one of the first to attack if conditions are favourable, apparently prompting others to follow (D. P. Watts, personal communication).

The 'Meat-scrap' Hypothesis

A complementary and frequently cited explanation for why hunting probability increases with party size is that there is a greater payoff for hunting in groups, thus an incentive to hunt with others. Many studies of social carnivores demonstrate an increase in per capita meat intake and/or net energy gain with group size (meta-analysis: Creel & Creel 2002). However, there is little evidence that chimpanzees hunt in response to an energy shortfall. Contrary to that expectation, hunting frequency at our research site was positively correlated with diet quality, even when controlling for increases in party size (Gilby & Wrangham 2007). In two other sites, hunting frequency was also higher during periods of high food availability, but there was no effect of food availability on hunting once party size was controlled for (Gombe: Gilby et al. 2006; Ngogo: Mitani & Watts 2005). No chimpanzee populations have been reported to hunt more when preferred plant foods are scarce.

Thus, hunting by chimpanzees does not appear to be motivated by an energy shortfall. This is not surprising, since their diet is chiefly composed of fruit, leaves and pith (Wrangham 1977; Goodall 1986). However, most researchers agree that meat is a concentrated source of vitamins, minerals and other essential micronutrients that are beneficial in small quantities (Teleki 1973, 1981; Takahata et al. 1984; Boesch 1994a; Stanford 1996; Mitani & Watts 2001; Milton 2003). Consequently, an individual might benefit by obtaining even a small amount of meat (Boesch & Boesch-Achermann 2000). If a male's likelihood of obtaining meat increases with the number of hunters, then social predation would be economically profitable, and therefore cooperative. A recent mathematical model supports this idea (C. Tennie, I. C. Gilby & R. Mundry, unpublished data).

Collaboration

Our fourth hypothesis is that larger parties create more opportunities for collaboration, whereby hunters 'perform different complementary roles all directed towards the same prey' (Boesch & Boesch-Achermann 2000). In support of this idea, these authors reported that 75% of hunts at Taï involve 'drivers', 'blockers' and 'ambushers', which all contribute to the capture of a single monkey. At most sites, however, the thickness of the forest and confusion of the hunt prevents reliable detailed classification of specific hunting roles (Mitani & Watts 2001; Hosaka et al. 2001; Gilby et al. 2006). Nevertheless, the collaboration hypothesis does generate two testable predictions for such sites. First, an individual male's hunting probability should increase with male party size. Second, collaboration will depend on the behaviour of other males (Boesch 2002). For example, the effectiveness of a driver's behaviour is contingent upon the participation of blockers and ambushers. A hunter must be confident that his partners will not lose their motivation and defect at a critical moment. Therefore, this predicts that a male should be more likely to hunt if a frequent association or grooming partner also hunts.

Social Exchange

The fifth hypothesis is that hunting probability increases when the hunters have opportunities to exchange meat for social favours.

Male social bonding

Chimpanzees have been reported to reciprocally exchange meat for grooming and coalitionary support in two communities (Mahale: Nishida et al. 1992; Ngogo: Mitani & Watts 2001; Mitani 2005). This raises the possibility that the potential for trading meat serves as an added incentive for hunting (Stanford et al. 1994b; Mitani & Watts 2001). The 'male social bonding' hypothesis predicts that an individual's probability of hunting will increase with the presence of a preferred association or grooming partner, which should be more likely in large parties.

Hunt-for-sex

Stanford et al. (1994b) proposed that males may be more likely to hunt if sexually receptive females are present. This now seems unlikely since there is little evidence to support the idea that male chimpanzees trade meat-for-sex with sexually receptive females (Mitani & Watts 2001; Gilby 2006). However, if this 'hunt-for-sex' idea was correct it could in theory explain why hunts are more likely in large parties, since sexually receptive females are a well-known predictor of party size (Stanford et al. 1994b; Matsumoto-Oda 1999; Anderson et al. 2002; Mitani et al. 2002; Emery Thompson & Wrangham 2006). Thus, the 'hunt-for-sex' hypothesis predicts that after statistically controlling for male party size, a male will be more likely to hunt if at least one sexually receptive female is present.

METHODS

Study Site and Population

The Kanyawara chimpanzee community ranges over an area of approximately 32 km^2 (Wilson 2001) within Kibale National Park, Uganda, and has been systematically studied since 1988. Individuals were habituated to the presence of human observers without provisioning. The ecological characteristics of the study site have been described in detail elsewhere (Chapman & Wrangham 1993). This study uses data collected between January 1996 and December 2004, during which the size and composition of the community remained relatively constant, with 10−12 adult males and 13−18 adult females. Among the adult males, there is only one suspected pair of maternal brothers and no suspicions of other genetic relationships.

Data Collection

Each day, a team of observers, which typically included two to three Kibale Chimpanzee Project research staff and one to two graduate students, located a chimpanzee party by consulting nesting information from the previous day, listening for vocalizations, or visiting recent feeding sites. The team followed the party for as long as possible, usually until the animals built their night nests. Whenever possible, one observer conducted a 10-min follow of a randomly chosen target individual within the party. At 2-min intervals, he used scan sampling (Altmann 1974) to record which (if any) chimpanzees were grooming with the target. After 10 min, the observer chose another target, rotating through all chimpanzees in the party.

Additionally, at 15-min intervals, another observer systematically recorded party composition and noted whether red colobus monkeys could be detected within 100 m of the chimpanzees (hereafter referred to as a 'red colobus encounter').

When a red colobus encounter occurred, the observers simultaneously used ad libitum sampling (Altmann 1974) to record which (if any) chimpanzees hunted. Here, we define 'hunting' as 'climbing in pursuit of prey' (Gilby et al. 2006; Gilby & Wrangham 2007). This simple binary variable can be recorded for the majority of chimpanzees present at an encounter, and is unlikely to vary among observers. When the chimpanzee party was widely scattered, the research team spread out so as to be able to monitor the behaviour of as many individuals as possible. At each successful hunt, the observers recorded which chimpanzees captured monkeys, and which ultimately obtained meat. After a hunt (successful or unsuccessful), the team compiled their observations into a single account and entered relevant data into hunt-specific data sheets. Confidence in the accuracy of the data comes from the presence of several observers (including R.W.W. and/or graduate students), dedicated to obtaining detailed documentation of each hunt through immediate collaborative discussion and sharing of reports. We were unable to assess observer reliability specifically in the hunting context, but observers scored highly in interobserver reliability tests for other data collection procedures (Kibale Chimpanzee Project, unpublished data).

Analysis

Choosing focal individuals

As described above, data on red colobus encounters and hunts came from party-level observations. However, many of our predictions pertain to the actions of an individual male within a party. Thus, for each analysis, we used a random number generator to choose (post hoc) one focal male out of a pool of candidates. For clarity, we identify the pool of candidate males for each analysis in the Results section.

Preferred grooming partners

We used data from the 10-min follows to identify preferred grooming partners. To reduce pseudoreplication and biased sampling of 'interesting' behaviour (which might prompt an observer to initiate a 10-min follow), we used only the last scan of each follow in our analyses. We calculated the following grooming index for each male dyad AB:

$$\frac{A_F(B_G) + B_F(A_G)}{A_F(B_P) + B_F(A_P)}$$

where $A_F(B_G)$ = the number of instances A was the target of a 10-min follow and was grooming with B, $B_F(A_G)$ = the number of instances B was the target of a 10-min follow and was grooming with A, $A_F(B_P)$ = the number of instances A was the target of a 10-min follow and B was in same party, and $B_F(A_P)$ = the number of instances B was the target of a 10-min follow and A was in the same party. We calculated this index for each of three 2-year time periods (1999–2000, 2001–2002, 2003–2004).

If the grooming index (for a given time period) for dyad AB was more than half a standard deviation above the means of both A and B, we classified A and B as 'preferred grooming partners'. There were five pairs of preferred grooming partners in 1999–2000, seven in 2001–2002 and eight in 2003–2004.

Preferred association partners

To identify preferred association partners, we used data from a recent study of association patterns among Kanyawara chimpanzees (I. C. Gilby & R. W. Wrangham, unpublished data). For the same three time periods used above, we calculated the simple ratio index of association (Cairns & Schwager 1987) for each adult male dyad, based on time spent in the same party. If the simple ratio index for dyad AB was more than half a standard deviation above the means of both A and B, then we classified A and B as having a 'mutual affinity' for one another. This procedure was repeated using two other independent indexes based on nearest neighbour frequency and time spent within 5 m of one another. Males were classified as preferred association partners if they showed mutual affinity for one another in at least two of the three indexes. These social bonds tended to last for several years. There were five pairs of preferred association partners in 1999–2000 and six in 2001–2002 and 2003–2004. Data were not sufficient to identify such pairs by this technique prior to 1999.

Statistics

We used SAS 9.1 (SAS Institute, Cary, NC, U.S.A.) for all statistical analysis. For all focal-level analyses, we used generalized estimating equations (GEE; Diggle et al. 2002) to control for repeated observations of the same male. All tests were two tailed, with significance set at $\alpha = 0.05$.

RESULTS

Between January 1996 and December 2003, there were 610 encounters with red colobus monkeys when at least one adult male chimpanzee was present in the party. A party-level hunt (hunting by at least one male) occurred in 99 (16%) of these encounters. Of these hunts, 49 (49.5%) were successful (resulting in at least one kill). For all focal-level analyses, we excluded 14 hunts for which observers were unable to identify all hunters.

Additive Probability

There were 98 encounters with red colobus monkeys when only one adult male chimpanzee was present. That male hunted in one of these encounters, thus the lone hunting rate (H) was 0.0102 (1/98). Using this value of H, we calculated the expected probability of a party-level hunt occurring for parties containing 1–11 males, using the predictive equation described in the Introduction. In all parties containing more than two males, the actual party-level hunting rate was significantly higher than that predicted by the additive probability hypothesis ($\chi^2_{10} = 171.7$, $P < 0.001$; Fig. 1).

Accordingly, there was a significant positive association between the probability that the focal male (randomly chosen post hoc from all males that were present at a red colobus encounter) hunted and male party size (GEE logistic regression: odds ratio = 1.23, $\chi^2_1 = 12.4$, $P = 0.0004$). The data indicate that focal male hunting probability reached a maximum in six-male parties (Fig. 2). Therefore, we fitted a logistic GEE model for focal hunting with a piecewise linear trend for male party size. This allowed focal hunting probability to increase with male party size up to a threshold
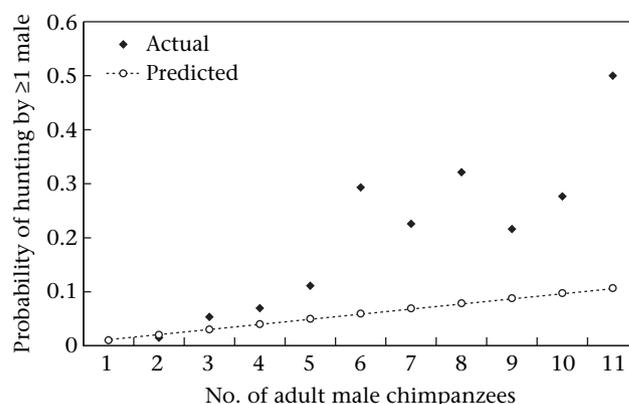

Figure 1. Party-level hunting rate (hunts/encounters) versus male party size. The observed hunting rate of parties with more than two males was significantly higher than that predicted by the additive probability hypothesis.

and then to level off or decrease. Indeed, there was a positive association between male party size and focal hunting probability in parties containing up to six males (odds ratio = 1.7, $\chi_1^2 = 11.7$, $P = 0.0006$), but no association between the number of males and focal hunting probability in larger parties ($\chi_1^2 = 0.35$, $P = 0.56$; Fig. 2, solid line). Since traditional goodness-of-fit tests are not available for GEE models, we calculated the sum of squared errors (SSE) by summing the squared difference between the observed outcome (hunt = 1, no hunt = 0) and the predicted probability over all observations for this threshold model and compared it to a model with a simple linear trend. The piecewise linear model with the threshold set at six males had a lower SSE (39.3) than the simple linear model (40.0), indicating that including an inflection point at six resulted in a better-fitting model. Similarly, it provided a better fit than models with inflection points at five (SSE = 39.5) or seven (SSE = 39.6).

At Gombe, Gilby et al. (2006) found a negative association between the presence of sexually receptive females and hunting probability. If a similar relationship holds in Kanyawara (see Hunt-for-Sex results, below), a possible explanation for the lack of a relationship with male party size in large parties is that parties with more than six males were more likely to contain a sexually receptive female (logistic regression: odds ratio = 1.36, $\chi_1^2 = 7.2$, $P = 0.007$). However, when we statistically controlled for the presence of sexually receptive females using multiple logistic regression, the results remained the same. The effect of male party size on hunting rate remained statistically significant in parties with up to six males (GEE logistic regression: odds ratio = 1.75, $\chi_1^2 = 13.9$, $P = 0.0002$) but not in larger parties (odds ratio = 0.96, $\chi_1^2 = 0.06$, $P = 0.81$).

The poor predictive power of the additive probability model, coupled with the strong relationship between individual hunting probability and male party size in small parties, allows us to reject the additive probability hypothesis.
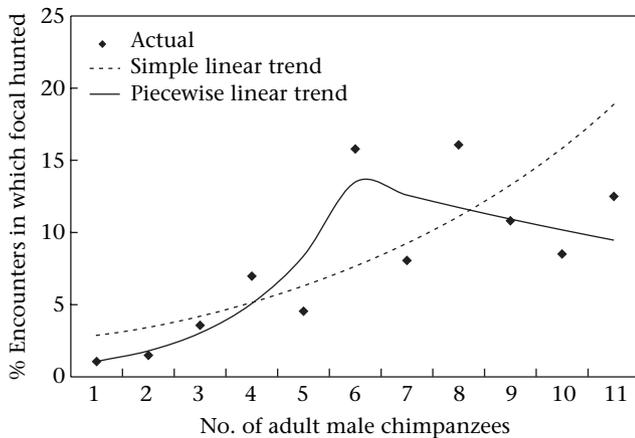
Figure 2. Relation between focal hunting probability and male party size. There was an overall positive association between male party size and the probability that the focal male hunted. However, a simple logistic regression with the number of adult males as a simple linear trend (dashed line) indicates a poor fit at large party sizes. Indeed, a logistic regression model with the number of adult males as a piecewise linear trend (solid line) indicated that there was no association between male party size and hunting by the focal male in parties with more than six males.

Impact Hunters

We classified MS and AJ as impact hunters because they had hunting rates (hunts/encounters) greater than 1 SD above the mean (MS: 0.205, AJ: 0.198; Table 1). In support of the impact-hunter hypothesis, the likelihood of a party-level hunt was considerably greater in 'impact' parties (AJ and/or MS present) than 'nonimpact' parties (logistic regression: odds ratio = 48.7, $\chi_1^2 = 14.62$, $P < 0.0001$), even after controlling for male party size using multiple regression (odds ratio = 16.94, $\chi_1^2 = 7.46$, $P = 0.006$; Fig. 3). In fact, there was only one hunt in the 170 encounters by nonimpact parties. These results demonstrate that the presence of an impact hunter was an important predictor of party-level hunting.

The influence of impact hunters could simply be due to their own high hunting rates, or additionally by promoting an increased rate of hunting by other males. We found that for a given encounter by an impact party, the probability that the focal male (randomly chosen post hoc from all nonimpact males that were present) hunted was much higher if an impact male hunted (logistic regression: odds ratio = 7555, $\chi_1^2 = 63.12$, $P < 0.0001$), even after controlling for male party size (odds ratio = 8690, $\chi_1^2 = 56.74$, $P < 0.0001$). Nonimpact males hunted on only 1.2% (4/333) of occasions when impact males were present but did not hunt. This, coupled with the low hunting rate by nonimpact parties, strongly supports the hypothesis that highly motivated hunters serve as catalysts for others.

The Meat-scrap Hypothesis

In accordance with the meat-scrap hypothesis, a focal hunter (randomly chosen post hoc from all males that hunted) was more likely to obtain meat (through capture, sharing and/or scrounging) as the number of hunters increased (GEE logistic regression: odds ratio = 1.38, $\chi_1^2 = 17.89$, $P < 0.0001$). This was probably because the probability of a hunt succeeding increased with the number of hunters (logistic regression: odds ratio = 1.71, $\chi_1^2 = 12.7$,

Table 1. Individual encounter, hunt and kill rates for adult male chimpanzees

Male ID	Red colobus encounters	Hunted	Hunts/ encounters	Kills	Kills/ hunts
AJ*	308	61	0.198	16	0.262
BB	229	12	0.052	6	0.500
BF	61	8	0.131	2	0.250
KK	263	32	0.122	5	0.156
LB	158	14	0.089	3	0.214
LK	392	20	0.051	2	0.100
LM	31	2	0.065	1	0.500
MS*	366	75	0.205	17	0.227
PG	112	5	0.045	1	0.200
SL	168	13	0.077	0	0.000
ST	291	16	0.055	6	0.375
SY	108	0	0.000		
TU	204	21	0.103	11	0.524
YB	317	13	0.041	4	0.308

Asterisks indicate 'impact' hunters, which had hunting rates greater than 1 standard deviation above the mean.
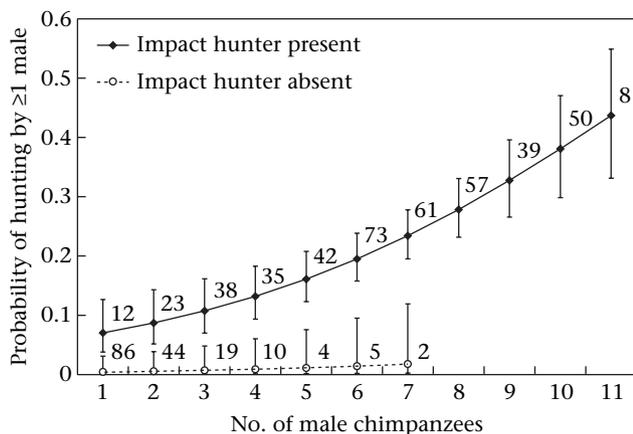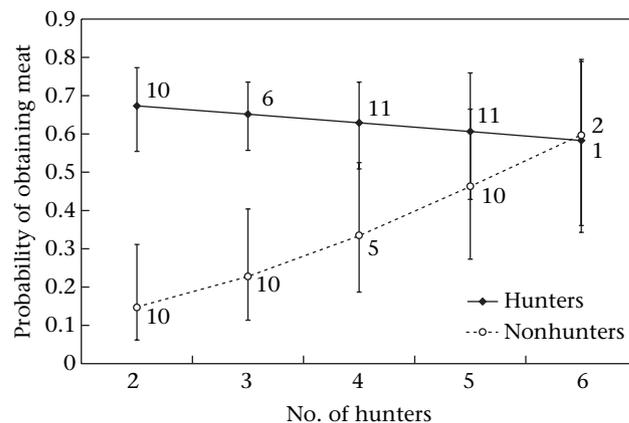
Figure 3. Probability of hunting by at least one male versus male party size. Regression lines are from the multiple logistic regression described in the text. Error bars represent 95% confidence intervals. Parties that contained at least one 'impact' hunter (AJ, MS) were significantly more likely to hunt than parties without an impact hunter.

Figure 4. The relation between the probability of obtaining meat, the number of hunters and a male's participation in a hunt. Values are point estimates from the multiple logistic regression described in the text. Error bars represent 95% confidence intervals, and numbers indicate sample sizes. When only a few males hunted, hunters were more likely to obtain meat than nonhunters. However, if many males hunted, nonhunters and hunters were equally likely to obtain meat.

$P = 0.0004$). These results suggest that once a hunt occurred, it was in a male's best interest to hunt rather than remain on the ground. However, an analysis of meat distribution among hunters and nonhunters at successful hunts suggests that the relative benefits of hunting versus scrounging diminished with the number of hunters. The focal hunter had an almost constant probability of obtaining meat (~ 0.65), independent of the number of other males that hunted (GEE logistic regression: $\chi_1^2 = 0.39$, $P = 0.53$; Fig. 4). In contrast, the probability that a focal nonhunter (randomly chosen post hoc from all nonhunters) obtained meat was lower, but rose with larger numbers of hunters (odds ratio $= 1.71$, $\chi_1^2 = 14.12$, $P = 0.0002$) to approach that of hunters (Fig. 4). Owing to small sample size, we excluded the four kills in which there were seven or more hunters. However, visual examination of these hunts' data gave no indication of differing results.

Therefore, assuming that a scrap of meat is beneficial, if several males are already hunting, it is in an individual's best interests to refrain from hunting and obtain meat by begging or scrounging.

Collaboration

The collaboration hypothesis predicted that a male would be more likely to hunt if his preferred association or grooming partner hunted. This was not the case. For the 53 hunts at which at least one pair of preferred association partners was in the party, the probability that the focal male (randomly chosen post hoc from all preferred association partners that were present) hunted did not increase if his preferred association partner hunted (GEE logistic regression: $\chi_1^2 = 0.9$, $P = 0.3$). Similarly, for the 58 hunts at which at least one pair of preferred grooming partners was present, the probability that the focal male (randomly chosen post hoc from all preferred grooming partners in the party) hunted was not affected by whether his preferred grooming partner hunted (GEE logistic regression: $\chi_1^2 = 1.39$, $P = 0.24$).

Social Exchange

Male social bonding

There was no evidence in support of the male social bonding hypothesis. The probability that the focal male (randomly chosen post hoc from all males that had at least one preferred grooming partner during that time period) hunted was not associated with the presence of his preferred grooming partner (GEE logistic regression: odds ratio $= 2.69$, $\chi_1^2 = 3.06$, $P = 0.08$). The fact that this relationship approached statistical significance is probably because the presence of a preferred grooming partner was positively correlated with adult male party size (GEE logistic regression: odds ratio $= 1.92$, $\chi_1^2 = 94.1$, $P < 0.0001$). Indeed, when we statistically controlled for adult male party size, the relation between hunting probability and the presence of a preferred grooming partner was far from statistically significant (GEE logistic regression: $\chi_1^2 = 0.67$, $P = 0.41$).

Similarly, the probability that the focal male (randomly chosen post hoc from all males that had a preferred association partner during that period) hunted was unaffected by the presence of his preferred association partner (GEE logistic regression: $\chi_1^2 = 0.25$, $P = 0.62$), even when we statistically controlled for adult male party size ($\chi_1^2 = 0.0001$, $P = 0.99$).

Hunt-for-sex

There was no association between the presence of at least one sexually receptive female and the probability that the focal male (randomly chosen post hoc from all males present) hunted when adult male party size was held constant (GEE logistic regression: odds ratio $= 0.55$, $\chi_1^2 = 2.99$, $P = 0.08$). In fact, the trend indicated that focal hunting probability decreased in the presence of sexually receptive females. These data offer clear evidence against the hunt-for-sex hypothesis.

DISCUSSION

Despite the theoretical importance of individual variation in the tendency to cooperate, there are few empirical data on the roles of specific individuals in group-level behaviour. We examined how individual variation may affect hunting in a social context. Our results show that specific 'impact' males had strong influences on the probability of hunting. They also suggest that the acquisition of even small amounts of meat may be sufficiently beneficial to provide an incentive for hunting with others. This implies that group hunting was economically profitable, and therefore cooperative. We frame our discussion of these points by reviewing each of our five hypotheses. We include evidence both from our Kanyawara study site and from other chimpanzee populations.

Hypotheses Rejected at Kanyawara and Elsewhere

Social exchange

Reciprocal exchange of meat, grooming and coalitionary support at some sites suggests that meat is a valuable tool for maintaining long-term cooperative relationships among males (reviewed in Muller & Mitani 2005). This has prompted the claim that the potential social benefit of obtaining (and subsequently sharing) meat serves as an added incentive for hunting (Stanford et al. 1994b; Mitani & Watts 2001). However, this was not the case at Kanyawara, where a male's likelihood of hunting was unaffected by the presence of his preferred association or grooming partner. We do not currently have data on coalition formation. However, at Ngogo, rates of coalition formation are highly correlated with association and grooming patterns (Mitani & Watts 1999), suggesting that the results would be similar.

Our study is the first to explicitly test the effects of association and grooming frequency on hunting probability. Nevertheless, our rejection of the male social bonding hypothesis is consistent with data from Gombe, where the hunting rates of focal males were not affected by male party size (Gilby et al. 2006), which was correlated with the presence of a closely bonded partner in our study.

Similarly, there was no evidence that the presence of sexually receptive females promoted hunting. In fact, there was a strong trend ($P = 0.08$) in the opposite direction: a focal male was less likely to hunt if at least one sexually receptive female was present. This is again consistent with data from Gombe, where males appear to forgo hunting opportunities in favour of mate guarding ('meat or sex', rather than 'meat-for-sex', Gilby et al. 2006), and do not share preferentially with sexually receptive females (Gilby 2006). Coupled with data from Ngogo, where there was no correlation between sexually receptive females and either hunting or sharing (Mitani & Watts 2001), this result adds to the growing body of evidence against meat-for-sex as an explanation for either hunting or sharing.

Thus, our results do not support the role of social exchange in the decision to hunt. Chimpanzees in captivity lack inhibitory control when faced with desired food items (Boysen & Berntson 1995; Boysen et al. 2001).

We therefore suggest that when given the chance to obtain a valuable food item, a male is unlikely to anticipate the social benefits of sharing it. Given that both our data and expectations from the laboratory challenge the social exchange hypothesis, we conclude that stronger evidence is required before it can be considered as viable.

Hypotheses Rejected at Kanyawara, Mixed Support Elsewhere

Additive probability

The additive probability hypothesis assumes that all males have equal intrinsic hunting tendencies, regardless of party size. By simple probability, large parties are then more likely to contain a male that will hunt (Gilby et al. 2006). However, in contrast to the core assumption of this model, we found that an individual male was significantly more likely to hunt in larger parties. This clearly shows a synergistic effect of multiple males.

This pattern is different from that found at Gombe, where there was no effect of party size on hunting by individual males (Gilby et al. 2006). This is likely to be a result of the relatively high hunting rate of single hunters at Gombe (Boesch 1994b). It remains to be seen whether chimpanzees in other populations follow the Gombe or Kanyawara pattern, since such analyses have not been applied elsewhere. Qualitatively, however, descriptions of hunting at other sites imply that as party size increases, a greater proportion of the party hunts (Muller & Mitani 2005). We suggest that ecological factors may be responsible for intersite variation in the rate at which single males hunt, which in turn affects whether the additive probability hypothesis applies.

Collaboration

Our results do not support collaborative hunting at Kanyawara. First, we found no evidence that preferred association or grooming partners coordinated their actions, which might be expected because of increased levels of trust under risky circumstances. Second, while the finding that individual hunting probability increased with male party size is consistent with the idea that males coordinate their actions, this was only true in relatively small parties. In parties with more than six males, the addition of another male did not increase a male's likelihood of hunting (Fig. 2). It is possible, although unlikely in our view, that too many males impede the ability of hunters to collaborate. We discuss a more parsimonious explanation for this pattern in the 'meat-scrap hypothesis' section below.

To assess the degree to which hunters collaborate, detailed observations of the precise movements of each individual are required. At most sites, including Kanyawara, such observations are prohibitively difficult. Qualitatively, however, collaboration has been judged to be 'rare' at Ngogo (Watts & Mitani 2002b) and Gombe (Busse 1977; Boesch 1994b). At Taï, in contrast, males have been reported to consistently adopt complementary roles, and 75% of hunts have been characterized as collaborative (Boesch 1994b; Boesch & Boesch-Achermann 2000; Boesch 2002). A possible explanation for the existence

of collaboration at Taï is that the physical characteristics of the forest there make it very difficult for hunters to succeed without collaboration (Boesch 1994b). Hunts in Gombe are most likely to occur and to succeed in woodland and semideciduous forest, where trees are short and the canopy is broken (Gilby et al. 2006). A similar pattern is observed at Ngogo, where hunts were more likely to occur in low and broken canopy than in primary forest (Watts & Mitani 2002b). It is possible that chimpanzees in Gombe and Ngogo collaborate when they need to (in primary evergreen forest), but not in areas where the chances of individual success are high.

Hypotheses Supported at Kanyawara and Elsewhere

The meat-scrap hypothesis

In obligate carnivores, the most common way to assess whether group hunting is economically profitable has been to determine the effect of the number of hunters on per capita meat consumption (or net energy gain). However, this pattern does not hold in most chimpanzee populations (Mitani & Watts 2001; Gilby et al. 2006; but see Boesch 1994b). This suggests that the profitability of group hunting for chimpanzees may differ from social carnivores. We suggest that because meat contains valuable micronutrients that complement a predominantly plant-based diet, obtaining a small amount might represent a favourable payoff to a chimpanzee. This predicts that group hunting would be favoured if it increased the chances that an individual obtained even a scrap of meat. Our data support this idea. As the number of hunters increased, a given male became more likely to get meat. Thus, we may conclude that hunting at Kanyawara is cooperative, at least to a point. At successful hunts with two to four hunters, hunters were more likely to obtain meat than nonhunters. However, at successful hunts with five or more hunters, nonhunters and hunters were equally likely to obtain meat (Fig. 4).

These results can explain why individual hunting probability reached an asymptote as male party size increased (Fig. 2). In small parties a male was more likely to obtain meat if he was one of the hunters, providing an incentive to hunt rather than cheat. However, in large parties, when scrounging was an equally effective strategy for getting meat, there was no longer a positive effect of party size on individual hunting probability. Further research is needed to identify the mechanism by which nonhunters in large parties were more likely to obtain meat. The most likely explanation is that successful hunts with many hunters yield greater absolute quantities of meat. The carcass(es) may be controlled by several individuals over the course of the meat-eating bout, thus creating more opportunities for nonhunters to beg or gather fallen scraps.

The meat-scrap hypothesis may also explain why studies of hunting at Gombe and Ngogo have failed to show that hunting is energetically profitable. At these sites, while the probability of a kill, the number of kills, and the total meat offtake (kg) increased with male party size, per capita meat availability did not (Gombe: Gilby et al. 2006; Ngogo: Watts & Mitani 2002a, b). At Gombe,

per capita net energy gain did not increase with the number of hunters (Boesch 1994b). However, if the probability of obtaining meat in any amount increased with party size, as we have shown, then social predation would be favoured in these communities.

Although the meat-scrap hypothesis has not previously been explicitly tested, data from other sites are consistent with our results. At Ngogo and Gombe, the number of males that obtained meat increased with party size (Ngogo: Watts & Mitani 2002b; Gombe: The Jane Goodall Institute's Center for Primate Studies, unpublished data).

Impact hunters

This study is the first to test the hypothesis that the positive association between male party size and party-level hunting in chimpanzees is explicable by the presence of particularly motivated hunters. This seemed reasonable, since our criterion for a party-level hunt was 'hunting by at least one male', and large parties were more likely to contain an 'impact' hunter. Indeed, we found that a hunt was considerably more likely to occur if MS and/or AJ were present, even after controlling for party size. In fact, parties without MS or AJ rarely hunted.

When MS and AJ were present, they also acted as hunting 'catalysts'. Other males were unlikely to hunt if MS or AJ remained on the ground. Perhaps, these males tended to wait for a decision from MS or AJ, who might be particularly adept at assessing the probability of success. If the most skilled hunters decided that a hunt was unlikely to succeed, then there would be little point in an average hunter launching an attack. Alternatively, average hunters might be initially wary of being the sole target of male colobus defence (which can be physically dangerous to chimpanzees), and wait for MS or AJ to make the initial strike. Once a hunt is in progress, the defensive efforts of the colobus must be spread among the hunters, thus reducing the costs for each individual. Detailed records of the timing of each male's movements would be required to further test this idea.

Since variation in intrinsic hunting rates among males has not yet been systematically described, the factors responsible for it are unknown. Informal observation suggests, however, that age is not a major factor, because certain individuals have been recognized as impact hunters for many years. Individual variation in skill could be important since the costs of hunting are likely to be lower for particularly skilled hunters.

To our knowledge, this is the first study to quantify the effect of specific chimpanzees on hunting dynamics. However, anecdotal evidence from other sites is consistent with our results. For example, at Taï, Boesch & Boesch (1989) attribute a significant change in overall success rate to the maturation of Snoopy, a particularly persistent hunter. Stanford et al. (1994a) show that 'skilful' hunters at Gombe caught more adults than less skilful hunters, thus influencing overall predation patterns. At Gombe and Ngogo, males often appear to base their hunting decisions on the actions of Frodo (I. C. Gilby, personal observation) and Monk (D. P. Watts, personal communication), respectively.

The effects of our impact hunters highlight the importance of individual behavioural tendencies as an

explanation for variation in cooperation within and between populations and species. For example, the death of a frequent initiator of cooperative territorial patrols at Ngogo resulted in a considerable decrease in patrolling frequency (D. P. Watts, personal communication). In species with role specialization (e.g. bottlenose dolphins, *Tursiops truncatus*: Gazda et al. 2005; African lions: Stander 1992), it is easy to imagine that the death of a crucial participant would drastically affect the dynamics of group action, assuming that no other individuals occupy the empty role.

Conclusions

Our data suggest that two previously unrecognized principles contribute to solving the problem of why more hunting occurs in larger groups. First is the importance of impact hunters. If certain individuals have intrinsically high hunting rates, their presence in a group makes hunting more likely both by their own efforts and by increasing the likelihood that others hunt. It is not known why, among chimpanzees, a few individuals often hunt at higher rates than others. Nevertheless, these individuals create low-cost opportunities for others to benefit by joining a hunt in progress.

Second is the idea that because chimpanzees benefit nutritionally from eating even small amounts of meat, it is not necessary for hunters to obtain energetic returns in proportion to effort expended. This principle can explain why chimpanzees are more likely to hunt even when additional hunters do not obtain greater quantities of meat.

Together, these results suggest that social predation in chimpanzees may be cooperative in an economic sense but may not reflect motivation for promoting collective action. If cooperative hunting emerges as a result of the action of impact hunters, the apparent cooperation of nonimpact hunters can be characterized as by-product mutualism. Thus, the critical question for understanding the solution to the collective action problem is very specific: why do impact hunters have high hunting rates? If the informal evidence suggesting that impact-hunting is characteristic of individuals over several years is supported, it will be possible to test the idea that impact hunters are cooperative in several contexts. Alternatively, they may be impulsive, skilled, risk-takers. Identification of the traits of impact hunters will facilitate exploration of the motivation behind social predation. If impact-hunting is found in other social carnivores it will likewise offer rich opportunities for analysing the mechanisms underlying economic cooperation and solutions to the collective action problem.

Acknowledgments

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