



Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*

IAN C. GILBY*, LYNN E. EBERLY†, LILIAN PINTEA* & ANNE E. PUSEY*

*The Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution and Behavior, University of Minnesota

†Division of Biostatistics, School of Public Health, University of Minnesota

(Received 29 September 2005; initial acceptance 2 November 2005;

final acceptance 4 January 2006; published online 6 June 2006; MS. number: A10257)

There has been considerable discussion of the factors that influence the hunting behaviour of male chimpanzees. Explanations invoking social benefits hinge upon the potential for males to share meat with sexually receptive females in exchange for mating ('meat for sex'), or to share meat with other males in exchange for social support ('male social bonding'). Ecological factors may also affect hunting: chimpanzees may hunt more frequently (1) in response to food shortages ('nutrient shortfall'); (2) when energy reserves are high ('nutrient surplus'); (3) in habitat types with good visibility and increased prey vulnerability; and/or (4) when ecological factors favour cooperative hunting. We used 25 years of data on chimpanzees in Gombe National Park, Tanzania, to examine the relative importance of social and ecological factors in the decision to hunt red colobus monkeys, *Colobus badius*. The presence of sexually receptive females was associated with a significant decrease in hunting probability, suggesting that males face a trade-off between hunting and mating ('meat or sex' rather than 'meat for sex'). Hunting by specific males did not vary with adult male party size, providing evidence against the male social-bonding hypothesis. After controlling for the effects of party size, diet quality was not associated with the probability of hunting or hunting successfully. Hunts were more likely to occur and to succeed in woodland and semi-deciduous forest than in evergreen forest, emphasizing the importance of visibility and prey mobility. Finally, per capita meat availability decreased with adult male party size, suggesting that hunting was not cooperative. These results provide evidence against social explanations for hunting in favour of more simple ecological alternatives.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Capture of mobile prey provides nutritional benefits, but even for specialized carnivores, can be costly in terms of energy expenditure and risk of injury (Packer & Ruttan 1988). Studies of hunting in a variety of species show that animals weigh these benefits and costs in hunting decisions. Ecological factors, particularly pursuit costs, are central to hunting studies (Creel & Creel 1995; Creel 1997; Packer & Caro 1997). African lions, *Panthera leo*, hunt more in areas where prey are most vulnerable

(Hopcraft et al. 2005), have better hunting success in long grass and on dark nights (Funston et al. 2001), and cooperate to capture large ungulates when the mutual benefits outweigh the costs (Grinnell et al. 1995). Similarly, wolves, *Canis lupis*, preferentially kill white-tailed deer, *Odocoileus virginianus*, in areas with increased stalking cover (Kunkel & Pletscher 2001). Wild chimpanzees have a diet composed chiefly of fruit and leaves, but they also capture and eat a variety of mammals, birds and other vertebrates (Wrangham 1977; Nishida et al. 1979; Goodall 1986), preying most frequently upon red colobus monkeys, *Colobus badius* (Uehara 1997; Mitani & Watts 2001). Recent studies of the factors that influence chimpanzee hunting decisions and success have emphasized the potential social benefits of hunting. Selective meat sharing may yield increased mating opportunities and/or aid in the maintenance of cooperative intrasexual relationships, thus providing added incentives for hunting. However, ecological factors are also likely to be

Correspondence and present address: I. C. Gilby, Department of Anthropology, Harvard University, 11 Divinity Ave, Cambridge, MA 02138, U.S.A. (email: gilby@fas.harvard.edu). L. E. Eberly is at the Division of Biostatistics, School of Public Health, University of Minnesota, Minneapolis, MN 55455, U.S.A. L. Pintea is now at The Jane Goodall Institute Africa Programs, 4245 N. Fairfax Drive, Arlington, VA 22203, U.S.A. A. E. Pusey is at the Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, MN 55108, U.S.A.

important determinants of hunting probability and success in chimpanzees, as they are in other predators.

In this study, we used 25 years of data from Gombe National Park, Tanzania to examine social and ecological explanations for male chimpanzee hunting behaviour. We used multivariate statistics to test several nonmutually exclusive hypotheses. This allowed us to examine the relative importance of a single variable while controlling for the potentially confounding effects of additional variables associated with alternative hypotheses.

Social Factors

Chimpanzees live in complex fission–fusion communities within which individuals travel in subgroups (parties) of changing composition (Nishida 1968; Wrangham & Smuts 1980; Goodall 1986). Males compete for dominance rank and may form reciprocal, cooperative social relationships or ‘alliances’ (de Waal 1989; Wrangham et al. 1992; Mitani et al. 2000). Females are considerably less social than males, except during periods of sexual receptivity (Goodall 1986; Mitani et al. 2002), when they develop a conspicuous anogenital swelling (Goodall 1986; Wallis 1997).

Male social bonding

The male social-bonding hypothesis proposes that the potential of using meat to foster intrasexual alliances provides a social incentive for hunting (Stanford et al. 1994b; Mitani & Watts 2001). This predicts that upon encountering a red colobus troop, a male chimpanzee will be more likely to hunt if there are many other adult males present, assuming that large parties are more likely to contain an ally (Mitani & Watts 2001). In support of this idea, several studies have reported that the probability of hunting (by at least one chimpanzee) increases with party size (Stanford et al. 1994b; Hosaka et al. 2001; Mitani & Watts 2001; R. W. Wrangham, personal communication). However, each male ultimately decides whether or not to hunt; therefore, it is more informative to conduct analyses at the level of the individual (i.e. the target of focal-animal sampling). No study to date has investigated the effect of party size on hunting by specific individuals.

Meat for sex

The ‘meat-for-sex’ hypothesis proposes that male chimpanzees hunt to obtain meat to entice swollen (sexually receptive) females to mate (Stanford et al. 1994b; Stanford 1998). This predicts that a male will be more likely to hunt in parties containing sexually receptive females, independently of the number of adult males. Using long-term data from Gombe, Stanford et al. (1994b) provided evidence consistent with the meat-for-sex hypothesis, reporting a positive correlation between the presence of swollen females and hunting frequency. In two communities in Kibale National Park, Uganda, however, there was no such correlation (Ngogo: Mitani & Watts 2001; Kanyawara: R. W. Wrangham, personal communication).

Ecological Factors

Nutrition

The availability of ripe fruit in chimpanzee habitat varies considerably over time, resulting in predictable and unpredictable nutrient shortfalls (Chapman et al. 1995; Wrangham et al. 1998). The ‘nutrient shortfall’ hypothesis proposes that hunting frequency will increase when fruit is scarce and chimpanzees need to supplement their diet with meat (Teleki 1973; Takahata et al. 1984; Stanford 1996, 1998). In support of this idea, two studies have reported that hunting frequency at Gombe was highest during the dry season (Stanford et al. 1994b; Gilby 2004), when body masses tend to be low (Pusey et al. 2005). However, it is unclear whether nutrition was responsible for this trend. An alternative, the ‘nutrient surplus’ hypothesis, proposes that a chimpanzee will be more likely to hunt when diet quality is high and it can more easily absorb the energetic costs of hunting (Mitani & Watts 2001). This idea is supported by data from Ngogo and Mahale Mountains National Park, Tanzania, where hunting frequencies were highest during times when ripe fruit was plentiful (Ngogo: Mitani & Watts 2001; Watts & Mitani 2002a, b; Mahale: Nishida et al. 1979; Takahata et al. 1984). However, these studies did not control for potentially confounding factors, such as party size, that are often correlated with fruit abundance and that affect hunting behaviour.

Vegetation type

Forest structure is likely to affect chimpanzee hunting behaviour. The habitat at Gombe is a mosaic of evergreen, semideciduous forest and deciduous woodland (Clutton-Brock & Gillett 1979). Hunting is arguably more costly in evergreen forest, where trees are tall, the canopy is thick and continuous, and the understory is dense, characteristics that reduce visibility and provide many escape routes for prey. Branches in the upper canopy are thin and flexible, increasing the risk of serious injury to chimpanzee hunters. In contrast, hunting costs should be lower in semideciduous forest and woodland, where the canopy is often broken and there is little or no vine cover or ground-layer vegetation. In the woodland habitat, trees reach only 12–15 m in height (Clutton-Brock & Gillett 1979). Thus, because of such contrasting characteristics, a male should be more likely to hunt (and succeed) in semideciduous forest or woodland than in evergreen forest. Several studies have supported this idea. Chimpanzees at Gombe and Ngogo were most likely to hunt and succeed in areas with broken canopy and/or secondary growth (Wrangham 1975; Stanford et al. 1994b; Watts & Mitani 2002b). Differences in hunting patterns between chimpanzees at Taï National Park, Côte d’Ivoire and Gombe may be due to consistent differences in forest structure (Boesch 1994).

Cooperation

Chimpanzees usually hunt red colobus monkeys in groups, but there is disagreement over the extent to which they hunt cooperatively. According to a well-known

economic definition, hunting is cooperative if the payoff to a hunter is higher by hunting with others than by hunting alone (Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995). Therefore, if chimpanzees hunt cooperatively, then (1) the probability that a male will hunt, (2) the probability that a male will make a kill and (3) per capita meat intake (Busse 1977; Watts & Mitani 2002a) should increase with adult male party size.

There has been mixed support for cooperative hunting among chimpanzees. An early study at Gombe showed that an individual male's probability of making a kill decreased with party size (Busse 1978). At Ngogo, per capita meat availability after successful hunts was independent of party size (Watts & Mitani 2002a). At Tai, however, a male's net energy gain was higher when he hunted cooperatively with others than when he did not hunt and relied upon obtaining meat from a successful hunter (Boesch 1994; Boesch & Boesch-Achermann 2000). While the type of cooperation that Boesch describes requires behavioural coordination, and our definition does not, the data suggest that, at Tai, there is a per capita energetic payoff to hunting in groups.

METHODS

Data collection on the Kasekela chimpanzee community at Gombe National Park has been consistent since 1974 (for details, see Goodall 1986). Observers conduct daily dawn-to-dusk focal follows of adult chimpanzees, systematically recording three main types of data: (1) party composition; (2) feeding by the focal chimpanzee; and (3) location. Location estimates, recorded at 15-min intervals, have a mean error of 133 m (Gilby 2004). The observers also write detailed narrative notes on the behaviour of the focal chimpanzee and significant party-level events, including encounters with colobus monkeys.

We extracted all reported encounters with colobus monkeys from the narrative notes between 1975 and 2001 (excluding 1994, for which data were not available). We defined an 'encounter' as when the observers recorded the presence of colobus monkeys within close range (~50 m) of the focal chimpanzee, regardless of whether any interest was shown in hunting (after Stanford et al. 1994b). We plotted the location of each encounter on a vegetation map derived from a 4-m multispectral IKONOS satellite image acquired on 30 June 2000. We smoothed the image using a 3×3 low-pass filter and classified the vegetation using the normalized difference vegetation index (NDVI) threshold in ERDAS Imagine (Leica Geosystems, Heerbrugg, Switzerland). Ground-truthing indicated that the user accuracy was 80% for woodland and semideciduous forest and 77% for evergreen forest (L. Pintea, unpublished data). Using this map, we recorded whether each colobus encounter occurred in evergreen forest, semideciduous forest or woodland. Owing to similarities in structure, we refer to woodland and semideciduous forest as 'woodland' throughout this paper. We determined the number of adult male chimpanzees and swollen females that were present in the party from the start of each encounter, ± 15 min. We classified males as

'adult' if they were at least 12 years old, the age at which males at Gombe consistently start to hunt successfully (I. C. Gilby, unpublished data). We classified only maximally tumescent females as 'swollen' (sexually receptive).

For each encounter with colobus monkeys, we recorded which males (if any) hunted and which captured monkeys. We defined hunting as 'climbing in pursuit of one or more monkeys'. This is similar to the definition used by Boesch & Boesch (1989), where hunters were identified as chimpanzees that climbed to the same height as the monkeys. We refer to encounters in which at least one adult male hunted as 'party-level' hunts and those in which the focal male hunted as 'focal-level' hunts. Based on Stanford (1998) and Wrangham & Bergmann-Riss (1990), we used the following values to estimate the number of kilograms of meat (including bones and viscera) captured during each successful hunt: infant colobus = 1 kg; juvenile = 3 kg; adult = 8 kg. If the observer did not record the age of the prey, we estimated its mass as 5 kg.

When possible, all chimpanzees that visited an artificial feeding area were weighed at least once a month during three periods: 1970–1985, 1991–1994 and 1996–2000 (for more detail, see Pusey et al. 2005). After statistically controlling for several confounding factors, Pusey et al. (2005) found that body mass varied significantly by month. We modified the Pusey et al. (2005) model to fit monthly effects specific to each year ($N = 204$ month/year combinations), rather than using separate, additive monthly and yearly effects. The resulting monthly 'multiplicative body mass' (MBM) effect is the month-specific average effect on median chimpanzee body mass, as predicted by this modification of the Pusey et al. (2005) model. For example, a MBM effect of 1.03 would indicate that, in that month, chimpanzees tended to weigh 3% more than the median body mass observed during the entire study period.

We consider body mass to be a reliable indicator of nutritional state. However, body mass measurements were distributed unevenly across months and years. As a result, there were mass data for fewer than 50% (148 of 312) of the months with hunting data. Rather than restrict our analyses to these months, we assessed whether monthly diet measures (recorded for all months) were correlated with body mass. We calculated two measures of diet quality for each month of the study, using feeding records of all focal chimpanzees that were followed during that month. We totalled the number of minutes that focal chimpanzees spent feeding and then calculated (1) leaf/pith consumption, the percentage of feeding time spent eating leaves or pith and (2) fruit consumption, the percentage of feeding time spent eating fruit. A repeated measures multiple regression of the month-specific MBM effect on the previous month's leaf/pith and fruit consumption values indicated that only leaf/pith consumption was a significant (negative) predictor of body mass ($F_{1,148} = 5.05$, $P = 0.03$, controlling for autocorrelated MBM effects in adjacent months). In other words, low average body mass in a specific month was associated with high leaf/pith consumption in the previous month. Therefore, we chose to use

leaf/pith consumption in a given month as an indicator of diet quality in that month.

Statistical Analysis

For each hypothesis, we ran party-level and focal-level analyses. Each hypothesis has one primary explanatory variable of interest, so we began with simple (unadjusted) logistic regressions with the outcome either 'hunt occurred' (yes/no) or 'hunt succeeded' (yes/no), as appropriate. Then, to illustrate the potentially confounding effects of the other explanatory variables, we ran multiple logistic regression (MLR) models with all interactions among adult male party size, number of swollen females (zero, one, two or more), vegetation type (woodland, evergreen) and leaf/pith consumption. We refer to these variables as 'confounding factors'. We ran four MLR models: (1) party-level hunting (MLR 1); (2) focal-level hunting (MLR 2); (3) party-level hunting success (MLR 3) and (4) focal-level hunting success (MLR 4). We reduced each model using manual backwards elimination, removing interaction terms with P values greater than 0.05 (type III analysis). We retained all main effects, regardless of significance. For all focal-level analyses, we used generalized estimating equations (GEE; Diggle et al. 2002) to control for repeated observations of the same male. We used SAS version 9.1 (SAS Institute, Cary, North Carolina, U.S.A.) for all analyses.

RESULTS

Hunting Totals

We identified 1646 encounters with colobus monkeys. We restricted party-level analyses to those encounters in which at least one adult male chimpanzee was present and the narrative notes contained sufficient detail to determine whether at least one male hunted (1087 encounters; Table 1). There were 991 encounters for which the focal chimpanzee was an adult male and it was clear whether or not he hunted. We used this subset for all focal-level analyses. The party-level hunting rate (hunts/encounters) was 0.69, compared to a focal hunting rate of 0.46 (Table 1). Fifty-three per cent of party-level hunts were successful, with a mean \pm SD of 1.76 ± 1.1 kills per successful hunt (range 1–7; Table 1). The focal male's success rate was 0.32 (Table 1).

Male Social Bonding

The odds that at least one male hunted increased significantly with adult male party size (unadjusted odds

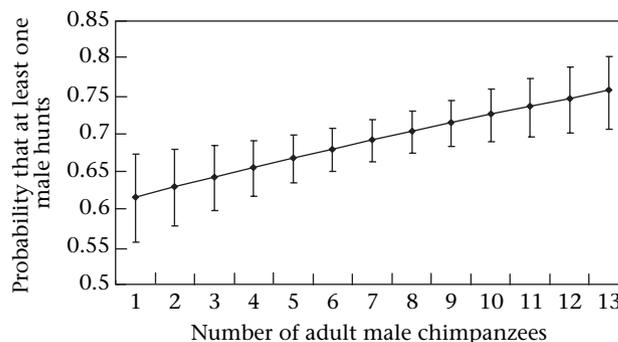


Figure 1. Relation between the probability of hunting by at least one male and adult male party size. The regression line is from an unadjusted logistic regression. Error bars represent 95% confidence intervals.

ratio = 1.06, $\chi^2_1 = 8.82$, $P = 0.003$; Fig. 1). The magnitude and significance of this association increased after controlling for the confounding factors (see Methods; MLR 1: odds ratio = 1.12, $P < 0.0001$; Table 2). There was no association between hunting by the focal male and adult male party size (unadjusted odds ratio = 0.96, $\chi^2_1 = 3.49$, $P = 0.06$). This result became significant when we controlled for the confounding factors ($\chi^2_1 = 7.02$, $P = 0.03$), but only for parties with two or more swollen females (odds ratio = 1.11, $P = 0.05$; Table 3, Fig. 2).

Meat for Sex

Unadjusted analysis revealed no association between the number of swollen females and the probability of party-level hunting ($\chi^2_2 = 1.29$, $P = 0.5$). However, multiple regression showed that the odds of party-level hunting were 44% lower in parties with one swollen female (odds ratio = 0.56, $P = 0.002$) and 55% lower in parties with two or more swollen females (odds ratio = 0.45, $P = 0.0002$), compared to parties with no swollen females (MLR 1; Table 2, Fig. 3). Similarly, there was a negative unadjusted association between hunting by the focal male and the number of swollen females ($\chi^2_2 = 5.90$, $P = 0.05$). This negative relationship remained when we controlled for the confounding factors, but was tempered by the aforementioned interaction between adult male party size and swollen females. In parties with three adult males, the odds that the focal male hunted were 69% lower in parties with two or more swollen females than in parties with no swollen females (odds ratio = 0.31, $P = 0.006$; Table 3, Fig. 2). In parties with 10 adult males, however, there was no such association ($P = 0.53$).

Table 1. Hunting totals

	Encounters	Hunts	Hunting rate	Successful hunts	Success rate	Kills	Kill rate
Party level*	1087	751	0.69	399	0.53	703	1.76
Focal level†	991	453	0.46	146	0.32	151	1.03

*At least one male was present during all encounters and participated in all hunts, successful hunts and kills.

†The focal chimpanzee was an adult male in all encounters and participated in all hunts, successful hunts and kills.

Table 2. Output from MLR 1: hunting by at least one adult male

Parameter	Category	Odds ratio	χ^2_1	<i>P</i>
Adult males		1.12	19.25	<0.0001
Swollen females	2+	0.45	13.67	0.0002
	1	0.56	9.45	0.002
	0	1.00	—	—
Vegetation	Woodland	1.34	3.72	0.05
	Evergreen	1.00	—	—
Leaf/pith		1.00	0.02	0.88

Output from a multiple logistic regression (MLR) of hunting by at least one male on adult male party size, swollen females, vegetation type and leaf/pith consumption. Odds ratios represent the effect of a one-unit increase in the continuous variables (adult males and leaf/pith consumption). For the categorical variables, odds ratios represent the effect relative to the reference group (swollen females: 0; vegetation: evergreen). Significant values are shown in bold.

There was a positive unadjusted association between party-level hunting success and the number of swollen females ($\chi^2_2 = 20.73$, $P < 0.0001$), but this relationship was not statistically significant when we controlled for confounding factors (MLR 3: $\chi^2_2 = 1.19$, $P = 0.5$; Table 4). There was no evidence of an unadjusted association between number of swollen females and focal male hunting success ($\chi^2_2 = 4.77$, $P = 0.11$), even in the multiple regression (MLR 4: $\chi^2_2 = 4.76$, $P = 0.09$; Table 5).

Nutrition

Party-level hunting was positively associated with diet quality: the odds that at least one male hunted decreased as leaf/pith consumption increased (unadjusted odds ratio = 0.98, $\chi^2_1 = 5.16$, $P = 0.02$). However, after controlling for the confounding factors, this association was no longer significant (MLR 1: $P = 0.88$; Table 2), probably because mean adult party size was also positively correlated with

both diet quality (Gilby 2004) and party-level hunting (see Male Social Bonding, above). Hunting by the focal male was also not associated with leaf/pith consumption ($\chi^2_1 = 0.14$, $P = 0.70$), even in the multiple regression (MLR 2: $P = 0.6$; Table 3).

Hunting success was positively associated with diet quality: a party-level hunt was less likely to succeed during months with high leaf/pith consumption (unadjusted odds ratio = 0.97, $\chi^2_1 = 7.53$, $P = 0.006$). Again, however, this relationship was no longer significant when we controlled for the confounding factors (MLR 3: $P = 0.86$; Table 4). The focal male was also less likely to succeed during months with high leaf/pith consumption (odds ratio = 0.97, $\chi^2_1 = 3.9$, $P = 0.05$), but again, this relationship was not significant in the multiple regression (MLR 4: $P = 0.08$; Table 5).

Vegetation Type

At least one male hunted in 73.6% (251/341) of encounters with red colobus monkeys in woodland habitat versus 67% (500/746) of similar encounters in evergreen habitat, a difference that was statistically significant (unadjusted odds ratio = 1.37, $\chi^2_1 = 4.83$, $P = 0.03$). This remained the case when the confounding factors were controlled for statistically (MLR 1: odds ratio = 1.34, $P = 0.05$; Table 2). Focal-level hunting showed the same pattern, but the difference was not statistically significant ($\chi^2_1 = 0.99$, $P = 0.32$), even after controlling for the confounding factors (MLR 2: $P = 0.3$; Table 3).

The probability of party-level hunting success was higher in woodland than in evergreen forest (odds ratio = 1.75, $\chi^2_1 = 13.02$, $P = 0.0003$), even when the confounding factors were controlled for (MLR 3: odds ratio = 1.80, $P = 0.0003$; Table 4). Similarly, the focal male was more likely to hunt successfully in woodland (39% success) than in evergreen forest (28% success, unadjusted odds ratio = 1.62, $\chi^2_1 = 5.27$, $P = 0.02$). When the

Table 3. Output from MLR 2: hunting by the focal male

Parameter	Category	Level of interacting variable	Odds ratio	χ^2_1	<i>P</i>
Adult males		2+ swollen females	1.11	3.85	0.05
		1 swollen female	0.91	2.41	0.12
		0 swollen females	0.96	1.67	0.19
Swollen females	2+	3 adult males	0.31	7.56	0.006
	1		1.19	0.56	0.45
	0		1.00	—	—
Swollen females	2+	10 adult males	0.86	0.39	0.53
	1		0.84	0.36	0.56
	0		1.00	—	—
Vegetation	Woodland		1.13	1.02	0.3
	Evergreen		1.00	—	—
Leaf/pith			0.99	0.27	0.6

Output from a GEE multiple logistic regression (MLR) of hunting by the focal male on adult male party size, swollen females, vegetation type and leaf/pith consumption. Owing to a significant interaction between swollen females and adult males, we report the odds ratios for these categories at different levels of the interacting variable. For example, the odds that the focal male hunted increased by 11% (odds ratio = 1.11, $P = 0.05$) with the addition of an adult male in parties with 2+ swollen females, but did not increase in parties with fewer than two swollen females. Significant values are shown in bold.

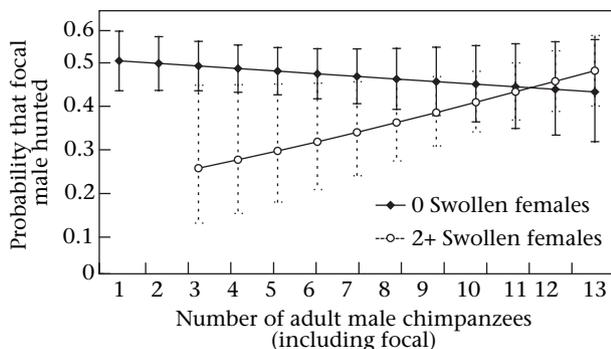


Figure 2. Relation between the probability of hunting by the focal male, adult male party size and number of swollen females. The regression lines are from a GEE multiple logistic regression (MLR 2, Table 3). Error bars represent 95% confidence intervals.

confounding factors were controlled for, this relationship remained statistically significant, but only in parties with fewer than two swollen females (MLR 4: interaction between vegetation type and swollen females: $\chi^2_1 = 6.08$, $P = 0.05$; Table 5).

Cooperation

The odds of party-level hunting success increased with adult male party size (unadjusted odds ratio = 1.16, $\chi^2_1 = 52.09$, $P < 0.0001$; Fig. 4). This association remained highly significant after we controlled for the confounding factors (MLR 3: odds ratio = 1.12, $P < 0.0001$; Table 4). However, there was no association between adult male party size and focal hunting success ($\chi^2_1 = 0.49$, $P = 0.48$), even in the multiple regression (MLR 4: $P = 0.7$; Table 5).

Adult male party size was positively correlated with the number of monkeys killed per hunt (mixed effects linear regression: parameter estimate = 0.12, $F_{1,749} = 91.58$, $P < 0.0001$) and total kilograms of meat secured (parameter estimate = 0.35, $F_{1,749} = 48.65$, $P < 0.0001$). However, the number of kilograms available per male decreased

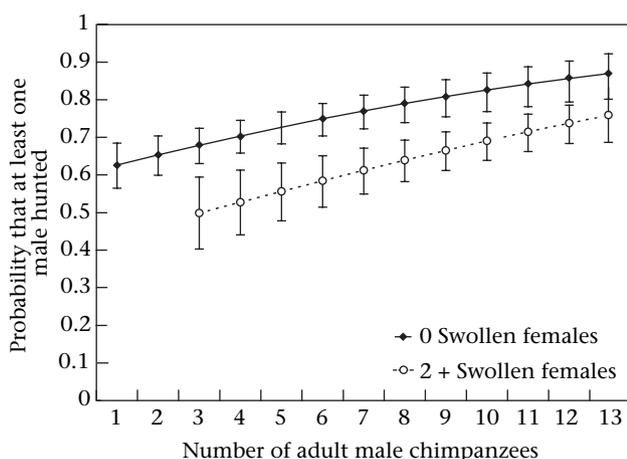


Figure 3. Relation between the probability of hunting by at least one male, adult male party size and number of swollen females. The regression lines are from a logistic regression (MLR 1, Table 2). Error bars represent 95% confidence intervals.

Table 4. Output from MLR 3: party-level hunting success

Parameter	Category	Odds ratio	χ^2_1	P
Adult males		1.12	14.94	<0.0001
Swollen females	2+	1.16	0.43	0.5
	1	1.25	1.19	0.3
	0	1.00	—	—
Vegetation	Woodland	1.80	12.97	0.0003
	Evergreen	1.00	—	—
Leaf/pith		1.00	0.03	0.86

Output from a multiple logistic regression (MLR) of hunting success by at least one male hunter on adult male party size, swollen females, vegetation type and leaf/pith consumption. Significant values are shown in bold.

significantly as adult male party size increased (parameter estimate = -0.022 , $F_{1,749} = 7.09$, $P = 0.008$).

A summary of the results from all hypotheses is given in Table 6.

Observer Reliability

The percentage of encounters in which hunting occurred (party-level hunting: 69%, focal-level hunting: 46%) was surprisingly high. To examine whether the Gombe field assistants biased their recording of 'encounters' towards those in which the chimpanzees showed an interest in hunting (thus inflating the hunting rate), we analysed data collected during a recent meat-sharing study at Gombe (Gilby 2006). During full-day focal follows of adult male chimpanzees during 12 months of data collection between 1999 and 2002, 94 encounters with colobus monkeys were recorded. In this data set, the probabilities of hunting were 40% and 18% for party-level and focal-level hunts, respectively, indicating that the hunting rate in the long-term study may indeed have been inflated.

In general, however, this observer bias did not appear to affect the overall results with respect to the hypotheses we tested. Consistent with the long-term data, analysis of the 1999–2002 data showed that the probability of hunting by at least one male was positively associated with adult male party size (odds ratio = 1.36, $\chi^2_1 = 11.54$, $P = 0.0007$), but hunting by the focal male was not ($\chi^2_1 = 1.62$, $P = 0.2$). In similar concordance with the long-term study, Gilby's data revealed no effect of monthly leaf/pith consumption on the probability of hunting (party level: $\chi^2_1 = 0.63$, $P = 0.43$; focal level: $\chi^2_1 = 0.09$, $P = 0.76$). Regarding vegetation type, however, results from the two data sets were slightly different. In Gilby's data set, focal males were more likely to hunt in woodland than in evergreen forest (odds ratio = 3.79, $\chi^2_1 = 3.92$, $P = 0.05$), but there was no effect of vegetation type on party-level hunting ($\chi^2_1 = 1.20$, $P = 0.27$). In the long-term data set, there was a significant effect of vegetation type on party-level hunting but not on focal-level hunting. While we cannot explain this difference, both data sets indicate that hunting by chimpanzees is more likely in woodland than in evergreen forest. Finally, in Gilby's data set, there was no effect of swollen females

Table 5. Output from MLR 4: hunting success of the focal male

Parameter	Category	Level of interacting variable	Odds ratio	χ^2_1	P
Males			0.98	0.19	0.7
Swollen females	2+	Vegetation = woodland	0.56	1.75	0.19
			1	2.75	0.10
			0	—	—
	2+	Vegetation = evergreen	1.54	1.64	0.20
			1	1.99	0.15
			0	—	—
Vegetation	Woodland	2+ swollen females	0.71	1.44	0.23
			Evergreen	1.00	—
	Woodland	1 swollen female	2.17	15.1	<0.0001
			Evergreen	1.00	—
	Woodland	0 swollen females	1.91	4.82	0.03
			Evergreen	1.00	—
Leaf/pith			0.97	3.08	0.08

Output from a GEE multiple logistic regression (MLR) of focal male hunting success on adult male party size, swollen females, vegetation type and leaf/pith consumption. Owing to a significant interaction between swollen females and vegetation type, we report the odds ratios for these categories at different levels of the interacting variable. Significant values are shown in bold.

on the probability of hunting by at least one male ($\chi^2_2 = 2.61$, $P = 0.3$, controlling for adult male party size) or by the focal male ($\chi^2_2 = 1.14$, $P = 0.6$). This result is not concordant with the negative effect of swollen females indicated by the long-term data. However, the power to detect the effects of swollen females and other factors was necessarily reduced by the smaller sample size of Gilby's data set.

DISCUSSION

We used 25 years of data from Gombe National Park, the longest running study of free-ranging chimpanzees, to examine male hunting behaviour. We focused upon hunts of red colobus monkeys, chimpanzees' preferred prey. At least one male hunted in 69% of all recorded encounters with colobus monkeys, which is consistent with data from earlier studies at Gombe (71.5%, [Stanford et al. 1994a](#);

72.6%, [Stanford et al. 1994b](#)) and Mahale (63%, [Hosaka et al. 2001](#)). However, we found that this rather high hunting rate may be due in part to a systematic sampling bias among the field assistants who collected the data. In a smaller data set collected by one of us (I. C. Gilby), the probability that at least one male hunted upon encountering red colobus monkeys was 40%, which is similar to the rate at Ngogo (37%, [Mitani & Watts 2001](#)), but still considerably higher than at Kanyawara (15%, R. W. Wrangham, personal communication). However, when we compared the long-term data set with Gilby's data, we found little evidence that this sampling bias affected the results concerning the factors influencing the decision to hunt.

This study is the first to use multivariate statistics to simultaneously measure the effects of chimpanzee party composition, vegetation type and nutritional state on hunting by specific chimpanzees. This approach yields new insights into the relative importance of social and ecological factors in the decision to hunt. We found little evidence to support social incentives for hunting. Instead, the results indicate that chimpanzees are sensitive to ecological factors in a manner similar to that of other predators.

Social Factors

Male social bonding

The male social-bonding hypothesis proposes that males hunt to obtain meat to foster intrasexual cooperative alliances and predicts a positive association between adult male party size and hunting probability ([Mitani & Watts 2001](#)). This prediction rests on the assumption that large parties are more likely to contain an allied pair. While there is evidence that allies associate preferentially ([Mitani et al. 2000](#)) and are often together in small parties, they do not travel together exclusively. Therefore, large parties should indeed be more likely to contain allied dyads. We found a positive association between adult male party size and

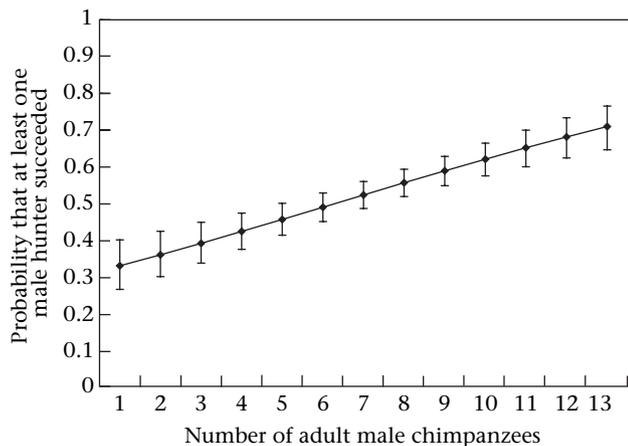


Figure 4. Relation between the probability of hunting success by at least one male and adult male party size. The regression line is from an unadjusted logistic regression. Error bars represent 95% confidence intervals.

Table 6. Summary of results, organized by hypothesis

Hypothesis	Explanatory variable	Dependent variable	Predicted effect	Observed effect
Male social bonding	Adult males (few → many)	Party hunt	+	+
		Focal hunt	+	0*
Meat for sex	Swollen females (0 → many)	Party hunt	+	–
		Focal hunt	+	–
		Party kill	+	0
		Focal kill	+	0
Nutrient shortfall	Diet quality (low → high)	Party hunt	–	0
		Focal hunt	–	0
		Party kill	–	0
		Focal kill	–	0
Nutrient surplus	Diet quality (low → high)	Party hunt	+	0
		Focal hunt	+	0
		Party kill	+	0
		Focal kill	+	0
Vegetation type	Evergreen → Woodland	Party hunt	+	+
		Focal hunt	+	0
		Party kill	+	+
		Focal kill	+	+†
Cooperative hunting	Adult males (few → many)	Party kill	+	+
		Focal kill	+	0
		Number of prey	+	+
		Total prey mass (kg)	+	+
		Per capita prey mass (kg)	+	–

*There was a positive effect of adult males on hunting by the focal male, but only in parties with 2+ swollen females.

†Woodland hunts by the focal male were more likely to succeed, but only in parties with fewer than two swollen females.

the probability of hunting by at least one male, a result that agrees with previously published studies of chimpanzee hunting behaviour (Stanford et al. 1994b; Mitani & Watts 2001). At first, this seems to support the male social-bonding hypothesis. However, examination of hunting by specific males (rather than by at least one male) casts doubt on this idea. Adult male party size did not affect hunting by the focal male, provided that there were fewer than two swollen females present. Although there was a positive association between adult male party size and hunting by the focal male in parties with two or more swollen females, it is unlikely that the presence of swollen females served as an added incentive for males to seek meat to foster alliances with other males. At Ngogo, males form coalitions to guard swollen females (Watts 1998), so it is possible that meat sharing may solidify such partnerships. However, coalitionary mate guarding is rarely observed at Gombe. We discuss a possible alternative explanation for our results in the following section.

Another key assumption of the male social-bonding hypothesis is that males use meat as 'currency' with which to establish and maintain intrasexual alliances. This notion was supported at Ngogo (Mitani & Watts 2001; Watts & Mitani 2002a), where males share reciprocally with each other. However, Gilby (2006) demonstrated that at Gombe, adult males do not preferentially share with frequent grooming partners or associates.

Meat for sex

Although a previous analysis of Gombe hunting data found a positive association between the presence of

swollen females and hunting (Stanford et al. 1994b), we found that hunting was significantly less likely to occur if swollen females were present. There are several possible reasons for such contrasting results. First, we examined 25 years of data, compared to Stanford et al. (1994b), who examined a relatively short period of just 10 years of data. Second, we restricted the definition of 'swollen' females to those that were maximally tumescent, whereas Stanford et al. (1994b) included females that were only partially swollen. Male chimpanzees rarely mate with females who are not maximally swollen (Goodall 1986; Wallis 1997), so it seems unlikely that the decision to hunt should be affected by the presence of partially swollen females. Third, we used a more restrictive definition of hunting. Our examination of the Gombe narrative notes indicated that sometimes the observers used the term 'hunt' to describe a mere interest in hunting, rather than active pursuit. We therefore used climbing as the main criterion for defining hunting. Finally, we used logistic regressions, the appropriate analysis for modelling a binomial response (Agresti 1996). Stanford et al. (1994b) used a linear regression model with the proportion of encounters that led to hunts as the response variable. A linear regression is not appropriate under these circumstances (Agresti 1996).

Our finding that males were less likely to hunt when swollen females were present does not support the meat-for-sex hypothesis and suggests that males face a trade-off between hunting and mating. 'Possessiveness' is a common mating strategy in which a high-ranking male prevents a swollen female from mating with other males (Tutin 1979; Goodall 1986). If a possessive male temporarily loses

sight of the female, she will often quickly mate with other males in the party (I. C. Gilby, personal observation). Therefore, upon encountering colobus monkeys, a possessive male must choose between hunting and mating (meat or sex). Similarly, middle- and low-ranking males, who normally have low mating success in parties with other males, might be able to 'sneak' a mating during the excitement that is usually associated with a colobus encounter. If they hunt, they may miss a rare mating opportunity. However, in large parties, mating competition increases dramatically. A possessive male's mate-guarding ability is compromised (Watts 1998), and middle- or low-ranking males must compete with many other males for the chance to mate. Therefore, in large parties, males should be less likely to forgo hunting in favour of mating. This hypothesis would explain why the negative effect of swollen females on hunting by the focal male was inversely related to adult male party size (Fig. 2). In parties with many males, there was no effect of swollen females on the focal male's likelihood of hunting.

These results add to a growing body of evidence against the meat-for-sex hypothesis as an explanation for hunting. In the two study communities at Kibale, there was no effect of swollen females on party-level hunting (Ngogo: Mitani & Watts 2001; Kanyawara: R. W. Wrangham, personal communication). Additionally, other studies have shown that males do not preferentially share with swollen females (Gombe: Gilby 2006) or copulate more (Ngogo: Mitani & Watts 2001) with females with which they frequently share food.

Ecological Factors

Nutrition

Results of our analysis suggest that the effects of diet quality on hunting are complex and are influenced by several confounding factors. Previous work has demonstrated that hunting frequency at Gombe is highest in the late dry season (Stanford et al. 1994a; Gilby 2004), when chimpanzee body masses generally tend to be low (Pusey et al. 2005). This association could be taken as evidence supporting the nutrient shortfall hypothesis, that chimpanzees hunt to obtain additional energy when high-quality plant food is scarce. In contrast, in our study, a simple regression showed that the odds of hunting upon encountering red colobus monkeys were lower in 'poor diet' months. Similarly, hunts were less likely to succeed when diet was poor. This appears to support the alternative hypothesis that chimpanzees hunt more, and hunt more 'intensely', during nutrient surplus, when the energetic costs of hunting may be more easily absorbed. This result is consistent with studies at other sites that have demonstrated a positive association between hunting probability and food availability (Ngogo: Mitani & Watts 2001; Watts & Mitani 2002a, b; Mahale: Nishida et al. 1979; Takahata et al. 1984). However, these studies failed to control for two important confounding factors. First, many studies have demonstrated that food availability and distribution (and hence diet quality) are positively correlated with party size (Goodall 1986;

Chapman et al. 1994; Matsumoto-Oda et al. 1998; Wrangham 2000; Anderson et al. 2002; Mitani et al. 2002), which is a well-known predictor of party-level hunting (Stanford et al. 1994b; Hosaka et al. 2001; Mitani & Watts 2001; R. W. Wrangham, personal communication). Second, there is evidence that the number of swollen females, which is also positively associated with party size (Goodall 1986; Matsumoto-Oda 1999; Boesch & Boesch-Achermann 2000; Wrangham 2000; Anderson et al. 2002; Mitani et al. 2002) increases with diet quality (Gilby 2004; Emery Thompson 2005). Therefore, we used multiple regression models to statistically control for party size and the number of swollen females. With these confounding factors held constant, diet quality was not significantly associated with the probability of hunting or hunting successfully. Therefore, while there is little doubt that meat is a valuable food source, we found no evidence suggesting that the Gombe chimpanzees base their hunting decisions on their nutritional state. It is possible, however, that deficiencies in protein, fat or trace minerals may play a role. More work is needed in this area.

Vegetation type

Upon encountering colobus monkeys, the probability that at least one male hunted was higher in woodland or semideciduous forest than in evergreen forest. Party-level hunts were also most likely to succeed in woodland and semideciduous forest. These results suggest that hunters have an advantage in areas where the trees are short (woodland) and/or the canopy is broken (semideciduous forest).

The results were slightly different when we examined the effect of vegetation type on hunting by focal males. Focal males were equally likely to hunt in woodland or semideciduous forest and evergreen forest, but the reasons for this are unclear. Focal males were more likely to hunt successfully in woodland than in evergreen forest, but only in parties with fewer than two swollen females. In parties with two or more swollen females, vegetation type did not affect the probability that a focal male hunted successfully. What accounts for this pattern? A male may abandon a hunting attempt if another male approaches the swollen female he is guarding (I. C. Gilby, personal observation). This scenario may be more likely to occur in woodland, where visibility is clear, and a male can see copulation attempts by other males. The presence of easily visible swollen females may therefore cancel out the positive effect of woodland on hunting success.

In general, our results are consistent with previously published data from Gombe showing that hunts are most likely to occur in areas with broken canopy (Wrangham 1975; Stanford et al. 1994b). Similarly, the Ngogo chimpanzees hunt more frequently in disturbed forest than primary forest (Watts & Mitani 2002b). These findings suggest that more open habitats provide increased visibility, reduced prey mobility and lower hunting costs for chimpanzees, a pattern that is similar to that of obligate carnivores.

Cooperation

In agreement with previously published research, this study offers little evidence to support cooperative hunting by the Gombe chimpanzees. We used a well-known economic definition of cooperation: 'joint action for mutual benefit' (Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995), which proposes that cooperation will evolve when individuals enjoy a greater payoff by hunting with others than when hunting solitarily. We found no evidence that focal males were more likely to hunt successfully in large parties than in small parties. Although the number of prey killed increased with adult male party size, per capita meat availability was significantly lower in large parties. However, we were unable to address the pattern of meat consumption. Meat may not be distributed evenly among party members (Goodall 1986; Nishida et al. 1992; Boesch 1994; Stanford et al. 1994b; Watts & Mitani 2002a), and the hunter that kills the prey may consume more meat than average (Boesch 1994; Boesch & Boesch-Achermann 2000). Therefore, it is possible that certain individuals may consume more meat even though the per capita meat availability decreases with party size. However, the number of adult males in the party did not affect the probability that the focal male hunted (except in parties with two or more swollen females, see *Meat for sex*, above), suggesting that potential cooperative partners did not provide an additional hunting incentive.

What explains the positive association between adult male party size and the probability of party-level hunting, if not cooperation? The answer may be rather simple. If each male had a constant probability of hunting, regardless of party size, then large parties would be more likely to contain at least one willing hunter (the 'additive probability' hypothesis). Our results are consistent with this hypothesis because adult male party size was positively associated with the probability that at least one male hunted, but it was not associated with the probability that the focal male hunted. Unfortunately, we lack consistent data on the exact number of hunters in each party, so it is unclear whether a constant proportion of the party usually hunted.

Conclusions

It is clear that the factors affecting male chimpanzee hunting behaviour are varied and complex. Indeed, there certainly may be factors that we did not consider or that we were unable to test. For example, the age composition of red colobus troops most likely affects the probability of chimpanzee hunting and success at Gombe (Stanford 1998), but the level of detail in the narrative notes from our data set was not sufficient to document this effect. Here we have considered the five main hypotheses that have been proposed in the chimpanzee hunting literature to date. The large sample size from the 25-year Gombe data set allowed us to systematically test each hypothesis, using multivariate statistics to control for potentially confounding variables. Our results do not support hypotheses that invoke social benefits to explain why male chimpanzees at Gombe hunt red colobus monkeys. Instead, our

results suggest that the Gombe chimpanzees attend to simple energetic and ecological factors, a pattern that is consistent with other predators, such as lions and wolves.

Acknowledgments

Without the hard work of Jane Goodall and the staff at the Gombe Stream Research Centre, this research would not have been possible. We are especially grateful to Jane Goodall for access to the data, and H. Matama, I. Yahaya, H. Mkono and E. Mpongo for decades of data collection and dedication to the project. We thank the Tanzanian Commission for Science and Technology (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania National Parks (TANAPA) for permission to continue the ongoing research at Gombe. Thanks to Brian Farm for developing data entry software, to Jane Waterman, Joann Schumacher-Stankey and Jennifer Williams for overseeing data entry, and to the scores of undergraduates and volunteers who entered data. Special thanks to Katie Lee, Kelly Hughes, Anna Wynn and Jason Beyer for helping to extract colobus encounters from the narrative notes. Thanks also to John Carlis for development of the relational database, and to Jin Suong Yoo and Mete Celik for computer programming. We thank Gary Oehlert for continuing his work with the weight data. Richard Wrangham, John Byers and two anonymous referees provided helpful comments on earlier versions of the manuscript. Long-term data collection was supported by the Jane Goodall Institute. Data entry was funded in part by National Science Foundation grants DBS-9021946, SBR-93109909, the College of Biological Sciences of the University of Minnesota, the Jane Goodall Institute, and the Windibrow Foundation. I.C.G. was supported by the L.S.B. Leakey Foundation, The University of Minnesota Graduate School and grants from Milton Harris. L.P. was supported by the L.S.B. Leakey Foundation. IKONOS imagery was courtesy of Space Imaging. The research presented here was described under Animal Subject Codes Number 0005A52421, approved by the Institutional Animal Care and Use Committee of the University of Minnesota.

References

- Agresti, A. 1996. *An Introduction to Categorical Data Analysis*. New York: J. Wiley.
- Anderson, D. P., Nordheim, E. V., Boesch, C. & Moermond, T. C. 2002. Factors influencing fission–fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 90–101. Cambridge: Cambridge University Press.
- Boesch, C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour*, **48**, 653–667.
- Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, **78**, 547–573.
- Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Taï Forest. Behavioural Ecology and Evolution*. Oxford: Oxford University Press.
- Busse, C. D. 1977. Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution*, **31**, 907–911.

- Busse, C. D. 1978. Do chimpanzees hunt cooperatively? *American Naturalist*, **112**, 767–770.
- Chapman, C. A., White, F. J. & Wrangham, R. W. 1994. Party size in chimpanzees and bonobos: a re-evaluation of theory based on two similarly forested sites. In: *Chimpanzee Cultures* (Ed. by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne), pp. 41–57. Cambridge, Massachusetts: Harvard University Press.
- Chapman, C. A., Wrangham, R. W. & Chapman, L. J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.
- Clements, K. C. & Stephens, D. W. 1995. Testing non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour*, **50**, 527–535.
- Clutton-Brock, T. H. & Gillett, J. B. 1979. A survey of forest composition in the Gombe National Park, Tanzania. *African Journal of Ecology*, **17**, 131–158.
- Creel, S. 1997. Cooperative hunting and group size: assumptions and currencies. *Animal Behaviour*, **54**, 1319–1324.
- Creel, S. & Creel, N. M. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **50**, 1325–1339.
- Diggle, P. J., Heagerty, P. J., Liang, K.-Y. & Zeger, S. L. 2002. *Analysis of Longitudinal Data*. New York: Oxford University Press.
- Emery Thompson, M. 2005. Endocrinology and ecology of female chimpanzee reproduction. Ph.D. thesis, Harvard University.
- Funston, P. J., Mills, M. G. L. & Biggs, H. C. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, **253**, 419–431.
- Gilby, I. C. 2004. Hunting and meat sharing among the chimpanzees of Gombe National Park, Tanzania. Ph.D. thesis, University of Minnesota.
- Gilby, I. C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, **71**, 953–963.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Grinnell, J., Packer, C. & Pusey, A. E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*, **49**, 95–105.
- Hopcraft, J. G. C., Sinclair, A. R. E. & Packer, C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.
- Hosaka, K., Nishida, T., Hamai, M., Matsumoto-Oda, A. & Uehara, S. 2001. Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. In: *All Apes Great and Small. Vol. 1. African Apes* (Ed. by B. Galdikas, N. Briggs, L. Sheeran, G. Shapiro & J. Goodall), pp. 107–130. New York: Kluwer Academic.
- Kunkel, K. & Pletscher, D. H. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management*, **65**, 520–530.
- Matsumoto-Oda, A. 1999. Mahale chimpanzees: grouping patterns and cycling females. *American Journal of Primatology*, **47**, 197–207.
- Matsumoto-Oda, A., Hosaka, K., Huffman, M. A. & Kawanaka, K. 1998. Factors affecting party size in chimpanzees of the Mahale mountains. *International Journal of Primatology*, **19**, 999–1011.
- Mesterton-Gibbons, M. & Dugatkin, L. A. 1992. Cooperation among unrelated individuals: evolutionary factors. *Quarterly Review of Biology*, **67**, 267–281.
- Mitani, J. C. & Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, **61**, 915–924.
- Mitani, J. C., Merriwether, D. A. & Zhang, C. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, **59**, 885–893.
- Mitani, J. C., Watts, D. P. & Lwanga, J. S. 2002. Ecological and social correlates of chimpanzee party size and composition. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 102–111. Cambridge: Cambridge University Press.
- Nishida, T. 1968. The social group of wild chimpanzees in the Mahali mountains. *Primates*, **9**, 167–224.
- Nishida, T., Uehara, S. & Nyundo, R. 1979. Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates*, **20**, 1–20.
- Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. & Uehara, S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: *Topics in Primatology* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal), pp. 159–174. Tokyo: University of Tokyo Press.
- Packer, C. & Caro, T. M. 1997. Foraging costs in social carnivores. *Animal Behaviour*, **54**, 1317–1318.
- Packer, C. & Ruttan, L. 1988. The evolution of cooperative hunting. *American Naturalist*, **132**, 159–198.
- Pusey, A. E., Oehlert, G. W., Williams, J. M. & Goodall, J. 2005. Influence of ecological and social factors on body mass of wild chimpanzees. *International Journal of Primatology*, **26**, 3–31.
- Stanford, C. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist*, **98**, 96–113.
- Stanford, C. B. 1998. *Chimpanzee and Red Colobus*. Cambridge, Massachusetts: Harvard University Press.
- Stanford, C. B., Wallis, J., Matama, H. & Goodall, J. 1994a. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *American Journal of Physical Anthropology*, **94**, 213–228.
- Stanford, C. B., Wallis, J., Mpongo, E. & Goodall, J. 1994b. Hunting decisions in wild chimpanzees. *Behaviour*, **131**, 1–18.
- Takahata, Y., Hasegawa, T. & Nishida, T. 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *International Journal of Primatology*, **5**, 213–233.
- Teleki, G. 1973. *The Predatory Behavior of Wild Chimpanzees*. Lewisburg, Pennsylvania: Bucknell University Press.
- Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, **6**, 29–38.
- Uehara, S. 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*, **38**, 193–214.
- de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, **18**, 433–459.
- Wallis, J. 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, **109**, 297–307.
- Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, **44**, 43–55.
- Watts, D. P. & Mitani, J. C. 2002a. Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 244–255. Cambridge: Cambridge University Press.
- Watts, D. P. & Mitani, J. C. 2002b. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, **23**, 1–28.
- Wrangham, R. W. 1975. The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. thesis, Cambridge University.

- Wrangham, R. W.** 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 503–538. London: Academic Press.
- Wrangham, R. W.** 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: *Primate Males: Causes and Consequences of Variation in Group Composition* (Ed. by P. M. Kappeler), pp. 248–258. Cambridge: Cambridge University Press.
- Wrangham, R. W. & Bergmann-Riss, E.** 1990. Rates of predation on mammals by Gombe chimpanzees, 1972–1975. *Primates*, **31**, 157–170.
- Wrangham, R. W. & Smuts, B.** 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility, Supplement*, **28**, 13–31.
- Wrangham, R. W., Clark, A. P. & Isabirye-Basuta, G.** 1992. Female social relationships and social organization of Kibale forest chimpanzees. In: *Topics in Primatology. Vol. 1. Human Origins* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal), pp. 81–98. Tokyo: Tokyo University Press.
- Wrangham, R. W., Conklin-Brittain, N. L. & Hunt, K. D.** 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance: I. Antifeedants. *International Journal of Primatology*, **19**, 949–970.