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ORIGINAL PAPER

Reciprocity and trades in wild West African chimpanzees

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Abstract Why do animals help other individuals and provide benefits to the recipient, sometimes at personal cost? In this study, we aim to determine if some of the helpful behaviors observed in a group of wild chimpanzees (Taï chimpanzee group, Côte d'Ivoire, West Africa) are exchanged among individuals resulting in a net benefit for both participants. We adopted an inclusive view of exchanges by considering that all commodities (i.e., social behaviors as grooming, sex, support, as well as resources, such as meat) can be exchanged. This would result in "market" type social interactions in which debts of one commodity can be met by giving the same or other commodities. We investigated whether both in-kind exchanges and trades of commodities occurred. The Taï chimpanzees reciprocated the amount of grooming they received and were more likely to give support in agonistic conflicts to those who also supported them. In addition, they traded support for meat and meat for sex. Both male and female chimpanzees exchanged many different commodities, which seemed to result in long-term balanced relationships. Our results suggest that wild chimpanzees rely on other group members to obtain many of the important commodities they need.

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Introduction

Animals that live in highly social groups are frequently dependent on others' help to acquire important resources, achieve specific goals, and fend off rivals. Wolves help other group members in raising their offspring, lion prides share their prey amongst each other, moray eel and grouper fish help each other to hunt, and humans regularly share food and provide childcare and assistance in labor to other individuals (Dugatkin 1997; Kappeler and van Schaik 2006). The benefit acquired by the receiver of such acts is straightforward and can come in the form of food, help in completing tasks, support in aggressive encounters, etc.; however, why an individual would invest in another at personal cost is unclear, especially in the case of non-kin. The reciprocal altruism model proposes that individuals take turns as giver and receiver, exchanging helpful acts, which would result in a net benefit for both partners (Trivers 1971). These exchanges can be of the same type of resource or helpful act (in-kind exchanges) or of different ones (trades), and the conditions under which each type of exchange is expected differ. In-kind exchanges are likely to occur with activities that require more than one individual (e.g., clearing crops, hunting large prey), with helpful services that can only be obtained from another individual (e.g., grooming of hard to reach places), or with resources that are unpredictably attained (e.g., meat), as a means to regularize resource access. Trades are more likely when there is some division of labor or when there are considerable differences among individuals in their capacity to acquire resources (i.e., differences in individuals' resource holding potential), so that individuals have to trade to obtain all the resources or services they require (Hawkes 1993; Noë and Hammerstein 1995; Barrett et al. 1999). Thus, any commodity (i.e., any resource or service one individual can give another) that represents a benefit to the receiver can be exchanged, either for the same or for different commodities.

Evidence supporting the reciprocal altruism model comes from a variety of species. For example, predator inspection by sticklebacks was conditional upon the presence of a previous cooperating "partner" (Milinksi 1987), hermaphrodite fish were shown to exchange sperm reciprocally (Leonard and Leukowiak 1984), and non-human primates were found to reciprocate grooming (Schino and Aureli 2008), support, and meat (Mitani 2006), and to trade grooming for support (Hemelrijk and Ek 1991; Mitani 2006; Schino 2006), and meat for sex (Gomes and Boesch 2009). Studies on forager societies found that humans too exchange meat, fish, and roots in a reciprocal fashion (Henri 1951; Gurven et al. 2000; Hames 2000; Tucker 2004; Hames and McCabe 2007). These studies showed that the amount of each resource given and received was correlated; however, in many cases, there was a large amount of variability not explained by the correlations obtained. For example, a meta-analysis across several different primate species showed that the correlation between grooming given and received was 0.58 (Schino and Aureli 2008). This imbalance could be an artifact of the statistical analyses used, a reflection of cheating, or cases of trading for other resources. If part of the grooming given was traded for food, for example, then this could explain the imbalance found in the in-kind exchange. However, most studies have focused on one or two commodities at a time, which precludes understanding how trading different commodities functions to balance out other exchanges. This will likely lead to underestimating the impact of reciprocal altruism. Determining which commodities are reciprocated and traded, to what extent they are exchanged, and which individuals are involved in these exchanges (e.g., females vs. males, high-ranking vs. low-ranking individuals) will allow us to understand the extent to which individuals rely on other group members to acquire important resources, and how exchanges shape their social interactions and bonds.

In this study, we aim to investigate whether wild chimpanzees living in the Taï National Park (Côte d'Ivoire) exchange grooming, meat, support given in aggressive interactions, and sex. We seek to understand if these four commodities are reciprocated and if so, if trades can, to a certain extent, account for imbalances in in-kind exchanges. Although kin selection could also explain some of the instances of sharing and helping among group members, previous studies showed that on average, only 5% of the adult dyads in one group of chimpanzees were closely related (Vigilant et al. 2001; Csillery et al. 2006), whereas the majority of the cooperative dyads in another group of chimpanzees were not related or were distantly related (Langergraber et al. 2007; Langergraber et al. 2009). These studies suggest that kin selection has only a limited impact on cooperation in wild chimpanzees.

In previous papers, we showed that in the Taï chimpanzees, both males and females exchange commodities (Gomes and Boesch 2009; Gomes et al. 2009). We found that they reciprocate grooming, and that the relationship between grooming given and received was more or less symmetrical (Gomes et al. 2009). Although the majority of the variability of grooming given seemed to be explained by grooming received, we do not know whether part of the grooming given was exchanged for other commodities and whether this could explain the remaining variability not accounted for by the in-kind exchange of grooming. We also found that the Taï chimpanzees traded meat and sex (Gomes et al. 2009); however, some of the variability in copulation rate or in meat transferred could be explained by trades for other commodities.

The four commodities we will focus on are likely to be exchanged because they benefit the receiver and comply with one or several of the characteristics of exchangeable commodities explained above (i.e., activities that require more than one individual, helpful services that can only be obtained from another individual, resources that are unpredictably attained, etc.). Grooming provides hygienic benefits through parasite removal (Mooring et al. 1996; Hawlena et al. 2007) and tension relief benefits by stimulating beta-endorphin release (Keverne et al. 1989), and it decreases the heart rate (Feh and de Mazieres 1993; Aureli et al. 1999). Non-human primates invest much of their time into grooming one another (reviewed in Spruijt et al. 1992), suggesting that the intrinsic benefits of receiving, and therefore exchanging grooming, are high. Like other social mammals, wild chimpanzees often rely on support from other group members to win social disputes in both intra- and inter-group encounters. By forming strong alliances with other group members, they are able to reinforce dominance relationships or challenge higher-ranking individuals from their own group (Goodall 1986; Nishida and Hosaka 1996; Boesch and Boesch-Acherman 2000). Thus, support in aggressive interactions is very valuable and likely to be an important commodity to exchange. Meat is a highly valued resource because it is high in protein and micronutrients and is risky and difficult to acquire (Hamilton and Busse 1978; Boesch and Boesch 1989; Mitani et al. 2002b; Gilby et al. 2006; Tennie et al. 2008). Studies have shown that the majority of the food-related aggressive interactions observed in wild chimpanzees are over meat, indicating that it is a highly contested resource (Boesch and Boesch-Acherman 2000; Wittig and Boesch 2003). Thus, individuals are likely to profit largely from both in-kind exchanges of meat (due to its risk- or variance-reduction effects on daily meat intake (Hawkes 1993)) and trades of meat for other valuable resources. Finally, although chimpanzees are highly promiscuous, females do not copulate an equal number of times with each of the males in a group and, at least in the Taï community, females reject some of the solicitations from males, thereby exerting some choice of mating partners (Stumpf and Boesch 2006). Therefore, females could "use" sex to obtain other valuable resources, for example meat (Gomes and Boesch 2009), support in aggressive interactions, or grooming. In this paper, we use detailed observational data to investigate whether these valuable commodities are exchanged, and determine to what extent wild chimpanzees living in the Taï National Park rely on others to obtain the resources and services they need. Some of the results presented in this paper differ slightly from those of previous publications (Gomes and Boesch 2009; Gomes et al. 2009), even though the relationships being studied (e.g., the relationship between grooming given and received) are apparently the same. Given that the goal of each of our publications is different (in previous papers, we investigated specific relationships, whereas here we are interested in the exchange of many different commodities), the analysis and the variables included in each one also differ, leading to slightly different results. These differences are explained in each case.

Methods

Study animals and field site

C.M.G. collected data on the South group of the Taï Chimpanzee Project (Taï National Park, Côte d'Ivoire) during a non-consecutive 22-month period between December 2003 and March 2006 (Gomes et al. 2009). The community consisted of 44 individuals: eight males (five adults, three adolescents), 16 females (14 adults, two adolescents), and 20 juveniles and infants all of which were fully habituated. However, during the study period, one adult male and four adult females disappeared or died (Herbinger et al. 2001; Deschner et al. 2003; Boesch et al. 2006).

Behavioral sampling

We recorded data on grooming (total seconds A was seen grooming B), support in aggressive interactions (Nishida and Hosaka 1996), copulation rate (number of times each male copulated with each female, corrected for the amount of time they were seen together during the estrous phase of the female), greeting vocalizations and, with the help of a field assistant, party composition. We obtained these data through all-day focal animal sampling (Altmann 1974) of one target per day, conducted on the five adult males and nine of the adult females, leading to a total of 91 dyads ($N=182$ combinations). We collected meat transfer data through ad libitum observations of hunting behavior and meat eating parties and quantified the total amount of meat (grams) each individual transferred/shared. Two field assistants helped collecting this data by scanning the meat eating party and collecting meat transfer and eating data on different individuals of the party (for details on the grooming, meat transfer, and copulation data collection, see Gomes and Boesch (2009); Gomes et al. (2009)). Data were entered into a Psion Organizer hand-held computer using "The Observer" (Noldus 1989). This data collection resulted in a total of ~3,000 h of focal observation (275 all-day follows): ~1,500 h of for males (138 all-day follows) and ~1,480 h of for females (137 all-day follows); and observations of 90 successful hunts.

Statistical analysis

General results are presented using the trimmed mean, which is insensitive to outliers (Quinn and Keough 2002), the first quartile (Q1), and third quartile (Q3) throughout. To determine whether the Taï chimpanzees exchanged commodities, we used generalized linear mixed models (Crawley 2002; Bolker 2007; Baayen 2008) which allowed us to analyze the relationship between grooming, giving support, transferring meat, and copulating, while controlling for other confounding variables (e.g., rank, association patterns, etc.). GLMM were carried out in R (R-DevelopmentCoreTeam 2004) using the lme4 package, version 0.9975 (Bates et al.2011).

We investigated 14 different GLMM (Fig. 1)[1]:

- *Grooming, Supporting*, and *Transferring meat* were set as response variables in separate models, and for each model, the remaining two behaviors were set as predictor variables. We constructed two models for each of these response variables: One with a binary response variable (0/1, Logistic model) and one with a continuous response variable (Gaussian model), resulting in a total of six models. For the former, we used the entire data set, while for the latter, we discarded all the data points for which the response variable was equal to zero (0). We did this because there is not an appropriate

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[1] As each predictor variable included in a model affect the remaining predictor variables and the response variable in a different way, it is important to test each variable both as a predictor and as a response variable.

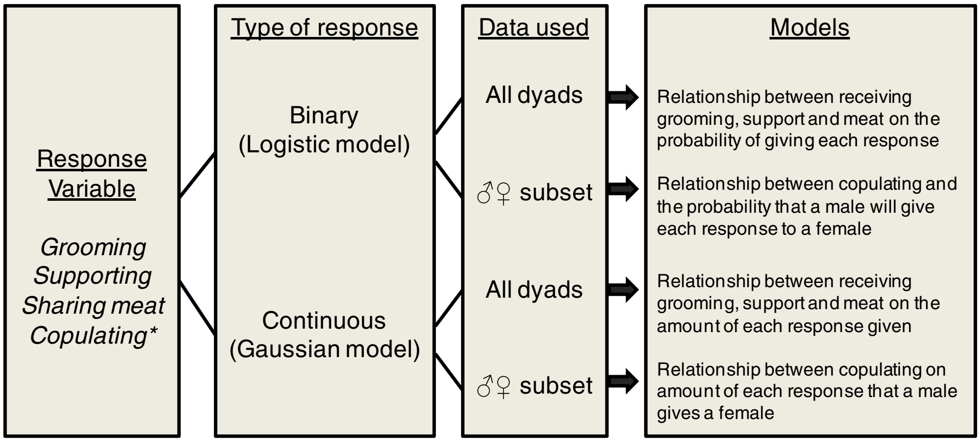

Fig. 1 Description of analyses. For the response variables *Grooming*, *Supporting*, and *Transferring meat*, we ran the four models presented here. In the case of *Copulating*, we only investigated the two models with the male/female subset and the remaining three variables as predictors

error structure for a GLMM with a continuous response variable with an excess of zeros (which is the case for all our variables of interest); thus, dividing the data set was the only viable solution. When meat transferred was tested as a continuous response variable (Gaussian model), we investigated both the number of sharing events and the amount of meat transferred (grams), assuming that each could reflect different patterns of sharing. However, only the model with number of sharing events was significant, so here, we only present the results of those models.

- For the subset of male–female dyads, we repeated the same procedure as in the previous point, but included *Copulating* as an additional predictor variable in each model, resulting in a total of six additional models. This allowed us to investigate whether *Copulating* was a good predictor of *Grooming*, *Supporting*, and *Transferring meat.*
- For the subset of male–female dyads, we constructed two models (i.e., a Logistic and a Gaussian model) with *Copulating* as a response variable and *Grooming*, *Supporting*, and *Transferring meat* as predictor variables. This allowed us to investigate whether *Grooming*, *Supporting*, and *Transferring meat* were good predictors of *Copulating.*

To assess the overall significance of each model, we compared the fit of the full model with that of the null model (i.e., one that only included the intercept and the random effects) by performing a likelihood-ratio test (LRT) that compared the log-likelihoods of both (Crawley 2002). We investigated whether the model was unstable due to multicollinearity between two or more predictor variables by bootstrapping the data 1,000 times to obtain parameter coefficients of each of the individual predictor variables (Manly 1997). This allowed us to verify that the confidence intervals (CI) for parameter estimates were small, which is evidence for a minor effect of multicollinearity. Finally, as we investigated many different models with the same data set, we did a Fisher's omnibus test on the set of p values of the models tested. The resulting highly significant p value of the Fisher's test ($p<0.0001$) indicates that there were no power problems or type I errors resulting from multiple testing.

Details of the models

Response variables

As mentioned above, *Grooming, Supporting*, and *Transferring meat* were used in separate models as both binary and continuous response variables. For the analyses with continuous response variables (Gaussian models), we used rates instead of total amounts or occurrences (i.e. for a behavior X and a dyad AB, X rate_{AB}=ABs' total number or amount of X interactions/observation time of AB). We did this to correct for differences in the number of hours we observed each dyad. We determined that the use of a Gaussian error structure for continuous response variables was justified by inspecting the histograms of the residuals of each model and by the use of Kolmogorov–Smirnov tests. The four variables complied with the requirements of normality.

Predictor variables

When used as predictor variables, *Grooming* was always included as a continuous one (total seconds A was seen grooming B), *Supporting* as a binary one (0/1, whether A was seen giving support to B in the 22-month study period), while *Transferring meat* was included as binary (0/1) or continuous predictor variable depending on which one had a better fit (based on the AIC of the full model, the type of predictor used for this variable is specified in the results). In all the above models, we included *Rank* of the giver, *Rank difference*, association patterns (dyadic association index, Nishida 1968), and *Sex* combination of the dyad as additional predictor variables to control for any confounding effects of proximity or similarity amongst individuals. As the effect of these variables is not relevant to the goals of this paper, and they were only included because of their possible confounding effect, we did not include them in the results. Finally, in each model, we tested for the significance of the interactions between each commodity (i.e., *Grooming, Supporting*, *Transferring meat*, and *Copulating*) and *Sex combination*, and each commodity and *Rank difference*. This allowed us to determine if the relationship between each pair of commodities was different for different sex classes (e.g., if male–male dyads exchanged meat for support but female–female dyads did not) or for dyads with different rank classes (e.g., if only dyads close in rank reciprocated grooming). To test the overall significance of an interaction, we performed a likelihood-ratio test (LRT) comparing log-likelihoods of the full model (i.e., one with the interaction term) and the reduced model (Field 2005). We accounted for multiple testing by carrying out Fisher's omnibus tests on the set of interactions of each analysis (Haccou and Meelis 1994; Quinn and Keough 2002). If this test was significant, we included in the final model only those interactions for which the LRT was significant, in addition to the *z*-transformed main effects of the interaction (Crawley 2002). We tested the significance of each fixed effect using LRT (Crawley 2002), and for the Logistic models, we used MCMC tests as well as the first. In addition to these fixed effects, we included the identity of the giver and receiver as random effects (Gomes et al. 2009). Because measures of effect size are not available for GLMM, we evaluated effect size by comparing the AIC of the full model and a reduced model, which did not include the variable of interest, and performed a LRT. This allowed us to assess the amount of variability explained by the variable excluded from the reduced model (Baayen 2008). The unit of measure was the dyad, so that each data point consisted of the total number of interactions of each behavioral category (continuous variables) or whether the behavior was seen or not (binary variables) throughout the entire 22-month study period per pair of giver–receiver (Gomes et al. 2009).

Results

Grooming

The 91 dyads sampled were observed grooming for a total of 87 h, including 22 h (25%) of mutual grooming and 65 h (75%) during which one individual groomed its partner (for more details on the general grooming patterns, see Gomes et al. (2009)).

Grooming as a binary (Logistic model) and continuous response variable (Gaussian model) In both models, the predictor variables had a significant overall effect on *Grooming* given (Logistic model, LRT: $\chi^2=32.97$, df=9, $N=182$, $p=0.0001$; Gaussian model: $\chi^2=115.97$, df=9, $N=161$, $p<0.0001$). However, the only behavior that significantly predicted *Grooming* given was *Grooming* received, whereas neither *Supporting* nor *Transferring meat* (binary variable) significantly predicted *Grooming* (Table 1)[2]. A model that did not include *Grooming* received had a significantly inferior fit than one that did, indicating that *Grooming* received explained an important amount of the variability of *Grooming* given (Logistic model, Model with *Grooming* received: AIC=114, df=12, Model without *Grooming* received: AIC=126, df=11, LRT: $\chi^2=14.26$, df=1, $p<0.0001$; Gaussian model, Model with *Grooming* received: AIC=505, df=12, Model without *Grooming* received: AIC=591, df=11, LRT: $\chi^2=81.31$, $p<0.0001$). None of the interaction effects were significant; therefore, these were not included in the final model.

Grooming and copulating (male–female subset) For this subset, we lacked enough variability to use *Grooming* given as a binary response variable because there were only four dyads in which the male never groomed the female. When *Grooming* was used as a continuous response variable, the variables included in the model had a significant effect on *Grooming* given (Gaussian model: $\chi^2=47.35$, df=7, $N=37$, $p<0.0001$), although *Copulating* did not significantly predict the amount of *Grooming given* (Table 1).

Therefore, giving grooming was only correlated with receiving grooming and individuals were more likely to groom, and gave more grooming to those who groomed them more than to those who groomed them less.

Supporting

We observed 70 instances of one individual supporting another in an aggressive interaction. Out of the 91 dyads observed, in 57 (63%) dyads, neither of the individuals were observed supporting the other; in 23 (25%) dyads, only one of the individuals in the pair was observed supporting its partner; and in 11 (12%) dyads, both supported each other on at least one occasion. In dyads in which support occurred, most supported their partner only once ($\overline{X}=1.44$, Q1=1, Q3=1.25, 0.04–0.67 times/day of observation).

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[2] Note that the results of this analysis differ slightly from the ones presented in Gomes et al. (2009). As the goal of each paper was different, so were the analyses. In this analysis, we incorporated all of the dyads, including those in which only one individual in the pair groomed its partner, whereas in Gomes et al. (2009) we did not.

Table 1 Commodities influencing if, and how much time one individual spent grooming another

Predictor variable	Logistic model		Gaussian model	
	b±se	*p* value	*b*±se	*p* value
Grooming	1.59±0.51	0.001	1.15±0.09	<0.0001
Support	0.93±0.92	0.31	−0.09±0.20	0.64
Meat transfer (0/1)	−0.67±0.79	0.40	−0.04±0.12	0.78
Copulation rate	–	–	1.32±.99	0.19

Supporting as a binary response variable (Logistic model) Overall, the predictor variables included had a significant effect on *Supporting* (χ^2=63.91, df=15, *N*=182, *p*<0.0001). The probability that an individual would support another was predicted by whether it received support and by the amount of meat it received (Table 2). However, the relationship between these variables varied with partner sex (Table 2). The relationship between *Support* given and received was positive for male–male and female–female dyads (GLMM, slope: ♂♂=4.6, *p*=0.05; ♀♀=1.45, *p*=0.03), whereas for male–female dyads, the relationship was not significant (GLMM, slope: ♂♀=−1.08, *p*=0.78; ♀♂=−0.37, *p*=0.93). The correlation between *Transferring meat* and *Supporting* was positive for male–male and male–female dyads (GLMM, slope: ♂♂=1.76, *p*=0.04; ♂♀=1.25, *p*=0.008; ♀♂=1.59, *p*=0.09), but not for female–female ones for which it was not significant (GLMM, slope: ♀♀=−0.36, *p*=0.14). However, given the small sample size of each of these subsets (*N*: ♂♂=20, ♂♀=45, ♀♂=45, ♀♀=72), the results must be interpreted with caution.

The model that included *Supporting* as a continuous response variable (Gaussian model) was not significant (χ^2=8.46, df=9, *N*=45, *p*=0.49). The same when we included *Supporting* as a binary response variable for the subset of male–female dyads to investigate the relationship between *Copulating* and *Supporting* (χ^2=9.26, df=7, *N*=39, *p*=0.23). This indicates that overall, the predictor variables included in these models had no explanatory value. Finally, we had too few data points (*N*=10) to analyze a model with *Supporting* as a continuous response variable for male–female dyads; thus, we were not able to evaluate the relationship between *Copulating* and the number of times one individual supported another.

Thus, only support received and meat received were correlated with *Supporting*.

Table 2 Commodities influencing if one individual supported another in an aggressive interaction

Predictor variable	Logistic model	
	b±se	*p* value
Grooming	−0.06±0.27	0.83
Support	1.55±0.55	0.005
Meat transfer	−2.45±1.35	0.08
Support * Sex class	9.89 (χ^2)	0.02
Meat transfer * Sex class	19.85 (χ^2)	<0.0001
Copulation rate	–	–

Transferring meat

We observed 508 transfers of meat. Out of the 91 dyads, 34 (37%) dyads were never seen transferring meat; in 36 (40%), only one individual of the pair shared with its partner; and in 21 (23%), both individuals of the pair shared meat with their partner on at least one occasion. However, the amount of meat each individual shared with each partner varied considerably ($\overline{X} = 820$ g, Q1=225 g, Q3=1.33 kg, 0.008–20.4 g/h of observation).

Transferring meat as a binary response variable (Logistic model) The predictor variables had a significant overall effect on meat given (χ^2=35.86, df=9, *N*=182, *p*<0.0001). However, the only behavior that had a significant effect on *Transferring meat* was *Supporting* (Table 3), and a model that did not include *Supporting* had a significantly inferior fit than one that did, indicating that *Supporting* explained an important amount of the variability of *Transferring meat* (model with support received: AIC=109, df=12, model without support received: AIC=112, df=11, LRT: χ^2=4.54, df=1, *p*=0.03). None of the interactions tested for (see "Predictor variables" section) reached significance and were therefore not included in the final model.

Transferring meat as a continuous response variable (Gaussian model) The predictor variables included had a significant overall effect on meat given (χ^2=20.13, df=7, *N*=78, *p*=0.005). However, none of the behavioral variables were significantly correlated with the number of times one individual shared meat with another (Table 3).

Table 3 Commodities influencing if, and how many times one individual transferred meat to another

Predictor variable	Logistic model		Gaussian model (freq)	
	b±se	*p* value	*b*±se	*p* value
Grooming	−0.54±0.23	0.25	−0.004±0.14	0.97
Support	2.76±0.70	0.0001	0.28±0.24	0.25
Meat transfer	−0.11±0.25	0.63	−0.23±0.13	0.08
Copulation rate	28.46±8.95	0.003	2.59±1.32	0.09

We used the rate of meat transfer events instead of the amount of meat transferred (grams) as a response variable because the model with amount transferred was not significant

Transferring meat and copulating (male–female subset) When meat transferred was included as a binary response variable (Logistic model), the predictor variables included in the model had a significant effect overall ($\chi^2=4.31$, df=3, $N=39$, $p<0.03$). Furthermore, *copulating,* significantly predicted whether a male would transfer meat to a female (Table 3). When *transferring meat* was included as a continuous response variable (Gaussian model: $\chi^2=13.98$, df=7, $N=28$, $p=0.052$), *Copulating* did not significantly predict the amount of meat a male gave a female (Table 3).

Therefore, only giving or not giving meat (binary variable) was predicted by other behavioral variables; it was correlated to support received and to the number of times the male copulated with a female.

Copulating

Thirty-nine male–female dyads were observed together while the females were in estrous (estrous females were observed 1,814 h). These dyads were seen copulating a total of 262 times (Gomes and Boesch 2009).

Copulating as a binary response variable (Logistic model) None of the variables included in the model were significant (Overall effect: $\chi^2=12.57$, df=6, $N=39$, $p=0.09$, Table 4), indicating that *Grooming, Supporting*, or *Transferring meat* to a female (binary predictor variable) did not increase the probability that she would copulate at all with the male.

Copulating as a continuous response variable (Gaussian model) The predictor variables included in the model had a significant effect on *Copulating* ($\chi^2=18.55$, df=6, $N=30$, $p<0.005$). However, *Transferring meat (*binary predictor variable) was the only variable that was correlated with *Copulating*, and the relationship was positive, indicating that males who transferred meat to a female copulated more frequently with the female than males who did not (Table 4)[3]. None of the interaction effects reached significance; therefore, they were not included in the final model.

Discussion

General exchange patterns in the Taï chimpanzees

Our results suggest that chimpanzees in the Taï Forest have both in-kind reciprocal exchanges and trades (Fig. 2). Although the setup of the models tested seems to indicate causality, as there is always a response and a predictor variable, we are not assuming that giving one commodity is preceded by giving another (e.g., males first give meat and then copulate with a female). We aim only at investigating whether correlations exist between giving and receiving commodities, and whether these suggest that individuals exchange resources and helpful acts. We found a number of such correlations that were not by-products of random giving (i.e., giving more to those with whom the target spent more time) or of giving to similar individuals. Furthermore, in the light of findings from other populations, it seems that kin selection has a limited effect on cooperation (Langergraber et al. 2009), and while it might explain some of the correlations we found, it probably cannot account for most of them. We conclude that most of these correlations seem to be reflecting instances of exchange amongst individuals in the Taï chimpanzee community. However, mutualism could also be playing a role in explaining some of the cooperative acts observed in chimpanzees, as the giver might be receiving a net benefit by helping another individual. This could be the

Table 4 Commodities influencing how many times a female copulated with a male

Predictor variable	Gaussian model	
	b±se	*p* value
Grooming	2.16±1.55	0.18
Support	3.33±3.36	0.33
Meat transfer (0/1)	6.81±3.49	0.02

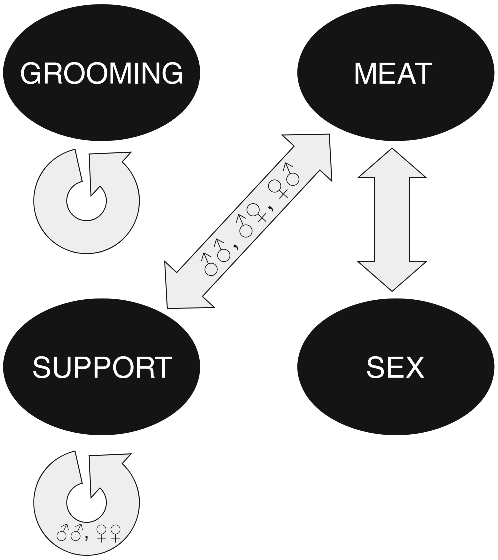

Fig. 2 Diagram of the commodities exchanged by chimpanzees in the Taï National Park. For cases in which not all sex classes engaged in a particular type of exchange, we pointed out the ones that did. Cases with no arrow represent exchange possibilities that were not reciprocal in the Taï chimpanzee group

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[3] Note that the results of this analysis differ slightly from the ones presented in (Gomes and Boesch 2009). The response variable in this analysis is copulation rate whereas in the previous paper it was total copulation counts.

case of support in aggressive encounters, in which cases the supporter (giver) might aggress a common enemy, resulting in an immediate net benefit for both the giver and receiver. Although there is no evident reason why cooperation driven by mutualism should result in a correlation between giving and receiving, it would be necessary to rule out this possibility by investigating in more depth the costs and benefits of support.

The correlation between the amounts of grooming given and received suggests that the Taï chimpanzees exchanged grooming for grooming, presumably resulting in both giver and receiver acquiring a net hygienic and tension relief benefit. However, the lack of significant correlation between grooming and any of the other commodities indicates that grooming was exclusively exchanged for grooming, explaining the high levels of symmetry found in the relationship between grooming given and received. The correlation between the amount of support given and received, suggest that chimpanzees exchange support for support; thus, a chimpanzee that helped another group member in an aggressive encounter with a third party was likely to receive support from that same partner in a future dispute. However, the results of the models of support should be interpreted with caution as the sample size was low and it is possible, in spite of the correlation found, that mutualism could also be playing an important role.

Our results also show that they trade different commodities. Both the support models and meat transfer models suggest that Taï chimpanzees traded support and meat. An individual who supported another was more likely to receive meat from that partner and vice versa (Tables 2 and 3). The lack of significant correlations between the amount, the rate of meat transfer, and other variables could be due either to a failure by Taï chimpanzees to take into account any other commodity when considering how much meat or how many times to share with other individuals, or to a problem with statistical power. We were unable to record all of the instances of meat transfer, even though two to three people were recording data on different individuals simultaneously, as it is virtually impossible to observe every sharing episode in a meat eating party because some individuals are usually out of sight. We would need more data to determine whether the analysis lacks power or if our results reflect the true nature of meat exchanges in chimpanzees. Finally, both the models of copulation (Gaussian) and meat transfer (Logistic) suggest that females and males traded meat and sex, and that what was important was whether or not the male had transferred meat to the female, and not the rate or amount of meat transferred, and the copulation rate, and not whether the female had copulated or not with the male. Thus, a male who shared meat with a particular female copulated more frequently with that female than one who did not share meat with her. Previous analyses indicated that this relationship was not a by-product of other factors such as begging, female age (studies have shown that female age in chimpanzees is a good proxy for female attractiveness, (Muller et al. 2006)), or gregariousness of the female (as a proxy for their likelihood of receiving meat), suggesting that in fact, males and females trade meat and sex (Gomes and Boesch 2009). The difference between the two copulation models (Logistic model not significant, Gaussian model significant) could be due to females being able to actively bias their frequency of copulation with each male based on their own preference, but not being able to avoid copulating at all with unpreferred males; or to paternal confusion. However, detailed data on female choice would be necessary to test these hypotheses.

Some differences in exchange depended on the sex of partner dyads. Only same-sex dyads engaged in in-kind exchanges of support, whereas male–female dyads did not reciprocate the support they received in aggressive encounters. Male–male and male–female dyads exchanged meat and support, but female–female dyads did not. Although these results should be interpreted with caution because they could be inaccurate due to small sample sizes, they suggest that males and females both engage in in-kind exchanges and trades, but the commodities they trade differ among sex classes. Furthermore, Taï chimpanzees sometimes interact selectively with particular partners depending on the sex of their partners. Both males and females seem to rely on same-sex partners who had previously supported them in aggressive encounters, but seem to be less selective when it comes to choosing partners with whom to exchange meat.

These findings show that exchanges were common place among chimpanzees in the Taï Forest and that many of the resources and services that they depend on were acquired from other group members (Fig. 2). For example, on average 34% of the meat a chimpanzee from the Taï Forest consumed was obtained from others, which they might have obtained through trades of meat for support or sex. We could not determine whether trades might have compensated for other unbalanced exchanges because no more than one predictor variable of interest had a significant effect in any of the models that tested amounts exchanged (Gaussian models). However, that the Taï chimpanzees seem to trade support, meat and sex suggests that individuals might balance out debts of a particular helpful act or resource with another type of commodity; for example, unbalanced exchanges of support for support might be compensated by transferring meat. Further studies which use Gaussian models to test for the exchange of several commodities simultaneously will aid in answering this question.

Differences among groups and species

Studies of other groups of chimpanzees have also found that they engage in both in-kind exchanges, and trades (Table 5):

Table 5 Review of the studies of reciprocity and trade in chimpanzees

Group	Habitat	Analytical method	Behaviors investigated	Variables included	Results		Ecological factors[a]	Sources
					In-kind reciprocity	Trade		
Mahale-M group	Natural	Matrix correlations	GR		GR		Average group size (79, 9M, 19F) Low density (3 chimp. per km^2)	Nishida and Hosaka (1996); Watts (2000); Boesch (2002); Matsumoto-Oda (2002)
Budongo-Sonso	Natural	Matrix correlations	GR	AG, SE, AS, RA	GR		Average group size (46, 12M, 11F) Average density (6 chimp. per km^2)	Wallis (2002); Arnold and Whiten (2003); Newton-Fisher (2003); Reynolds (2005); Newton-Fisher and Lee (2011)
Kibale-Ngogo	Natural	Matrix correlations	GR, SU, ME	AG, AS, RA, GE	GR, SU, ME	GR and SU, GR and ME, SU and ME	Large group size (140, 24M, 45F)	Watts (2000); Mitani and Watts (2001); Mitani et al. (2002a); Mitani et al. (2002b); Watts (2002); Mitani (2006); Watts (2007)
		Binomial test	ME, MS			No evidence	Average density (4 chimp. per km^2) Apparent low female choice (more male coercion)	
Gombe	Natural	Linear regressions (GEE)	GR, ME	SE	Not tested	Partial support for ME and GR	Average group size (55, 10M, 20F) Average density (5 chimp. per km^2) Apparent low female choice	Goodall (1986); Wallis (2002); Williams et al. (2002a); Williams et al. (2002b); Gilby (2006); Murray et al. (2006)
		Linear regressions (GEE) and sign tests	ME, MS		Not tested	No effect		Gilby (2006); Gilby et al. (2010)
Kibale-Kanyawara		Spearman correlation	male SU of alpha male, MS	RA	Not tested	male SU of alpha male and MS	Average group size (41, 9M. 13F) Low density (3 chimp. per km^2) Apparent low female choice	Wrangham et al. (1996); Muller (2002); Duffy et al. (2007)
	Natural	Linear regression (GEE)	ME, MS		Not tested	No effect		Gilby et al. (2010)
Tai-North group	Natural	Matrix correlation	GR	AG, AS, RA	GR	Not tested	Average group size (61, 7M, 21F) Low density (3 chimp. per km^2) High female choice	Boesch and Boesch-Acherman (2000); Herbinger et al. (2001)
Tai-South group	Natural	GLMM	GR, SU, ME, MS	AG, SE, AS, RA	GR, SU	SU and ME, ME and MS	Average group size (44, 8M, 16F) Low density (2 chimp. per km^2) High female choice	Herbinger et al. (2001); Stumpf and Boesch (2006); Gomes and Boesch (2009); Gomes et al. (2009); Riedel et al. (2010)
							Steepness of dominance hierarchy[c]: 0.83(all), 0.82 (MM), 0.55 (FF), 0.1 (MF) Highly gregarious females	
Arnhem zoo	Captive (observational)	Matrix permutation and Pearson correlation	SU, GR	SE, AS, GE	SU	Not tested	Small group size (23, 4M, 9F) Low density (2 chimp. per km^2) Low food competition Effect of habitat size	de Waal and Luttrell (1988)
		Matrix correlation	GR, SU, FO, MS	AG, RA, SE	GR, SU	GR and SU[b] GR and MS	Effect of dominance rank stability	Hemelrijk (1990); Hemelrijk and Ek (1991); Hemelrijk et al. (1992)
Yerkes Primate Center	Captive (experimental)	Matrix permutation and Pearson correlation	FO, GR	AS, RA	FO	GR and FO	Small group size (19, 1M, 8F) High density (25 chimp. per km^2) Low food competition	de Waal (1989)

Table 5 (continued)

Group	Habitat	Analytical method	Behaviors investigated	Variables included	Results		Ecological factors[a]	Sources
					In-kind reciprocity	Trade		
		Matrix permutation and Pearson correlation	FO, GR		FO, GR	GR and FO	Small group (20, 1M, 8F) High density (27 chimp. per km^2) Low food competition	de Waal (1997)
Walter Zoo	Captive (experimental)	GLMM	FO, GR	AS, RA, SE, GE	FO, GR	Not tested	Small group size (13, 3M, 8F) High density (37 chimp. per km^2) Low food competition Steepness of dominance hierarchy: 0.18 (all)	Jaeggi (2010)

GR grooming, *SU* support in aggressive conflicts, *ME* transferring meat, *MS* mating success, *FO* sharing food, *AG* age, *SE* sex combination of the dyad, *AS* association, *RA* rank, *GE* genetic relatedness

[a] Group size: The numbers included in the table are total group size, number of adult males, number of adult females. These are approximates as the numbers sometimes varied from one year to another. Group size is categorized based on the reported numbers for natural populations: Average group size > 37 and < 67 chimpanzees, Small group size ≤ 37 chimpanzees, Large group size ≥ 67 chimpanzees. Density: Categorized based on the reported numbers for natural populations: Average density < 6 and > 3 chimpanzees per km^2 , Low density ≤ 3 chimpanzees per km^2 , High density ≥ 6 chimpanzees per km^2 . For general descriptions and characteristics of each chimpanzee group see Ghiglieri (1984); Goodall (1986); Nishida (1990); Wrangham et al. (1994); Mc Grew et al. (1996); Boesch and Boesch-Acherman (2000); Boesch et al. (2002); Reynolds (2005).

[b] The trade of grooming for support disappeared during the period with an unclear alpha male

[c] Calculated based on the slope of a linear regression line through the normalized David's scores of the pant grunts (de Vries 1995; de Vries et al. 2006). We report the slope of the regression of the whole group and of each sex combination (MM, FF, MF). All of the regressions were significant (p=0.0005)

The Mahale and Budongo chimpanzees were shown to exchange grooming for grooming (Nishida and Hosaka 1996; Arnold and Whiten 2003); the Ngogo chimpanzees were shown to have in-kind exchanges of grooming, support and meat, and to trade grooming for support, grooming for meat, and support for meat (Watts 2002; Mitani 2006); whereas no other group of chimpanzees (Ngogo, Kanyawara nor Gombe) was observed to engage in exchanges of meat for sex (Mitani and Watts 2001; Gilby et al. 2010). Several observational studies of captive chimpanzees also showed that they engage in in-kind exchanges and trades of different commodities (Table 5); whereas other studies have used artificial setups (e.g., the exchange of tokens) to investigate the extent to which chimpanzees are capable of cooperating with each other, the proximate mechanism(s) explaining exchanges (e.g., similarity-based, emotionally based or cognitive-based reciprocity, (de Waal and Luttrell 1988; de Waal 2000; Aureli and Schino 2004; Schino et al. 2007)), the cognitive capacities of chimpanzees, and the differences of these with humans (Brosnan and de Waal 2005; Jensen et al. 2006; Melis et al. 2006; Melis et al. 2008; Brosnan et al. 2009; Yamamoto and Tanaka 2009). Although these represent an important contribution to our understanding of reciprocity and cooperation, the level at which they study cooperation is beyond the scope of this paper. That the commodities exchanged by chimpanzees in different groups were different is not surprising (see Table 5). According to biological markets theory (Noë and Hammerstein 1995), exchanges among animals are dynamic processes that change with social and environmental circumstances: thus, different species, groups, or even the same group at different time periods are expected to have different patterns of exchange based on variation in the characteristics of the local resources and in competition within the groups. Resources that are easily obtained by all individuals and thus less contested are less likely to be exchanged than resources that are unpredictable and harder to obtain. Furthermore, members of groups with medium to high levels of competition, who vary in resource holding potential (RHP) are more likely to engage in trades in which low-ranking individuals seek to obtain the resources they cannot obtain on their own, than are members of groups with low competition and similar levels of RHP. For example, in groups in which contest competition is low, grooming (a service that all non-injured adult individuals are equally capable of giving) is expected to be exchanged mainly for grooming, whereas in groups in which contest competition is high, grooming is expected to be traded for other contested commodities, such as food or support in aggressive interactions (Noë and Hammerstein 1995; Barrett et al. 1999; Henzi and Barrett 1999). Some support for this hypothesis comes from studies of chacma baboons, bonobos, samango monkeys, white-faced capuchins, savanna baboons, and gray-cheeked mangabeys, in which groups with less competition have more balanced grooming patterns than groups with more competition (Barrett et al. 1999; Payne et al. 2003; Manson et al. 2004; Stevens et al. 2005; Chancellor and Isbell 2009). However, if despotism reaches levels at which individuals can obtain desired commodities by force, then the incentive to exchange is lost and other hypotheses, such as the "sharing-under-pressure" model, will probably better explain instances of resource transfer (Wrangham 1975; Blurton-Jones 1984). In several bonobo and chimpanzee populations, this model explains food transfers, and in a few cases, despotism is associated to a lack of reciprocity (Fruth and Hohmann 2002; Stevens et al. 2005; Gilby 2006; Jaeggi et al. 2010). Differences in the competitive regime between the Taï and Ngogo group (e.g., Taï might have less intra-group freeding competition than Ngogo, due perhaps to lower population density (Table 5); evidence of this could be the high gregariousness of females at Taï compared to other Eastern African groups (Riedel et al. 2010)) could explain why the Taï chimpanzees exchanged only grooming for grooming, whereas the Ngogo chimpanzees traded grooming for meat and support. Furthermore, differences in the degree of female choice and in the level of despotism among groups (Table 5) could explain why meat and sex were traded in the Taï group but not in other chimpanzee populations. However, further studies which take into account the level of competition, the steepness of dominance hierarchies (see Table 5 for measure of steepness of the Taï chimpanzees), and other behavioral and ecological factors are needed to test these hypotheses.

The variation observed among different chimpanzee groups could also be due to analytical problems. Most of the previous studies on reciprocity in wild chimpanzees have used univariate analyses (Table 5) which preclude testing the effect of all exchangeable commodities simultaneously while controlling for many confounding factors. This could lead to correlations resulting as a by-product of other exchanges (e.g., a correlation between support and meat resulting from the in-kind exchanges of support and meat) or of the effect of other confounding factors (e.g., association, rank, sex) [4]. In addition, precise estimates of exchanges that do not underestimate the symmetry of a relationship are difficult to obtain unless all exchangeable commodities are included in the same analyses and the appropriate time scale is used (Gomes et al. 2009). To avoid such problems, future studies must determine a priori the appropriate time scale at which exchanges must be analyzed (see Gomes et al. 2009 for an example) and make use of modern multiple regression techniques which allow the inclusion of all exchangeable commodities and confounding factors simultaneously in one analysis.

This study presents evidence showing how group living animals can depend on one another to acquire important resources and services. Wild chimpanzees living in the Taï Forest seem to obtain these commodities by exchanging them with other group members. These exchanges provide them with meat and support in aggressive interactions, and allow them to stay clean and healthy through the grooming they obtain from others, especially of hard to reach body parts. In the absence of partners willing to contribute to their well being, certain individuals would be unable to acquire important commodities that are perhaps necessary for their survival. For example, individuals would have a hard time keeping certain body parts clean; female chimpanzees, who rarely hunt or obtain meat on their own (Boesch 1994; Gomes and Boesch 2009), would hardly ever eat meat; low-ranking males, who are usually unable to monopolize estrous females (Boesch and Boesch-Acherman 2000), would perhaps have difficulties gaining access to them, especially when they are periovulatory. Additional helpful acts that occur less frequently but play a very important role in the survival of certain individuals, such as adoption of orphans or care for injured individuals (Boesch 2009), are perhaps also exchanged or given only to trusted cooperating partners. The maintenance of reciprocal relationships might be essential to establish the trust and familiarity necessary to make these types of long-term investments and develop relationships similar to what we consider friendship.

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[4] Many studies have used matrix correlations which allow investigating the relationship between two variables while controlling for a third confounding factor. Although this was the appropriate analysis, and best one available at the time these studies were done, it does not allow investigating the relationships of more than three variables simultaneously. In light of the statistics available now, it would be interesting to reanalyze these data to determine whether there are any differences in the relationships found.

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