

Original Article

“Decision-making” in conflicts of wild chimpanzees (*Pan troglodytes*): an extension of the Relational Model

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Received: 25 April 2002 / **Revised:** 6 May 2003 / **Accepted:** 4 June 2003 / **Published online:** 11 July 2003

Abstract >We examined the “decision-making” process of aggressive interactions within a community of wild chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d’Ivoire (West Africa). Costs and benefits were investigated for 876 dyadic aggressive interactions among 18 adults (including 4 independent adolescents) of either sex. An extended version of the Relational Model was developed to describe the dynamics of the “decision-making” process in Taï chimpanzees, which suggests that the net benefit determines the occurrence of conflicts. Both sexes fought more frequently for the resources that were most important to them, food for females and social contexts for males. Individuals used two different strategies according to their likelihood of winning the aggressive interaction, determined by the dominance relationship of the conflict partners. Dominant initiators had longer and more intense aggressive interactions, but they limited their social disadvantages by fighting non-cooperative partners. Subordinate initiators had shorter and less intense aggressive interactions, but risked more social costs, which they could reduce afterwards by reconciliation. Both strategies included a positive overall net benefit. The extended

Relational Model fits the complexity of wild chimpanzee conflicts and allows for more flexibility in the “decision-making” compared to the original version.

Keywords Extended Relational Model · Conflict management · Likelihood of winning · Aggressive interactions · Chimpanzees

Communicated by E. Sterck

An erratum to this article can be found at <http://dx.doi.org/10.1007/s00265-003-0696-y>

Introduction

Group-living animals face the problem of competing over resources and mating partners with the same social partners that they cooperate with in protection against predators and in resource acquisition (Wrangham 1980; Walters and Seyfarth 1987; van Hooff and van Schaik 1992; de Waal 2000a). The dilemma is that an out-competed cooperation partner might withhold assistance in the next situation when cooperation is required. Therefore the use of aggression to resolve competitive situations carries advantages and disadvantages. This has led to a number of mechanisms being proposed that function as counter-disadvantage regulations (e.g. dominance hierarchy: Popp and de Vore 1979; post-conflict management: Kappeler and van Schaik 1992; meat-sharing: Boesch 1994). The most recent and comprehensive model for aggressive competition including counter-disadvantage mechanisms is the Relational Model (RM) (de Waal 1996).

The RM considers aggression, as well as tolerance and avoidance, as possible reactions to a conflict of interest—a competitive situation of two individuals having incompatible goals (van der Dennen and Falger 1990). The model predicts that whenever there is a conflict of interest, the tendency to take aggressive action increases with the number of opportunities for competition, as well as the resource value and the reparability of the relationship, while it decreases with the risk of injury and the value of the relationship (de Waal 2000b). An individual is viewed as going through a “decision-making” process during a conflict of interest, weighing the costs against the benefits. Since we do not want to imply any deliberate intention in the “decision-making”, we have used quotation marks. Although the RM is a convincing model, it has never been tested as a complete model with data of one species. In this paper, we assess this “decision-making” process

in wild chimpanzees using a cost-benefit estimation based on the RM, where the net benefit applies to benefits minus costs.

In the RM, the benefit is taken as the value of the resource. According to the socio-ecological model, food is proposed as the most beneficial resource for females whereas a sexual partner holds the most benefit for a male (Janson 2000). High rank, determining priority of access to females, is very beneficial to male primates (Dixson 1998). In the RM, cost of aggression is taken as the risk of injury. Injury obtained during fighting can entail tremendous costs through infection and disability, hampering food acquisition, travelling and defence against predators (Palombit 1993). In the RM, social costs are represented by the negative effects aggression produces by disturbing the relationship between partners (e.g. unwillingness to support or to share food). The more valuable the relationship, the more partners suffer from the disturbance (Aureli and Smucny 2000). However, the disturbance can be reduced by reconciliation, such that relationships of former opponents return to their baseline level, and these dyads seem to interact like before (Cords 1992). In the RM, the tendency to reconcile is referred to as the reparability of the relationship. The opportunity for competition, suggested as a predictor in the RM, seems to be more a predictor for the number of conflicts of interests individuals face rather than for their aggressive tendency. Although the aggression rate increases with competition (Janson 1988; Barton and Whiten 1993; Sterck and Steenbeek 1997; Wittig and Boesch 2003), the individual's aggressive tendency per conflict of interest should not be affected when the other factors stay constant. Therefore, the opportunity for competition is not considered as a predictor in our study.

Despite the fact that several costs and benefits are taken into account, the RM does not explicitly consider two other important factors. First, whilst predicting a higher tendency for aggression when the value of the resource is high, it only evaluates the potential benefit of the resource, without considering that the resource has to be accessed to gain the benefit. This requires winning the contest. Different fighting abilities of conflict partners influence the outcome of the contest (Huntingford and Turner 1987). In stable social groups, where the same two individuals compete repeatedly, dyadic dominance relationships often emerge as linear rankings at group level (Jackson 1988). Conflict partners with small rank differences have more equally matched fighting abilities. In consequence, the probability of winning should increase with the rank difference for the dominant initiator, but should decrease for the subordinate who fights a stronger individual. Except for the highest and the lowest ranking member of the community, individuals are facing conflict situations where each can be either dominant or subordinate to the conflict partner. In this manner, the

likelihood of winning a contest, a precondition for gaining the value of the resource (the benefit), is an important component added to the RM.

Second, the RM incorporates the risk of injury as the only cost of aggression. Although most aggressive interactions end without injuries (Bernstein et al. 1983; Whitten and Smith 1984), are they really free of cost? Aggression requires energy expenditure and this energetic cost of fighting has been shown to increase with duration (Smith and Taylor 1993; Hack 1997; Neat et al. 1998). Moreover, longer conflicts are usually followed by aggressive post-conflict interactions (R.M. Wittig and C. Boesch, unpublished data). Thus, third parties might join the conflict the longer an aggressive interaction continues, which involves additional costs of aggression. As energy expenditure increases with conflict duration and long conflicts involve additional aggression costs, we have added duration as second necessary component to the RM.

Furthermore, the RM predicts that the tendency to initiate aggression increases with reparability of the relationship, independent of whether there will be negative effects of the aggression. However, repairing a relationship is important only when there is something to repair. Cords and Thurnheer (1993) have shown that the occurrence of reconciliation is dependent on the value of the relationship of former opponents. Therefore, the value of the relationship and its reparability are dependent on their contribution to the RM. Both factors have to be considered together in the “decision-making” process, as repairing the relationship can counteract the social costs.

In general, animals can accept higher costs as long as the net benefit is positive (Parker and Rubenstein 1981). This might lead to different strategies by the same individual depending on the conflict situation: the same resource provides a different benefit to different individuals and different opponents require different fighting intensities or incur different social costs. Thus the dyadic character of conflict situations has to be considered by a competitor when deciding about aggression.

Chimpanzees represent a good model to test the “decision-making” process. Chimpanzees live in multi-male multi-female communities and face intra- and inter-sexual competition with multiple partners. A formal linear hierarchy is found among all adult members of the community based on dyadic dominance relationships (Wittig and Boesch 2003). They have frequent bouts of aggression that occur in different contexts, with different partners and different intensities (Goodall 1986). Alternatively, individuals can avoid aggression before it arises by just leaving the party, due to the fission-fusion character of the chimpanzee society. Finally chimpanzees build and maintain long-term relationships and often reconcile after aggressive interactions (Arnold and Whiten 2001; Preuschoft et al. 2002).

The aim of this paper is to test the extended RM with aggressive interactions of chimpanzees in the Taï National Park, Côte d'Ivoire. This test investigates how chimpanzees handle the conflict situation, taking into account the conflict's costs and benefits. The extended RM includes as benefit a combination of the benefit of the resource—assessed by the value of the resource—and the likelihood of winning, whereas costs include the cost of aggression and the social costs—assessed by the value of the relationship—minus the part of the social costs that are reduced by relationship repair. Our extended version of the RM predicts that aggression is expected when the net benefit is positive.

We tested the extended model using a step-by-step procedure, adding more parameters in each step, to show schematically how the “decision-making” process may operate for chimpanzees. First, the resource arouses the individual's interest. The individual assesses its likelihood of winning and how much aggression to invest, taking into account the identity of the competitor. Finally, the individual estimates the disturbance the aggression will cause to its relationship with the competitor and if this is repairable. Thus the potential gain in net benefit may be estimated, allowing an individual to “decide” whether to initiate aggression in this particular situation and how to handle the conflict. Each “decision” is highly dependent on the identity of the individuals in the dyad. Therefore our analysis is based on dyadic data and not on individual data. For simplicity, the term “conflict” is used instead of aggressive interaction.

Step 1: estimating the benefit

- a. The benefit of the resource: individuals are predicted to initiate conflicts more frequently in accordance with the value of the resource to them. We expect females to initiate more conflicts over food and males over oestrous females.
- b. The likelihood of winning: individuals are predicted to initiate conflicts more frequently the higher their likelihood of winning. We expect dominants to initiate and to win more conflicts than subordinates.

Step 2: estimating the costs of aggression

Individuals are predicted to risk more the higher the benefit of the resource is to them as long as they have a chance to access it. We expect chimpanzee initiators to have longer and more intense fights the higher the value of the resource is to them, and when they are dominant in the dyad. However, although dominant initiators are able to risk more than subordinates, in order to minimise

costs, individuals are predicted to avoid escalation of aggression. We expect, therefore, short and less intense fights when the rank difference to the opponent is large.

Step 3: estimating the social costs

- a. The social costs: individuals are predicted to keep the disturbance of their relationship with the conflict partner small. We expect chimpanzees to initiate less conflicts with high-benefit partners. If they initiate conflicts, then they are shorter and less intense (to minimise the costs of aggression), and mainly for high-benefit resources in dyads that they are likely to win (to maximise the benefit).
- b. Reducing social costs: individuals are predicted to reduce social costs more frequently when these costs are high. We expect chimpanzees to have a high chance of reconciling when they initiate conflicts with high-benefit partners (to reduce social cost).

Methods

Study site and subjects

Data were collected in the Taï Chimpanzee Project study area, in the Taï National Park, Côte d'Ivoire (West Africa, 5°52'N, 7°22'W). The study was carried out between October 1996 and April 1999 on the "North-community", which has been observed continuously since 1979 (further information: Boesch and Boesch-Achermann 2000). Almost all individuals, except for the female Ricci and her adolescent son Nino, were fully habituated to humans and were followed from nest to nest. During the observation period, Nino became fully habituated. In October 1996, the community consisted of 4 males (3 adults, 1 adolescent), 14 females (11 adults, 3 adolescents) and 13 juveniles and infants. During the observation period, five chimpanzees disappeared or died (one adult male, two adolescent females, two juveniles) and six infants were born.

Data collection and data set

R.M.W. collected the following three types of data during all-day follows on the four males and ten habituated adult females: (1) all-day focal animal sampling (Altmann 1974) on one target chimpanzee per day, recording activities (feed, rest, travel, etc.), social interactions (aggressive and affiliative) and vocalisations; (2) composition of the target's party every 10 min; (3) identity and number of females with genital swellings. Data were entered into a Psion Organiser hand-held

computer using The Observer (Noldus Information Technology 1989). In addition, fast interactions were recorded on audio tape and later entered into the day's computer file.

We aimed to change the target chimpanzee each day, observing females once and males twice per month. However, there was some variability in individual observation frequency due to the fission-fusion character of chimpanzee societies, death and the habituation level. The result was 80 all-day follows of males (Macho/Marius: 31 days each, Brutus/Nino: 9 days each) and 123 all-day follows of females (between 10 and 15 days per female). R.M.W. collected dyadic conflicts with complete information 1,071. Of these, 876 dyadic conflicts were analysed, as we excluded conflicts involving juveniles and infants.

Operational definitions

Conflict variables

A conflict was defined as a dyadic aggressive interaction that started with the first aggressive behaviour exchanged and ended with either submission (e.g. greeting, crouching, etc.), flight (fleeing, retreating, etc.), reciprocal screaming, or non-aggressive behaviour, which was not immediately followed by further aggression. Aggressive behaviours were classified into five ordinal intensities according to the aggression's likelihood of injuring the partner (Table 1). For each conflict, the most intense aggressive behaviour used determined the intensity score for that conflict.

[Table 1. will appear here. See end of document.]

Context variables

We observed conflicts within three different contexts. In sex contexts, conflicts are with or over oestrus females, either to copulate with them or to prevent others' copulation attempts. Food conflicts are over food resources. In the social contexts, conflicts show or challenge dominance (e.g. subordinates approaching without greeting followed by aggression) or conflicts arise from competition for social partners. However, it is partly a default option (as conflicts can only occur with other social partners present), which other studies have summarised in an "unknown" category (e.g. de Waal and Hoekstra 1980).

Dominance variables

Hierarchies in chimpanzees are classically determined by greeting vocalisations (de Waal 1978). We used “pant-grunts” among males and additionally “greeting-hoo” and “greeting-pant” among females to determine the hierarchy (Wittig and Boesch 2003). The hierarchy was linear (improved linearity test: $h'=0.80$, $P<0.0001$, de Vries 1995), with males dominant over females, which enabled us to clearly determine initiator’s rank and the rank difference (rank of subordinate minus rank of dominant) of a dyad (Table 1). One rank change occurred in the males during the data collection period due to the death of Brutus, the β -male. Since the two lower ranking males raised rank accordingly, conflicts between them and the α -male had two rank differences each in the data set, depending on whether the conflict occurred before or after the rank change. The winner of the conflict was defined as the one able to access the resource. In food contexts, the winner was the one possessing the food after the conflict. In sex contexts, the winner was able to assert his or her choice (e.g. a female refused copulation, a male interrupted a copulation of another male). In social contexts, the winner was the one who showed neither submission, nor screaming nor flight or, in cases of competition over the access to social partners, the one who affiliated with this social partner afterwards. We defined conflicts as a draw when neither conflict partner won. Cases ending in a draw were not considered in the analysis of the initiator’s likelihood of winning (step 2), as sample size was too small (less than 4% of conflicts).

Social variables

Association is defined as being present in the same party (being within visibility). We used the dyadic association index (DAI) to measure how frequently two individuals were associated:

$$DAI_{AB} = \frac{\sum (A + B)}{\sum A + \sum B - \sum (A + B)}$$

, where A is the time individual A was seen, B is the time individual B was seen and $A+B$ is the time A and B were seen together (Nishida 1968). We gave the relationship benefit three categories according to the presence of food-sharing and support events within the dyads (Table 1). Dyads of high relationship benefit are called friends. Reconciliation occurs when the first post-conflict interaction is socio-positive body-contact among former opponents. We used the corrected conciliatory tendency (CCT) for the probability that a dyad will reconcile after a conflict (Veenema et al. 1994). CCT is the quotient of the number of reconciliation events occurring sooner than the baseline time minus the number of reconciliation events occurring later than the baseline time,

divided by number of conflicts. We calculated the baseline time as the average time interval between two consecutive friendly interactions of the same dyad on the same day.

Some variables are affected by the sex of the chimpanzees (DAI: higher for males than females, Boesch and Boesch-Achermann 2000; CCT: higher for males than females, Preuschoft et al. 2002; dominance-rank: males dominant over females, Bygott 1979). For the multivariate analysis, we corrected for sex differences by calculating indices for DAI, CCT and rank difference. The indices relate data to average values of sex combinations in order to enable a comparison between the sexes (detailed description: Table 1).

Statistical process

To calculate expected frequencies, we corrected for the frequency of occurrence of each context. As conflicts could occur only when there was a partner present, we excluded data when chimpanzees were alone. Social conflicts could happen anytime (expected frequency: 1.0). However, food conflicts could occur only when chimpanzees were feeding. Males, like females, showed an average feeding time of about 45% of their time budget (expected frequency=0.45). Conflicts in a sex context could occur only when at least one female had a genital swelling. For male focals, oestrous females were present on 48 of the 80 days and focal females were in oestrus on 23 of the 123 days. As a result, expected frequencies are different for male-male conflicts (0.6), mixed sex conflicts (0.35) and female-female conflicts (0), since only conflicts with the focal animal were recorded and competition over sex among females was not expected. To enable a comparison between expected and observed frequencies, we standardised the frequencies by setting the sum of expected frequencies within each sex combination to 1.

When comparing among five and fewer individuals, standard non-parametric statistics are not applicable. Therefore, we applied a permutation test that follows the network subgroup analysis test of Dow and de Waal (1989). We created a matrix for each context and sex combination with the difference of observed minus expected frequencies of each dyad. We sampled randomly one data set (one specific matrix) with replacement and calculated the mean. The procedure was repeated 1,000 times and we checked whether zero (value when observed and expected frequencies are identical) was outside or inside the 95% confidence interval (two-sided test).

An optimal data set for multivariate testing should not include repeated measurements. However, some dyads fought several times in the same conflict situations. Therefore, we applied a balancing process for the data set with the following procedure: we compared all 876 conflicts and summarised conflicts in 1 data point that had the same initiator and receiver of aggression and were identical

in all variables of Table 1, except for conflict duration and intensity. For these last two variables, we calculated means and medians, respectively, to represent the identical conflict situations. The result of this balancing process was a data set of 409 conflicts, which we used for the multivariate analyses.

Generalised linear models (GLMs) are an extension of classical linear models, such as linear multiple regression or ANOVAs (McCullagh and Nelder 1989; Agresti 1996), and are an appropriate method to examine the functional relationship between a dependent variable and one or more independent variables (Hardy and Field 1998). GLMs have been successfully applied in studies on reconciliation and dominance relationships (Call et al. 1999; Côté and Festa-Bianchet 2001).

We used GLMs to study the effects of several independent variables on multiple dependent variables following the stepwise model design (Table 2). When analysing categorical dependent variables, we chose a binomial or ordinal multinomial error distribution, depending on the dependent variable (Table 1), and a logit link function (McCullagh and Nelder 1989). The best model for a dependent variable was selected using the best subset method, an iterative method that is based on likelihood statistics. The significance of the fitted terms was assessed using the Wald statistic at the final iteration of the algorithm (Dobson 1990). The estimate-coefficient β describes the strength of the effect that each independent variable-parameter had on the variation in the dependent variable. A positive β indicates an effect in favour of the first parameter of the dependent variable that enters the model, while a negative β indicates an effect in favour of the last parameter of the dependent variable that enters the model. For ordinal multinomial dependent variables, the first and the last parameter stand for parameters, respectively. The order of entering the dependent parameters in the model is the same as the parameter definitions in Table 1. Finally, the effects of the independent variable-parameters were tested.

[Table 2. will appear here. See end of document.]

Conflict duration d , the only continuous dependent variable, was log transformed [$d' = \log_{10}(d+1)$], to stabilise the variance. Homogeneity of variance was not obtained in the sex context, which was excluded from this particular test. The general linear model based on the least-square method was used to estimate the effects of the variables on the continuous dependent variable. Afterwards, we calculated the effect size for the significant variables and excluded trivial effects (effect size ≤ 0.1) from the model (Cohen 1988). For interactions of variables, we used a Fisher LSD post-hoc test (equivalent to t -test) with Bonferroni correction.

Furthermore, we controlled for over-representation of individuals as initiators of conflicts, since the balancing process controlled for multiple representation of conflict situations rather than the

number of conflict situations in which one individual initiated aggression. We tested all best models by adding the identity of the initiator as an independent variable, similar to the procedure of Côté and Festa-Bianchet (2001). It should be noted that, if two independent variables are correlated, then only the better predictor of the dependent variable shows a significant effect. Therefore, the explanatory power of any significant independent variable was proved to be independent from individual variation and over-representation when it remained significant (Bland and Altman 1995). However, we could not control initiator's sex with this method, as individuals are either male or female, resulting in zero variance of the initiator's sex. For the sake of simplicity, we present only the remaining significant variables of the best models in the results. For this test, the significance level was taken as $P < 0.05$.

All multivariate analyses were performed in STATISTICA 99 edition (StatSoft 1999). STATISTICA calls the test for categorical dependent variables a generalised linear model (GLZ), and the test for continuous dependent variables a general linear model (GLM). Two-sided exact tests were used for all non-parametric statistics because of small samples (Mundry and Fischer 1998), and were carried out in STATXACT 5 (Cytel Software 2001).

Results

Step 1: benefit

Benefit of the resource: did chimpanzees fight more in particular contexts (Table 2: step 1a)? Table 3 compares the frequency of initiated conflicts in the different contexts of each individual with the random expectation. The average frequencies suggest that females in same sex and mixed-sex dyads used more aggression in competition over food. However, aggression among males was more common in social contexts, and males attacked females more in food and sex contexts. We compared the relative difference between observed with expected frequencies for each individual. Females fought more frequently over food than in social contexts with other females (Wilcoxon exact: $T=10$, $N=12$, $P=0.021$), and more frequently over food than in social and sex contexts when attacking males (Friedman exact: $T_2=6.049$, $N=11$, $P=0.049$). For males, we applied the permutation test, due to the low number of individuals (Table 3). The six male-male dyads fought more often in social contexts (permutation test: $P=0.006$) and less often over food (permutation test: $P=0.018$), while they fought as expected over sex (permutation test: $P=0.238$). However, the 47 dyads of males attacking females did not show a preference in any context

(permutation test: social, $P=0.808$; food, $P=0.104$; sex, $P=0.055$). Thus, females fought more over food and males fought males more in social contexts.

[Table 3. will appear here. See end of document.]

Likelihood of winning: how was the chance of winning a conflict affected by the dominance relationship and the context of the conflict (Table 2: step 1b)? Likelihood of winning a conflict was significantly affected by two variables (GLZ: $LR \chi_{5,380}^2 = 84.19$, $P<0.0001$; Table 4). Dominant initiators were more likely to win conflicts (92%, $\beta=2.53$) than subordinate initiators (60%, $\beta=-2.53$). However, the likelihood of winning decreased with rank difference for dominant initiators whereas the opposite was true for subordinates (Fig. 1). The initiator's likelihood of winning was greater the larger the relative dominance of the initiator (Fig. 1: from very subordinate to highly dominant). In consequence, dominants initiated aggression more frequently with increasing rank difference (see "N" in Fig. 1, as the categories "dom-large" and "sub-large" etc. represent dyads from two different perspectives). Thus, the more dominant an initiator was over his opponent, the higher was his likelihood of winning the conflict and the more conflicts he initiated.

[Table 4. will appear here. See end of document.]



Fig. 1. Likelihood of winning a conflict in Taï chimpanzees. The proportion of initiator winning (*white*) compared to initiator losing (*black*) the conflict is displayed as a function of the interaction between Initiator's Rank and Rank Difference. The interaction is presented from the highest to the lowest likelihood of winning (*dom* dominant initiator, *sub* subordinate initiator, *big* large rank difference, *middle* middle rank difference, *small* small rank difference)

Step 2: cost of aggression

Conflict intensity: how was the intensity of the fight affected by the resource and the partner's dominance relationship (Table 2: step 2a)? Aggression type was only significantly affected by rank difference between opponents (GLZ: $LR \chi_{4,409}^2 = 17.11$, $P=0.0018$; Table 5). Dyads with a large rank difference were more likely to use non-contact aggression (large: 81%, $\beta=0.63$) than dyads with closer rank conditions (middle: 63%, $\beta=-0.34$; small: 64%, $\beta=-0.29$), independent of the context. Did chimpanzees then prefer low levels of intensity when subordinate and high levels when dominant to their conflict partner (Table 2: step 2b)? Conflict intensity was only significantly

affected by initiator's rank (GLZ: $LR \chi^2_{3,409} = 23.62$, $P < 0.0001$; Table 6). Looking at non-contact and contact aggression separately (Fig. 2), we found that subordinates initiated conflicts with lower levels of intensity for both non-contact (threats, level 1) and contact aggression (single physical contact, level 4). Dominants, however, preferred to initiate conflicts with higher levels of intensity for both aggression types (non-contact aggression: displays, level 2+3; contact aggression: multiple physical contact, level 5). Thus both types of aggression occurred in the repertoire of subordinates and dominants, but subordinates mainly initiated the lower and dominants the higher intensity variants of both types. In addition, both preferred non-contact aggression when the rank difference was large.

[Table 5. will appear here. See end of document.]

[Table 6. will appear here. See end of document.]



Fig. 2. Intensity of conflicts in Tai chimpanzees. The percentage of conflicts for dominant (*grey*) and subordinate (*white*) initiators as well as for all conflicts (*black*) is presented for each level of intensity. Intensity levels 1–3 are non-physical contact conflicts; intensity levels 4+5 are physical contact conflicts (Table 1)

Conflict duration: in addition to intensity, duration of the conflict was considered as a cost of aggression (Table 2: step 2c). Two variables significantly influenced the duration of a conflict (GLM: $F_{10,347} = 3.44$, $P = 0.0003$; Table 7). Males initiated longer conflicts than females and conflicts in social contexts were significantly longer than in food contexts (Fig. 3). Since males fought more in social contexts and females more in food contexts, but the interaction of both significant effects was not significant in the GLM ($F_1 = 2.27$, $P = 0.1332$), we investigated the interaction separately again. We found that male-initiated social conflicts were longer and had the largest range, whereas none of the other combinations were significantly different (Fig. 3; Fisher LSD with Bonferroni correction: significance level of $P < 0.016$; male-social: range=1–61 s, male-food: range=1–21 s, female-social: range=1–22 s, female-food: range=1–33 s). Thus, the effects of initiator's sex and conflict context was partly due to males initiating long conflicts in social contexts.

[Table 7. will appear here. See end of document.]



Fig. 3. Duration of conflicts in Tai chimpanzees. The mean duration (seconds±SE) is presented for each parameter of the significant variables of the model of conflict duration and also for the interaction. Post-hoc statistic for the interaction is shown in the graph in case of significance (significance level was Bonferroni-corrected to $P<0.016$)

Step 3: social cost

Social costs: how did chimpanzees distribute their social costs (Table 2: step 3a)? Conflict-induced social costs were significantly affected by three variables (GLZ: $LR \chi^2_{8,409} = 90.97$, $P<0.0001$; Table 8). Dominant initiators initiated more conflicts with low-benefit partners (low: 37.9%, $\beta=0.48$), while subordinate initiators initiated more conflicts with opponents of higher benefit (medium+high: 67.4%, $\beta=-0.48$). Moreover, the interaction of dominance and rank difference had the strongest effect of all significant variables on social costs (Table 8, β -coefficients). Considering dominant and subordinate initiators separately showed that dominants initiated more aggression with friends when the rank difference was small and more with non-friends when rank difference was large (Fig. 4). Conversely subordinate initiators attacked friends more when the rank difference was large and non-friends when rank difference was small (Fig. 4). Thus dominant, like subordinate, individuals started conflicts with friends more frequently as their relative likelihood of winning decreased (dom-small: $\beta=-0.95$, sub-large: $\beta=-0.94$). In addition, the sex combination of opponents had an effect (Table 8). Mixed pairs fought relatively less with low-benefit partners and relatively more with partners of a high-benefit relationship, whereas in conflicts among opponents of same sex, it was the opposite (conflicts per sex combination with low-benefit/high-benefit partners: m-m=36.3%/15.9%; f-f=49.0%/6.9%; m-f=28.8%/24.7%; f-m=22.0%/19.5%; all conflicts=36.7%/16.1%).

[Table 8. will appear here. See end of document.]



Fig. 4. Relationship benefit of opponents representing the social costs of conflicts in Tai chimpanzees. The percentage of conflicts between high-benefit (*black*) and low-benefit (*white*) partners is displayed as a function of the interaction between Initiator's Rank and Rank Difference. For simplicity, medium-benefit partners are not presented, but when including medium-benefit partners conflicts total 100%. Social costs are presented from high to low likelihood of winning (*dom* dominant initiator, *sub* subordinate initiator, *big* large rank difference, *middle* middle rank difference, *small* small rank difference)

Reduction of social cost: when were chimpanzees more likely to reduce social costs (Table 2: step 3b)? Reduction of social costs was only significantly affected by relationship benefit of the opponents (GLZ: $LR \chi^2_{6,409} = 58.81$, $P < 0.0001$; Table 9). The tendency to reconcile between opponents increased strongly with relationship benefit, such that among friends more conflicts showed a high CCT index (high relationship benefit: 63.6% with high CCT index, 36.4% with low CCT index, $\beta = -1.20$), and among lower-benefit partners more conflicts showed a low CCT index (medium relationship benefit: 23.8% high CCT index, 76.2% low CCT index, $\beta = 0.57$; low relationship benefit: 23.3% high CCT index, 76.7% low CCT index, $\beta = 0.63$). Thus social costs were more likely to be reduced among friends.

[Table 9. will appear here. See end of document.]

Discussion

Tai chimpanzees consider costs and benefits when determining whom, when and how to fight—how to handle a conflict situation. All variables considered in the RM (value of the resource, risk of injury, value and reparability of the relationship) were found to significantly affect the “decision-making” process of Tai chimpanzees. Our results also revealed the limits of the RM. While the RM does not consider different aggression tendencies for dominant and subordinate initiators, we found that these differed in Tai chimpanzees, as they considered their likelihood of winning the conflict in their conflict “decisions”. Moreover, the RM could not directly explain the within-individual variation in costs of aggression and social costs that we observed in Tai chimpanzees. The extension of the RM we propose remedies these shortcomings.

Adult chimpanzees fought more in contexts that had a high potential benefit to them. Female chimpanzees in Tai initiated more aggression over food than in social conflicts. This result corresponds with the findings in Gombe chimpanzees, where females also fought frequently over food (Goodall 1986). The females’ focus on food is not surprising as better-fed primate females have a higher overall fitness (e.g. baboons: Altmann et al. 1985; Japanese macaques: Mori 1979; rhesus macaques: Small 1981). In contrast, males preferentially engaged in social conflicts. Considering the fact that access to oestrous females represents the key resource for reproductive success of males, this result is surprising. However, males might achieve high ranks by winning conflicts in non-sexual contexts, which in itself might be sufficient to reach their reproductive goals, either through female choice (Matsumoto-Oda 1999) or because subordinate males are reluctant to challenge dominants in a sexual context. Therefore, engaging in social conflicts might

be a more effective strategy to maximise reproductive success in male chimpanzees, since high-ranking males in Pan species sire more offspring than low-ranking ones (Gerloff et al. 1999; Constable et al. 2001). Thus, individuals initiated more conflicts as the benefit of the resource increased (Fig. 5).



Fig. 5. Schematic illustration modelling the factors affecting two fighting strategies in Tai chimpanzees. The illustration follows our proposed order of the “decision-making” process. How the costs or benefits considered in each step affect the variation in initiation frequencies of conflicts is shown, and also how social costs affect the variation in the frequency of reduction of social costs. The positive or negative slopes of the graphs are based on the observed frequencies of conflicts in Tai chimpanzees (see Fig. 1, 2, 3, and 4), using a *straight line* for simplicity. Two strategies were found: strategy A is used by dominant initiators (*thick white arrow*) whereas strategy B is used by subordinate initiators (*thin black arrow*). The outcome of the two strategies is represented by the net benefit in relation to the relative initiation frequency of conflicts for dominant (*A, white*) or subordinate (*B, black*) initiators. The outcomes of both strategies are presented in a simplified form (the most likely outcome) and are shown together in one graph to clarify the trade-off used by subordinate conflict partners: subordinate initiators trade their lower frequency of winning a conflict for a greater positive net benefit, when they are winning, and a smaller negative net benefit, when they are losing, compared to dominant initiators (see Discussion)

In accordance with the general mammalian pattern of dominant individuals being more aggressive than subordinates (e.g. carnivores: Creel et al. 1997; perissodactyla: Clutton-Brock et al. 1976; primates: Hrdy and Hrdy 1976; ungulates: Côté 2000), Tai chimpanzees of both sexes initiated more conflicts the higher their dominance position. Furthermore, Tai chimpanzees also won more conflicts the more dominant they were over their opponent. Neither result is surprising as they reflect the character of a dominance hierarchy. Thus, individuals initiated more conflicts as the likelihood of winning increased (Fig. 5).

Contrary to expectation, subordinate initiators often won, suggesting that Tai chimpanzees use a sufficient “decision-making” process. This may be due to the egalitarian character of chimpanzee societies, which enables subordinate individuals to compete successfully (van Schaik 1989). Alternatively, subordinate winners may have had potential dominant supporters in the party, as the mere presence of supporters can change the outcome of a dyadic conflict (de Waal 1982). A third explanation may be that sex-related differences in fighting “decisions” help females to win food conflicts against males, since males seem to avoid food conflicts more often than females,

although they are generally dominant over females. Thus, subordinate initiators may choose their opponents more carefully than dominants do by monitoring the situation more precisely. The factors enabling subordinates to win require further examination.

Tai chimpanzees handled their costs of aggression economically, their investment in duration and intensity of aggression being shaped by the potential benefit of the context and their likelihood of accessing the benefit. Individuals used non-contact aggression more frequently when the winner was predictable due to a large rank difference. Males fought for a longer time in contexts that were more beneficial for them. While it may seem questionable that fighting for an extra second represents a significant increase of energetic costs, the range of conflict duration shows that male chimpanzees fought up to 1 min in social contexts, almost 3 times as long as the maximum conflict duration over food. A continuous performance of muscles in humans can lead to energetic problems within 1 min due to usage of ATP reserves (Keul et al. 1967), phosphocreatine shortage (McKenna et al. 1999) or neuronal firing fatigue (Ross et al. 2001). In contrast, females did not fight much longer over food than in social contexts, even though food is the most important context for them. This might reflect female experience that longer fights draw more combatants (R.M. Wittig and C. Boesch, unpublished data). Thus a food-specific risk arises, as food owners can lose control over the resource to a third party during a conflict, a risk that individuals seem not to face when competing for rank. Tai chimpanzees risk high costs of aggression only when this is required to achieve a positive outcome.

Subordinate initiators used lower levels of contact and non-contact aggression than dominants. It must be adaptive for subordinate initiators to minimise costs of aggression as they are less often able to offset their costs by accessing the benefit. Crowley (2000) detected a similar mixed evolutionary stable strategy (EES) for asymmetric contest situations. He investigated a general form of the hawk-dove game (Maynard Smith and Parker 1976), which included the fighters' knowledge about their own fighting ability and that of their conflict partner. The main EES combined a cautious strategy (dove) for subordinate partners with a daring strategy (hawk) for dominants (Crowley 2000). Similarly, dominant opponents in Tai chimpanzees initiated more conflicts with high costs of aggression, whereas subordinate opponents initiated more conflicts with low costs of aggression (Fig. 5).

Tai chimpanzees risked different social costs depending on their likelihood of winning. Social costs originate from the disturbance of a cooperative relationship when one partner withholds cooperation (de Waal 1996). Thus, a disturbed relationship with non-cooperative partners is unlikely to create social costs. In Tai, the effect of the initiator's rank on the relationship benefit of opponents

clearly showed that subordinates initiated more conflicts with cooperative partners. Consequently subordinate initiators generally risked more social costs than dominant ones (Fig. 5). This general trend was also reflected by the fact that both types of initiators, dominant as well as subordinate, risked more social costs the lower their relative likelihood of winning. It was probably unnecessary for a dominant to fight a friend when the outcome of the conflict was predetermined, but dominants risked a fight when the outcome was less predictable. Why, however, did subordinate initiators also not fight more with friends with a small rank difference? A partnership does not provide the same value to each partner (Cords and Aureli 2000). Dominant individuals are likely to provide better-quality food and support to subordinates than the other way around. Therefore, subordinate initiators should have been more careful with highly dominant friends. Instead, however, they initiated fewer conflicts with closely ranked opponents. Opponents of a small rank difference fought harder and therefore those conflicts may have induced a stronger disturbance to the relationship. Subordinates thus were probably more careful with friends when facing the risk of a difficult relationship repair. Subordinate initiators generally risked more social costs than dominants, except when reparation of the relationship could be difficult—suggesting more gentle slopes of social costs (Fig. 5) compared to other graphs in Fig. 5.

Such a strategy is only adaptive if high social costs were reduced more frequently than low ones after the conflict. Indeed, Taï chimpanzees were more likely to reduce higher than lower social costs (Fig. 5). This higher reconciliation frequency with friends has also been seen in other primates (reviewed in Aureli et al. 2002). Since social costs seemed to be easily reduced afterwards, why did Taï chimpanzees not fight friends more frequently? Reconciliation, however, is not free of risk, as individuals have to approach former opponents, which may lead to further aggression (e.g. Aureli and van Schaik 1991; Cords 1992). Moreover, reconciliation might fail if the same relationship is repeatedly disturbed, with a bigger disturbance possibly requiring longer and more intense reconciliation.

How did Taï chimpanzees “decide” to fight for a resource? They were more likely to initiate conflicts for resources that were highly beneficial to them, but they used less aggression when the chance of winning was lower. The likelihood of winning therefore served as the key factor in the “decision-making” process, and two different alternative strategies can be identified (Fig. 5):

1. Dominant initiators fought harder, but they did not risk undue costs of aggression. Additionally, they risked fewer social costs by fighting less with partners of higher benefit. Thus, dominant conflict partners fight over highly beneficial resources, investing more in aggression costs but less in social costs. Dominant initiators gain a medium positive net benefit when winning and

face a medium negative net benefit when losing, since costs of aggression are non-reducible and have to be subtracted from the benefit. In consequence, as dominant initiators almost always win, their strategy has a predictable outcome: often obtained medium positive net benefit (Fig. 5).

2. Subordinate initiators had lower costs of aggression, but took higher social costs, except when reparation of the relationship could be difficult. Hence, subordinate conflict partners also fight over high-benefit resources, but invest less in aggression costs and more in social costs.

Subordinate initiators gain a high positive net benefit when winning and face low negative net benefit when losing, since they have low costs of aggression and the social costs are reducible. In consequence, subordinate initiators trade their lower chance to win the conflict for a higher positive and a lower negative net benefit compared to dominant initiators. This trade-off is a risky strategy: rarely obtained high positive net benefit (Fig. 5).

The extended RM describes the “decision-making” process in Tai chimpanzees well, although one can never be sure that all potential effects have been identified. We did not investigate situations directly when chimpanzees reacted non-aggressively during a conflict of interest. Nevertheless, we found that females initiated fewer social conflicts, whereas males initiated fewer conflicts over food. Furthermore, one partner initiated the conflict while the other one had not yet “decided” to initiate aggression. Therefore, Tai chimpanzees seem to avoid aggression when the resource is not beneficial to them and when their “decision-making” process does not offer a positive net benefit. However, the “decision-making” process is not perfect as sometimes initiators misjudged the situation and lost the conflict. Still, the overall net benefit in both strategies was positive, as subordinate initiators showed a trade-off for their lower winning rate by going for a larger net benefit (Fig. 5).

Tai chimpanzees demonstrate a very flexible “decision-making” process before initiating a conflict. Clearly more factors are taken into account than initially suggested by the RM. “Decisions” are made in an economical fashion to increase the benefit for the initiator while diminishing the costs. The extended RM proposed here fits well with the social complexity observed in wild chimpanzees. The extended RM, providing a powerful way of investigating conflict management, may help to answer further questions about when aggression is avoided and how effective the mechanisms are for managing a conflict (de Waal and Aureli 2000). Hence, comparative studies are required, to test this model on other primate species, to make within- and between-species differences in conflict “decisions” apparent.

Acknowledgements We thank the “Ministère de la Recherche Scientifique”, the “Ministère de l’Agriculture et des Ressource Animales” of Côte d’Ivoire, the director of the Taï National Park and the “Projet Autonome pour la Conservation du Parc National de Taï” for permission to conduct this study. We also thank the “Centre Suisse de la Recherche Scientifique” in Abidjan, the staff of the “Station du Centre de Recherche en Ecologie” and of the “Projet Chimpanzé Taï”, especially Kpazahi Honora Néné and Nohon Gregoire Kohon, for support in Côte d’Ivoire. We are grateful to Gunter Weiss and Daniel Stahl for their statistical advice, and to Filippo Aureli, Josep Call, Nadia Corp, Diane Doran, Julia Fisher, Elaine Madsen, Martha Robbins, Liesbeth Sterck and Frans de Waal for constructive comments. Special thanks are due to Cathy Crockford for constant stimulating discussions and encouragement. This research was funded by the Swiss National Foundation and the Max Planck Society.

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Table 1. Variables and their parameters considered in the statistical models (parameters are *italicised* for better contrast). *No.* follows the order in which variables were considered for tests of the stepwise model design (Table 2), m-m: male-male, m-f: male-female, f-f: female-female

No	Name	Distribution	Parameter definitions	Correction
1	Initiator's Sex	Binomial	<i>m</i> male aggressor; <i>f</i> female aggressor	
2	Recipient's Sex	Binomial	<i>m</i> male aggressed; <i>f</i> female aggressed	
3	Conflict Context	Multinomial	<i>social</i> conflict about hierarchy or social partners; <i>sex</i> conflict about oestrous females; <i>food</i> conflict about food or possession of tool	
4	Initiator's Victory Outcome	Multinomial	<i>w</i> initiator wins aggressive interaction; <i>l</i> initiator loses; <i>n</i> no winner	
5	Initiator's Rank	Binomial	<i>d</i> aggressor dominant over aggressed; <i>s</i> aggressor subordinate to aggressed	
6	Rank Difference (r.d.)	Ordinal multinomial	Categories of r.d. in m-m dyads (4 males): <i>small</i> for rank neighbours, <i>middle</i> for r.d.=2, <i>large</i> for r.d.=3; categories of r.d. in f-f dyads (12 females): <i>small</i> for r.d.≤3, <i>middle</i> for 3<r.d.≤6; <i>large</i> for r.d.>6; categories of r.d. in m-f dyads (16 individuals) <i>small</i> for r.d.≤5, <i>middle</i> for 5<r.d.≤10, <i>large</i> for r.d.>10	Sex combination, because of different numbers of individuals
7	Aggression Type	Binomial	<i>non-contact</i> aggression conflict intensities 1-3; <i>contact</i> aggression conflict intensities 4+5	
8	Conflict Intensity	Ordinal multinomial	<i>1</i> threat: single aggressive vocalisation or gesture; <i>2</i> display (or "bluff") without locomotion of the aggressor; <i>3</i> display with locomotion of the aggressor; <i>4</i> single physical contact aggression; <i>5</i> multiple physical contact aggressions	
9	Conflict Duration	Nominal	Duration (<i>d</i>) is measured in seconds from the first aggressive behaviour to the end of the conflict (submission, flight,	$d' = \log_{10}(d+1)$

No	Name	Distribution	reciprocal screaming, non-aggressive behaviour)	Correction
10	Relationship Benefit	Ordinal multinomial	Parameter definitions <i>low</i> no food sharing, no support within dyad; <i>medium</i> either food sharing or support within the dyad; <i>high</i> both food sharing and support within the dyad	
11	Association Index	Ordinal binomial	<i>rare</i> in m-m dyads: $DAI \leq 0.5$, in other dyads: $DAI \leq 0.25$; <i>frequent</i> in m-m dyads: $DAI > 0.5$, in other dyads: $DAI > 0.25$	Sex combination
12	Corrected Conciliatory Tendency (CCT) Index	Ordinal binomial	<i>low</i> Corrected Conciliatory Tendency (CCT) $<$ mean CCT of the specific sex combination; <i>high</i> CCT \geq mean CCT of the specific sex combination	Sex combination

Table 2. Variables considered for the tests in the different steps of the stepwise model design. Set of variables is marked with + when considered as independent variables for the test: *set W*/Initiator's Sex, Receiver's Sex, Sex Combination; *set X* Conflict Context, interaction (Conflict Context×Initiators's Sex), Initiator's Rank, Rank Difference, interaction (Initiator's Rank×Rank Difference); *set Y* Conflict Intensity, Conflict Duration; *set Z* Relationship Benefit, Association Index

Step	Part	Factor of the extended RM	Dependent variable	Independent variables			
				set W	set X	set Y	set Z
1	a	Benefit of the resource	Conflict Context	+			
	b	Likelihood of winning	Initiator's Victory Outcome	+	+		
2	a	Cost of aggression	Aggression Type	+	+		
	b		Conflict Intensity	+	+		
	c		Conflict Duration	+	+		
3	a	Social cost	Relationship Benefit	+	+		
	b	Reduction of social cost	Corrected Conciliatory Tendency Index	+	+		+

Table 3. Frequency (in %) of conflicts initiated by females and males per conflict context and sex of conflict partner in Tai chimpanzees. *Expected* are the standardised expected frequencies within each sex combination (see Methods). Note that females did not compete over sex

Context	N			Sex			N			Sex		
	Female-female conflicts	Social	Food	Female	Male	Sex	Female-male conflicts	Social	Food	Female	Male	Sex
Females	Female-female conflicts			Sex			Female-male conflicts			Sex		
Belle	14	86	14	2	50	50	2	50	50	0	0	0
Castor	19	42	58	4	25	50	4	25	50	25	25	25
Dilly	26	35	65	3	67	33	3	67	33	0	0	0
Fossey	7	57	43	2	0	0	2	0	0	100	100	100
Goma	10	40	60	2	50	50	2	50	50	0	0	0
Kana	3	33	67	0	-	-	0	-	-	-	-	-
Loukoum	40	13	87	18	39	61	18	39	61	0	0	0
Mystère	19	53	47	3	33	67	3	33	67	0	0	0
Narcisse	6	83	17	4	100	0	4	100	0	0	0	0
Perla	15	27	73	1	0	100	1	0	100	0	0	0
Ricci	8	62	38	5	20	80	5	20	80	0	0	0
Venus	12	58	42	5	60	40	5	60	40	40	40	40
Average		49	51		40	45		40	45	15	15	15
Expected		69	31		56	25		56	25	19	19	19
Males	Male-male conflicts			Sex			Male-female conflicts			Sex		
Brutus	19	58	37	5	42	55	5	42	55	3	3	3
Macho	356	80	9	11	41	30	100	41	30	29	29	29
Marius	29	90	3	7	51	45	77	51	4	45	45	45
Nino	0	-	-	-	58	25	36	58	25	17	17	17
Average		76	16	8	48	28		48	28	24	24	24
Expected		49	22	29	56	25		56	25	19	19	19

Table 4. Factors affecting the likelihood of winning a conflict in Tai chimpanzees (Table 2: step 1b). The table presents the significant variables and the estimate-coefficient (β) of the parameters; independent parameters: *dom* dominant initiator, *sub* subordinate initiator, *small* small rank difference, *middle* middle rank difference, *large* large rank difference; order of entering the dependent parameters in the model: winner, loser

Independent variables	Dependent variable		Parameters	β	Wald	P
	Initiators	Victory Outcome				
	Wald	P				
1	Initiator's Rank	40.15	dom	2.53	40.15	<0.0001
			sub	-2.53		
2	Initiator's Rank \times Rank Difference	16.76	dom-small	-1.24	16.75	0.0002
			sub-small	1.24		
			dom-middle	-0.45		
			sub-middle	0.45		
			dom-large	1.69		
			sub-large	-1.69		
				1.94	0.1636	
				13.18	0.0003	

Table 5. Factors affecting intensity and duration of conflicts in Tai chimpanzees (Table 2: step 2a). Significant variables for the model of aggression type are presented. The GLZ estimate-coefficient (β) of the parameters is shown. Order of entering the dependent parameters in the model: non-contact aggression, contact aggression

Independent variable	Dependent variable		Parameters	β	Wald	P
	Wald	P				
1 Rank Difference	8.41	0.0149	Small	-0.29	2.87	0.0905
			Middle	-0.34	3.75	0.0529
			Large	0.63	8.40	0.0037

Table 6. Factors affecting intensity of conflicts in Tai chimpanzees (Table 2: step 2b). Significant variables for the model of conflict intensity are presented. The GLZ estimate-coefficient (β) of the parameters is shown. Order of entering the dependent parameters in the model: 1, 2, 3, 4, 5

Independent variable	Dependent variable		Parameters	β	Wald	P
	Conflict Intensity					
	Wald	P				
1 Initiator's Rank	5.30	0.0213	Dominant	-0.39	5.30	0.0213
			Subordinate	0.39		

Table 7. Factors affecting duration of conflicts in Tai chimpanzees (Table 2: step 2c). Significant variables for the model of conflict duration are presented. GLM post-hoc statistics are given

	Independent variables	Dependent variable		Post-hoc	P
		Conflict Duration	P		
1	Initiator's Sex	8.89	0.0031	Fisher LSD	0.0351
2	Conflict Context	5.95	0.0153	Fisher LSD	0.0065

Table 8. Factors affecting social costs in Tai chimpanzees (Table 2: step 3a). Significant variables for the model of social costs are presented and the estimate-coefficient (β) of the parameters is given. Independent parameters: *dom* dominant initiator, *sub* subordinate initiator, *small* small rank difference, *middle* middle rank difference, *large* large rank difference, *m* male, *f* female. Order of entering the dependent parameters in the model: low, medium, high

Independent variables	Dependent variable		Parameters	β	Wald	P
	Relationship Benefit					
	Wald	P				
1 Initiator's Rank \times Rank Difference	25.69	<0.0001	dom-small	-0.95	23.55	<0.0001
			sub-small	0.95		
			dom-middle	0.01	0.01	0.9760
			sub-middle	-0.01		
			dom-large	0.94	16.60	<0.0001
2 Sex Combination	8.57	0.0034	sub-large	-0.94		
			m-m	0.46	8.57	0.0034
			f-f	0.46		
			m-f	-0.46		
3 Initiator's Rank	6.55	0.0105	f-m	-0.46		
			dom	0.48	6.55	0.0105
			sub	-0.48		

Table 9. Factors affecting reduction of social costs in Tai chimpanzees (Table 2: step 3b). Significant variables for the model of reduction of social costs are presented and the estimate-coefficient (β) of the parameters is given. Order of entering the dependent parameters in the model: low, high

Independent variable	Dependent variable		Parameters	β	Wald	P
	CCT Index	P				
1 Relationship Benefit	Wald	13.07				
			low	0.63	4.83	0.0279
			medium	0.57	4.73	0.0298
			high	-1.20	13.03	0.0003