1   Title: **Social instability raises the stakes during social grooming**

2   **among wild male chimpanzees**

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Summary

Explaining cooperative behaviour is fundamental issue for evolutionary biology. The problem any cooperative strategy faces is minimizing risks of non-reciprocation (cheating) in interactions with immediate costs and delayed benefits. One of a variety of proposed strategies, the raise-the-stakes (RTS) strategy posits that individuals establish cooperation by increasing investment across interactions from an initial interaction. This model has received little quantitative support, however, probably because individuals of many social species engage in repeated interactions from a young age. In some situations, however, such as following conflicts, after prolonged absences, or during social instability, established relationships may become unreliable predictors of future behaviour, create an environment for RTS. We investigated grooming interactions among wild male chimpanzees (*Pan troglodytes*), testing RTS in these specific contexts. We found evidence that male chimpanzees employed RTS during social instability, but not under the other conditions. However, this patterning of grooming interactions was, we suggest, less to do with preventing cheating and more to do with avoiding the elevated risks of intra-male aggression during the period of social instability: social instability raises the stakes for grooming by creating a more hazardous marketplace in which to trade.

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Introduction

Explaining cooperative behaviour is a fundamental question for evolutionary biology (West et al. 2006). While cooperation between related individuals is often accounted for by indirect benefits and inclusive fitness theory (Hamilton 1964a, b), cooperation between unrelated individuals is typically explained by invoking the theory of reciprocal altruism (Trivers, 1971) with its exchange of direct costs and benefits, albeit delayed in time. Functionally, this is mutualism rather than altruism as all actors receive direct fitness benefits and is better described as direct reciprocity (Clutton-Brock 2009).

The problem faced for any cooperative strategy is how to minimize risks of non-reciprocation (cheating) in interactions in which costs are immediate but benefits are delayed. A variety of strategies have been proposed, building on the iterated prisoner's dilemma (IPD) model suggested by Trivers (1971). Axelrod and Hamilton's (1981) 'tit-for-tat' strategy (TfT), under which individuals start out cooperating and match their opponent's behaviour in previous interactions, refusing to cooperate only if the partner does so first, is evolutionarily stable. TfT has found some support but seems restricted to simple social exchanges (e.g. serranid coral-reef hermaphroditic fish: Fischer, 1988), or artificial experimental situations (e.g. predator inspection by sticklebacks and guppies: Milinski 1987; Dugatkin 1988). Strategies based on an IPD model assume cooperation to be an 'all-or-nothing' affair, and that interacting individuals have no other potential social partners (Noë 1990, 2001); in consequence, a variety of further models with more applicability to biological systems have been proposed, such as Biological Markets theory (Noë 2001, 2006; Noë and

72 Hammerstein 1994, 1995), pseudo-reciprocity (Connor 1986), parcelling (Connor

73 1992) and raise-the-stakes (Roberts and Sherratt 1998; Sherratt and Roberts 2002).

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75   Raise-the-stakes (RTS) describes a strategy in which co-operators increase

76 investment in a social interaction if the partner matches or betters their opponent's last

77 move. It allows cooperation to be incremental, rather than 'all-or-nothing', and

78 individuals' investment in a relationship can vary over a series of interactions

79 (Roberts and Sherratt 1998; Sherratt and Roberts 1999). RTS allows the animals to

80 'test the water', before investing in potentially costly cooperative behaviours; at the

81 very least, it allows them to limit their losses. This strategy is robust against 'subtle

82 cheaters': individuals that invest less than in previous interactions (Roberts & Sherratt

83 1998; Van den Berg and De Witte 2006) and generates predictions that can be easily

84 tested in animal systems (Keller and Reeve 1998). Support for RTS has been found in

85 species as diverse as the sawfly *Perga affinis*, where cohesion among gregarious larva

86 is maintained through tapping signals and the group's investment (Fletcher 2008), and

87 humans *Homo sapiens*, where subjects increased monetary donations to a social

88 partner if that partner matched their investment (Roberts and Renwick 2003; Majolo

89 et al. 2006; Van den Berg and De Witte 2006) but not where the partner was a

90 previously established friend (Majolo et al. 2006; Krebs 1970).

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92   The initial presentation of the RTS strategy was supported by data on

93 grooming reciprocity in impala *Aepyceros melampus* (Roberts and Sherratt 1998) and

94 social grooming should be an ideal behaviour with which to test the usefulness of

95 RTS as an explanation for reciprocity: the total amount of grooming that one

96 individual performs for another is easily broken down into smaller 'episodes' of

97 investment, and that investment can be quantified by time spent giving grooming

98 (Roberts and Sherratt 1998; Keller and Reeve 1998). Grooming offers benefits to the

99 recipient, in terms of ectoparasite removal (Mooring et al. 2004) and stress reduction

100 (Aureli et al. 1999; Gust et al. 1993; Kaburu et al. 2012) at some costs to the groomer,

101 such as reduced vigilance (Maestripieri 1993; Cords 1995; Mooring and Hart, 1995)

102 and resting time (Dunbar 1992). Studies of grooming in non-human primates,

103 suggested as an example system for RTS by Keller and Reeve (1998), have failed to

104 find support for this strategy, however (Barrett et al. 2000; Manson et al. 2004;

105 Fruteau et al. 2011).

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107   RTS assumes an initial interaction from which reciprocity can develop and so

108 appears most applicable to situations where individuals are forming new cooperative

109 relationships (*sensu* Hinde 1976). In many animal groups, however, most observed

110 social interactions are merely the latest of a series of interactions that may have

111 started in infancy: the relevance of RTS for understanding persistent reciprocity

112 between members of complex social groups has therefore been questioned (Barrett et

113 al. 2000; Barrett and Henzi 2006). There are several possible scenarios under which

114 this history of interactions may be negated, at least temporarily. These could include

115 aggressive conflicts, prolonged absences from a group or periods of high social

116 instability. If this occurs, and individuals cannot rely on their prior history of

117 interactions to predict future behaviour, they may need to use strategies such as RTS

118 to re-establish cooperative relationships. The impact of such contexts on grooming

119 strategy has not been examined.

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Here we examine grooming exchanges among wild male chimpanzees (*Pan troglodytes*) for evidence of the RTS strategy. The grooming behaviour of adult male chimpanzees offers a good model system for the investigation of reciprocity. Previous work has shown that chimpanzees tend to reciprocate grooming exchanges (Newton-Fisher 1997, 2002; Newton-Fisher & Lee 2011; Watts, 2000; Mitani 2006; Arnold and Whiten 2003; Gomes et al. 2009; Boesch and Boesch-Achermann, 2000). Furthermore, chimpanzees tend to break down grooming bouts into small episodes (*sensu* Barrett et al. 2000), the length of which can vary both within and across bouts. The chimpanzee social system is characterised by fluid associations, with any particular set of individuals often only stable on a timescale of minutes or hours and individuals may be out of contact with particular others for hours or days as a result (Reynolds 1965; Nishida 1968).

Given the results of previous studies of primate grooming exchanges (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011), we predict that RTS will not be a strategy employed during social stability (*prediction 1*). In contrast, we predict that they will adopt RTS in contexts where relationships may be 'reset': that is, where prior histories of interaction may become unreliable predictors of the behaviour of social partners, thus creating a need to re-establish grooming relationships. We focus on three specific contexts:

1. *The aftermath of aggressive conflicts*. Across a range of primate species both aggressor and victim tend to be more anxious after a conflict (reviewed in Aureli and Smuncy 2000), especially where they had previously shown a high level of affiliation (Kutsukake and Castles 2001; Aureli, 1997; Cords and Aureli 2000). Conflicts can potentially jeopardize the relationship between two individuals (Aureli and de Waal 2000; Cords and Aureli 2000; Aureli et al.

146   2002; Silk 2002) and former opponents may try to repair their relationships

147   (Cords and Aureli 2000) by reconciling (de Waal and van Roosmalen 1979; Silk

148   2002), suggesting that they can no longer rely on prior history to guide future

149   cooperation. Reconciliatory tendency in wild chimpanzees is relatively low,

150   however, occurring in only 12-16% of dyads (Arnold & Whiten, 2001;

151   Kutsukake & Castles, 2004; cf. 27-35% in captivity: de Waal & van

152   Roosmalen; Preuschoft et al 2002), so RTS may provide an alternative strategy

153   (*prediction 2*).

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155   2.   *After prolonged absence*. Male chimpanzees may be apart from others for many

156   days or weeks if they pursue a consortship mating strategy, by which they

157   isolate themselves and a single (cycling) female from the rest of the social

158   group in an attempt to gain exclusive mating access (Tutin 1979; Goodall 1986;

159   Nishida 1997; Matsumoto-Oda 1999). The duration of this separation, together

160   with shifting patterns of interactions between other males, may create a context

161   in which males re-joining the other members of the social group may be unable

162   to rely on past history and need to employ the RTS strategy to re-establish

163   cooperative relationships (*prediction 3*).

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165   3.   *During periods of social instability*. Loss of key individuals through predation

166   or, particularly in chimpanzees, conspecific lethal violence (Newton-Fisher &

167   Emery Thompson 2012), may disrupt existing patterns of social interaction

168   and/or destabilise rank hierarchies (Wey et al. 2008; Cheney and Seyfarth

169   2009). During our study period, a phase of elevated aggression rates and high

170   instability in the male hierarchy followed the killing of the incumbent alpha-

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171   male of study community (Kaburu et al. 2013). We use this dramatic shift to

172   examine whether male chimpanzees employ RTS in their grooming interactions

173   in periods of high social instability (*prediction 4*).

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175   **Materials and Methods**

176   *Data collection*

177

178   The study was conducted between February and November 2011 on the *M-*

179 *group* chimpanzee community of the Mahale Mountains National Park, Tanzania (for

180 descriptions of the field site see: Nishida 1990, 2012; Nakamura and Nishida 2012).

181 The study group initially consisted of 10 adult males (≥16 yr), 5 adolescent males (9-

182 15 yr), 2 juvenile males (5-8 yr), 3 infant males (0-4 yr), 23 adult females (≥14 yr), 7

183 adolescent females (7-13 yr), 5 juvenile females (3-6 yr), and 5 infant females (0-2

184 yr). During data collection, two females gave birth, one female joined the community,

185 while two cycling females disappeared (and were assumed to have dispersed to

186 another group), and one adult male, the alpha, was killed (Kaburu et al. 2013).

187

188   Eight adult males were followed through day-long focal sessions (Altmann

189 1974). Each day, the individual previously sampled less frequently was selected as

190 focal animal in an effort to equalise number of hours of observation across

191 individuals. To assure independency between the focal samples, the same animal was

192 not followed during two subsequent days. A total of 397 hours of observation were

193 recorded (Table 1; mean ± SD / focal male = 49 ± 5 hours).

194

195   Data concerning grooming bouts were collected using both focal animal and

196   *ad libitum* sampling. Grooming sessions were thoroughly described by voice using a

197   dictaphone. Specifically, the identity of the partners, the time spent giving or

198   receiving grooming, and events when one or both the individuals stopped grooming

199   were recorded. Bouts that were underway at the beginning of the observation period

200   and/or whose pattern could not be accurately observed due to poor visibility were

201   discarded. Additionally, from focal animal samples, we collected directed aggressive

202   interactions in which an individual attacked a specific partner either by physical

203   contact (e.g. kicking, hitting, slapping) or by chasing or agonistic displays.

204

205   *Data analysis*

206

207   A grooming bout was defined as a dyadic grooming interaction where one or

208   both individuals exchanged episodes of grooming, and it was considered ended when

209   both males engaged in other activities, including simple resting, for more than 30s

210   (after Newton-Fisher and Lee 2011). We defined intra-bout episodes as unbroken

211   continuous grooming given by one individual. An episode ended when neither of the

212   groomer's hands was in contact with the recipient.

213

214   We looked for evidence of RTS both across and within grooming bouts, and

215   tested our predictions for the absence (during social stability) and presence (in

216   specific contexts) of the RTS strategy as detailed below. Except where indicated, all

217   analyses were conducted using SPSS (ver. 20).

218

To test *prediction 1*, we analysed grooming interactions collected in the period February-September 2011, which corresponded to a period of social stability (Kaburu et al., 2013). If RTS was used as a strategy across grooming interactions, then we expected to see (a) an increase in the length of episodes across grooming bouts, as evidence of increasing investment in a cooperative relationship, and (b) the amount of grooming performed in one bout to match the amount received in the previous bout, as the strategy requires at least matching of the partner's previous investment. We used two-tailed Spearman's rank correlations to examine the relationship between length of episodes and order of occurrence, for each male's grooming history for each grooming partner. We restricted this analysis to those males recorded performing at least five episodes. To avoid pseudo-replication, the contribution of each male to each of his grooming dyads was tested individually, giving 45 possible dyads and 90 possible groomer-receiver combinations. These results were combined using a weighted Z-test (Stouffer et al. 1949; Whitlock 2005), implemented by the program MetaP (Dongliang 2009). This method is preferable to Fisher's test for combining probabilities (Sokal and Rohlf, 1981) as it is not sensitive to small (hence significant) p-values and treats large and small p-values equally: the weighted Z-test is less likely to result in a type I error (Whitlock, 2005). In order to control for the different contributions of each male to the dataset, weights were selected as the number of grooming episodes that individuals performed.

We used a Linear Mixed Model (LMM) to test whether the amount of grooming performed in one bout matched the amount received in the previous bout. LMM offers the opportunity to assess the effect of multiple independent variable(s) while controlling for repeated sampling of the same individuals (treated as random

244   factors: Pinheiro and Bates 2000). Our dependent variable was duration of grooming

245   performed, while duration of grooming received in the previous bout involving the

246   same dyad was set as an independent factor. Grooming durations were log-

247   transformed to normalise the data. We controlled for the differential contribution of

248   dyads by including dyad identity as a factor. Identities of groomer and recipient were

249   treated as random factors, while the number of grooming bouts was set as repeated

250   measurement. It was possible to conduct this type of analysis as each focal animal

251   was followed for the whole day, which offered the opportunity to identify the

252   temporal sequence of grooming interactions between each grooming pair. Grooming

253   bouts in chimpanzees can be either unidirectional (only one individual takes the role

254   of groomer) or bidirectional, with the latter involving either alternating or

255   simultaneous grooming; many bouts include a combination of these structures.

256   Unidirectional grooming is common (e.g. Newton-Fisher and Lee 2011; Gomes et al.

257   2009; see results), and we included episodes from unidirectional bouts as well as

258   those where both members of the dyad groomed as unidirectional grooming is likely

259   to play an important role in ensuring that grooming is reciprocated over time (Gomes

260   et al 2009).

261   Following Barrett et al. (2000), we tested for evidence of RTS within bouts by

262   examining whether duration of grooming episodes matched or exceeded previous

263   episodes both performed and received, for each reciprocated bout in which partners

264   alternated the roles of groomers and receivers. We assigned a plus sign when either

265   the initiator (i.e. the individual who started the bout) or the reciprocator (i.e. the

266   individual who returned the grooming) increased or matched grooming time

267   throughout the bout compared to either their own previous episodes or partner's

268   previous contribution, excluding periods of simultaneous (mutual) grooming. We

269 grouped bouts on the basis of the number of intra-bout episodes, and analysed only

270 those groups where at least 5 dyads contributed data. We used two-tailed sign-test to

271 assess whether the number of bouts in which there was a consistent increase in the

272 duration of grooming episodes (indicated by a plus sign) significantly exceeded the

273 number of bouts in which there was no consistent increase in grooming episode

274 duration (indicated by a minus sign). The p-values from these multiple tests were then

275 combined with the weighted Stouffer's Z-method. In this case weights were selected

276 as the number of bouts that contributed to each group.

277

278 *Context 1: after conflicts*

279

280   Following Arnold and Whiten (2001), we defined the post-conflict context as

281 the 30-minute period following an aggressive interaction. The window of opportunity

282 for grooming provided by this context is short, and so we looked for evidence of RTS

283 exclusively within bouts. We extracted grooming interactions between former

284 opponents from post-conflict contexts and analysed bouts containing at least three

285 episodes, as explained above.

286

287 *Context 2: After prolonged absence*

288

289   During the study, two adult males (*PR & AL*) engaged in consortship

290 behaviour; in both cases with the same cycling female (*EF*). The consortship between

291 *PR* and *EF* started on 7th of March. This was interrupted after 42 days (on 18th of

292 April), but resumed on the 21st of April, lasting another month (until 24th of May).

293 The consortship between *AL* and *EF* started on the 6th of August 2011, and lasted 52

294   days (concluding on 27th of September). We examined all grooming bouts recorded

295   within one month after each male resumed normal association with the other adult

296   males. We tested for RTS both across and within-bouts as explained above. Unlike for

297   the analysis conducted during social stability, we carried out one-tailed Spearman's

298   rank correlation tests as we predicted a positive relationship (an increase in episode

299   length across bouts).

300

301   *Context 3: Social instability*

302

303   The alpha male (*PM*) for most of our study period was killed in a coalitional

304   attack on 2nd of October, triggering a period (hereafter: the 'unstable period') of high

305   rank instability and increased aggression rates (Kaburu et al. 2013). We extracted

306   grooming data collected in this period, and compared grooming interactions with

307   those collected in the period prior to this event (hereafter: the 'stable period'). For this

308   comparison we included grooming bouts recorded both from focal and *ad libitum*

309   observations, and grooming data collected from the two non-focal males (*DW* and

310   *XM*). Across the two periods, we used Wilcoxon signed-rank tests (two-tailed) to

311   compare (a) the mean duration of grooming bouts for each dyad ($N = 35$); (b) the

312   mean episode length and the number of episodes per bout for each male ($N = 9$), and

313   (c) rates of both bouts and episodes for focal males ($N = 7$). We had previously

314   determined that rates of aggression were significantly elevated in the 'unstable period'

315   (average rate per male: 0.45 vs. 0.16 interactions/hr; $T = -2.37$, $N = 9$, $P = 0.018$:

316   Kaburu et al, 2013); to investigate whether rates of aggression changed within this

317   period, we derived daily rates of aggression by dividing the number of aggressive

318   interactions recorded during each observation day by the observation time, and used a

13

319 two-tailed Spearman's rank correlation test. Additionally, since, in chimpanzees,

320 during social instability males are often observed disrupting grooming interactions

321 between rivals (de Waal 1982, 1984; Nishida 2012; personal observations), we tested

322 whether, in the period following *PM*'s death, temporal variation in episode length was

323 predicted by aggression rates. To this end, we ran an LMM analysis in which males'

324 daily mean grooming episode length was treated as dependent variable, while rates of

325 aggressive interactions males participated either as aggressor or as a victim were

326 entered as fixed factors. The ID of the males was entered as random factor and the

327 number of days males were recorded grooming was included as repeated measure.

328 Finally, we tested for RTS both across and within bouts, as described above.

329 **Results**

330   We collected 593 complete grooming bouts and 2168 grooming episodes in

331 the stable period, corresponding to 51hr 45min of grooming time, with a mean across

332 dyads of 13.17 bouts ($\pm$ SD = $\pm$ 12.30; median = 9), and 48.18 episodes ($\pm$ SD = $\pm$

333 45.41; median = 38). Mean bout length was 5min 16s ($\pm$ SD = $\pm$ 7 min 36s; median =

334 2 min 42s). Grooming rate was 1.10 bouts/hr, and 9 min 58s of grooming/hr. Mean

335 episode length was 1min 34s ($\pm$ SD = $\pm$ 1min 45s; median = 1 min, range = 1s −

336 20min 2s). Most bouts (69%: 412/593) were unidirectional. The majority (51%:

337 93/181) of bidirectional bouts were a mixture of alternating and simultaneous

338 grooming; 29% (52/181) combined unidirectional and simultaneous grooming, while

339 only a small proportion were exclusively alternating (15%: 27/181) or simultaneous

340 (5%: 9/181) grooming.

341   Across bouts, mean episode duration tended to significantly decrease over

342 time, with 65% of the individuals showing a negative trend (weighted Z-test: mean r_s

343 = − 0.09, $P < 0.001$; Table 2). Additionally, the duration of grooming performed did

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344   not match that received in the previous intra-dyadic bout (LMM: *Estimate ± SE =*

345   0.10 ± 0.07, *Wald* = 2.014, *P* = 0.158).

346   Within bout, groomers did not increase the length of grooming episodes in

347   response to the duration of their own previous contribution (weighted Stouffer's Z

348   method: N = 3, *P* = 0.97; Table 3). Additionally, the number of bouts in which

349   individuals increased episode duration in response to the duration of partner's

350   previous episode length was significantly lower than the number of bouts in which

351   there was no increase of episode duration (weighted Stouffer's Z method: *N* = 2, *P* <

352   0.001; table 3). Therefore, male chimpanzees did not raise the stakes during social

353   stability supporting prediction 1.

354

355   *Context 1: after conflicts*

356

357   Of 114 aggressive interactions involving focal individual, only 23 were

358   followed by a grooming session between former opponents. Of these, more than half

359   (52%: 12/23) were unidirectional, whilst the others were a combination of mutual and

360   alternating grooming. We found no convincing evidence that males consistently

361   increased the duration of grooming episodes during post-conflict grooming bouts

362   either in relation to their own previous contribution or to partner's (Table 4). Our data

363   therefore do not support prediction 2: male chimpanzees did not raise the stakes in

364   post-conflict grooming.

365

366   *Context 2: After prolonged absence*

367

368   We collected 112 grooming bouts between the consorting male and the other

369   adult males across the two post-consortship months. These bouts included 455

370   episodes, totalling 7hr 48min of grooming. Most groomers tended to significantly

371   decrease episode duration over time (weighted Z-test: mean $r_s = -0.04$, $P < 0.001$;

372   Table 2) and the amount of grooming an individual received during a bout did not

373   significantly predict the amount of grooming he gave the partner in the subsequent

374   bout (LMM: *Estimate* $\pm$ *SE* $= 0.17 \pm 0.11$, *Wald* $= 1.032$, $P = 0.449$). Within bout,

375   males did not show significant increase in episode duration either in relation to their

376   own previous contribution, or to partner's (Table 5). Our data therefore do not

377   support prediction 3: male chimpanzees did not raise the stakes following periods of

378   absence.

379

380   *Context 3: Social instability*

381

382   We recorded 18hrs 10min of grooming across 254 bouts during the 'unstable

383   period', consisting of 773 episodes, with a dyadic mean of 7.06 bouts ($\pm$ SD $= 7.28$;

384   median $= 6.50$) and 21.47 episodes ($\pm$ SD $= 27.22$; median $= 11.50$). In this 'unstable

385   period', males appeared to change their grooming behaviour when compared to the

386   previous 'stable period'. Grooming bouts were significantly shorter (median bout

387   length: 'stable period' $= 290s$; 'unstable period' $= 186s$; Wilcoxon signed-test: $Z = -$

388   2.072, $N = 35$, $P = 0.038$) also showing a strong trend towards shorter episodes

389   (median episode length: 'stable' $= 96s$, 'unstable' $= 65s$: $Z = -1.955$, $N = 9$, $P =$

390   0.051). Median rates of both episodes ('stable'$= 2.41$/hr; 'unstable'$= 5.39$/hr: $Z = -$

391   2.028, $N = 7$, $P = 0.043$) and bouts ('stable'$= 0.88$/hr; 'unstable' $= 2$/hr: $Z = -2.197$,

392    $N = 7$, $P = 0.028$) increased significantly, while the number of episodes per bout

393 significantly decreased (median 'stable' = 3.16 episodes/bout, 'unstable'= 2.32

394 episodes/bout: $Z = -2.547$, $N = 9$, $P = 0.011$). Overall, these results show that during

395 the unstable period, males engaged in shorter but more frequent grooming bouts,

396 which contained fewer and shorter grooming episodes.

397

398   Mean length of grooming episodes increased across bouts in the period of

399 social instability, with individuals significantly increasing episode duration over time

400 in more than half of the dyads (weighted Z-test: average: $r_s = +0.063$, $P < 0.001$;

401 Table 2). Additionally, the amount of grooming individuals received during a bout

402 significantly matched the amount of grooming they gave their partner in the following

403 bout (LMM: *Estimate* ± *SE* = 0.22 ± 0.10, *Wald* = 4.590, $P = 0.035$). Only 23 bouts,

404 which correspond to 9% of the total number of bouts collected during social

405 instability, incorporated more than two intra-bout episodes. Within those bouts,

406 individuals did not significantly increase grooming episode duration in relation to

407 their own previous contribution (weighted Stouffer's Z-method: $N = 2$, $P = 1$; Table

408 6). Similarly, the number of bouts in which individuals did not increase episode

409 duration in response to partner's previous contribution significantly exceeded the

410 number of bouts in which episode duration increased throughout the bout (weighted

411 Stouffer's Z-method: $N = 2$, $P < 0.001$; Table 6). These results indicate that *M-group*

412 males during social instability raised the stakes across bouts by increasing episode

413 length across subsequent grooming interactions and matching partner's grooming

414 investment in the previous bout, which supports prediction 4, although they did not

415 raise the stakes within bout.

416   While rates of aggression were higher in the 'unstable period' than in the

417 'stable period' (Kaburu et al., 2013), these tended to decrease across the period,

418   although the relationship did not reach significance ($r_s = -0.316$, $N = 32$, $P = 0.078$).

419   Finally, daily variation in episode length was not significantly predicted by aggression

420   rates (LMM: *Estimate $\pm$ SE* = 0.31 $\pm$ 0.30, *Wald* = 1.097, *P* = 0.299).

421

422   **Discussion**

423

424   We found no support for raise-the-stakes as a grooming-allocation strategy

425   among wild male chimpanzees during periods of social stability (supporting our

426   *prediction 1*), a result consistent with studies on monkeys (*Papio cynocephalus*:

427   Barrett et al. 2000; *Macaca radiata* & *Cebus capuchinus*: Manson et al 2004;

428   *Cercocebus atys* & *Chlorocebus aethiops*: Fruteau et al. 2011). Male chimpanzees

429   might not raise the stakes not only because of the long history of social interactions

430   that characterize group members, but also because of the time limits that constrain

431   them. In other words, as during a day individuals have to engage in a broad range of

432   activities, including grooming more than one partner (Henzi et al. 1997; Dunbar,

433   1992), increasing grooming time with a partner might not always be a viable strategy

434   (Barrett et al. 2000). Contrary to our *predictions 2* and *3*, male chimpanzees did not

435   use the strategy in either post-conflict situations or after prolonged absence. However,

436   we did find support for raise-the-stakes during social instability, supporting our

437   *prediction 4*: in this context, individuals matched partner's contribution from the

438   previous bout and showed a general tendency to increase their grooming investment

439   across bouts, which was not a by-product of the decrease of aggression rates across

440   the unstable period. .

441

442   These findings suggest that RTS might be a viable strategy not only while

443   cooperating with strangers but also in periods of social instability when relationships

444   – prior histories of interaction – between the individuals become unreliable. Such

445   instability may create conditions of uncertainty and unpredictability, comparable to

446   situations in which individuals have to cooperate with strangers.

447

448   Grooming is commonly viewed as a means to build trust (Seyfarth 1977,

449   1980; Dunbar 1988, 1991; Henzi et al. 2000; Watts, 2002) to create a platform (a

450   relationship) upon which future cooperation and contingent fitness benefits can be

451   based (Hinde, 1976). Under this 'valuable relationships' model (Kummer 1978; Cords

452   and Aureli 2000), we can conclude that trust was not sufficiently disrupted by either

453   long absences caused by consortships or routine acts of aggression to require a RTS

454   strategy to rebuild a relationship. The analysis of post-conflict contexts reveals also

455   that not only did male chimpanzees not increase their investment, but also that

456   former opponents rarely engaged in grooming bouts after conflicts, which is

457   consistent with previous studies on this community (Kutsukake and Castle,

458   2004). It is possible that given the social stability that characterized the

459   majority of the study period, with low rates of male-male aggression (Kaburu

460   et al., 2013), aggressive interactions and the shifting of social interactions

461   between group members might have had a minimal negative impact on social

462   relationships between former opponents or for consorting males, and, thus,

463   males might have not needed to rebuild predictable cooperative relationships

464   'from scratch' after conflicts, or after a prolonged absence.Additionally, Male

465   chimpanzees might have no need to employ a RTS strategy to rebuild trust or repair

relationships after conflict or long periods apart if grooming is traded for other commodities and for itself (Newton-Fisher & Lee, 2011; Watts 2002; Mitani 2006; Gomes and Boesch 2011), or if groomers receive immediate benefits by decreasing their stress levels (Shutt et al. 2007) or feeding on the parasites removed (Tanaka and Takenfushi, 1993; Onishi et al., 2013; Johnson et al., 2010). Male chimpanzees, however, raised the stakes when there was an increase in social instability. The unexpected and unusual coalitional killing of the alpha male appeared to have offered a condition that led individuals to (re)-build predictable cooperative relationships: the trust on which social relationships were built broke down and needed to be re-established. Our study therefore provides the first evidence of raise-the-stakes in primate social grooming, albeit restricting to a particular context.

The presence of a raise the stakes pattern across bouts, including unidirectional grooming (see data analysis), and its simultaneous absence within bout confirms that unidirectional grooming plays an important role in male strategies to enforce grooming reciprocation. In contrast, studies on monkeys have generally focused exclusively on grooming bouts in which both partners groomed (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011). While this makes sense for species whose grooming bouts are predominantly reciprocated within bout, such as vervet monkeys (*Chlorocebus aethiops*) and sooty mangabeys (*Cercocebus atys*) as 90% of their grooming bouts were found to be reciprocated (Fruteau et al. 2011), this approach is less understandable for species in which reciprocated bouts are less than half of the total number of bouts, which is the case of, for instance, chacma baboons (31-51%: Barrett et al. 1999), bonnet macaques (5-7%: Manson et al. 2004), and white-faced capuchins (12-27%: Manson et al. 2004). The results presented in this

491   chapter indicate that unidirectional grooming should receive more consideration in

492   future studies and its importance in the analysis of grooming interactions should not

493   be discounted.

494   Since our analysis is based on an unusual social context (i.e. social instability

495   due to the alpha male's death) and on a relatively small sample size (e.g. only two

496   males were recorded spending a considerable amount of time far from the other group

497   members) our results need to be taken with caution. Nevertheless, our study

498   highlights the importance of considering the possibility that individuals adopt some

499   strategies to enforce reciprocation and avoid cheating in specific contexts, rather than

500   as a general approach. Given the complexity of chimpanzee social system and

501   grooming patterning, it would not be plausible to suppose that male chimpanzees

502   engage in a single strategy to assure reciprocation. In contrast, it is more likely that

503   they change the strategies adopted in relation to, for instance, the stability of the

504   hierarchy, rank relationships, or the presence of bystanders. Therefore, future work

505   might attempt to test for the RTS strategy in specific social contexts in which a re-

506   establishment of predictable cooperative relationships is needed, such as during social

507   instability among male baboons following the immigration of new males (Wittig et al.

508   2008; Beehner et al. 2005), or in chimpanzee communities, such as *Kanyawara*

509   (Kibale, Uganda) that exhibit higher rates of aggressive interactions (Muller 2002; *cfr.*

510   Kaburu et al., 2013), or that show higher levels of post-conflict grooming (e.g.

511   *Ngogo*: Watts, 2006). This might potentially shed light on whether partners that can

512   no longer rely on their prior history of interactions resort to a RTS strategy to re-

513   establish cooperative relationships.

514

515   **Acknowledgement**

523

524 Table 1. Number of focal observation hours on each of 8 adult male chimpanzees.

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Focal Individuals	Focal Observation Time
AL	49hr 45min
BB	54hr 53min
CT	48hr 54min
DE	53hr 11min
FN	46hr 01min
OR	47hr 03min
PM*	40hr 14min
PR	57hr 15min

535 **PM* was killed on the 2nd of October 2011 (Kaburu et al. 2013).

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538 Table 2. Spearman rank correlation between length and order of occurrence of

539 grooming episodes. The grooming contribution of each male to each of the grooming

540 dyad he was part of was tested individually and the results were combined through

541 weighted Z-test. Only males that performed at least 5 grooming episodes were

542 included in the analysis. The table shows 1) the context from which grooming data

543 were extracted, 2) the range of p values, 3) the range of coefficients of Spearman's

544 correlations (r_s) and 4) the percentage of individuals showing a positive trend

545 (grooming episodes increased over time) and a negative trend (grooming episodes

546 decreased). RTS in post-conflict context was analysed exclusively within-bout (Table

547 4).

Context	N	p range	r_s range	% r_s (+)	% r_s (-)
Social stability	71	$0.00<p<0.934$	$-1<r_s<0.835$	35 %	65%
After prolonged absence	25	$0.019<p<0.466$	$-0.9<r_s<0.6$	40%	60%
Social instability	39	$0.01<p<0.497$	$-0.80<r_s<0.771$	57%	43%

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	Increase across bouts								
	in response to their own previous contribution							in response to partner's previous contribution	
	Initiator			Reciprocator					
N	Yes	No	Sign test *P*	Yes	No	Sign test *P*			Sign test *P*
3	15	20	0.5	-	-	-	5	30	<0.000
4	6	4	0.754	5	5	1	1	9	0.021
5	1	3	-	3	1	-	1	3	-
6	0	3	-	0	3	-	0	3	-
7	0	1	-	1	0	-	0	2	-
23	0	1	-	0	1	-	0	1	-

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562   N = number of intra-bout episodes.

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571 Table 4. Sign tests to assess whether groomers increase episode duration in response

572 to their own previous contribution or to partner's in post-conflict context. The test

573 was run only when at least five dyads contributed to a group, but we included also

574 groups for which the test was not run to show the trend.

	Increase across bout								
	in response to their own previous contribution						in response partner's previous contribution		
	Initiator			Reciprocator					
N	Yes	No	Sign test *P*	Yes	No	Sign test *P*	Yes	No	Sign test *P*
	2	5	0.453				1	6	0.125
4	1	1	-	0	2	-	0	2	-
7	0	1	-	0	1	-	0	1	-
21	0	1	-	0	1	-	0	1	-

575

576 N = number of intra-bout episodes.

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586 Table 5. Sign tests to assess whether groomers increase episode duration in response

587 to their own previous contribution or to partner's after a prolonged absence due to

588 consortship. The test was run only when at least five dyads contributed to a group, but

589 we included also groups for which the test was not run to show the trend.

590

	Increase across bout								
	in response to their own previous contribution							in response to partner's previous contribution	
	Initiator			Reciprocator					
N	**Yes**	**No**	**Sign test** *P*	**Yes**	**No**	**Sign test** *P*	**Yes**	**No**	**Sign test** *P*
3	1	4	0.375				0	5	0.063
4	2	0	-	0	2	-	0	2	-
7	0	1	-	0	1	-	0	1	-

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592 N = number of intra-bout episodes.

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604 Table 6. Sign tests to assess whether groomers increase episode duration in response

605 to their own previous contribution or to partner's during social instability. The test

606 was run only when at least five dyads contributed to a group, but we included also

607 groups for which the test was not run to show the trend.

608

	Increase across bout								
	in response to their own previous contribution							in response to partner's previous contribution	
	Initiator			Reciprocator					
N	Yes	No	Sign test *P*	Yes	No	Sign test *P*	Yes	No	Sign test *P*
3	7	6	1				0	13	< 0.001
4	3	2	1	3	2	1	0	5	0.06
5	0	2	-	0	2	-	0	2	-
6	0	1	-	0	1	-	0	1	-
7	0	2	-	0	2	-	0	2	-

609

610 N = number of intra-bout episodes.

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