1 **Reciprocity in group-living animals: partner control *versus***

2 **partner choice**

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14

15 ABSTRACT

16 Reciprocity is probably the most debated of the evolutionary explanations for

17 cooperation. Part of the confusion surrounding this debate stems from a failure to note

18 that two different processes can underlie reciprocity: partner control and partner

19 choice. We suggest that the common observation that group-living animals direct their

20 cooperative behaviours preferentially to those individuals from which they receive

21 most cooperation is to be interpreted as the result of the sum of the two separate

22 processes of partner control and partner choice. We review evidence that partner

23 choice is the prevalent process in primates and propose explanations for this pattern.

24   We make predictions that highlight the need for studies that separate the effects of

25   partner control and partner choice in a broader variety of group-living taxa.

26

27   *Key words*: cooperation, reciprocity, partner control, partner choice, proximate

28   mechanisms.

29

30   CONTENTS

45

46   **I. INTRODUCTION**

47   In the endless debate about reciprocity, an aspect that is often neglected is the

48   need to distinguish between the two different processes that can underlie reciprocal

49 exchanges of cooperative behaviours (Noë & Voelkl, 2013). The first study to

50 distinguish these two processes was probably Bull & Rice (1991; see Eshel & Cavalli-

51 Sforza, 1982 for an earlier insight), that named them 'partner fidelity' (later called

52 'partner control' by Noë, 2006) and 'partner choice'. In partner-control models (e.g.

53 Axelrod & Hamilton, 1981) dyads of interacting individuals are conceptually isolated

54 from other dyads and the behaviour of each subject depends only on the previous

55 behaviour of the partner. As there is no possibility of switching partner, individuals

56 must try to control the behaviour of the partner by rewarding cooperation and

57 sanctioning uncooperative behaviour. In partner-choice models (e.g. Campennì &

58 Schino, 2014) individuals choose their partners on the basis of the benefits they offer,

59 and the need to sanction uncooperative partners is replaced by partner switching and

60 outbidding competition. Partner choice features pre-eminently in biological market

61 models, and proponents of biological market theory have repeatedly emphasized the

62 distinctiveness of the two processes (Noë & Hammerstein, 1994, 1995; Noë, 2006).

63 Empirical tests of biological market theory have however tended to focus on market

64 effects, rather than on distinguishing and separating the effects of partner control and

65 partner choice (e.g. Henzi & Barrett, 2002; Fruteau *et al.*, 2009).

66   In our opinion, the failure to distinguish and separate the two processes of

67 partner control and partner choice has hampered empirical research and biased

68 recognition of the presence of reciprocity, especially among group-living animals.

69 Herein, we discuss why distinguishing the two processes is important, review the

70 (few) attempts to quantify their relative prevalence, and make predictions about their

71 distribution in nature.

72

73 **II. THE CONSEQUENCES OF NOT DISTINGUISHING**

74   A common assumption of research on reciprocity is that the only way actually

75   to demonstrate reciprocity is to show the existence of a temporal contingency between

76   the receipt of cooperation and the giving of cooperation (and/or between failure to

77   receive cooperation and subsequent retaliation) (Hauser *et al.*, 2003; Silk, 2003). This

78   assumption implicitly equates reciprocity with partner control and, given the relative

79   rarity of convincing examples of true temporal contingencies between giving and

80   receiving cooperative acts, it leads to the conclusion that reciprocity must be rare (e.g.

81   Stevens, Cushman & Hauser, 2005; see Cheney *et al.*, 2010, and Olendorf, Getty &

82   Scribner, 2004 for two examples of temporal contingencies studies). In fact, temporal

83   contingencies between giving and receiving only test for partner control, and say

84   nothing about partner choice (Carter, 2014). Thus, the emphasis on temporal

85   contingencies, and the failure to note that they are predicted by partner control only,

86   caused a widespread underestimation of the prevalence of reciprocity.

87   While empiricists focused on partner control (although apparently implying

88   that the results apply to all forms of reciprocity), theoreticians began producing

89   models of the evolution of cooperation by partner choice (Sherratt & Roberts, 1998;

90   Aktipis, 2004; McNamara *et al.*, 2008; Castro & Toro, 2010; Campennì & Schino,

91   2014; see McNamara & Leimar, 2010 for a review on the role of variation in

92   promoting the evolution of cooperation, especially by partner choice). It is now

93   abundantly clear that partner choice can indeed promote the evolution of cooperation.

94   Furthermore, theoretical models have shown that partner choice can also lead to

95   patterns of reciprocal exchange similar to those observed in animals (see Section VII

96   for details). Notwithstanding this new emphasis on partner choice, the contrast

97   between the easiness with which cooperation evolves in a variety of partner-control

98   models and the difficulties of showing empirical evidence for these models has led

99   some authors to hypothesize that proximate constraints may limit the evolvability of

100   reciprocity (thus again implicitly extrapolating from partner control to all forms of

101   reciprocity; Stevens & Hauser, 2004).

102   A corollary of the neglect of partner choice is that evidence that animals direct

103   their cooperative acts preferentially to those individuals from which they receive most

104   cooperation is dismissed as showing 'only a correlation' (Silk, 2013). Such evidence

105   however is (in stark contrast to the limited evidence about temporal contingencies)

106   truly overwhelming, so that we believe it should not be dismissed lightly.

107

108   **III. ACROSS-DYAD CORRELATIONS BETWEEN GIVING AND**

109   **RECEIVING**

110   One of the oldest ways of assessing the relations between giving and receiving

111   cooperation is to carry out a correlation across dyads between cooperation given and

112   cooperation received. Regardless of the statistical technique employed [matrix

113   correlations or some variation of generalized linear mixed models (GLMMs)] these

114   analyses enter dyadic values of cooperation given (i.e. cooperation given by each

115   subject to each other subject) as the dependent variable and dyadic values of

116   cooperation received as one of the independent variables. Kinship and/or other

117   potential confounding factors are usually added as additional independent variables.

118   Typically, dyadic values are calculated on the basis of a relatively long observation

119   period (e.g. grooming rates averaged across several months of observation).

120   In addition to many empirical studies (e.g. Silk, 1992; Watts, 2002; Carne,

121   Wiper & Semple, 2011), three meta-analyses have addressed the relationship between

122   giving and receiving cooperative behaviour in primates. These meta-analyses

123   summarized studies conducted on dozens of different primate species and hundreds of

124   different individuals. Schino (2007; also including a single temporal relations study)

125   assessed the relationship between grooming and agonistic support; Schino & Aureli

126   (2008) examined the relationship between giving and receiving grooming; Jaeggi &

127   Gurven (2013; including data on humans) investigated the relationships between

128   grooming and food sharing and between giving and receiving food. All three of these

129   studies found significant positive weighted average correlations across dyads between

130   giving and receiving cooperative acts. Overall, the results of these meta-analyses

131   provide extremely robust and convincing evidence for reciprocal exchanges in

132   primates. Note, however, that they are silent as to the underlying processes.

133   Across-dyad positive correlations between cooperation given and received are

134   not limited to primates. Recent studies have broadened the phylogenetic scope of such

135   analyses and have obtained similar results in several other species, including jackdaws

136   (*Corvus monedula*) that exchange food and interchange food for allopreening (De

137   Kort, Emery & Clayton, 2006), coatis (*Nasua nasua*) that exchange agonistic support

138   (Romero & Aureli, 2008), spotted hyenas (*Crocuta crocuta*) that interchange

139   communal defence at carcasses for tolerance while feeding (Smith, Memenis &

140   Holekamp, 2007), rooks (*Corvus frugileus*) that exchange food and interchange food

141   for allopreening and agonistic support (Scheid, Schmidt & Noë, 2008), ravens

142   (*Corvus corax*) that exchange agonistic support and interchange allopreening for

143   support (Fraser & Bugnyar, 2012), and vampire bats (*Desmodus rotundus*) that

144   exchange regurgitated blood and interchange blood for allogrooming (Carter &

145   Wilkinson, 2013).

146   Overall, evidence that group-living animals (including humans) direct most of

147   their cooperative acts towards those individuals from which they receive most

148 cooperative acts seems unassailable. It is clear that we need an interpretation for such

149 a common phenomenon.

150

151 **IV. THE MEANING OF ACROSS-DYAD CORRELATIONS**

152 We propose that across-dyad correlations between cooperative acts given and

153 received are the result of the sum of the two separate processes of partner control and

154 partner choice. Due to the nature of these dyadic data, no information is available on

155 the temporal relationships between single cooperative events. In principle, it is

156 possible to imagine two extremes of a continuum. At one end of the continuum, a

157 significant positive dyadic correlation can result from a tight temporal relationship

158 between giving and receiving (each act of giving is immediately returned). At the

159 other end of the continuum, it can derive from interindividual preferences based on a

160 comparison of the overall amount of cooperation received from each group member,

161 in the complete absence of a temporal relationship between giving and receiving (see

162 Section VII and Campennì & Schino, 2014, for a model showing that when partner

163 choice is based on a comparison of the amount of cooperation received from group

164 members, across-dyad correlations between cooperation given and received emerge).

165 The first extreme of the continuum would correspond to strict partner control in the

166 absence of partner choice; the other extreme would correspond to partner choice in

167 the absence of partner control. As already noted, real animals probably use a mixture

168 of the two strategies and the across-dyad correlations we observe empirically thus

169 reflect the sum of these two processes.

170 It follows from the above reasoning that across-dyad correlations do provide

171 evidence for reciprocity, but they do not tell us anything about the relative

172 contributions of the two processes. The paucity of convincing evidence of partner

173   control together with the abundance of across-dyad correlations between cooperative

174   acts given and received suggest that partner choice may be the prevalent process, but

175   we have relatively little quantitative evidence from studies that compare the two

176   processes. Below, we review this evidence.

177

178   **V. TRYING TO DISTINGUISH**

179   A few studies have tried to estimate the relative contributions of partner

180   control and partner choice in the same species and setting by evaluating both the

181   temporal relationships between individual cooperative events and the across-dyad

182   correlations between overall cooperation given and received. Schino, Ventura &

183   Troisi (2003) and Schino, Polizzi di Sorrentino & Tiddi (2007) observed no short-

184   term temporal relations between giving and receiving grooming or between grooming

185   and agonistic support in Japanese macaques (*Macaca fuscata*). At the same time,

186   macaques showed strong positive across-dyad correlations between grooming given

187   and received and between grooming and support. Tiddi *et al.* (2011) observed no

188   short-term temporal relationship between grooming and tolerance over a clumped

189   food resource coupled with strong across-dyad correlations in wild tufted capuchin

190   monkeys (*Cebus apella*). Kaburu & Newton-Fisher (2015) observed no short-term

191   exchange of grooming for sexual access together with a positive across-dyad

192   relationship between male mating success and grooming by males to females in a

193   community of wild chimpanzees (*Pan troglodytes*) characterized by egalitarian

194   dominance relationships. Jaeggi, Stevens & Van Schaik (2010) and Jaeggi *et al*.

195   (2013) observed no short-term temporal relationship between grooming and food

196   sharing in chimpanzees, while long-term food sharing given was best predicted by

197   food sharing received. In bonobos (*Pan paniscus*) food sharing increased the short-

term exchange of grooming and was also, in the long-term, best predicted by

relationship quality (Jaeggi *et al.*, 2010, 2013). Finally, Carter & Wilkinson (2013)

conducted a fasting experiment in vampire bats. They found that, within dyads, blood

given in a particular trial was not predicted by blood received in the previous trial. At

the same time, blood given was strongly correlated with blood received across dyads.

In all these studies (with the possible exception of the bonobo studies of

Jaeggi *et al.* (2010, 2013) partner control appeared to exert weak or no effect on

cooperative behaviours (see Table 1 for details regarding the time windows used to

test for immediate reciprocation) and our interpretation is therefore that the positive

across-dyad correlations have to be ascribed (almost) entirely to partner choice.

Other studies used refined statistical techniques to identify (and then remove)

the effects of partner control. Schino, Di Giuseppe & Visalberghi (2009), Schino &

Pellegrini (2009) and Campennì *et al.* (2015) used survival analysis to identify the

time window over which having received grooming increased the probability of

returning grooming to the same partner, thus obtaining an objective (i.e. data-driven)

estimate of immediate reciprocation (Table 1). These studies revealed significant

short-term temporal relationships between giving and receiving grooming (i.e.

animals showed an increased probability of immediately returning grooming,

compared to their baseline). However, only 7–35% of the grooming episodes were

immediately reciprocated, showing that temporal relationships between events played

a limited role in guiding animal decisions about cooperation. When all the cases of

immediate reciprocation were excluded from analysis (thus removing any effect of

partner control), across-dyad correlations remained significant, again showing an

important effect of partner choice (Schino *et al.*, 2009; Schino & Pellegrini, 2009;

Campennì *et al.*, 2015). Gomes & Boesch (2009) reported similar results on

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223   exchanges of meat for sexual access in wild chimpanzees. Note also that, although it

224   is obviously possible that an act of cooperation received can sometimes affect the

225   likelihood of returning cooperation past the measured time window, this effect is

226   likely to be small. It is clear that any partner-control effect of cooperation received

227   must decrease monotonically with time, so that the magnitude of this effect after it is

228   no longer operationally measurable must be negligible.

229   Applying new methods of network dynamics, Hooper *et al.* (2013) tested

230   'stationary' (i.e. long-term) and 'dynamic' (i.e. short-term) reciprocity in the

231   exchange of manioc beer among Tsimane horticulturalists. They found robust long-

232   term reciprocity, while short-term reciprocity only applied to socially distant partners.

233   Fruteau *et al.* (2011) found little evidence for two specific partner-control

234   strategies ('parcelling' and 'raise the stake') in the grooming exchanges of wild

235   mangabeys (*Cercocebus atys*) and vervet monkeys (*Chlorocebus aethiops*). Finally,

236   Sabbatini *et al.* (2012) conducted a food-sharing experiment on tufted capuchin

237   monkeys in which animals were tested in triads or in dyads. In triadic tests, partner

238   choice exerted a stronger effect than partner control (effect sizes r=0.289 and r=0.194,

239   respectively; unpublished data from Sabbatini *et al.* 2012). Interestingly, partner

240   control appeared to play a reduced role in triadic compared to dyadic tests. This

241   suggests a causal role for the possibility of partner choice in reducing the scope of

242   partner control. Bshary & Grutter (2002) similarly reported that in a cleaner fish

243   mutualism (*Labroides dimidiatus* with clients *Ctenochaetus striatus*), increased

244   possibilities of partner choice were associated with reduced partner control.

245   Overall, the available evidence shows that partner choice is the prevailing

246   process whenever both processes have been studied simultaneously.

247

VI. THE PROXIMATE MECHANISMS UNDERLYING RECIPROCITY

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249   Before drawing conclusions from the evidence reviewed above, we will

250 discuss briefly the proximate mechanisms underlying reciprocity. This topic is

251 traditionally neglected; most authors that do discuss proximate mechanisms adopt

252 (rather uncritically) the classification proposed by Brosnan & de Waal (2002). Below,

253 we build on the work of Brosnan & de Waal (2002) and propose three hypothetical

254 proximate mechanisms for reciprocity that overcome some of the difficulties

255 encountered by their original formulation. Proximate mechanisms can be thought of

256 as evolved answers to recurrent problems, and can therefore be expected to implement

257 adaptive responses appropriate to the costs and benefits of the situation. The three

258 mechanisms we discuss below are therefore likely to have evolved under different

259 social and ecological conditions.

260

261 **(1) Hard-wired reciprocity**

262   This mechanism replaces Brosnan & de Waal's (2002) symmetry-based

263 reciprocity that, in its original formulation, cannot be evolutionarily stable (M.

264 Campennì & G. Schino, in preparation). Hard-wired reciprocity can be hypothesized

265 to evolve whenever reciprocity is needed in one-shot interactions (i.e. interactions that

266 are unlikely to be repeated). The animal responds 'instinctively' to the receipt of a

267 cooperative act by immediately returning it. This mechanism is characterized by short

268 delays between receiving and giving and by a one-to-one relationship in the

269 currencies exchanged (one kind of cooperation is always exchanged with the same

270 other kind of cooperation). It requires neither individual recognition, nor stable social

271 relationships, and is likely to be found in cognitively unsophisticated animals (e.g.

272 egg trading in simultaneous hermaphrodites; Fischer, 1980; Sella, 1985) or in animals

273   that do not form stable social groups [e.g. grooming in impalas (*Aepyceros*

274   *melampus*); Connor, 1995]. It is inherently a partner-control mechanism, although, in

275   a biological market perspective, it can be conceived to allow some flexibility in

276   exchange rates in relation to the conditions of the market place.

277

278   **(2) Emotionally based reciprocity**

279   To the extent that emotions can be conceived as task-specific computational

280   mechanisms (LeDoux, 2012; Cosmides & Tooby, 2013), it is possible to hypothesize

281   that a system of 'emotional bookkeeping' (Schino & Aureli, 2009) evolved to support

282   reciprocity in group-living animals, i.e. under conditions of continuous social

283   interaction with individually recognizable group mates.

284   Our formulation of emotionally based reciprocity is derived from Brosnan &

285   de Waal's (2002) attitudinal reciprocity, but acts over a longer time frame. Through

286   this mechanism, cooperation received triggers partner-specific positive emotions that

287   promote subsequent cooperation. What motivates an animal to engage in emotionally

288   based cooperation is the social attachment that it has developed with group

289   companions (social attachment that itself depends also on the receipt of cooperative

290   behaviours). Emotions thus constitute a bookkeeping system that can act over

291   relatively long time frames and allow easy and flexible conversion among multiple

292   currencies (Schino & Aureli, 2009). Emotionally based reciprocity requires the

293   formation of differentiated social relationships that guide social decision-making, but

294   no special cognitive abilities are otherwise needed. The formation of differential

295   social relationships (from strong social bonds to simple cohabitation) is inherently a

296   partner-choice mechanism that promotes outbidding competition (Campennì &

297   Schino, 2014). In humans emotions associated with cooperative exchanges (e.g. anger

298   or gratitude) presumably play a role also as a partner-control mechanism (van't Wout

299   *et al*., 2006; McCullough, Kimeldorf & Cohen, 2008). We know very little about the

300   short-term emotional consequences of cooperation in animals. In primates,

301   displacement activities have been proposed as a measure of anxiety-like emotions

302   (Maestripieri *et al*., 1992; Schino *et al*., 1996) and used to gauge the emotional

303   consequences of receiving grooming. Overall, rather inconsistent results have been

304   obtained (Schino *et al.*, 1988; Radford, 2012; Molesti & Majolo, 2013; Semple,

305   Harrison & Lehmann, 2013).

306

307   **(3) Calculated reciprocity**

308   Calculated reciprocity can be hypothesized to evolve as a response to the need

309   to be able to engage in reciprocal exchanges in rare and or/novel situations and/or

310   when interacting with unfamiliar individuals. Alternatively, it can be conceived as a

311   by-product of selection for the general ability to plan future actions.

312   An animal that engages in calculated reciprocity is supposed to be motivated

313   by the expectation of a future return benefit (the reciprocated cooperation). Calculated

314   reciprocity thus requires advanced cognitive abilities such as the capacity to plan

315   social interactions or some form of 'future thinking'. Note that, unlike Brosnan & de

316   Waal's (2002) original formulation, we propose the defining characteristic of

317   calculated reciprocity should not be the reliance on some computation of costs and

318   benefits but the role played by expected benefits as the key motivating factor. This

319   also allows calculated reciprocity to be empirically distinguished from emotionally

320   based reciprocity (Schino & Pellegrini, 2011). Calculated reciprocity is likely to be

321   rare outside humans (see Section VIII). It can in principle underlie both partner-

322   control and partner-choice processes.

323

VII. MODELLING RECIPROCITY IN GROUP-LIVING ANIMALS

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325   Most theoretical studies of cooperation and reciprocity focus on modelling

326   their evolution rather than on attempting to reproduce existing patterns of exchanges

327   of cooperative acts as observed in group-living animals (see Section II for partner-

328   choice models and Bshary & Bronstein, 2011, for a review and classification of

329   partner-control models). A few recent theoretical studies have used agent-based

330   simulations to model and reproduce empirically observed patterns of social

331   interactions. In these models, artificial agents (that may or may not be set in space)

332   exchange positive or negative interactions based on their past experiences and/or on

333   their spatial proximity with other agents. These models may be relevant for

334   understanding the proximate mechanisms underlying reciprocity and its emergence

335   from animal decision rules.

336   Puga-Gonzalez, Hildenbrandt & Hemelrijk (2009) and Puga-Gonzalez,

337   Hoscheid & Hemelrijk (2015) have shown that across-dyad correlations between

338   cooperative acts given and received can emerge as a consequence of the spatial

339   structuring of agents. When 'social bonds' (in the form of a tendency to follow

340   specific individuals) were added to these models, the pattern of reciprocity

341   strengthened. Evers *et al.* (2014, 2015) modelled the emotional consequences of

342   affiliation and fear, and showed that individual-specific emotional states can generate

343   patterns of reciprocity consistent with a mechanism of emotional bookkeeping.

344   Although the aim of these models was only to reproduce existing patterns of

345   reciprocal cooperation in animals, one could argue for the necessity to test also

346   whether the strategies implemented in the agents were evolutionarily robust, i.e. if

347   they competed successfully against other (notably, selfish) strategies. M. Campennì &

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348   G. Schino (in preparation) found that when cooperative acts are based on

349   interindividual proximity, reciprocal patterns of exchange emerge (thus confirming

350   the results of Puga-Gonzalez *et al.*, 2015). Nevertheless, such a strategy was

351   unsuccessful in an evolutionary test in which it had to compete against selfish agents

352   that never cooperated. Generally speaking, any strategy that does not include a

353   mechanism that controls or excludes cheaters is likely to be evolutionarily

354   unsuccessful.

355   Campennì & Schino (2014) implemented the same strategy of partner choice

356   based on benefits received in both a 'single-generation' and an evolutionary model. In

357   their model, agents choose to cooperate with those partners from which they had

358   received the most cooperation. They showed that a strategy of pure partner choice can

359   both reproduce emergent patterns of reciprocal exchange (i.e. across-dyads

360   correlations) and compete successfully against selfish agents in an evolutionary test.

361   Note that in this model agents were obligate cooperators, and there was therefore no

362   possibility of partner control. This study provided theoretical (simulation-based)

363   support for a role of partner choice in the evolution and maintenance of reciprocal

364   cooperation in group-living animals.

365   Agent-based models appear to be a promising tool for understanding the

366   emergence of reciprocity, but they need to incorporate both tests aimed at reproducing

367   existing patterns of behaviour as observed in real animals and tests aimed at

368   evaluating the evolutionary plausibility of the implemented strategies.

369

370   **VIII. INFERENCES AND PREDICTIONS**

371   Two inferences can be drawn tentatively from the available evidence. First, if

372   one accepts that across-dyad correlations between cooperative acts given and received

373 do provide useful insight, then one must conclude that reciprocity is indeed common,

374 at least in group-living animals. This is in sharp contrast to some commonly held

375 opinions (Stevens *et al.*, 2005, Clutton-Brock, 2009). Second, partner choice seems to

376 play a larger role than partner control in guiding animal decisions about cooperation.

377 This is again in contrast to common (often implicit) assumptions.

378 Our focus herein is on the second of these conclusions, and thus we should ask

379 the following questions: is this to be considered a conclusion of general applicability

380 or is it in some way taxonomically restricted? Are there conditions or animal taxa

381 where partner control can instead be expected to prevail?

382 Noë & Voelkl (2013) suggested that partner choice should prevail in one-shot

383 interactions, while when animals engage in longer-term relationships progressively

384 larger amounts of partner control should become apparent. We note, however, that in

385 group-living animals (that are likely to have long-lasting relationships) the costs of

386 partner sampling and partner switching are greatly reduced, a factor that should

387 favour partner choice and thus promote cooperation through outbidding competition

388 (Johnstone & Bshary, 2008). Also, stable social relationships facilitate emotionally

389 based reciprocity that, in turn, makes partner choice an easy option for a variety of

390 animals.

391 With a single exception (Carter & Wilkinson, 2013), all studies that tried to

392 compare partner control and partner choice in the same species and setting have been

393 conducted on primates, most concluding that partner choice is the prevalent process

394 (see Section V). Thus, there is an urgent need for similar studies in other taxa. Group-

395 living primate and non-primate species share two important aspects that make us

396 suggest that partner choice may be the prevalent process across taxa. First, positive

397 across-dyad correlations between cooperative acts given and received are common in

398   various taxa (Section III). Second, long-term social bonds have important fitness

399   consequences in group-living primate and non-primate species (Silk, 2007; Silk *et al.*,

400   2010; Cameron, Setsaas & Linklater, 2009; Frère *et al.*, 2010), suggesting that the

401   formation of differentiated social relationships has been subject to positive selection

402   in a variety of taxa. Long-term differentiated social relationships and emotionally

403   based reciprocity are closely linked, and similar mechanisms of emotionally based

404   partner choice may have been favoured by natural selection whenever animals

405   capable of interindividual recognition came to live in permanent groups (Schino &

406   Aureli, 2009).

407   By contrast, animals that do not form long-term social relationships must

408   necessarily rely on hard-wired reciprocity for their cooperative exchanges. Under

409   these conditions, short-term reciprocation based on partner-control processes is likely

410   to be the prevalent process, unless it is possible and inexpensive to 'sample' different

411   potential partners before the actual cooperative exchange takes place.

412   We offer two possible explanations for why partner control is comparatively

413   rare among group-living animals, both based on an assessment of the proximate

414   mechanisms likely to underlie reciprocity. The first explanation is that partner control

415   may require immediate reciprocation and thus be limited in scope. Stevens & Hauser

416   (2004) identified several possible cognitive constraints (limited memory, limited

417   computational ability, temporal discounting) that may limit the ability of animals to

418   engage in reciprocal cooperation. We have argued elsewhere (Schino & Aureli, 2009;

419   see also Carter, 2014) that these proximate constraints can be easily sidestepped by a

420   proximate mechanism based on emotional bookkeeping. Emotional bookkeeping,

421   however, is essentially a partner-choice mechanism, and the only way to overcome

422   the cognitive constraints identified by Stevens & Hauser (2004) in a partner-control

423   process would be for reciprocity to be always immediate (possibly through hard-wired

424   reciprocity).

425   Although immediate reciprocation does exist (e.g. immediate grooming

426   reciprocity in primates; Barrett *et al.*, 1999), its scope is clearly limited to those cases

427   in which the exchanged currencies are simultaneously available and needed. For

428   example, exchanges of grooming and agonistic support can only occur when support

429   is needed, so that a tight temporal relationship reduces dramatically the possibility of

430   exchange. Accordingly, reciprocal exchanges of grooming and support appear to

431   occur on a much longer time frame that involves partner choice based on overall

432   grooming/support received rather than short-term temporal relationships between

433   events (Schino *et al.*, 2007).

434   The second explanation for why partner control is relatively rare among

435   group-living animals is that partner control may alternatively require some form of

436   'planning' of social interactions and thus be taxonomically restricted to species with

437   advanced cognitive capacities. Partner control may occur when cooperation is

438   proximately motivated by the expectation of a return benefit (i.e. calculated

439   reciprocity). We are aware of only a few studies of non-human animals whose results

440   can be interpreted as a test of calculated reciprocity (as defined above). Dufour *et al.*

441   (2009) reported that a single pair of orang-utan (*Pongo pygmaeus*) exchanged tokens

442   that were valuable only for the partner showing turn taking and signalling. This

443   suggested giving was associated with the expectation that the partner returned the

444   favour. Pelé *et al.* (2009) tested a larger number of apes in a similar setting, and did

445   not observe systematic exchanges that could be interpreted as motivated by the

446   expectation of a return benefit. Similarly, Pelé *et al.* (2010) did not observe systematic

447   exchanges of tokens in tufted capuchin monkeys or Tonkean macaques (*Macaca*

448 *tonkeana*). In a more naturalistic study, Schino & Pellegrini (2011) showed that

449 female mandrills (*Mandrillus sphinx*) did not groom the alpha male immediately

450 before attacking another group member (even if the male was more likely to provide

451 support immediately after grooming), thus suggesting that the expectation to receive

452 support did not motivate the females to groom the male. Interestingly, Sebastian-

453 Enesco & Warneken (2015) recently showed that 5-year-old, but not 3-year-old

454 children adjusted their sharing of a toy in anticipation of future reciprocation, thus

455 highlighting the late development of calculated reciprocity (see also House *et al.*,

456 2013, for comparable results on the development of contingent reciprocity). They also

457 suggested that the mechanisms necessary for partner choice may develop in children

458 earlier than those necessary for partner control. Overall, we argue that partner control

459 may be relatively rare because it is restricted either in scope (being limited to those

460 cases where immediate reciprocation is possible) or taxonomically (being limited to

461 humans and possibly a few other species capable of calculated reciprocity).

462

463 **IX. CONCLUSIONS**

464 (1) Distinguishing between partner-control and partner-choice processes allows a

465 better understanding of the importance of reciprocal cooperation in animals. The

466 available evidence seems to suggest that partner choice is the prevalent process

467 underlying reciprocity in group-living animals. This conclusion, however, is drawn

468 from a taxonomically biased sample of observational studies including almost only

469 nonhuman primates.

470 (2) Three priorities emerge for future research. First, we need studies that quantify

471 simultaneously partner control and partner choice in a broader variety of taxa, in order

472 to assess the generality of our conclusions. Second, we need studies that

19

473 experimentally manipulate the occurrence of reciprocation in order to assess if and

474 how this manipulation differentially affects parter control and partner choice. Third,

475 we need studies that experimentally manipulate the possibility of partner control and

476 partner choice in order to assess how one process is affected by the presence/absence

477 of the other. Fulfilling these three needs will require the joint effort of researchers

478 with disparate backgrounds and expertise.

479

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483

484 **XI. REFERENCES**

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700

Table 1. Assumed and measured time windows for immediate reciprocation in studies of reciprocity.

Species	Assumed/measured	Duration	Reference
Cebus apella	Assumed	About 1 min	Sabbatini *et al.* (2012)
Cebus nigritus	Assumed	2 h	Tiddi *et al.* (2011)
Cecrocebus atys and *Chlorocebus aethiops*	Assumed	30 and 20 s, respectively	Fruteau *et al.* (2011)
Desmodus rotundus	Assumed	Unclear (about 2 weeks)	Carter & Wilkinson (2013)
Macaca fuscata	Assumed	1 min	Schino *et al.* (2003)
Macaca fuscata	Assumed	30 min	Schino *et al.* (2007)
Pan paniscus and *P. troglodytes*	Assumed	1 h	Jaeggi *et al.* (2013)
Pan troglodytes	Assumed	30 s	Kaburu & Newton-Fisher (2015)
Callithrix jaccus	Measured	2 min	Campennì *et al.* (2015)
Cebus apella	Measured	7 min	Schino *et al.* (2009)
Homo sapiens	Measured	3 days	Hooper *et al.* (2013)
Mandrillus sphinx	Measured	4.5 min	Schino & Pellegrini (2009)