

Bystanders, parcelling, and an absence of trust in the grooming interactions of wild chimpanzees

Item Type	Journal article
Authors	Kaburu, Stefano S. K.;Newton-Fisher, Nicholas E.
Citation	Kaburu, S.S.K., and Newton-Fisher, N.E. (2016) 'Bystanders, parcelling, and an absence of trust in the grooming interactions of wild male chimpanzees', Scientific Reports, 6, DOI:10.1038/srep20634
Publisher	Nature
Journal	Scientific Reports
Rights	Attribution-NonCommercial-NoDerivs 3.0 United States
Download date	2026-05-16 04:53:21
License	http://creativecommons.org/licenses/by-nc-nd/3.0/us/
Link to Item	http://hdl.handle.net/2436/622133

1 Title: **Bystanders, parcelling, and an absence of trust in the grooming**
2 **interactions of wild male chimpanzees.**

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16 Running title: Bystanders and the parcelling of social grooming

17 Keywords: *Pan troglodytes*, cooperation, allogrooming, Mahale, M-group,
18 dominance rank

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24 The evolution of cooperation remains a central issue in socio-biology with the
25 fundamental problem of how individuals minimize the risks of being short-changed
26 ('cheated') should their behavioural investment in another not be returned. Economic
27 decisions that individuals make during interactions may depend upon the presence of
28 potential partners nearby, which offers co-operators a temptation to defect from the
29 current partner. The parcelling model posits that donors subdivide services into parcels to
30 force cooperation, and this is contingent on opportunities for defection; that is, the
31 presence of bystanders. Here we test this model and the effect of bystander presence
32 using grooming interactions of wild chimpanzees. We found that with more bystanders,
33 initiators gave less grooming at the beginning of the bout and were more likely to
34 abandon a grooming bout, while bouts were less likely to be reciprocated. We also found
35 that the groomer's initial investment was not higher among frequent groomers or stronger
36 reciprocators, suggesting that contrary to current assumptions, grooming decisions are not
37 based on trust, or bonds, within dyads. Our work highlights the importance of considering
38 immediate social context and the influence of bystanders for understanding the evolution
39 of the behavioural strategies that produce cooperation.

40 **Introduction**

41 In group-living species, many social interactions occur in the presence of others. The
42 influence of such bystanders has attracted increasing attention, both in their role as an
43 audience that influences performance (audience effect: e.g. *Gallus gallus domesticus*¹,
44 *Pan troglodytes*²), and as eavesdroppers who acquire information that they can later
45 exploit³ (e.g. *Astatotilapia burtoni*⁴, *Procambarus clarkia*⁵). This interest has led to
46 investigation into the importance of bystanders as a selective influence on the evolution
47 of cooperative behaviour; eavesdroppers may benefit by identifying individuals with
48 whom they can cooperate in future³. The focus on the information extracted by
49 bystanders^{4,5}, and whether actors attempt to manipulate this information (e.g. *Betta*
50 *splendens*⁶, *Pongo* spp.⁷), however overshadows a more direct role for bystanders in the
51 evolution of cooperation through widening the range of options open to actors by offering
52 alternative partners with which to cooperate.

53 Understanding the evolution of cooperation in social animals remains a central
54 issue in socio-biology^{8,9}, with the fundamental problem of how individuals minimize the
55 risks of being short-changed ('cheated') should their behavioural investment in another
56 not be returned. Economic decisions that individuals make when interacting with group
57 members may well depend upon the presence of potential partners nearby, and it is
58 therefore vital to determine the extent to which individuals respond to bystander
59 presence^{10,11}. The importance of bystanders is highlighted in two particular theoretical
60 approaches, Noë and colleagues'^{10,11} biological markets theory (BMT) and Connor's
61 parcelling model^{12,13} (see also Friedman & Hammerstein¹⁴) for the evolution of
62 cooperative exchanges.

63 From a purely dyadic perspective, Connor's parcelling seems little different to a
64 tit-for-tat strategy¹⁵: one individual provides a small level of cooperative investment, and
65 continues to do so as long as its partner does likewise¹². However, central to Connor's
66 model is the concept that the existence of bystanders generates a temptation to defect
67 from the current partner, and that this drives the parcelling (subdividing) of a social
68 interaction such that the partner is forced into cooperating in order to extract significant
69 benefit from the interaction, while minimising the cost to the actor should the partner
70 defect (i.e. refuse to cooperate or select another partner)^{12, 13}. When individuals have easy
71 opportunities to find alternative partners, such that the costs of searching are low,
72 defection – the lack of reciprocation – is more likely to occur and the donor should give
73 smaller parcels in order to limit its losses^{12, 13}.

74 Superficially similar to parcelling is Roberts & Sherratt's raise-the-stakes (RTS)¹⁶
75 model, which proposes that cooperative acts should be delivered through a pattern of
76 variable investment. However, unlike parcelling, RTS is a purely dyadic model that does
77 not consider the potential influence of bystanders. RTS actors are concerned solely with
78 their investment, and whether or not it is matched; the presence or absence of third parties
79 is irrelevant. As a behavioural strategy, RTS is not so much concerned with partner
80 control (forcing a partner into a cooperative interaction) but with reserving significant
81 cooperative investment for social partners who demonstrate a willingness to do likewise.
82 To date, there is little empirical support for RTS¹⁷.

83 Biological markets theory^{10,11} predicts that individuals should alter their
84 investment in an interaction in relation to the availability of other potential partners,
85 which may be in the form of local markets: individuals who are close at hand, i.e.

86 bystanders. Gumert¹⁸ found that male long-tailed macaques (*Macaca fascicularis*)
87 respond to local market conditions in their grooming of females, a result interpretable as
88 a bystander effect. Unlike parcelling, however, BMT predicts on only the total amount of
89 investment as a function of market conditions, and does not predict the internal
90 structuring of interactions. Thus while both parcelling and BMT predict a bystander
91 effect, the division of behaviour into parcels is not predicted, or accounted for, by BMT.

92 Social grooming exchanges provide an excellent system within which to explore
93 models of social cooperation¹⁹⁻²⁷. Grooming provides hygienic, stress relief, and possibly
94 thermal benefits to the recipient²⁸⁻³⁰, while the groomer has to endure possible energetic
95 and opportunity costs³¹. While such costs may be small, also incurred by the recipient, or
96 in some cases perhaps trivial³², fitness is relative and, where recipients are reproductive
97 rivals of groomers, providing such rivals with benefits generates net costs for the
98 groomer³³ and even marginal gains in fitness may be important. Both parasite load and
99 stress are driven by factors extrinsic to an individual and so will accumulate with time,
100 creating an on-going demand for grooming that varies between individuals.

101 Here we test the effect of bystander presence on grooming interactions among
102 wild chimpanzees (*Pan troglodytes*) of the M-group community of the Mahale Mountains
103 National Park (Tanzania). We focus on adult males, as they are more gregarious than
104 adult females and exhibit higher rates of grooming^{34,35}. Male chimpanzees tend to engage
105 in a broad range of mutually cooperative behaviours, such as support in agonistic
106 interactions and sharing of food^{34,35} with social exchanges little influenced by kinship³⁶.
107 These males are also direct reproductive rivals in that they compete with one another for
108 the same limited set of paternity opportunities. Chimpanzees are an ideal species with

109 which to investigate the influence of bystanders, as the fission-fusion social system
110 shuffles the identity and number of community members within a party³⁷, so that the
111 proximity and association between individuals can change frequently and
112 unpredictably³⁸. Occasionally, individuals of the same social group can be so far apart
113 that defection might not be viable because the costs of searching for alternative partners
114 would be prohibitive.

115 In addition, chimpanzees' grooming bouts can take various and complex
116 forms^{17,24,25,27,39}. As with our previous work^{17,24,25}, we follow Barrett et al.²⁰ & Manson et
117 al.⁴⁰ in defining a grooming bout as an interaction between two individuals, rather than
118 the behaviour of a single individual. Within a bout, grooming effort²⁴ is typically broken
119 up into short episodes¹⁷ of varying number and duration (which may correspond to the
120 'parcels' in Connor's model), and the exchange of these can be highly dynamic. At its
121 simplest, a bout consists of a single episode performed by one groomer, but typically a
122 groomer will perform a sequence of episodes, interspersed by short breaks (< 30s) where
123 the groomer is effectively resting but poised to continue grooming. In some bouts, termed
124 'unidirectional', this sequence will terminate without the recipient performing any
125 grooming in response: the groomer may stop, or the recipient may depart. In other bouts,
126 termed 'bidirectional', both individuals perform a sequence of episodes that vary in
127 duration and may be asynchronous such that individuals alternate the roles of groomer
128 and recipient, or overlapping such that grooming is simultaneous ('mutual'). Sequences
129 of grooming episodes are typically not aligned (or necessarily matched in duration), so
130 that 'mutual' grooming appears to result from coincidental overlap²⁷, and can end or
131 resume purely as the result of the grooming decisions of one of the groomers. Many bouts

132 include a combination of these structures. In only a small proportion of bouts (e.g. 3% for
133 the Sonso community, 1994-1995²⁴) do individuals start simultaneously and groom in
134 this manner throughout.

135 We have reported previously our tests of both raise-the-stakes (for which we find
136 no support¹⁷) and biological market theory, as applied to primate grooming^{24,25}. Here, we
137 test Connor's parcelling model^{12,13} by exploring whether the presence of bystanders
138 influences both the initiator's investment and the partner's decision to reciprocate (note
139 that we are not concerned here with the extent to which the initiator's partner
140 reciprocates, but whether or not the initiator's effort results in the receipt of grooming
141 though a bidirectional bout).

142 We focus on the initial phase of a grooming bout, defined as the period during
143 which the initiator is grooming alone before the bout either terminates as a unidirectional
144 bout, or becomes bidirectional through the participation of the recipient. The initial phase
145 of a grooming bout should be particularly important as the initiator is essentially
146 gambling their investment on an unknown or uncertain outcome, whether this comes
147 about through economic exchange or via a mechanism of relationships. Given that the
148 groomer has yet to see any return on their investment, the initial phase should be
149 particularly sensitive to bystander effects and initiators may abandon bouts if their current
150 partner appears unwilling to provide the grooming in response²⁷. Unlike later phases
151 within a (bidirectional) bout, the initial phase is unaffected by previous grooming
152 performed or received, and so any decision to abandon a bout during this period will not
153 be influenced by the accrual of grooming benefits or a decline the rate of their accrual,
154 while the potential effect of bystanders may diminish in later phases.

155 Following from Connor’s parcelling model, with more (male) bystanders we
156 expect: less investment (i.e. less grooming effort: prediction 1), as well as fewer
157 (prediction 2) and smaller (prediction 3) parcels (episodes of grooming), from an initiator
158 during the initial phase of the grooming bout, and a higher probability of unidirectional
159 bouts (prediction 4). As episodes of grooming can vary in duration, such that a given
160 amount of grooming (grooming effort) can in principle be provided by multiple shorter
161 episodes or fewer longer episodes, we also tested the relationships between grooming
162 effort, number and length of episodes.

163 We recognise that rank differences within a dyad can influence economic
164 decision-making if subordinates trade grooming for rank-related or rank-restricted
165 commodities^{20,25,41} and so include social dominance rank in our analyses. ‘Grooming up
166 the hierarchy’ is a well-known pattern in primate grooming⁴² which may be the result of
167 lower-ranking individuals attempting to access services restricted to higher ranking
168 individuals, such as effective agonistic support, sharing of valued food items, or tolerance
169 ^{20,25,42,43}. However, our previous work²⁵ showed that the distribution of grooming
170 amongst the male chimpanzees of the Mahale Mountains National Park was not related to
171 social dominance rank during the period of this study, that social tolerance was not a
172 rank-restricted commodity, and that grooming was not exchanged for agonistic support or
173 meat. In consequence, we do not expect to see an effect of rank difference in the tests of
174 these predictions.

175 Parcel size may be contingent also on the expectation by the donor of receiving
176 grooming from the recipient: the more likely it is that the recipient will reciprocate
177 grooming, the bigger the donor’s parcel ought to be. Despite a growing set of findings

178 supporting a view that primate grooming exchanges are driven by immediate economic
179 considerations^{18-21,24-27,44-47}, the orthodox view remains that the interchange of grooming,
180 at least amongst catarrhine primates, functions primarily to build a platform of trust
181 (“bonds”), which in turn facilitates fitness benefits^{32,48,49}; this is why such primates
182 groom at a level assumed to exceed the need for hygienic functions^{50,51}. If this
183 relationship model holds, it follows that the expectation of reciprocity in any single
184 grooming bout should be contingent on the nature of the relationship, and thus the level
185 of trust between individuals. If the relationship model is correct, then dyads that groom
186 frequently and/or dyads that exchange grooming more reciprocally should be those with a
187 greater degree of trust^{21,22,48}. This conclusion is valid whether the expectation is for
188 immediate (within-bout) or delayed (across-bout) reciprocity, and thus the amount of
189 grooming invested by the initiator of any particular bout should be positively related to
190 the degree of trust, the strength of the “bond” between the individuals.

191 Few studies have tested this prediction. Barrett et al.²¹ found no significant
192 difference between frequent and infrequent grooming dyads in the duration of the first
193 episode of grooming among chacma baboons (*Papio ursinus*). Fruteau et al.²⁶, by
194 contrast, did find a significant difference in first episode duration between frequent and
195 infrequent groomers, among both mangabeys (*Cercocebus atys*) and vervet monkeys
196 (*Chlorocebus aethiops*), but in the opposite direction: dyads that groomed more
197 frequently tended to give shorter first episodes than did infrequent groomers. The
198 relationship between initial investment and the degree of reciprocity has not been
199 investigated and we provide the first test of this among wild chimpanzees. Under the
200 relationship model, we predict that groomer’s initial investment should be greater among

201 frequent groomers (prediction 5) and/or strong reciprocators (prediction 6) than among
202 infrequent groomers and weak reciprocators, respectively.

203

204 **Results**

205 *Groomer's initial investment*

206 Across 774 bouts, we recorded 33 hours of grooming in the initial phase with a mean (\pm
207 SD) per bout duration of 153.6 ± 179.9 s (median = 95.5s): 139.9 ± 174 s (median = 81.5s)
208 during unidirectional bouts and 197.5 ± 191.6 s (median = 133.5s) during bidirectional
209 bouts. The initial phase of unidirectional bouts (by definition, this is equal to the total
210 bout) consisted on average of 1.9 ± 1.6 episodes (median = 1; range = 1-13), of $72.6 \pm$
211 73.4 s (median = 51.8s) in duration. The initial phase of bi-directional bouts consisted on
212 average of 2.2 ± 1.7 episodes (median = 2; range = 1-9), of 96.3 ± 91.4 s (median = 74s)
213 in duration. Both the number of episodes and mean episode length predicted grooming
214 effort in the initial phase (LMM: number of episodes: $\beta \pm SE = 75.99 \pm 1.61$, $t = 47.26$, p
215 < 0.001 ; episode length: $\beta \pm SE = 1.387 \pm 0.03$, $t = 41.10$, $p < 0.001$). Number and length
216 of episodes were not collinear (both variables, VIF = 1.00), and one did not predict the
217 other (LMM: $\beta \pm SE = -1.821 \pm 1.702$, $t = -1.07$, $p = 0.291$); chimpanzees appeared to vary
218 their grooming effort by altering either the number or length of episodes.

219 Only 4% of grooming bouts were interrupted; this was less likely to occur with
220 more male bystanders (GLMM: $\beta \pm SE = -0.418 \pm 0.174$, $t = -2.40$, $p = 0.02$), although
221 the number of male bystanders did not depend on the context during which the grooming
222 interaction occurred (GLMM: $\beta \pm SE = -0.02 \pm 0.062$, $t = -0.39$, $p = 0.69$).

223 The number of male bystanders (i.e. those within 10m) significantly predicted
224 both groomer's initial investment (LMM: $\beta \pm SE = -10.93 \pm 5.07$, $t = -2.155$, $p = 0.03$:
225 Table 1) and number of initial episodes (GLMM: $\beta \pm SE = -0.09 \pm 0.022$, $t = -4.26$, $p <$
226 0.001 : Table 2): groomers tended to invest less grooming effort through fewer episodes
227 when there were more male bystanders, supporting predictions 1 & 2. As expected, rank
228 distance was not a significant predictor of grooming effort (LMM: $\beta \pm SE = -0.002 \pm$
229 0.02 , $t = 0.13$, $p = 0.886$: Table 1), indicating that initiators did not adjust their
230 investment during the initial phase in relation to partner's rank. This is consistent with
231 our previous finding that subordinates did not give grooming in exchange for rank-related
232 commodities (e.g. agonistic support) during the study period²⁵. There was no effect of
233 bystanders on grooming effort in bi-directional bouts after the initial phase (LMM: $\beta \pm$
234 $SE = -30.71 \pm 25.539$, $t = -1.202$, $p = 0.22$), confirming the significance of the initial
235 phase of grooming bouts for partner choice decisions.

236 In contrast with our prediction 3, there was no effect of the number of bystanders
237 on mean episode length (LMM: $\beta \pm SE = -1.154 \pm 2.219$, $t = -0.520$, $p = 0.597$: Table 1),
238 suggesting that male chimpanzees were adjusting their total investment in the initial
239 phase of the grooming bout by changing the number of episodes, not their size. Episode
240 length was also unaffected by the rank-distance between the initiator and recipient
241 (LMM: $\beta \pm SE = -0.01 \pm 0.009$, $t = 1.135$, $p = 0.254$; Table 1). Using absolute rank (Elo-
242 rating) of the recipient in place of rank-distance, we found that higher ranked recipients
243 received shorter episodes in the initial phase (LMM: $\beta \pm SE = -0.027 \pm 0.014$, $t = -1.997$,
244 $p = 0.047$). We found no relationship between the absolute rank of the initiator and
245 episode length (LMM: $\beta \pm SE = -0.002 \pm 0.013$, $t = -0.148$, $p = 0.881$). The male

246 chimpanzees in our sample showed a relatively flat, or structurally egalitarian, dominance
247 hierarchy²⁵; it will be interesting to see whether chimpanzees under more structurally
248 despotic hierarchies demonstrate a more defined relationship between recipient rank and
249 grooming episode length.

250 *Grooming pattern and identity of the individual who terminated the bout*

251 Both the number of bystanders (GLMM: $\beta \pm SE = -0.158 \pm 0.072$, $t = -2.20$, $p =$
252 0.028) and rank distance (GLMM: $\beta \pm SE = 0.0008 \pm 0.0003$, $t = 3.36$, $p < 0.001$)
253 predicted the occurrence of bidirectional bouts (Table 2): grooming bouts were more
254 likely to be unidirectional when there were more males around (Figure 1) and when rank
255 distance between partners was larger. Since we assigned the number '1' to bidirectional
256 bouts, and positive rank distances correspond to bouts directed from dominants to
257 subordinates, the positive relationship between grooming pattern and rank difference
258 suggests that bouts were more likely to be bi-directional when initiated by higher-ranking
259 males with lower-ranking partners. Furthermore, grooming was more likely to be
260 terminated by the initiator when there were more bystanders (GLMM: $\beta \pm SE = -0.0483$
261 ± 0.0119 , $t = -4.07$, $p < 0.001$: Table 2 & Figure 2) and during feeding contexts (GLMM:
262 $\beta \pm SE = 0.0539 \pm 0.0249$, $t = 2.16$, $p = 0.031$, Table 2), a finding that suggests groomers
263 are sensitive to opportunity costs.

264 *Groomer's initial investment and trust*

265 We classified 12 dyads as frequent groomers, while 9 dyads had a grooming
266 reciprocity index greater than 0.8. Six dyads were both frequent groomers and strong
267 reciprocators. We found no support for prediction 5: groomer's initial investment was not
268 significantly longer among frequent groomers (mean grooming $\pm SD$: $165.26s \pm 49.21s$;

269 median: 153.21s) than it was among infrequent groomers (mean grooming \pm SD: 159.71s
270 \pm 84.96s; median: 148.88s; Mann-Whitney U test: $N_{\text{frequent}} = 12$, $N_{\text{infrequent}} = 32$, $W = 209$,
271 $p = 0.664$). We also found no support for prediction 6: strong reciprocators did not invest
272 significantly more in the initial phase of a bout (mean grooming \pm SD: 145.64s \pm 47.62s;
273 median: 145s) than weak reciprocators (mean grooming \pm SD: 165.23s \pm 82.21s; median
274 = 152s; $N_{\text{strong}} = 9$, $N_{\text{weak}} = 35$, $W = 139$, $p = 0.600$).

275 **Discussion**

276 Our study shows a clear influence of bystanders on the initial phase of chimpanzee
277 grooming bouts and suggests that chimpanzees use a parcelling-like strategy, at least in
278 this phase. When more bystanders were present, we found that: (1) initiators invested less
279 in their grooming bouts and provided both less grooming and fewer parcels; (2) bouts
280 were less likely to be reciprocated; and (3) initiators were more likely to abandon the
281 grooming if the recipient did not reciprocate. These results suggest that male
282 chimpanzees make economic decisions on how much to invest in grooming interactions
283 that are based not only on whether the partner reciprocates, but also on whether there are
284 other potential social partners in close proximity. This is a key aspect of Connor's
285 parcelling model^{12,13}. Previous studies of non-human primates have described time-
286 matching within grooming bouts in some^{20,24,40,43}, although not all^{23,57,52,53}, species
287 studied. While time-matching is consistent with parcelling, and occurs in chimpanzees²⁴,
288 our demonstration of a contingency between the initial investment in a potentially
289 cooperative interaction, and opportunity for defection, is perhaps the strongest support
290 yet for the parcelling model from grooming interactions of non-human primates. We add
291 a note of caution in that our results are based on interactions of only 8 focal animals and

292 10 individuals in total, although this represented the entire exchange network for male
293 chimpanzees in this social group and is comparable to other studies of this species.

294 Contrary to our expectations, we found evidence that dominance rank influenced
295 episode length: initiators gave shorter episodes when they groomed high-ranking males,
296 regardless of rank distance. Given that high-ranking individuals were more likely to
297 terminate bouts³⁹, this might suggest that lower ranking initiators anticipated a higher
298 likelihood of non-reciprocation and limited their losses accordingly. Alternatively, short
299 episodes may be response to risk of aggression from the higher-ranking partner: male
300 chimpanzees have been observed to attack current grooming partners⁵⁴, personal observations,
301 and similarly, in Japanese macaques (*Macaca fuscata*) groomers are more likely to
302 receive aggression from recipients in post-grooming contexts than during controls⁵⁵.
303 Grooming requires a commitment of attention from the actor(s) and shorter episodes
304 allow more frequent periods of vigilance to be interspersed during either the initial phase
305 or across a complete bout. We have shown previously that chimpanzees give shorter
306 grooming episodes when aggression rates are particularly high¹⁷. In this light, our finding
307 that bi-directional grooming was more likely when bouts were initiated by high-ranking
308 individuals might be the result of lower-ranking males being coerced into reciprocating,
309 out of fear of receiving aggression from a more powerful individual. More generally,
310 increased vigilance though shortening episodes may compromise grooming efficiency,
311 result in less grooming in a bout, or extend the bout duration and so increase opportunity
312 costs in order to maintain the amount of grooming performed or exchanged. These
313 possibilities warrant further investigation, particularly in relation to variation between
314 social groups in structural despotism²⁵.

315 We found no support for predictions derived from the relationship model of
316 primate grooming interactions. There was no influence of grooming frequency on the
317 grooming invested in the initial phase, and we found initiators in dyads with a history of
318 grooming reciprocity, who should under the relationship model trust their partner and
319 expect to receive grooming in return, were no different in their initial investment to those
320 without such a history. Thus the grooming relationship (the history of reciprocal
321 exchanges) of a dyad appeared irrelevant to the behaviour of an individual initiating a
322 grooming bout, and we have no evidence that individuals who had received high levels of
323 reciprocity in the past from their current partner trusted that they would do so again. This
324 finding calls into question the concept that grooming builds trust between individuals.
325 Our findings echo the results of Machanda et al.²⁷, who also found no support for
326 predictions derived from the relationship model in their study of simultaneous, or mutual,
327 grooming in chimpanzees, as well as our recent finding that male grooming of cycling
328 ('oestrus') females could not be explained by the relationship model⁵⁶. In light of these
329 results, and the growing body of work supporting a markets-based model of economic
330 exchange^{18-21,24-27,44-47}, a critical re-evaluation of the appropriateness of the relationship
331 ('bonding') model as an explanation for grooming in chimpanzees, as well as other
332 catarrhine primates, seems overdue³³. It may even be the case that immediate benefits
333 drive most if not all social interactions: Gilby⁵⁷ found this to be the case for meat sharing,
334 with individuals in possession of carcasses paying harassing 'beggars' to leave in order to
335 increase their own intake rates rather than sharing food with frequent grooming partners
336 (surprising only under the assumption that grooming builds social bonds).

337 We have presented evidence elsewhere as to the importance of market forces on the
338 grooming decisions of male chimpanzees²⁵. From a market forces perspective, bystander
339 effects can be seen as the product of partner choice strategies responding to local
340 economic conditions, implying that individuals make choices within local markets – their
341 immediate social environments¹⁸ – rather than a broader market presented by their global
342 social environment (the social group, or population, depending on social dynamics of
343 particular species). As a consequence of search and opportunity costs, local markets
344 become essentially isolated from one another. However, biological market theory is a
345 model to account for the evolution of partner choice strategies^{10,11,41} and, as such,
346 individuals embodying those strategies should be equipped to respond to average market
347 conditions (levels of supply and demand) across their global market, as well as evaluating
348 local conditions. Thus a biological markets model should predict that partner choice
349 decisions depend on local market conditions – bystanders – weighted by expected
350 average returns from selecting instead from the supply in the global market. While local
351 markets might be isolated from one another, they should be regarded as nested within a
352 global market. Such nesting and the consequent bystander effects potentially complicate
353 tests of biological market models. In species such as chimpanzees where a social group
354 (the global market place for an individual) is fragmented into discrete sub-groups
355 (parties), or the macaques studied by Gumert¹⁸, it may be necessary to consider both local
356 and global market conditions, the later devalued by average search and opportunity costs,
357 when determining the level of supply or demand to which an animal may be responding.
358 That said, structuring of social groups into discrete sub-groups also provides
359 opportunities to test between different market conditions within a single social group,

360 should local conditions vary sufficiently that individuals respond to these differences
361 when choosing social partners. More generally, existence of bystander effects and local
362 markets suggest that search costs should be given more explicit consideration in testing
363 biological market models across taxa.

364 Here, we focused on the initial phase of grooming bouts and showed that this is
365 particularly important for partner-choice decisions, with the presence of bystanders
366 having no effect on later phases of bidirectional bouts. If we consider bystanders to
367 represent a local market of alternative suppliers of grooming, then the question is why we
368 need to consider parcelling at all as an explanation? The obvious answer is that
369 chimpanzees deliver their grooming effort in discrete episodes within bouts – they parcel
370 their grooming – an effect that is not predicted (although not precluded) by biological
371 market theory. Furthermore, individuals continue to parcel their grooming throughout
372 bidirectional bouts¹⁷, but without an effect of bystanders (or local markets). Parcelling
373 provides an additional layer of explanation to that offered by biological market theory
374 and, given the complexity of these grooming interactions, we feel that parcelling should
375 be seen as a strategy available to chimpanzees rather than a model that can fully account
376 for the evolutionary dynamics of cooperative grooming exchanges.

377 Overall, our study shows that male chimpanzees modify the amount of grooming
378 investment in the initial phase of the bout in relation to the number of male bystanders:
379 when there are more males in close proximity, initiators tend to give less grooming, with
380 fewer grooming episodes, and are more likely to interrupt a bout in the absence of
381 immediate reciprocation, making unidirectional bouts more likely to occur. Our results
382 show that the number of bystanders present during a grooming interactions can affect

383 parcel size, at least in terms of the amount of grooming invested, as predicted by
384 Connor's model and highlight the importance of considering the presence of other
385 individuals during cooperative interactions, and the distinction between local and global
386 markets, as a way towards a better understanding of the evolved behavioural strategies
387 that generate cooperative interactions.

388 **Methods**

389 *Study site and subjects*

390 We studied the grooming behaviour of adult male chimpanzees of M-group
391 community from the Mahale Mountains National Park, Tanzania (06°15'S; 29°55'E),
392 between February and November 2011. This community has been continuously studied
393 for over 30 years³⁵; as a result our study subjects were fully habituated to human
394 observation, and grooming interactions could be recorded in detail at close range. The
395 community consisted of 60 individuals, including ten adult males (≥ 16 years old) and 23
396 adult females (≥ 14 years old)¹⁷. This research was carried out in accordance with the
397 approved guidelines for the ethical treatment of primates, was approved by the Ethics
398 Committee of University of Kent and adhered to the legal requirements of Tanzania and
399 the UK .

400

401 *Data collection and analysis*

402 We collected data through long-day focal follows on eight adult males. Data on
403 grooming and agonistic interactions were collected using all-occurrence sampling⁵⁸
404 within focal parties (i.e. all occurrences of these interactions that occurred in a party that

405 contained a nominal focal animal, where party is defined as a subgroup produced by the
406 fluid fission-fusion social system). Thus we sampled the grooming interactions of all 10
407 adult males. Each day the focal animal with the fewest hours of observation was selected
408 in order to balance the number of hours of observation across adult males (logistic
409 constraints meant that we did not select two males as focal animals), and this individual
410 was followed when parties fissioned. Parties were followed for as long as possible from
411 first encounter until nesting. If contact with chimpanzees was lost due to terrain and/or
412 chimpanzee movement patterns, we searched for and observed the next party encountered
413 that contained one of the predetermined focal animals. We recorded data through audio
414 narration, or by pen and paper. We conducted 141 focal follows for a total of 800.9 h of
415 observation.

416 We defined grooming as the visual examination, searching and manipulation of
417 the skin and hair with one or both hands, with the occasional use of the lower lip to part
418 the hair. When a male initiated a grooming bout, we recorded: (1) the identity of the
419 individual who approached the partner either to give or receive grooming, together with
420 the time of the approach; (2) the identity of other males within 10m (whom we labelled
421 bystanders); (3) the changes in the identity of groomer and recipient, including the
422 initiator; (4) the end time of the grooming bout, and the identity of the individual who
423 terminated the bout. A grooming bout was considered to have ended when neither
424 individual groomed for at least 30s^{24,25}. We recorded the context in which grooming
425 occurred, on the basis of the activity of the grooming dyad prior to the beginning of the
426 bout, as well as the activity of the majority of the male bystanders. We classified three
427 types of contexts: feeding, resting and travelling. Finally, we noted whether the grooming

428 bout was interrupted by aggression either from third parties or performed by one of the
429 participants in the grooming bout.

430 We examined grooming bouts as pairwise (dyadic) interactions. Bouts were
431 classified as either bidirectional when both individuals contributed some grooming²⁰,
432 whether simultaneously or by taking turns, or unidirectional when only one individual
433 groomed. A grooming episode was defined as an uninterrupted period of grooming given
434 by one individual, ending when neither of groomer's hands was in contact with partner's
435 body¹⁷. A groomer's initial investment was defined as the amount (duration) of grooming
436 given by an individual at the beginning of a bout before either the bout was terminated
437 (resulting in an unidirectional bout) or the receipt of grooming from the partner (resulting
438 in bidirectional bout). For the purposes of data analysis, we excluded bouts that started
439 prior to the observation and those whose pattern could not be accurately described due to
440 poor visibility. Similarly, bidirectional bouts in which a clear initiator could not be
441 identified (e.g. if partners started grooming each other simultaneously: n = 66 bouts) were
442 discarded. This gave us a total of 774 grooming bouts: 588 unidirectional and 186
443 bidirectional.

444 To determine social dominance rank we used the outcome of agonistic
445 interactions to calculate dominance rank order using Elo-ratings^{25,59} implemented in R
446 3.2.1. We defined agonistic interactions as those instances in which a male attacked
447 another group member either through physical contact (e.g. slap, bite) or charging
448 displays and/or chasing^{17,25}. We determined rank difference by subtracting the Elo-rating
449 of the recipient from the Elo-rating of the groomer. Since high Elo-rating values

450 correspond to high ranks⁵⁹, negative rank differences correspond to grooming interactions
451 directed from subordinates to dominants.

452 We tested whether groomer's investment in the initial phase was predicted by the
453 number and mean length of episodes in this phase, using the *lmer* function in the package
454 'lme4' (in R 3.1.2) to perform a Linear Mixed Model (LMM) analysis. We set grooming
455 effort (i.e. duration) as the dependent variable, while the number and mean duration of
456 initial episodes were entered as independent fixed factors. We ran a similar model to
457 assess whether mean episode length predicted the number of episodes. We used the *drop1*
458 function in R to compute a likelihood ratio test and thereby assess whether the
459 independent factor(s) exerted a significant effect on the dependent variable.

460 To assess whether the number of male bystanders significantly affected the
461 likelihood that a grooming bout was interrupted, and depended on the context of the
462 grooming interaction, we ran two different Generalized Linear Mixed Model (GLMM)
463 analyses, using the *glmer* function in the package 'lme4'. In one model we included
464 information on whether or not the bout was interrupted as binomial dependent variable,
465 with the number of bystanders set as independent factor. In a separate model, we
466 considered the number of male bystanders a dependent variable entered as count data
467 with Poisson distribution, while the context was included as independent factor.

468 To test whether groomers' initial investment (prediction 1), and the mean length
469 of grooming episodes (prediction 3) were affected by the number of male bystanders and
470 rank difference between partners, we ran two Linear Mixed Model analyses with the *lmer*
471 command and the *drop1* function in R 3.1.2. The initiator's initial investment and the

472 mean length of episodes were entered as continuous dependent variables in separate
473 models, while in each model the number of male bystanders, rank difference between
474 partners, the context during which the grooming interaction occurred and a binary
475 variable describing whether the bout was interrupted were set as fixed factors. To
476 determine whether the initial phase was distinct from the remainder of bi-directional
477 bouts in its sensitivity to bystander effects (one of our initial assumptions), we
478 investigated whether the remaining investment provided by an initiator was influenced by
479 the number of bystanders and/or the rank distance between partners. To this end, we used
480 an LMM analysis with the total grooming effort in each bout, minus that in the respective
481 initial phase, as the dependent variable and with the number of bystanders and rank
482 distance between partners as fixed factors.

483 We used a Generalized Linear Mixed Model with negative binomial distribution
484 to assess the effect of bystander and dominance rank on the number of grooming episodes
485 given by initiators (prediction 2) in the initial phase of the bout, using the *glmmadmb*
486 function in R 3.1.2. In this model, the number of episodes was entered as count data, with
487 the number of male bystanders, rank difference, context and whether the bout was
488 interrupted included as fixed factors, as above. We used two Generalized Linear Mixed
489 Models with binomial distributions (logistic GLMM) to test (a) whether reciprocation
490 was less likely with more bystanders (i.e. bouts were more likely to be unidirectional,
491 prediction 4), and (b) whether the initiator or the recipient were more likely to terminate a
492 unidirectional bout in the presence of bystanders, again using the *glmmadmb* function. In
493 the first of these models, we set grooming pattern (unidirectional vs. bidirectional) as the
494 dependent variable; in the second, the identity of the individual who terminated the bout

495 (initiator vs. recipient; only for unidirectional bouts). The number of bystanders, rank
496 difference, context and whether the bout was interrupted were entered as fixed factors in
497 both models.

498 In all these models (LMM and GLMM), the identity of the dyad and the day on
499 which each bouts occurred (as a category variable, such that all bouts on the same day
500 were given the same value) were included as random factors (intercepts) with nested
501 structure (within-day bouts nested within dyads) in order to control for the different
502 contribution that each dyad gave to the data set, and for the non-independency of the
503 grooming bouts that were exchanged within a day.

504 To test predictions 5 and 6, we categorised dyads on the basis of the frequency of
505 grooming exchanged and the strength of grooming reciprocity. To identify the dyads that
506 exchanged grooming time more frequently, we calculated the time spent grooming
507 (grooming effort) for each dyad as a proportion of the total observation time for both
508 members of that dyad. We ranked dyads on this proportion from the highest to lowest
509 and, following Koski *et al.*⁶⁰, defined dyads in the top quartile as frequent groomers
510 whilst the other dyads were considered infrequent groomers. To determine the degree of
511 grooming reciprocity for each dyad, we calculated its reciprocity index $RI^{24,25}$:

$$512 \quad RI = 1 - \left| \frac{g_{Ab}}{(g_{Ab} + g_{Ba})} - \frac{g_{Ba}}{(g_{Ab} + g_{Ba})} \right| \quad (1)$$

513 in which g_{Ab} is the grooming that individual A directed towards B, g_{Ba} is the grooming
514 that B directed towards A and $g_{Ab} + g_{Ba}$ is the total grooming exchanged between A and
515 B. This index can range between 0 (no reciprocity) and 1 (complete reciprocity). Dyads
516 with an RI equal or greater than 0.8 were defined as strongly reciprocating²⁴.

517 We used Mann-Whitney U tests to compare the groomer's initial investment
518 across dyads. As initial grooming investments in different bouts are potentially not
519 independent when they occur within the same dyad, we calculated mean groomer's initial
520 investment for each dyad and compared these values between dyads that were frequent
521 and infrequent groomers, and between the strongly reciprocating and other dyads.

522 **Acknowledgments**

523 We are grateful to the Tanzania Commission for Science and Technology, the Tanzania
524 Wildlife Research Institute and the Mahale Mountains Wildlife Research Centre for
525 allowing research in the park. We would like to express our gratitude also to our
526 Tanzanian research assistants for their invaluable assistance during data collection.
527 Research was funded by the Leverhulme Trust (grant # F/00236/Z) and the Wenner-Gren
528 Foundation (grant # 8216). All research protocols reported were reviewed and approved
529 by the Ethics Committee of the University of Kent and compiled to the legal
530 requirements of both Tanzania and the United Kingdom.

531 **Contributions**

532 NENF and SSKK designed the study; SSKK collected and analyzed the data; NENF and
533 SSKK wrote the paper.

534 **Competing interests**

535 The authors declare no competing financial interests.

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686 **Figures**

687

688 **Figure 1.** Mean number of male bystanders (within 10m of the grooming dyad) during
689 unidirectional and bidirectional grooming bouts. When there were more bystanders,
690 grooming bouts tended to be unidirectional

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692 **Figure 2.** Mean number of male bystanders (within 10m of the grooming dyad) in bouts
693 terminated by either initiator or recipient. Initiators were more likely to terminate
694 unidirectional grooming bouts when there were more male bystanders.

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710 **Tables**

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712 **Table 1.** Mixed model analyses showing the effect of the number of male bystanders and
 713 rank difference on the duration of groomer’s initial investment and the mean episode
 714 length. Significant results are presented in bold.

Analysis	Dependent	Predictor	β	SE	t	p
LMM	Initial investment	Intercept	200.014	19.715	10.145	-
		Rank distance	0.002	0.020	0.130	0.886
		# of bystanders	-10.93	5.070	-2.155	0.03
		Context	-21.860	13.386	-1.633	0.103
		Interrupted	-40.852	31.237	-1.308	0.188
LMM	Mean episode length	Intercept	90.402	8.55	10.571	-
		Rank distance	0.01	0.009	1.135	0.254
		# of bystanders	-1.154	2.219	-0.520	0.597
		Context	-7.385	5.861	-1.260	0.207
		Interrupted	-16.740	13.698	-1.222	0.219

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717 **Table 2.** Generalized Mixed Model analysis showing the effect of rank distance and
 718 number of bystanders on grooming pattern (unidirectional vs. bidirectional) and the
 719 identity of the individual who terminated the grooming bout (initiator vs. recipient).

Analysis	Dependent	Predictor	β	SE	z	p
Negative binomial GLMM	Number of episodes	Intercept	0.907	0.0785	11.56	<0.001
		Rank distance	-1.08 x 10 ⁻⁴	8.46x 10 ⁻⁵	-1.28	0.20
		# of bystanders	-0.09	0.022	-4.26	<0.001
		Context	-0.08	0.057	-1.39	0.16
		Interrupted	-0.097	0.136	-0.72	0.47
GLMM	Grooming pattern	Intercept	-1.126	0.267	-4.21	<0.001
		Rank distance	0.0008	0.0003	3.36	<0.001
		# of bystanders	-0.158	0.072	-2.20	0.028
		Context	0.08	0.183	0.44	0.661
		Interrupted	0.314	0.400	0.79	0.432
Binomial GLMM	Who terminates bout	Intercept	-1.95	0.035	-5.63	<0.001
		Rank distance	-6.07 x 10 ⁻⁵	3.91x 10 ⁻⁴	-0.16	0.876
		# of bystanders	-0.0483	0.0119	-4.07	<0.001
		Context	0.0539	0.0249	2.16	0.031
		Interrupted	-0.007	0.0575	-0.01	0.990

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