

Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate

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When foraging in a social group, individuals are faced with the choice of sampling their environment directly or exploiting the discoveries of others. The evolutionary dynamics of this trade-off have been explored mathematically through the producer-scrounger game, which has highlighted socially exploitative behaviours as a major potential cost of group living. However, our understanding of the tight interplay that can exist between social dominance and scrounging behaviour is limited. To date, only two theoretical studies have explored this relationship systematically, demonstrating that because scrounging requires joining a competitor at a resource, it should become exclusive to high-ranking individuals when resources are monopolisable. In this study, we explore the predictions of this model through observations of the natural social foraging behaviour of a wild population of chacma baboons (*Papio ursinus*). We collected data through over 800 hours of focal follows of 101 adults and juveniles across two troops over two 3-month periods. By recording over 7,900 social foraging decisions at two spatial scales we show that, when resources are large and economically indefensible, the joining behaviour required for scrounging can occur across all social ranks. When, in contrast, dominant individuals can aggressively appropriate a resource, such joining behaviour becomes increasingly difficult to employ with decreasing social rank because adult individuals can only join others lower ranking than themselves. Our study supports theoretical predictions and highlights potentially important individual constraints on the ability to use social information associated with low social rank, driven by competition with dominant conspecifics over monopolisable resources.

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12 **Abstract**

13 When foraging in a social group, individuals are faced with the choice of sampling their
14 environment directly or exploiting the discoveries of others. The evolutionary dynamics of this
15 trade-off have been explored mathematically through the producer-scrounger game, which has
16 highlighted socially exploitative behaviours as a major potential cost of group living. However,
17 our understanding of the tight interplay that can exist between social dominance and
18 scrounging behaviour is limited. To date, only two theoretical studies have explored this
19 relationship systematically, demonstrating that because scrounging requires joining a
20 competitor at a resource, it should become exclusive to high-ranking individuals when
21 resources are monopolisable. In this study, we explore the predictions of this model through
22 observations of the natural social foraging behaviour of a wild population of chacma baboons
23 (*Papio ursinus*). We collected data through over 800 hours of focal follows of 101 adults and
24 juveniles across two troops over two 3-month periods. By recording over 7,900 social foraging
25 decisions at two spatial scales we show that, when resources are large and economically
26 indefensible, the joining behaviour required for scrounging can occur across all social ranks.
27 When, in contrast, dominant individuals can aggressively appropriate a resource, such joining
28 behaviour becomes increasingly difficult to employ with decreasing social rank because adult
29 individuals can only join others lower ranking than themselves. Our study supports theoretical
30 predictions and highlights potentially important individual constraints on the ability to use
31 social information associated with low social rank, driven by competition with dominant
32 conspecifics over monopolisable resources.

33 **Introduction**

34 Socially exploitative behaviours occur when individuals make use of the resources of
35 competitors. A wide range of both theoretical and empirical studies over recent decades
36 (Giraldeau & Dubois, 2008) have highlighted such behaviours as a major potential cost of group
37 living. Because resources such as food, mates, breeding territories, or safety from predation
38 generally show variation in their distribution through space or time, individuals should benefit
39 from gathering information about their local environment to improve decision-making (Valone,
40 1989, 2006; McNamara, Green & Olsson, 2006). However, when the collection of information
41 requires search effort, selection should favour the avoidance of these costs by exploiting the
42 efforts of others in a social group (for review see Valone & Templeton, 2002; Danchin et al.,
43 2004; Rieucou & Giraldeau, 2011).

44

45 The dynamics of these interactions have been formalised as the producer-scrounger game
46 (Barnard & Sibly, 1981; Barnard, 1984; Vickery et al., 1991). Supported by a wide range of
47 empirical studies (e.g., Koops & Giraldeau, 1996; Mottley & Giraldeau, 2000; Morand-Ferron,
48 Giraldeau & Lefebvre, 2007), the producer-scrounger game has emerged as the prevailing
49 theoretical framework in which to study social foraging decisions (Vickery et al., 1991;
50 Giraldeau & Caraco, 2000). In this game, producers actively search for resources, while
51 scroungers exploit the discoveries of producers. The two tactics are considered mutually
52 exclusive. Scrounging is thus under negative frequency-dependent selection since its success,
53 being dependent on the efforts of producers, is determined by the relative frequencies of the
54 two tactics within a group. This dynamic is expected to lead populations to an evolutionarily or

55 behaviourally stable mix of producing and scrounging (Giraldeau & Dubois, 2008; Fawcett,
56 Hamblin & Giraldeau, 2013). As such, scrounging behaviour has the potential to reduce the per
57 capita rate of discovery of new resources (Vickery et al., 1991), which may act to reduce
58 average individual fitness in a population (Coolen, Giraldeau & Vickery, 2007).

59

60 The basic producer-scrounger model assumes that an individual's phenotype has no influence
61 on its decision or ability to play either tactic. All individuals are essentially equivalent, and are
62 expected to receive equal payoffs. However, many empirical studies have shown that an
63 individual's tactic choice may be strongly influenced or constrained by its phenotype (e.g.,
64 Beauchamp, 2001; Stahl et al., 2001; di Bitetti & Janson, 2001; Kurvers et al., 2010). This has
65 potentially important fitness implications, since theory predicts that phenotype-limited games
66 may not reach an evolutionarily stable mix of strategies, resulting in differential payoffs across
67 individuals (Parker, 1982).

68

69 Since scrounging behaviour represents the exploitation of another's resource, one might expect
70 it to be strongly influenced by social dominance. Specifically, the competitive advantage of
71 high-ranking individuals should allow them to scrounge from others more easily (Parker, 1974;
72 Maynard Smith & Parker, 1976; Hammerstein, 1981). Despite this expectation, empirical
73 studies have not been unanimous. While some experiments have demonstrated a clear positive
74 relationship between social dominance and scrounging behaviour (Stahl et al., 2001; Liker &
75 Barta, 2002; Lendvai, Liker & Barta, 2006; McCormack, Jablonski & Brown, 2007), a number of
76 other studies have not (Bugnyar & Kotrschal, 2002; Robinette Ha & Ha, 2003; Beauchamp,

77 2006; Teichroeb, White & Chapman, 2015). This conflict might be reconciled by considering
78 more systematically the spatiotemporal distribution of resources faced by different taxa in both
79 naturalistic and experimental settings. The competitive benefits of social dominance are
80 expected to be associated with priority of access to resources, manifest as contest competition
81 (Kaufmann, 1983; Łomnicki, 2009). Consistent with this, resource defence theory predicts that
82 individuals should be more aggressive when defending a resource in accordance with both its
83 value and how easily it can be defended (Grant, 1993; Grant & Guha, 1993; Robb & Grant,
84 1998). Empirical studies into dominance and resource defence have demonstrated higher
85 foraging success for socially dominant individuals only when presented with limited food
86 patches that are monopolisable (Theimer, 1987; Vahl et al., 2005).

87

88 Some researchers have suggested that the integration of producer-scrouter and resource
89 defence theory might elucidate an interesting relationship between socially exploitative
90 behaviour and dominance (Barta & Giraldeau, 1998; Giraldeau & Dubois, 2008). Specifically,
91 dominant individuals should benefit disproportionately if they can use their competitive
92 advantage to ensure that only they can use social information effectively. Two studies (Barta &
93 Giraldeau, 1998; Lee et al., 2016) have explored this hypothesis by modelling the effects of
94 between-individual asymmetries in competitive ability on producer-scrouter dynamics in a
95 group. They found that when social rank conferred no competitive advantage to an individual –
96 that is, resources were not monopolisable – groups converged on basic producer-scrouter
97 equilibria in which all individuals behave equivalently and receive equal payoffs. In contrast,
98 when individuals could use their social rank to gain a competitive advantage in monopolising a

99 resource, scrounging behaviour was strongly associated with dominance, and dominant
100 individuals achieved the highest payoffs (Barta & Giraldeau, 1998; Lee et al., 2016). The driving
101 force behind this pattern was the fact that scrounging behaviour requires that a competitor is
102 joined at a resource in space and time, forging a causal link between the degree to which
103 contest competition acts and constraints on an individual's ability to use social information (Lee
104 et al., 2016). However, to date there has been no attempt to test these predictions empirically,
105 either in the laboratory or under naturalistic conditions.

106

107 In this study, we explore a key prediction generated by the unification of producer-scrounger
108 and resource defence theories, namely that there should be a strong link between social
109 dominance and the scrounger tactic only when resources are monopolisable. We did this by
110 studying the natural social foraging decisions made by wild chacma baboons (*Papio ursinus*)
111 across two spatial scales that are expected to differ in the degree to which dominant individuals
112 can monopolise food. At the first spatial scale – the 'patch' – resource clumps were too large to
113 be monopolised independently, while at the second – the 'sub-patch' – resource clumps were
114 smaller and monopolisation was possible (see Methods for further details on how these spatial
115 scales were defined). Because our focus was on naturalistic behaviour, we did not manipulate
116 the information available to individuals while foraging to manufacture a situation where joining
117 a competitor always represented the exclusive use of social information, which could accurately
118 be termed scrounging (Vickery et al., 1991). Rather, we consider the observable joining
119 behaviours of individuals as they foraged, representing competitive interactions fundamental to
120 the predictions of producer-scrounger theory (Lee et al., 2016). In this way, we explore the

121 competitive constraints that social rank may impose on an individual's ability to use social
122 information through joining behaviour, and the relation of such constraints to resource
123 monopolisability in a naturalistic setting in which information use is expected to be important.
124 We made the following three predictions: 1) joining behaviour should show a strong positive
125 association with dominance rank at the smaller, sub-patch level but not at the larger, patch
126 level; 2) individuals should join those to whom they are dominant at the sub-patch level, but
127 there should be no systematic asymmetry in dominance when joining occurs at the patch level;
128 and 3) joining should be associated with competitive exclusion (i.e., resource monopolisation)
129 at the sub-patch level, but not at the patch level.

130

131 **Materials and Methods**

132 *Study Site and Species*

133 Fieldwork was conducted at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E), during two three-
134 month periods between August and October in 2012 and 2013. Two groups of chacma
135 baboons, hereafter referred to as troop 'J' (group size: $N_{2012} = 54$; $N_{2013} = 58$) and troop 'L' (N_{2012}
136 $= 51$; $N_{2013} = 62$), were the focus of study. All baboons were individually recognisable and
137 habituated to the presence of observers at close proximity. Each group was followed daily from
138 dawn until dusk (see Huchard et al., 2009 for further information). For each year, data were
139 collected for all individual baboons >6 months of age (the age at which young baboons begin to
140 forage independently of their mother) at the start of the study period, resulting in a total
141 sample of 101 individuals (2012: 54 adults, 43 juveniles; 2013: 50 adults, 41 juveniles).

142 Differences in the sample of individuals across years were due to death, emigration, or passing
143 the minimum age threshold.

144

145 Chacma baboons are an ideal model system for our study, since they live in large, stable social
146 groups in which linear dominance hierarchies are clear (Altmann & Altmann, 1973), individuals
147 generally feed at the same time as each other (King & Cowlshaw, 2009), and socially

148 exploitative foraging interactions are common (King, Isaac & Cowlshaw, 2009; Marshall et al.,
149 2012). Furthermore, our study troops spent approximately 80% of their foraging time during

150 the study period in a riparian woodland environment, characterised by large trees including

151 *Faidherbia albida*, *Salvadora persica*, *Acacia erioloba*, *Acacia tortilis*, and *Prosopis glandulosa*.

152 Within this feeding environment, we defined two spatial scales between which the ability of

153 dominant individuals to monopolise food were predicted to differ: the patch and the sub-patch.

154

155 The patch represents the scale traditionally used in foraging theory and ecology, and is defined

156 as a spatially discrete unit of a food resource (Wiens, 1976). Here, we refined this definition

157 such that the operational definition of a patch was a single tree or shrub, or a collection of

158 conspecifics growing together with a continuous canopy separated by no more than 1 m

159 (median surface area = 156 m², interquartile range = 28-237 m²; $n = 59$; see Marshall et al.,

160 2012 for further details). In contrast, the sub-patch was defined as the area in a patch within

161 which an individual could feed without travelling (i.e., within arm's reach of a stationary

162 baboon, approximately 2.25 m²). This is equivalent to the 'feeding station' scale that has

163 received some attention in the foraging literature (Kotliar & Wiens, 1990; see Searle, Hobbs &

164 Shipley, 2005 for a review). Given the large size of patches compared with sub-patches,
165 dominant individuals should be able to competitively exclude subordinate others more easily at
166 the latter scale.

167

168 *Data Collection and Processing*

169 Information regarding individual social foraging decisions and interactions at each spatial scale
170 was recorded through focal sampling (Altmann, 1974) on Motorola ES400 Personal Digital
171 Assistants and Google Nexus 4 Smartphones using a customised data capture application in the
172 database-driven software Cybertracker v.3.317 (<http://cybertracker.org>). Focal follows lasted
173 between 15 and 30 minutes, and the same individual was not studied more than once within a
174 6-hour period. Individuals were selected for focal observation using a pseudorandom sampling
175 process, which ensured even coverage across different times of day (based on four consecutive
176 3-hour time blocks from 06:00 to 18:00) and different months.

177

178 A patch entry event was recorded whenever the focal individual searched for or consumed food
179 in a new patch for 5 seconds or more. While in a patch, the focal individual could move
180 between sub-patches. A sub-patch entry was recorded when an individual relocated into a new
181 area of a patch to forage, and either remained stationary for ≥ 5 seconds while standing, or sat
182 for ≥ 1 second, to forage in this location. In this way, foraging behaviour at each spatial scale
183 was studied at the level of investment, since entries need not have resulted in successful food
184 consumption (although in almost all cases did). At each spatial scale, a specific foraging decision
185 was assigned to every entry event. The decision was defined as 'produce' if the patch or sub-

186 patch being entered was unoccupied, and 'join' if occupied by a conspecific. Note that join
187 events at the sub-patch level need not have been preceded by a join event at the patch level,
188 because 1) a focal individual could enter an unoccupied patch and subsequently be joined by
189 others, providing opportunities for future join events at the sub-patch level; and 2) focal follows
190 could begin with the focal individual already occupying a patch.

191

192 For each join event, the number and identity of individuals occupying the resource was
193 recorded. In cases where visibility was poor, a minimum number of occupants was estimated
194 and, where known, their identity recorded. Since individuals being joined could either remain
195 in, or be supplanted from, their patch or sub-patch, we recorded whether or not a join event
196 was associated with competitive exclusion. We defined supplanting, representing competitive
197 exclusion, as an approach-retreat interaction (Rowell, 1966; Silk et al., 2010) at a given patch or
198 sub-patch that resulted in the entry and exit of the approaching and retreating individuals,
199 respectively.

200

201 Since the size of a patch is variable, while sub-patch size is fixed, the relationship between them
202 is such that at the smallest, or 'critical', patch sizes they reach equivalence. With this in mind,
203 social foraging decisions were included only where a sub-patch structure could be defined (i.e.,
204 where the occupied patch held more than one sub-patch), such that the sub-patch always
205 represented a smaller spatial scale nested within the patch. Study at the sub-patch scale thus
206 captured social foraging dynamics at a resolution higher than at the patch scale, allowing us to
207 avoid conflating processes working at the two different spatial scales. Specifically,

208 monopolisation of food at the patch scale always required the defence of an area at least (but
209 generally considerably more than) double that required at the sub-patch scale. The data were
210 then filtered further to exclude all ambiguous foraging decisions that could not clearly be
211 classified as either produce or join (<10%). A total of 801 focal hours were carried out across
212 the two study periods on 101 individual baboons (mean \pm s.e. = 7.9 ± 0.1 hours per individual),
213 resulting in a dataset of 1861 patch entry and 5050 sub-patch entry decisions for analysis. All
214 observers completed a period of intensive training in the field to ensure high levels of accuracy
215 and consistency in recognising patch and sub-patch boundaries, entry events, foraging
216 decisions, and competitive exclusion. Observers were also naïve to the predictions of the study
217 relating to associations between joining behaviour and social dominance at the two spatial
218 scales.

219

220 A dominance hierarchy was generated for each troop-year combination using pairwise agonistic
221 interactions occurring within each study period. These interactions were collected both during
222 focal follows and through ad libitum sampling, and were used to make actor-receiver matrices
223 indicating the number of agonistic interactions occurring between each dyad in each direction.
224 No dominance interactions occurring during foraging decisions were included in the matrices. In
225 addition, all interactions involving individuals not yet weaned from their mother were excluded,
226 because dominance asymmetry at this age is strongly influenced by the mother's presence and
227 behaviour (Cheney, 1977). Each actor-receiver matrix ($N_{2012,J} = 1010$; $N_{2012,L} = 1025$; $N_{2013,J} =$
228 833 ; $N_{2013,L} = 1073$) was reordered using Matman 1.1.4 (Noldus Information Technology 2003),
229 optimised by selecting the hierarchy with the lowest level of conflict (i.e., minimising the

230 number of interactions inconsistent with the predicted hierarchy) using a heuristic search
231 algorithm with ten thousand randomisations. Linearity was supported for all four hierarchies
232 (Landau's corrected linearity index: $h'_{2012,J} = 0.19$; $h'_{2012,L} = 0.32$; $h'_{2013,J} = 0.18$; $h'_{2013,L} = 0.15$, $p <$
233 0.001 in all cases), highlighting the rarity of interactions inconsistent with the predicted
234 hierarchy ($n_{2012,J} = 67$; $n_{2012,L} = 81$; $n_{2013,J} = 43$; $n_{2013,L} = 71$). Individuals not yet weaned were then
235 re-entered into the appropriate dominance hierarchy based on their maternal rank (i.e., one
236 position below their mother, consistent with the well-documented maternal reinforcement of
237 offspring rank in chacma baboons; Cheney, 1977), producing complete hierarchies that
238 included all members of the group for each year. To control for differences in the size of groups
239 within and across years, all absolute ranks (ranging from 1 to n) were standardised to between
240 0 (lowest rank) and 1 (highest rank) following $1 - ((1-r)/(1-n))$, where r is the absolute rank of an
241 individual.

242

243 Our wholly observational research adhered to the Guidelines for the Use of Animals in
244 Behavioural Research and Teaching (Animal Behaviour 2012. 83:301–309), and our protocols
245 were assessed and approved by the Ethics Committee of the Zoological Society of London
246 (BPE/0518). Our study was approved by the Ministry of Environment and Tourism in Namibia
247 (Research Permits 1696/2012 and 1786/2013).

248

249 *Statistical analyses*

250 Our analysis was divided into three sections consistent with the three main predictions outlined
251 above. First, we used generalised linear mixed-effects modelling (GLMM) to explore how the

252 relationship between social dominance and joining behaviour changed across spatial scales due
253 to differences in resource monopolisability. Our main prediction was that all individuals would
254 exhibit joining behaviour at the patch scale, but that there would be a strong positive
255 relationship between rank and joining at the sub-patch scale. However, since juvenile baboons
256 are often tolerated at feeding sites (e.g., Huchard et al., 2013), we predicted that this positive
257 relationship (and thus an interaction between spatial scale and dominance rank) would only
258 hold for adults. We thus constructed our statistical model with a three-way interaction
259 between spatial scale ('patch' or 'sub-patch'), dominance rank, and age class ('juvenile' or
260 'adult'). The response variable was given as a binary indicator of the decision at each entry to
261 either 'produce' or 'join', scored as 0 or 1, respectively. We fit a binomial error structure to the
262 GLMMs. Model selection was conducted by using a likelihood ratio test to judge whether the
263 model with or without the three-way interaction term provided the better fit to the data, and if
264 the latter, whether those models with or without two-way interactions between spatial scale,
265 dominance rank, and age class provided the better fit. Troop and year were included as control
266 fixed effects, and were thus retained in all models. Focal identity and focal follow number were
267 included as random intercepts in all models.

268

269 Second, we asked whether join 'events' were consistently associated with asymmetries in social
270 rank at each spatial scale. Our main prediction was that individuals would consistently join
271 others lower ranked than themselves at the sub-patch level, but would join others regardless of
272 rank differences at the patch level. Again, we predicted that the relationship at the sub-patch
273 level would not hold for juvenile individuals. To test this second set of predictions, we used a

274 randomisation method to compare the joining behaviour we observed to the patterns of joining
275 that would be expected if individuals joined others randomly with respect to rank difference.
276 We employed this method because any relationship between dominance rank and joining
277 frequency demonstrated in our first analysis would indicate that a crude comparison of the
278 rank difference between joining and joined individuals could lead us to erroneous conclusions.
279 For example, if high ranked individuals joined more frequently than low ranked individuals at a
280 given spatial scale, our data would suggest that individuals on average joined others lower
281 ranked than themselves at this spatial scale in the case that their actual joining behaviour was
282 random with respect to rank difference, simply because individuals with above average social
283 rank necessarily have more individuals subordinate to them than dominant to them. Our
284 observation variable for this analysis was a binary indicator of whether the joining individual
285 was dominant or subordinate to the joined individual. For those events where multiple
286 individuals were joined in a patch (36%) or sub-patch (2%), the direction of their average rank
287 difference with the focal individual was used. We generated expectations of rank differences
288 under joining behaviour that was random with respect to rank difference by randomly
289 resampling from the appropriate troop only the identity of the joined individual for each
290 observed join event, and calculating the difference in rank between the actual joiner and this
291 randomly sampled individual. We repeated this process 10,000 times to generate a distribution
292 of the expected proportion of join events in which the joining individual would be subordinate
293 to the joined individual if individuals joined randomly with respect to rank difference. We
294 define that our observed estimates for the proportion of events with a subordinate joiner
295 would deviate from random expectations when they fall outside of the 95% tolerance intervals

296 of the random distribution. We built four sets of random distributions to compare our
297 observational estimates to: one for adult joiners and one for juvenile joiners at both the patch
298 and the sub-patch scale.

299

300 Third, we built a generalised linear model to establish whether join events at different spatial
301 scales were associated with differences in the competitive exclusion experienced by the joined
302 individual. Competitive exclusion was modelled as a binary response variable: individuals were
303 either supplanted from the resource or were not. Fixed effects were included as an interaction
304 between spatial scale and age class, assessed using likelihood ratio tests as described above.

305 Since these data were not available for patch level decisions in 2012, only decisions from 2013
306 were used in this analysis. Troop was included as a control fixed effect, and so was retained in
307 all models, and focal identity and focal follow number were included as random intercepts. We
308 predicted that joining behaviour in adults would cause competitive exclusion of the joined
309 individual at the sub-patch but not the patch scale, and that joining behaviour in juveniles
310 would result in lower levels of competitive exclusion at the sub-patch scale compared with
311 adults.

312

313 All analyses were conducted in R version 3.0.2. using the lme4 package (Bates et al., 2013; R
314 Core Team, 2013).

315

316 **Results**

317 *Dominance and social foraging decisions at different spatial scales*

318 At the patch scale, joining behaviour was common regardless of social rank (Table 1; Fig. 1a),
319 consistent with our predictions. Although there was some increase in joining with social
320 dominance in adults, even the lowest ranked individuals entered occupied patches
321 approximately 55% (95% confidence intervals: 41% and 67%) of the time. While joining was in
322 general much less common at the sub-patch scale, there was a strong positive relationship in
323 adults between dominance and joining behaviour (twice that at the patch scale) that was
324 consistent with our predictions (Table 1; Fig. 1b). The lowest ranked adults had around a 1%
325 probability (95% confidence intervals: 0% and 2%) of joining when entering a new sub-patch,
326 while mid-ranked and top-ranked adults did so approximately 4% (95% confidence intervals: 3%
327 and 6%) and 11% (95% confidence intervals: 8% and 17%) of the time, respectively.

328

329 As predicted, the effects of social rank on the probability of joining were weaker in juveniles,
330 and this held across both spatial scales such that there was in general no relationship between
331 dominance and joining frequency in juveniles (Table 1; Fig.1). In addition, juveniles were on
332 average more likely than adults to join at the patch scale, but this primarily reflected low-
333 ranking juveniles joining much more frequently than similarly ranked adults when entering a
334 new patch. This effect was somewhat weakened at the sub-patch scale: low-ranked juveniles
335 joined more frequently when entering a new sub-patch than similarly ranked adults but the
336 pattern was reversed for high-ranked juveniles.

337

338 *Social constraints on joining behaviour at different spatial scales*

339 At the patch scale, there was no evidence that adult individuals joined others systematically
340 higher or lower ranked than themselves compared with the rank asymmetries expected if
341 individuals joined others randomly with respect to their rank difference (Fig.2a, $N_{patch,adult} =$
342 313). Although adults were less likely to join individuals dominant to them at this spatial scale,
343 this could be explained under joining behaviour that was random with respect to rank
344 difference by the finding in our first analysis that the frequency of joining behaviour increased
345 slightly with increasing rank (Fig.1a).

346

347 At the sub-patch scale, adult individuals joined individuals dominant to themselves in 9% of join
348 events, and so were less likely to do so than would have been expected if individuals joined
349 others randomly with respect to rank difference (Fig.2b; $N_{sub-patch,adult} = 154$) and given the fact
350 that high ranked individuals are much more likely than low ranked individuals to join others at
351 this spatial scale (Fig.1b). We thus found support for our prediction that adult individuals would
352 consistently join others lower ranked than themselves at the sub-patch level.

353

354 Comparisons between observed and random joining behaviour for juveniles were broadly
355 similar to those for adults. At the patch scale, the rank asymmetries at observed join events did
356 not deviate from expectations under joining behaviour random with respect to rank difference
357 (Fig. 2c; $N_{patch,juvenile} = 349$). At the sub-patch scale, we observed juveniles joining others to
358 whom they were subordinate in 49% of cases. Although this shows that juveniles were
359 frequently able to join others dominant to themselves, they nonetheless did so less often than
360 expected under random joining (Fig. 2d; $N_{sub-patch,juvenile} = 147$). Despite the fact that our first

361 analysis found no relationship between dominance and joining frequency for juveniles at the
362 sub-patch level (Fig.1b), the random distribution at this spatial scale reflects the fact that
363 juveniles are on average below average in rank.

364

365 *Competitive exclusion at different spatial scales*

366 Joining caused competitive exclusion at the sub-patch scale much more than it did at the patch
367 scale (Table 1). In adults, joining at the patch scale was associated with competitive exclusion in
368 9% of cases. This figure increased to 79% at the sub-patch scale. Joining by juveniles was less
369 likely to result in competitive exclusion at both spatial scales (patch: 3%; sub-patch: 51%).

370

371 **Discussion**

372 We provide empirical evidence that joining behaviour should be more strongly related to social
373 rank when the competitive asymmetries associated with dominance are stronger, in support of
374 previous theoretical predictions (Barta & Giraldeau, 1998; Lee et al., 2016). We show that
375 changes in resource monopolisability can mediate this shift in competitive asymmetry through
376 changes in competitive exclusion at different spatial scales. At the larger patch scale, adults
377 could join others regardless of any differences in their social ranks, and did so frequently. At the
378 smaller sub-patch scale, joining was a rarer event – likely reflecting the higher finder's share at
379 this spatial scale (Vickery et al., 1991) – but also represented a more exclusive tactic, almost
380 non-existent in the lowest-ranking individuals but increasing in probability with social
381 dominance. When resources are monopolisable, socially subordinate individuals may thus be
382 constrained in their ability to exploit available social information when its use requires joining

383 behaviour, as is assumed by producer-scrounger theory. Since the size of a resource is expected
384 to influence its economic defensibility (Grant, 1993), our study supports calls to unify producer-
385 scrounger and resource defence theory in order to better understand the relationship between
386 dominance and socially exploitative behaviours (Barta & Giraldeau, 1998; Dubois, Giraldeau &
387 Grant, 2003; Dubois & Giraldeau, 2005; Giraldeau & Dubois, 2008). However, our study also
388 highlights two areas in which our understanding of the evolutionary ecology of animal
389 information use is still lacking, requiring further theoretical and empirical developments.

390

391 First, we showed a strong increase in the frequency of joining at higher ranks for adults at the
392 sub-patch scale, where single individuals could use their dominance to exclude competitors.
393 However, the pattern we observed was weaker than that predicted by Barta and Giraldeau
394 (1998), who suggested a complete absence of scrounging in all but the most dominant
395 individuals when resources could be effectively monopolised. We found that even middle- and
396 low-ranking adults can scrounge from others, provided that the others they join are even lower
397 ranked than themselves. The failure of the producer-scrounger model to predict this pattern
398 likely reflects two of its assumptions. Specifically, the model is built such that any individual
399 playing scrounger can access all the discoveries of others, since (1) resources are assumed to be
400 so rare that they are discovered one-at-a-time and (2) scroungers can access perfect social
401 information and so detect each discovery (Vickery *et al.* 1991b; Giraldeau & Caraco 2000; cf.
402 Ohtsuka & Toquenaga 2009). When resources can be monopolised, these conditions mean that
403 only the highest-ranked individuals will benefit from scrounging behaviour. However, in many
404 groups of social foragers multiple patches can be discovered at the same time (and

405 simultaneous discoveries or options will likely be the norm for many other types of resource
406 too). As such, scrounging individuals will be unable to access all resource discoveries even if
407 they have perfect social information (Ohtsuka & Toquenaga, 2009; Afshar & Giraldeau, 2014).
408 Furthermore, since individuals within social groups are unlikely to be in close proximity at all
409 times (Krause & Ruxton, 2002; for this study population, see Cowlshaw, 1999; Castles et al.,
410 2014), scrounging individuals are unlikely to possess perfect social information regarding all
411 discoveries occurring at the group level (Barta, Flynn & Giraldeau, 1997; Hirsch, 2007), and any
412 temporal and energetic costs associated with scrounging may vary both within and between
413 individuals.

414

415 Under the conditions of simultaneous discoveries and imperfect access to social information,
416 the most dominant individuals will be unable to monopolise all resource discoveries, regardless
417 of the economic defensibility of single resource patches. Instead, as shown here, the difference
418 in rank between individuals across a hierarchy should play an important role in mediating
419 scrounging behaviour. This finding is consistent with the predictions of a recent game theoretic
420 model (Lee et al., 2016), which proposes that if the highest ranking animals in a group do not
421 detect a particular patch discovery, and/or are occupied at another discovery, then middle and
422 lower ranking animals can benefit from scrounging, provided that the producers from whom
423 they are scrounging are lower ranking than themselves. Our result that joining at the sub-patch
424 level still increases with social rank likely reflects the fact that higher ranked individuals have
425 more competitors who are subordinate to them. The most dominant individual should thus be
426 unconstrained in its ability to act upon opportunities to scrounge, and constraints should

427 increase down the dominance hierarchy. Furthermore, theory predicts that if more dominant
428 individuals are more effective at monopolising other's resource discoveries, then they should
429 continue to scrounge even under conditions that drive lower-ranked individuals to switch to the
430 producer tactic (e.g., when the finder's share is large; Lee et al., 2016). Individuals may also
431 benefit from positioning themselves so as to maximise scrounging opportunities (Barta, Flynn &
432 Giraldeau, 1997; di Bitetti & Janson, 2001; Hirsch, 2007). Since dominant individuals may be
433 better able to secure more central positions in the group, this may improve their ability to
434 detect, and increase their proximity to, the discoveries of others (Barta, Flynn & Giraldeau,
435 1997; King, Isaac & Cowlshaw, 2009), and further reinforce the effects of dominance on
436 scrounging behaviour.

437

438 Second, we showed that the relationship between social dominance and joining is strongly
439 influenced by age class. In stark contrast to adults, juvenile baboons showed no general
440 relationship between social dominance and joining, particularly at the sub-patch level. Indeed,
441 juvenile behaviour accounted for almost all instances where a subordinate joined a higher-
442 ranking individual at this spatial scale. There are two likely explanations for this pattern. Firstly,
443 rank acquisition in chacma baboons is mediated primarily through maternal reinforcement.
444 Specifically, a mother will use aggressive behaviours to establish the dominance of her
445 developing offspring over others subordinate to her (Cheney, 1977; Holekamp & Smale, 1991;
446 Lea et al., 2014). Consequently, social rank during early life might be particularly sensitive to
447 context, such that social interactions between juveniles may only reflect rank differences
448 between their mothers in the presence of the dominant mother. In the absence of the

449 dominant mother, older but 'subordinate' juveniles might use their larger size to join younger,
450 smaller, but more 'dominant' competitors. Secondly, there is evidence that juvenile baboons,
451 like the juveniles of several other primate species (Janson, 1985), are more frequently tolerated
452 at feeding sites than adults. The presence of co-foraging juveniles may impose only a minimal
453 direct cost to adults, but permitting close kin access to resources may provide inclusive fitness
454 benefits. In particular, father-offspring relationships in chacma baboons afford juveniles access
455 to high-quality feeding sites (Huchard et al., 2013). Such toleration may mean that, in addition
456 to better access to monopolisable resources, low-ranked juveniles may not be constrained in
457 their ability to use social information in the same way that similarly ranked adults will be. Our
458 findings do not provide strong evidence in support of either tolerance or juvenile rank
459 instability in disrupting the expected positive relationship between social rank and joining
460 behaviour when resources are monopolisable. However, given that we might expect juvenile
461 rank stability to disrupt rank asymmetries but still to involve competitive exclusion when
462 resources are monopolisable, the fact that the probability of competitive exclusion was reduced
463 for juveniles compared with adults at the sub-patch scale might suggest that toleration is
464 playing a bigger role in our observations.

465

466 Our study demonstrates the way in which the monopolisability of resources may drive social
467 constraints on a subordinate individual's ability to use joining behaviour to access them. We
468 also show that such constraints may be relaxed in juveniles. Since resources generally show
469 some uncertainty in their distribution through space and time, information use is likely to play a
470 key role in resource acquisition. Our study illustrates how competitive processes associated

471 with dominance might facilitate or constrain an individual's ability to benefit from collecting
472 social information when its use requires joining behaviour, as in the producer-scrounger
473 framework (Barta & Giraldeau, 1998; Lee et al., 2016). An important step in future research will
474 be to develop frameworks that simultaneously consider how resource distributions underpin 1)
475 the strength and type of competition between individuals, 2) the benefits of collecting
476 information socially versus personally, and 3) the rate at which such information becomes out-
477 dated. This approach will elucidate the environmental conditions that should generate
478 interdependencies between contest competition and social information use by highlighting
479 when social information use should be dependent on joining behaviour at a resource. These
480 insights will allow better characterisation of the ways in which competition can modulate
481 relationships between an individual's ability to use information and its access to resources, and
482 the implications of such modulations for the dynamics of natural populations.

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662

Table 1 (on next page)

Factors predicting the probability of joining behaviour and competitive exclusion associated with joining.

1

Response	<i>N</i>	Fixed Effect	β	s.e.	χ^2	<i>p</i>
Probability of joining	6911	Intercept	-0.05	0.26		
		Spatial scale (Sub-patch)	-4.51	0.28		
		Rank	1.10	0.38		
		Age class (Juvenile)	1.57	0.30		
		Troop (L)	0.20	0.15		
		Year (2013)	0.27	0.12		
		Spatial scale (Sub-patch) * Rank	1.18	0.37	10.30	0.001
		Rank * Age class (Juvenile)	-1.68	0.54	9.03	0.003
		Spatial scale (Sub-patch) * Age class (Juvenile)	-0.68	0.21	10.40	0.001
Probability of competitive exclusion	385	Intercept	-2.44	0.47		
		Spatial scale (Sub-patch)	4.55	0.65	164.27	<0.001
		Age class (Juvenile)	-1.61	0.47	14.06	<0.001
		Troop	-0.89	0.44		

Model reference categories: Spatial scale (Patch), Age class (Adult), Troop (J), Year (2012).

Figure 1(on next page)

Predicted relationship between the probability of joining behaviour and dominance rank at the (a) patch and (b) sub-patch level.

For both panels, solid and dashed lines represent the predicted values for adults and juveniles, respectively. Shaded green (adults) and purple (juveniles) regions are bounded by upper and lower 95% confidence intervals. Note the difference in scale of the two y-axes, reflecting the much lower levels of joining across all individuals at the sub-patch compared with patch scale.

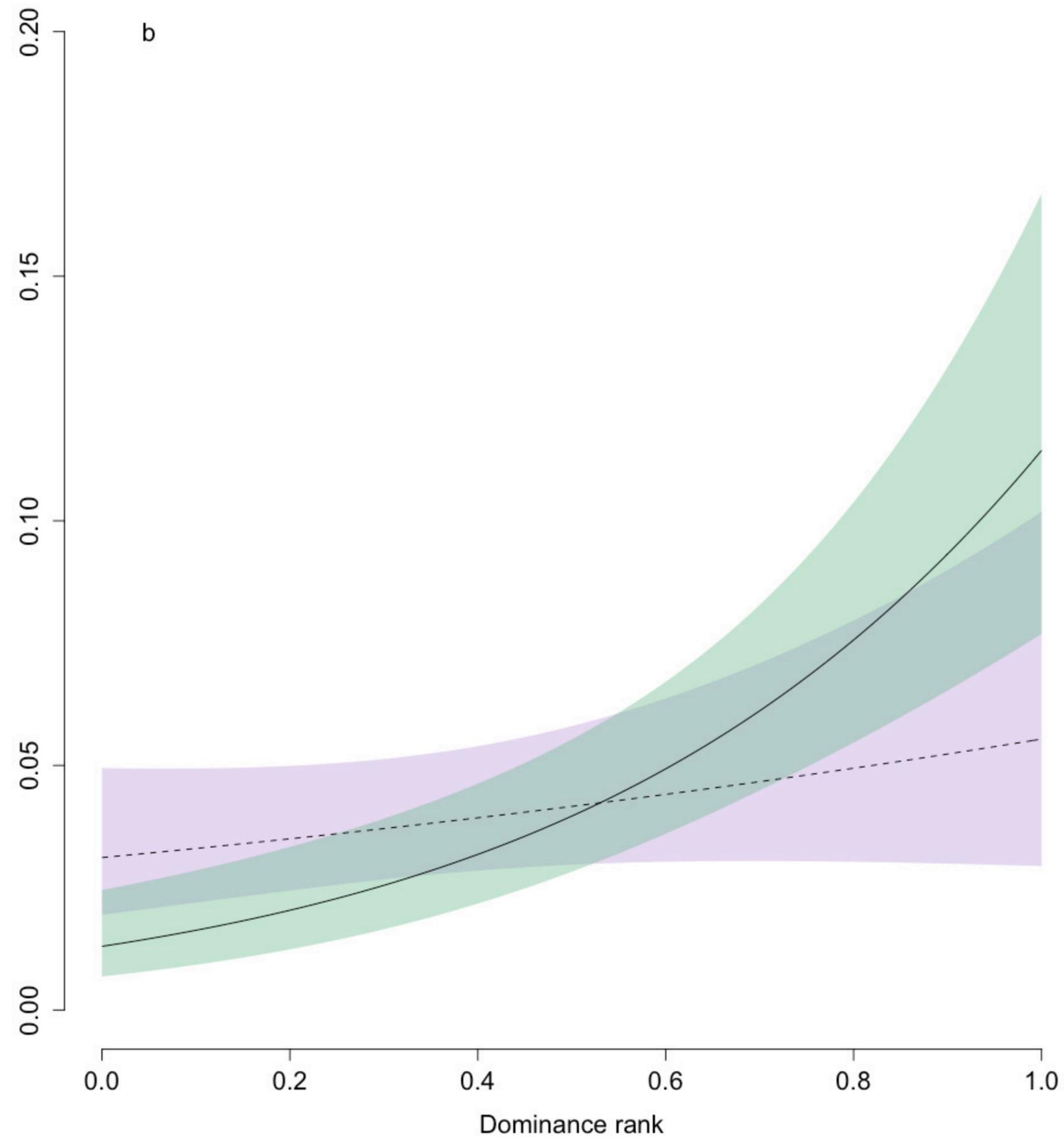
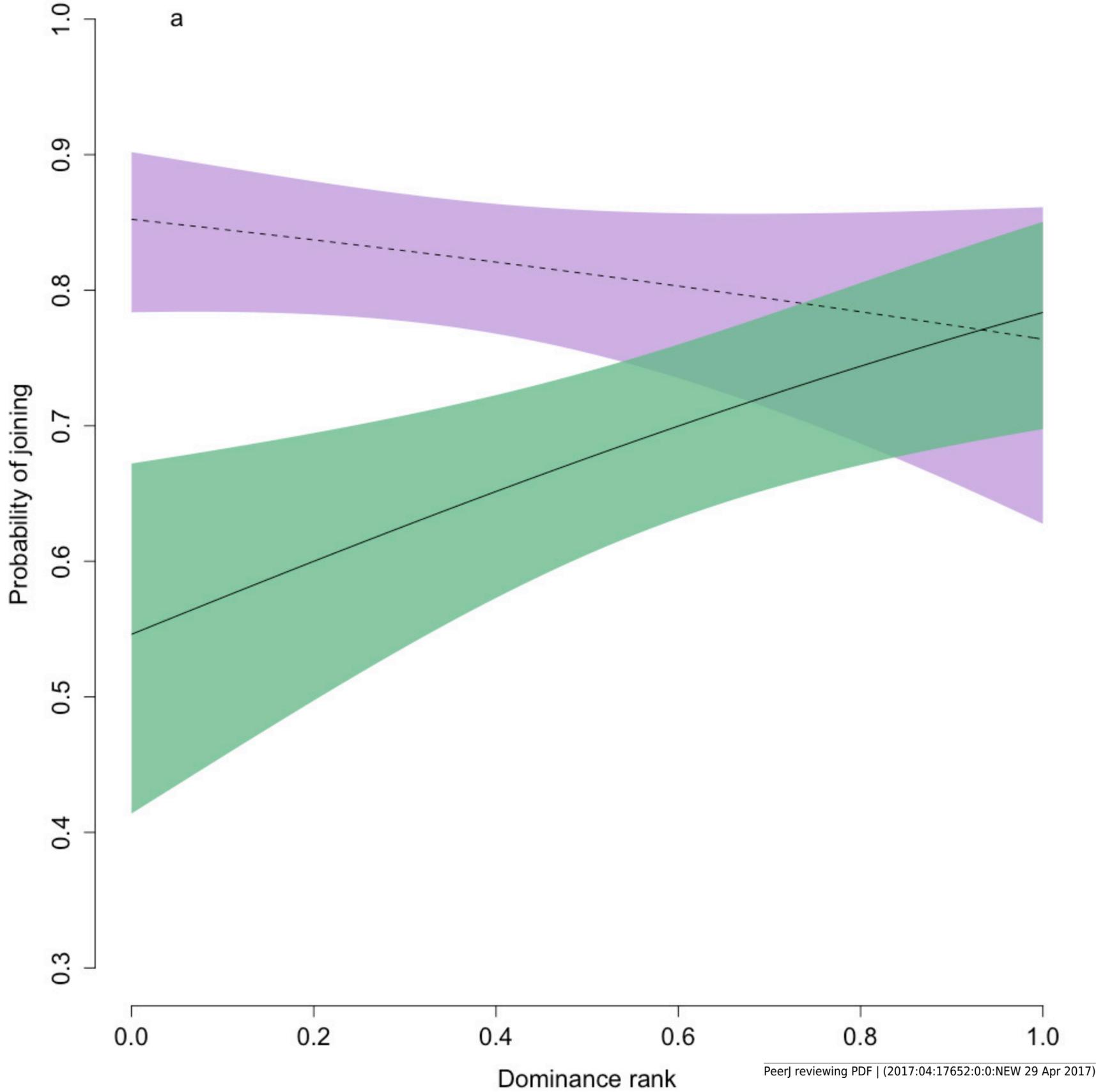


Figure 2 (on next page)

Comparison of observed dominance asymmetry during join events with simulated joining behaviour that is random with respect to rank difference.

Probability density distributions show expectations for the proportion of join events in which the joining individuals would be subordinate to the joined individual if their behaviour was random with respect to the rank of the joined individual. The distributions are for adults (a) and juveniles (b) at the patch level, and adults (c) and juveniles (d) at the sub-patch level, generated through 10,000 iterations of randomly selecting the individual to be joined at each join event. For each distribution, dotted vertical lines indicate the 95% tolerance intervals and solid vertical lines indicate our observed value.

