

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

Alexander E. G. Lee ^{Corresp., 1,2,3}, Guy Cowlshaw ²

¹ Department of Zoology, University of Oxford, Oxford, United Kingdom

² The Institute of Zoology, Zoological Society of London, London, United Kingdom

³ Centre of Excellence in Biological Interactions, Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland

Corresponding Author: Alexander E. G. Lee

Email address: allee@jyu.fi

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 of individuals of low social rank to use social information, driven by competition with dominant conspecifics over monopolisable resources.

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

3

4

Alexander E. G. Lee^{1,2,3,*} and Guy Cowlshaw²

5

6

¹ Department of Zoology, University of Oxford, Oxford, UK

7

² The Institute of Zoology, Zoological Society of London, Regent's Park, London, UK

8

³ Centre of Excellence in Biological Interactions, Department of Biological and Environmental Sciences,

9

University of Jyväskylä, Jyväskylä, Finland

10

11

* Author for correspondence. Email address: allee@jyu.fi

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-scrouter 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 of
31 individuals of low social rank to use social information, 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 have
36 highlighted such behaviours as a major potential cost of group living (Giraldeau & Dubois,
37 2008). 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 personal collection of
41 information requires search effort or risk taking, selection should favour the avoidance of these
42 costs through the collection and use of social information, where individuals attend to the
43 behaviours of others in a social group to exploit their efforts and knowledge (for review see
44 Valone & Templeton, 2002; Danchin et al., 2004; Rieucou & Giraldeau, 2011).

45

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

55 determined by the relative frequencies of the two tactics within a group. This dynamic is
56 expected to lead populations to an evolutionarily or behaviourally stable mix of producing and
57 scrounging (Giraldeau & Dubois, 2008; Fawcett, Hamblin & Giraldeau, 2013). As such,
58 scrounging behaviour has the potential to reduce the per capita rate of discovery of new
59 resources (Vickery et al., 1991), which may act to reduce average individual fitness in a
60 population (Coolen, Giraldeau & Vickery, 2007).

61

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

70

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

77 Barta, 2002; Lendvai, Liker & Barta, 2006; McCormack, Jablonski & Brown, 2007), a number of
78 other studies have not (Bugnyar & Kotrschal, 2002; Robinette Ha & Ha, 2003; Beauchamp,
79 2006; Teichroeb, White & Chapman, 2015). This conflict might be reconciled by considering
80 more systematically the spatiotemporal distribution of resources faced by different taxa in both
81 naturalistic and experimental settings. The competitive benefits of social dominance are
82 expected to be associated with priority of access to resources, manifest as contest competition
83 (Kaufmann, 1983; Łomnicki, 2009). Consistent with this, resource defence theory predicts that
84 individuals should be more aggressive when defending a resource in accordance with both its
85 value and how easily it can be defended (Grant, 1993; Grant & Guha, 1993; Robb & Grant,
86 1998). Empirical studies into dominance and resource defence have demonstrated higher
87 foraging success for socially dominant individuals only when presented with limited food
88 patches that are monopolisable (Theimer, 1987; Vahl et al., 2005).

89

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

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

108

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

121 behaviours of individuals as they foraged, representing competitive interactions fundamental to
122 the predictions of producer-scrounger theory (Lee et al., 2016). In this way, we explore the
123 competitive constraints that social rank may impose on an individual's ability to use social
124 information through joining behaviour, and the relation of such constraints to resource
125 monopolisability in a naturalistic setting in which information use is expected to be important.
126 We make the following three predictions: 1) joining behaviour should show a strong positive
127 association with dominance rank at the smaller, sub-patch level but not at the larger, patch
128 level; 2) individuals should join those to whom they are dominant at the sub-patch level, but
129 there should be no systematic asymmetry in dominance when joining occurs at the patch level;
130 and 3) joining should be associated with competitive exclusion (i.e., resource monopolisation)
131 at the sub-patch level, but not at the patch level.

132

133 **Materials and Methods**

134 *Study Site and Species*

135 Fieldwork was conducted at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E), during two three-
136 month periods between August and October in 2012 and 2013. Two groups of chacma
137 baboons, hereafter referred to as troop 'J' (group size and compositions: $N_{J,2012} = 54$, adult
138 females = 16, adult males = 15, juveniles = 23; $N_{J,2013} = 58$, adult females = 18, adult males = 9,
139 juveniles = 31) and troop 'L' ($N_{L,2012} = 51$, adult females = 18, adult males = 6, juveniles = 27;
140 $N_{L,2013} = 62$, adult females = 19, adult males = 11, juveniles = 32), were the focus of study. All
141 baboons were individually recognisable and habituated to the presence of observers at close
142 proximity. Each group was followed daily from dawn until dusk (see Huchard et al., 2009 for

143 further information). For each year, data were collected for all individual baboons >6 months of
144 age (the age at which young baboons begin to forage independently of their mother) at the
145 start of the study period, resulting in a total sample of 101 individuals (2012: 54 adults, 43
146 juveniles; 2013: 50 adults, 41 juveniles). Differences in the sample of individuals across years
147 were due to death, emigration, or passing the minimum age threshold.

148

149 Chacma baboons are an ideal model system for our study, since they live in large, stable social
150 groups in which linear dominance hierarchies are clear (Altmann & Altmann, 1973), individuals
151 generally feed at the same time (King & Cowlshaw, 2009), the use of social information while
152 foraging has been demonstrated in field-based experiments (Carter, Torrents Ticó & Cowlshaw,
153 2016), and socially exploitative foraging interactions are common (King, Isaac & Cowlshaw,
154 2009; Marshall et al., 2012). Furthermore, our study troops spent approximately 80% of their
155 foraging time during the study period in a riparian woodland environment, characterised by
156 large trees including *Faidherbia albida*, *Salvadora persica*, *Acacia erioloba*, *Acacia tortilis*, and
157 *Prosopis glandulosa*. Within this feeding environment, we defined two spatial scales between
158 which the ability of dominant individuals to monopolise food were predicted to differ: the
159 patch and the sub-patch.

160

161 The patch represents the scale traditionally used in foraging theory and ecology, and is defined
162 as a spatially discrete unit of a food resource (Wiens, 1976). Here, we refined this definition
163 such that the operational definition of a patch was a single tree or shrub, or a collection of
164 conspecific trees or shrubs growing together with a continuous canopy separated by no more

165 than 1 m (median surface area = 156 m², interquartile range = 28-237 m²; $n = 59$; see Marshall
166 et al., 2012 for further details). In contrast, the sub-patch was defined as the area in a patch
167 within which an individual could feed without travelling (i.e., within arm's reach of a stationary
168 baboon, approximately 2.25 m²). This is equivalent to the 'feeding station' scale that has
169 received some attention in the foraging literature (Kotliar & Wiens, 1990; see Searle, Hobbs &
170 Shipley, 2005 for a review). Given the large size of patches compared with sub-patches,
171 dominant individuals should be able to competitively exclude subordinate others more easily at
172 the latter scale.

173

174 *Data Collection and Processing*

175 Information regarding individual social foraging decisions and interactions at each spatial scale
176 was recorded through focal sampling (Altmann, 1974) on Motorola ES400 Personal Digital
177 Assistants and Google Nexus 4 Smartphones using a customised data capture application in the
178 database-driven software Cybertracker v.3.317 (<http://cybertracker.org>). Focal follows lasted
179 between 15 and 30 minutes, and the same individual was not studied more than once within a
180 6-hour period. Individuals were selected for focal observation using a pseudorandom sampling
181 process, which ensured even coverage across different times of day (based on four consecutive
182 3-hour time blocks from 06:00 to 18:00) and different months.

183

184 A patch entry event was recorded whenever the focal individual searched for or consumed food
185 in a new patch for 5 seconds or more. While in a patch, the focal individual could move
186 between sub-patches. A sub-patch entry was recorded when an individual relocated into a new

187 area of a patch to forage, and either remained stationary for ≥ 5 seconds while standing, or sat
188 for ≥ 1 second, to forage in this location. In this way, foraging behaviour at each spatial scale
189 was studied at the level of investment, since entries need not have resulted in successful food
190 consumption (although in almost all cases did). At each spatial scale, a specific foraging decision
191 was assigned to every entry event. The decision was defined as 'produce' if the patch or sub-
192 patch being entered was unoccupied, and 'join' if occupied by a conspecific. Note that join
193 events at the sub-patch level need not have been preceded by a join event at the patch level,
194 because 1) a focal individual could enter an unoccupied patch and subsequently be joined by
195 others, providing opportunities for future join events at the sub-patch level; and 2) focal follows
196 could begin with the focal individual already occupying a patch.

197

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

206

207 Since the size of a patch is variable, while sub-patch size is fixed, the relationship between them
208 is such that at the smallest, or 'critical', patch sizes they reach equivalence. With this in mind,

209 social foraging decisions were included only where a sub-patch structure could be defined (i.e.,
210 where the occupied patch held more than one sub-patch), such that the sub-patch always
211 represented a smaller spatial scale nested within the patch. Study at the sub-patch scale thus
212 captured social foraging dynamics at a resolution higher than at the patch scale, allowing us to
213 avoid conflating processes working at the two different spatial scales. Specifically,
214 monopolisation of food at the patch scale always required the defence of an area at least (but
215 generally considerably more than) double that required at the sub-patch scale. The data were
216 then filtered further to exclude all ambiguous foraging decisions that could not clearly be
217 classified as either produce or join (<10%). A total of 801 focal hours were carried out across
218 the two study periods on 101 individual baboons (mean \pm s.e. = 7.9 ± 0.1 hours per individual),
219 resulting in a dataset of 1861 patch entry and 5050 sub-patch entry decisions for analysis. All
220 observers completed a period of intensive training in the field to ensure high levels of accuracy
221 and consistency in recognising patch and sub-patch boundaries, entry events, foraging
222 decisions, and competitive exclusion. Observers were also naïve to the predictions of the study
223 relating to associations between joining behaviour and social dominance at the two spatial
224 scales.

225

226 A dominance hierarchy was generated for each troop-year combination using pairwise agonistic
227 interactions occurring within each study period. These interactions were collected both during
228 focal follows and through ad libitum sampling, and were used to make actor-receiver matrices
229 indicating the number of agonistic interactions occurring between each dyad in each direction.
230 No dominance interactions occurring during foraging decisions were included in the matrices. In

231 addition, all interactions involving individuals not yet weaned from their mother were excluded,
232 because dominance asymmetry at this age is strongly influenced by the mother's presence and
233 behaviour (Cheney, 1977). Each actor-receiver matrix ($N_{2012,J} = 1010$; $N_{2012,L} = 1025$; $N_{2013,J} =$
234 833 ; $N_{2013,L} = 1073$) was reordered using Matman 1.1.4 (Noldus Information Technology 2003),
235 optimised by selecting the hierarchy with the lowest level of conflict (i.e., minimising the
236 number of interactions inconsistent with the predicted hierarchy) using a heuristic search
237 algorithm with ten thousand randomisations. Linearity was supported for all four hierarchies
238 (Landau's corrected linearity index: $h'_{2012,J} = 0.19$; $h'_{2012,L} = 0.32$; $h'_{2013,J} = 0.18$; $h'_{2013,L} = 0.15$, $p <$
239 0.001 in all cases), highlighting the rarity of interactions inconsistent with the predicted
240 hierarchy ($n_{2012,J} = 67$ (7%); $n_{2012,L} = 81$ (8%); $n_{2013,J} = 43$ (5%); $n_{2013,L} = 71$ (7%)). Individuals not
241 yet weaned were then re-entered into the appropriate dominance hierarchy based on their
242 maternal rank (i.e., one position below their mother, consistent with the well-documented
243 maternal reinforcement of offspring rank in chacma baboons; Cheney, 1977), producing
244 complete hierarchies that included all members of the group for each year. To control for
245 differences in the size of groups within and across years, all absolute ranks (ranging from 1 to n)
246 were standardised to between 0 (lowest rank) and 1 (highest rank) following $1 - ((1-r)/(1-n))$,
247 where r is the absolute rank of an individual.

248

249 Our wholly observational research adhered to the Guidelines for the Use of Animals in
250 Behavioural Research and Teaching (Animal Behaviour 2012. 83:301–309), and our protocols
251 were assessed and approved by the Ethics Committee of the Zoological Society of London

252 (BPE/0518). Our study was approved by the Ministry of Environment and Tourism in Namibia
253 (Research Permits 1696/2012 and 1786/2013).

254

255 *Statistical analyses*

256 Our analysis was divided into three sections consistent with the three main predictions outlined
257 above. First, we used generalised linear mixed-effects modelling (GLMM) to explore how the
258 relationship between social dominance and joining behaviour changed across spatial scales due
259 to differences in resource monopolisability. Our main prediction was that all individuals would
260 exhibit joining behaviour at the patch scale, but that there would be a strong positive
261 relationship between rank and joining at the sub-patch scale. However, since juvenile baboons
262 are often tolerated at feeding sites (e.g., Huchard et al., 2013), we predicted that this positive
263 relationship (and thus an interaction between spatial scale and dominance rank) would only
264 hold for adults. While differences between adults and juveniles were not the focus of this study,
265 it was important to include age class in our statistical models to fully understand any
266 relationships between resource monopolisability, contest competition, and joining behaviour.
267 We thus constructed our statistical model with a three-way interaction between spatial scale
268 ('patch' or 'sub-patch'), dominance rank, and age class ('juvenile' or 'adult'). The response
269 variable was given as a binary indicator of the decision at each entry to either 'produce' or
270 'join', scored as 0 or 1, respectively. We fit a binomial error structure to the GLMMs. Model
271 selection was conducted by using a likelihood ratio test ($\alpha = 0.05$) to judge whether the model
272 with or without the three-way interaction term provided the better fit to the data, and if the
273 latter, whether those models with or without two-way interactions between spatial scale,

274 dominance rank, and age class provided the better fit. Troop and year were included as control
275 fixed effects, and were thus retained in all models. Focal identity and focal follow number were
276 included as random intercepts in all models.

277

278 Second, we asked whether join 'events' were consistently associated with asymmetries in social
279 rank at each spatial scale. Our main prediction was that individuals would consistently join
280 others lower ranked than themselves at the sub-patch level, but would join others regardless of
281 rank differences at the patch level. Again, we predicted that the relationship at the sub-patch
282 level would not hold for juvenile individuals. To test this second set of predictions, we used a
283 randomisation method to compare the joining behaviour we observed to the patterns of joining
284 that would be expected if individuals joined others randomly with respect to rank difference.

285 We employed this method because any relationship between dominance rank and joining
286 frequency demonstrated in our first analysis would indicate that a crude comparison of the
287 rank difference between joining and joined individuals could lead us to erroneous conclusions.

288 For example, if high ranked individuals joined more frequently than low ranked individuals at a
289 given spatial scale, our data would suggest that individuals on average joined others lower

290 ranked than themselves at this spatial scale in the case that their actual joining behaviour was
291 random with respect to rank difference, simply because individuals with above average social

292 rank necessarily have more individuals subordinate to them than dominant to them. Our

293 observation variable for this analysis was a binary indicator of whether the joining individual

294 was dominant or subordinate to the joined individual. For those events where multiple

295 individuals were joined in a patch (36%) or sub-patch (2%), the direction of their average rank

296 difference with the focal individual was used. We generated expectations of rank differences
297 under random joining behaviour with respect to rank difference by randomly resampling from
298 the appropriate troop only the identity of the joined individual for each observed join event,
299 and calculating the difference in rank between the actual joiner and this randomly sampled
300 individual. We repeated this process 10,000 times to generate a distribution of the expected
301 proportion of join events in which the joining individual would be subordinate to the joined
302 individual if individuals joined randomly with respect to rank difference. [We defined that our](#)
303 [observed estimates for the proportion of events with a subordinate joiner deviated from](#)
304 [random expectations when they fell outside of the 95% tolerance intervals of the random](#)
305 [distribution.](#) We built four sets of random distributions to which we could compare our
306 observational estimates: one for adult joiners and one for juvenile joiners at both the patch and
307 the sub-patch scale.

308

309 Third, we built a GLMM to establish whether join events at different spatial scales were
310 associated with differences in the competitive exclusion experienced by the joined individual.
311 Competitive exclusion was modelled as a binary response variable: individuals were either
312 supplanted from the resource or were not. Fixed effects were included as an interaction
313 between spatial scale and age class, and were assessed using likelihood ratio tests as described
314 above. Since these data were not available for patch level decisions in 2012, only decisions from
315 2013 were used in this analysis. Troop was included as a control fixed effect, and so was
316 retained in all models, and focal identity and focal follow number were included as random
317 intercepts. We predicted that joining behaviour in adults would cause competitive exclusion of

318 the joined individual at the sub-patch but not the patch scale, and that joining behaviour in
319 juveniles would result in lower levels of competitive exclusion at the sub-patch scale compared
320 with adults.

321

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

324

325 **Results**

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

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

337

338 As predicted, the effects of social rank on the probability of joining were weaker in juveniles,
339 and this held across both spatial scales such that there was in general no relationship between

340 dominance and joining frequency in juveniles (Table 1; Fig.1). In addition, juveniles were on
341 average more likely than adults to join at the patch scale, but this primarily reflected low-
342 ranking juveniles joining much more frequently than similarly ranked adults when entering a
343 new patch. This effect was somewhat weakened at the sub-patch scale: low-ranked juveniles
344 joined more frequently when entering a new sub-patch than similarly ranked adults but the
345 pattern was reversed for high-ranked juveniles.

346

347 Combined, our results reflect support for the three possible two-way interactions between
348 spatial scale, dominance rank, and age class (Table 1). Our lack of support for a three-way
349 interaction between these effects (likelihood ratio test: $\chi^2 = 0.70$, $p = 0.41$) reflects the fact that
350 there was some increase in joining with social rank in adults at both spatial scales. This meant
351 that a stronger effect of dominance in adults at the sub-patch versus patch level, combined
352 with no clear relationship between joining frequency and social rank in juveniles at either
353 spatial scale, was captured by a general (i.e., not age class-specific) increase in joining with
354 dominance at the sub-patch level and a general (i.e., not spatial scale-specific) decrease in the
355 effect of dominance on joining in juveniles.

356

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

358 At the patch scale, there was no evidence that adult individuals joined others systematically
359 higher or lower ranked than themselves compared with the rank asymmetries expected if
360 individuals joined others randomly with respect to their rank difference (Fig.2a, $N_{patch,adult} =$
361 313). Although adults were less likely to join individuals dominant to them at this spatial scale,

362 this could be explained under joining behaviour that was random with respect to rank
363 difference by the finding in our first analysis that the frequency of joining behaviour increased
364 slightly with increasing rank (Fig.1a).

365

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

372

373 Comparisons between observed and random joining behaviour for juveniles were broadly
374 similar to those for adults. At the patch scale, the rank asymmetries at observed join events did
375 not deviate from expectations under joining behaviour random with respect to rank difference
376 (Fig. 2c; $N_{patch,juvenile} = 349$). At the sub-patch scale, we observed juveniles joining others to
377 whom they were subordinate in 49% of cases. Although this shows that juveniles were
378 frequently able to join others dominant to themselves, they nonetheless did so less often than
379 expected under random joining (Fig. 2d; $N_{sub-patch,juvenile} = 147$). Despite the fact that our first
380 analysis found no relationship between dominance and joining frequency for juveniles at the
381 sub-patch level (Fig.1b), the random distribution at this spatial scale reflects the fact that
382 juveniles are usually below average in rank.

383

384 *Competitive exclusion at different spatial scales*

385 Joining caused competitive exclusion at the sub-patch scale much more than it did at the patch
386 scale (Table 1). In adults, joining at the patch scale was associated with competitive exclusion in
387 9% of cases. This figure increased to 79% at the sub-patch scale. Joining by juveniles was less
388 likely to result in competitive exclusion at both spatial scales (patch: 3%; sub-patch: 51%).

389

390 **Discussion**

391 We provide empirical evidence that joining behaviour should be more strongly related to social
392 rank when the competitive asymmetries associated with dominance are stronger, in support of
393 previous theoretical predictions (Barta & Giraldeau, 1998; Lee et al., 2016). We show that
394 changes in resource monopolisability can mediate this shift in competitive asymmetry through
395 changes in competitive exclusion at different spatial scales. At the larger patch scale, adults
396 could join others regardless of any differences in their social ranks, and did so frequently. At the
397 smaller sub-patch scale, joining was a rarer event – likely reflecting the higher finder’s share at
398 this spatial scale (Vickery et al., 1991) – but also represented a more exclusive tactic, almost
399 non-existent in the lowest-ranking individuals but increasing in probability with social
400 dominance. When resources are monopolisable, socially subordinate individuals may thus be
401 constrained in their ability to exploit available social information when its use requires joining
402 behaviour, as is assumed by producer-scrounger theory. Since the size of a resource is expected
403 to influence its economic defensibility (Grant, 1993), our study supports calls to unify producer-
404 scrounger and resource defence theory in order to better understand the relationship between
405 dominance and socially exploitative behaviours (Barta & Giraldeau, 1998; Dubois, Giraldeau &

406 Grant, 2003; Dubois & Giraldeau, 2005; Giraldeau & Dubois, 2008). However, our study also
407 highlights two areas in which our understanding of the evolutionary ecology of animal
408 information use is still lacking, requiring further theoretical and empirical developments.
409
410 First, we showed a strong increase in the frequency of joining at higher ranks for adults at the
411 sub-patch scale, where single individuals could use their dominance to exclude competitors.
412 However, the pattern we observed was weaker than that predicted by Barta and Giraldeau
413 (1998), who suggested a complete absence of scrounging in all but the most dominant
414 individuals when resources could be effectively monopolised. We found that even middle- and
415 low-ranking adults can scrounge from others, provided that the others they join are even lower
416 ranked than themselves. The failure of the producer-scrounger model to predict this pattern
417 likely reflects two of its assumptions. Specifically, the model is built such that any individual
418 playing scrounger can access all the discoveries of others, since (1) resources are assumed to be
419 so rare that they are discovered one-at-a-time and (2) scroungers can access perfect social
420 information and so detect each discovery (Vickery *et al.* 1991b; Giraldeau & Caraco 2000; cf.
421 Ohtsuka & Toquenaga 2009). When resources can be monopolised, these conditions mean that
422 only the highest-ranked individuals will benefit from scrounging behaviour. However, in many
423 groups of social foragers multiple patches can be discovered at the same time (and
424 simultaneous discoveries or options will likely be the norm for many other types of resource
425 too). As such, scrounging individuals will be unable to access all resource discoveries even if
426 they have perfect social information (Ohtsuka & Toquenaga, 2009; Afshar & Giraldeau, 2014).
427 Furthermore, since individuals within social groups are unlikely to be in close proximity at all

428 times (Krause & Ruxton, 2002; for this study population, see Cowlshaw, 1999; Castles et al.,
429 2014), scrounging individuals are unlikely to possess perfect social information regarding all
430 discoveries occurring at the group level (Barta, Flynn & Giraldeau, 1997; Hirsch, 2007), and any
431 temporal and energetic costs associated with scrounging may vary both within and between
432 individuals.

433

434 Under the conditions of simultaneous discoveries and imperfect access to social information,
435 the most dominant individuals will be unable to monopolise all resource discoveries, regardless
436 of the economic defensibility of single resource patches. Instead, as shown here, the difference
437 in rank between individuals across a hierarchy should play an important role in mediating
438 scrounging behaviour. This finding is consistent with the predictions of a recent game theoretic
439 model (Lee et al., 2016), which proposes that if the highest ranking animals in a group do not
440 detect a particular patch discovery, and/or are occupied at another discovery, then middle and
441 lower ranking animals can benefit from scrounging, provided that the producers from whom
442 they are scrounging are lower ranking than themselves. Our result that joining at the sub-patch
443 level still increases with social rank likely reflects the fact that higher ranked individuals have
444 more competitors who are subordinate to them. The most dominant individual should thus be
445 unconstrained in its ability to act upon opportunities to scrounge, and constraints should
446 increase down the dominance hierarchy. Furthermore, theory predicts that if more dominant
447 individuals are more effective at monopolising other's resource discoveries, then they should
448 continue to scrounge even under conditions that drive lower-ranked individuals to switch to the
449 producer tactic (e.g., when the finder's share is large; Lee et al., 2016). Individuals may also

450 benefit from positioning themselves so as to maximise scrounging opportunities (Barta, Flynn &
451 Giraldeau, 1997; di Bitetti & Janson, 2001; Hirsch, 2007). Since dominant individuals may be
452 better able to secure more central positions in the group, this may improve their ability to
453 detect, and increase their proximity to, the discoveries of others (Barta, Flynn & Giraldeau,
454 1997; King, Isaac & Cowlshaw, 2009), and further reinforce the effects of dominance on
455 scrounging behaviour.

456

457 Second, we showed that the relationship between social dominance and joining is strongly
458 influenced by age class. In stark contrast to adults, juvenile baboons showed no general
459 relationship between social dominance and joining, particularly at the sub-patch level. While an
460 adult baboon's ability to join competitors at this spatial scale depended strongly on their
461 relative dominance, juveniles were less constrained by their social status. Indeed, juvenile
462 behaviour accounted for almost all instances where a subordinate joined a higher-ranking
463 individual at the sub-patch level. There are two likely explanations for this pattern. Firstly, rank
464 acquisition in chacma baboons is mediated primarily through maternal reinforcement.
465 Specifically, a mother will use aggressive behaviours to establish the dominance of her
466 developing offspring over others subordinate to her (Cheney, 1977; Holekamp & Smale, 1991;
467 Lea et al., 2014). Consequently, social rank during early life might be particularly sensitive to
468 context, such that social interactions between juveniles may only reflect rank differences
469 between their mothers in the presence of the dominant mother. In the absence of the
470 dominant mother, older but 'subordinate' juveniles might use their larger size to join younger,
471 smaller, but more 'dominant' competitors. Secondly, there is evidence that juvenile baboons,

472 like the juveniles of several other primate species (Janson, 1985), are more frequently tolerated
473 at feeding sites than adults. The presence of co-foraging juveniles may impose only a minimal
474 direct cost to adults, but permitting close kin access to resources may provide inclusive fitness
475 benefits. In particular, father-offspring relationships in chacma baboons afford juveniles access
476 to high-quality feeding sites (Huchard et al., 2013). Such toleration may mean that, in addition
477 to better access to monopolisable resources, low-ranked juveniles may not be constrained in
478 their ability to use social information in the same way that similarly ranked adults will be. Our
479 findings do not provide strong evidence in support of either tolerance or juvenile rank
480 instability in disrupting the expected positive relationship between social rank and joining
481 behaviour when resources are monopolisable. However, we might expect juvenile rank stability
482 to disrupt rank asymmetries but still to involve competitive exclusion when resources are
483 monopolisable, while toleration of juveniles should result in reduced levels of competitive
484 exclusion. The fact that the probability of competitive exclusion was reduced for juveniles
485 compared with adults at the sub-patch scale might suggest that toleration is playing a bigger
486 role than juvenile rank instability in our observations.

487

488 Our study demonstrates the way in which the monopolisability of resources may drive social
489 constraints on a subordinate individual's ability to use joining behaviour to access them. We
490 also show that such constraints may be relaxed in juveniles. Since resources generally show
491 some uncertainty in their distribution through space and time, information use is likely to play a
492 key role in resource acquisition. Our study illustrates how competitive processes associated
493 with dominance might facilitate or constrain an individual's ability to benefit from collecting

494 social information when its use requires joining behaviour, as in the producer-scrounger
495 framework (Barta & Giraldeau, 1998; Lee et al., 2016). An important step in future research will
496 be to develop frameworks that simultaneously consider how resource distributions underpin 1)
497 the strength and type of competition between individuals, 2) the benefits of collecting
498 information socially versus personally, and 3) the rate at which such information becomes out-
499 dated. This approach will elucidate the environmental conditions that should generate
500 interdependencies between contest competition and social information use by highlighting
501 when social information use should be dependent on joining behaviour at a resource. These
502 insights will allow better characterisation of the ways in which competition can modulate
503 relationships between an individual's ability to use information and its access to resources, and
504 the implications of such modulations for the dynamics of natural populations.

505 **Acknowledgements**

506 We would like to say a big thank you to James Ounsley, Cassandra Raby, Rebecca Boulton,
507 Matthis Petit, Eveline Rijksen, Miles Keighley, Maddie Castles, Stef Oberprieler, Alice Baniel,
508 Stella Diamant, Katie Hatton, Julien Collet, Chris Smith, Boris Granovski, Caitlin Miller, Alecia
509 Carter, Elise Huchard, Hannah Wilmot, and Willem Odendaal for their work and support in the
510 field. Thanks also to Tim Coulson, Marcus Rowcliffe, Ben Sheldon, David Macdonald, Daniel van
511 der Post, Andrés López-Sepulcre, Alexander Weiss, and three anonymous reviewers for
512 constructive comments and discussions. Permission to work at the field site was kindly granted
513 by Tsaobis Nature Park, the Wittreich and Snyman families, and the Ministry of Lands and
514 Resettlement. We also thank the Gobabeb Training and Research Centre for affiliation in
515 Namibia. This study is a publication of the ZSL Institute of Zoology's Tsaobis Baboon Project.

516 **References**

- 517 Afshar M., Giraldeau L-A. 2014. A unified modelling approach for producer–scrounger games in
518 complex ecological conditions. *Animal Behaviour* 96:167–176. DOI:
519 10.1016/j.anbehav.2014.07.022.
- 520 Altmann J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour* 49:227–265.
521 DOI: 10.1163/156853974X00534.
- 522 Altmann SA., Altmann J. 1973. *Baboon ecology*. Chicago, IL: University of Chicago Press.
- 523 Barnard CJ. 1984. *Producers and scroungers: strategies of exploitation and parasitism*. London,
524 UK: Chapman & Hall.
- 525 Barnard CJ., Sibly RM. 1981. Producers and scroungers: a general model and its application to
526 captive flocks of house sparrows. *Animal Behaviour* 29:543–550. DOI: 10.1016/S0003-
527 3472(81)80117-0.
- 528 Barta Z., Flynn R., Giraldeau L-A. 1997. Geometry for a selfish foraging group: a genetic
529 algorithm approach. *Proceedings of the Royal Society B: Biological Sciences* 264:1233–
530 1238. DOI: 10.1098/rspb.1997.0170.
- 531 Barta Z., Giraldeau L-A. 1998. The effect of dominance hierarchy on the use of alternative
532 foraging tactics: a phenotype-limited producing-scrounging game. *Behavioral Ecology and*
533 *Sociobiology* 42:217–223. DOI: 10.1007/s002650050433.
- 534 Bates D., Maechler M., Bolker B., Walker S. 2013. lme4: Linear mixed-effects models using Eigen
535 and S4. R package version 1.0-5.

- 536 Beauchamp G. 2001. Consistency and flexibility in the scrounging behaviour of zebra finches.
537 *Canadian Journal of Zoology* 79:540–544. DOI: 10.1139/cjz-79-3-540.
- 538 Beauchamp G. 2006. Phenotypic Correlates of Scrounging Behavior in Zebra Finches: Role of
539 Foraging Efficiency and Dominance. *Ethology* 112:873–878. DOI: 10.1111/j.1439-
540 0310.2006.01241.x.
- 541 di Bitetti MS., Janson CH. 2001. Social foraging and the finder's share in capuchin monkeys,
542 *Cebus apella*. *Animal Behaviour* 62:47–56. DOI: 10.1006/anbe.2000.1730.
- 543 Bugnyar T., Kotrschal K. 2002. Scrounging tactics in free-ranging ravens, *Corvus corax*. *Ethology*
544 108:993–1009. DOI: 10.1046/j.1439-0310.2002.00832.x.
- 545 Carter A., Torrents Ticó M., Cowlshaw G. 2016. Sequential phenotypic constraints on social
546 information use in wild baboons. *eLife*:1–21. DOI: 10.7554/eLife.13125.
- 547 Castles M., Heinsohn R., Marshall HH., Lee AEG., Cowlshaw G., Carter AJ. 2014. Social networks
548 created with different techniques are not comparable. *Animal Behaviour* 96:59–67. DOI:
549 10.1016/j.anbehav.2014.07.023.
- 550 Cheney DL. 1977. The acquisition of rank and the development of reciprocal alliances among
551 free-ranging immature baboons. *Behavioral Ecology and Sociobiology* 2:303–318. DOI:
552 10.1007/BF00299742.
- 553 Coolen I., Giraldeau L-A., Vickery W. 2007. Scrounging behavior regulates population dynamics.
554 *Oikos* 116:533–539. DOI: 10.1111/j.2006.0030-1299.15213.x.
- 555 Cowlshaw G. 1999. Ecological and social determinants of spacing behaviour in desert baboon

- 556 groups. *Behavioral Ecology and Sociobiology* 45:67–77. DOI: 10.1007/s002650050540.
- 557 Danchin E., Giraldeau L-A., Valone TJ., Wagner RH. 2004. Public information: from nosy
558 neighbors to cultural evolution. *Science* 305:487–491. DOI: 10.1126/science.1098254.
- 559 Dubois F., Giraldeau L-A. 2005. Fighting for resources: the economics of defense and
560 appropriation. *Ecology* 86:3–11. DOI: 10.1890/04-0566.
- 561 Dubois F., Giraldeau L-A., Grant JWA. 2003. Resource defense in a group-foraging context.
562 *Behavioral Ecology* 14:2–9. DOI: 10.1093/beheco/14.1.2.
- 563 Fawcett TW., Hamblin S., Giraldeau L-A. 2013. Exposing the behavioral gambit: The evolution of
564 learning and decision rules. *Behavioral Ecology* 24:2–11. DOI: 10.1093/beheco/ars085.
- 565 Giraldeau L-A., Caraco T. 2000. *Social foraging theory*. Princeton, NJ: Princeton University Press.
- 566 Giraldeau L-A., Dubois F. 2008. Social Foraging and the Study of Exploitative Behavior. *Advances*
567 *in the Study of Behavior* 38:59–104. DOI: 10.1016/S0065-3454(08)00002-8.
- 568 Grant JWA. 1993. Whether or not to defend? The influence of resource distribution. *Marine*
569 *and Freshwater Behaviour and Physiology* 23:137–153. DOI:
570 10.1080/10236249309378862.
- 571 Grant JWA., Guha RT. 1993. Spatial clumping of food increases its monopolization and defense
572 by convict cichlids, *Cichlasoma nigrofasciatum*. *Behavioral Ecology* 4:293–296. DOI:
573 10.1093/beheco/4.4.293.
- 574 Hammerstein P. 1981. The role of asymmetries in animal contests. *Animal Behaviour* 29:193–
575 205. DOI: 10.1016/S0003-3472(81)80166-2.

- 576 Hirsch BT. 2007. Costs and benefits of within-group spatial position: a feeding competition
577 model. *The Quarterly review of biology* 82:9–27. DOI: 10.1086/511657.
- 578 Holekamp KE., Smale L. 1991. Dominance Acquisition During Mammalian Social Development:
579 The “Inheritance” of Maternal Rank. *American Zoologist* 317:306–317. DOI:
580 10.1093/icb/31.2.306.
- 581 Huchard E., Alvergne A., Féjan D., Knapp LA., Cowlshaw G., Raymond M. 2009. More than
582 friends? Behavioural and genetic aspects of heterosexual associations in wild chacma
583 baboons. *Behavioral Ecology and Sociobiology* 64:769–781. DOI: 10.1007/s00265-009-
584 0894-3.
- 585 Huchard E., Charpentier MJ., Marshall HH., King AJ., Knapp LA., Cowlshaw G. 2013. Paternal
586 effects on access to resources in a promiscuous primate society. *Behavioral Ecology*
587 24:229–236. DOI: 10.1093/beheco/ars158.
- 588 Janson CH. 1985. Aggressive competition and individual food consumption in wild brown
589 capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology* 18:125–138. DOI:
590 10.1007/BF00299041.
- 591 Kaufmann J. 1983. On The Definitions and Functions of Dominance and Territoriality. *Biology*
592 *Review* 58:1–20. DOI: 10.1111/j.1469-185X.1983.tb00379.x.
- 593 King AJ., Cowlshaw G. 2009. All together now: behavioural synchrony in baboons. *Animal*
594 *Behaviour* 78:1381–1387. DOI: 10.1016/j.anbehav.2009.09.009.
- 595 King AJ., Isaac NJB., Cowlshaw G. 2009. Ecological, social, and reproductive factors shape

- 596 producer-scrounger dynamics in baboons. *Behavioral Ecology* 20:1039–1049. DOI:
597 10.1093/beheco/arp095.
- 598 Koops MA., Giraldeau L-A. 1996. Producer–scrounger foraging games in starlings: a test of rate-
599 maximizing and risk-sensitive models. *Animal Behaviour* 51:773–783. DOI:
600 10.1006/anbe.1996.0082.
- 601 Kotliar NB., Wiens JA. 1990. Multiple scales of patchiness and patch structure: a hierarchical
602 framework for the study of heterogeneity. *Oikos* 59:253–260.
- 603 Krause J., Ruxton GD. 2002. *Living in groups*. Oxford, UK: Oxford University Press.
- 604 Kurvers RHJM., van Oers K., Nolet BA., Jonker RM., van Wieren SE., Prins HHT., Ydenberg RC.
605 2010. Personality predicts the use of social information. *Ecology letters* 13:829–37. DOI:
606 10.1111/j.1461-0248.2010.01473.x.
- 607 Lea AJ., Learn NH., Theus MJ., Altmann J., Alberts SC. 2014. Complex sources of variance in
608 female dominance rank in a nepotistic society. *Animal Behaviour* 94:87–99. DOI:
609 10.1016/j.anbehav.2014.05.019.
- 610 Lee AEG., Ounsley JP., Coulson T., Rowcliffe JM., Cowlshaw G. 2016. Information use and
611 resource competition: an integrative framework. *Proceedings of the Royal Society B:
612 Biological Sciences*:20152550. DOI: <http://dx.doi.org/10.1098/rspb.2015.2550>.
- 613 Lendvai ÁZ., Liker A., Barta Z. 2006. The effects of energy reserves and dominance on the use of
614 social-foraging strategies in the house sparrow. *Animal Behaviour* 72:747–752. DOI:
615 10.1016/j.anbehav.2005.10.032.

- 616 Liker A., Barta Z. 2002. The effects of dominance on social foraging tactic use in house sparrows.
617 *Behaviour* 139:1061–1076. DOI: 10.1163/15685390260337903.
- 618 Łomnicki A. 2009. Scramble and contest competition, unequal resource allocation, and resource
619 monopolization as determinants of population dynamics. *Evolutionary Ecology Research*
620 11:371–380.
- 621 Marshall HH., Carter AJ., Coulson T., Rowcliffe JM., Cowlshaw G. 2012. Exploring foraging
622 decisions in a social primate using discrete-choice models. *The American Naturalist*
623 180:481–95. DOI: 10.1086/667587.
- 624 Maynard Smith J., Parker GA. 1976. The logic of asymmetric contests. *Animal Behaviour*
625 24:159–175. DOI: 10.1016/S0003-3472(76)80110-8.
- 626 McCormack JE., Jablonski PG., Brown JL. 2007. Producer-scrounger roles and joining based on
627 dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). *Behaviour*
628 144:967–982. DOI: 10.1163/156853907781492717.
- 629 McNamara JM., Green RF., Olsson O. 2006. Bayes' theorem and its applications in animal
630 behaviour. *Oikos* 112:243–251. DOI: 10.1111/j.0030-1299.2006.14228.x.
- 631 Morand-Ferron J., Giraldeau L-A., Lefebvre L. 2007. Wild Carib grackles play a producer
632 scrounger game. *Behavioral Ecology* 18:916–921. DOI: 10.1093/beheco/arm058.
- 633 Mottley K., Giraldeau L-A. 2000. Experimental evidence that group foragers can converge on
634 predicted producer-scrounger equilibria. *Animal Behaviour* 60:341–350. DOI:
635 10.1006/anbe.2000.1474.

- 636 Ohtsuka Y., Toquenaga Y. 2009. The patch distributed producer-scrounger game. *Journal of*
637 *Theoretical Biology* 260:261–266. DOI: 10.1016/j.jtbi.2009.06.002.
- 638 Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of*
639 *Theoretical Biology* 47:223–243. DOI: 10.1016/0022-5193(74)90111-8.
- 640 Parker GA. 1982. Phenotype-limited evolutionarily stable strategies. In: King's College
641 Sociobiology Group ed. *Current Problems in Sociobiology*. Cambridge, UK: Cambridge
642 University Press, 173–201.
- 643 R Core Team. 2013. *R: A language and environment for statistical computing*. Vienna, Austria: R
644 Foundation for Statistical Computing.
- 645 Rieucau G., Giraldeau L-A. 2011. Exploring the costs and benefits of social information use: an
646 appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society*
647 *B: Biological Sciences* 366:949–957. DOI: 10.1098/rstb.2010.0325.
- 648 Robb SE., Grant JWA. 1998. Interactions between the spatial and temporal clumping of food
649 affect the intensity of aggression in Japanese medaka. *Animal Behaviour* 56:29–34. DOI:
650 10.1006/anbe.1998.0735.
- 651 Robinette Ha R., Ha JC. 2003. Effects of ecology and prey characteristics on the use of
652 alternative social foraging tactics in crows, *Corvus caurinus*. *Animal Behaviour* 66:309–316.
653 DOI: 10.1006/anbe.2003.2182.
- 654 Rowell TE. 1966. Hierarchy in the organization of a captive baboon group. *Animal Behaviour*
655 14:430–443. DOI: 10.1016/S0003-3472(66)80042-8.

- 656 Searle KR., Hobbs NT., Shipley LA. 2005. Should I stay or should I go ? Patch departure decisions
657 by herbivores at multiple scales. *Oikos* 111:417–424. DOI: 10.1111/j.0030-
658 1299.2005.13918.x.
- 659 Silk JB., Beehner JC., Bergman TJ., Crockford C., Engh AL., Moscovice LR., Wittig RM., Seyfarth
660 RM., Cheney DL. 2010. Strong and consistent social bonds enhance the longevity of female
661 baboons. *Current biology : CB* 20:1359–61. DOI: 10.1016/j.cub.2010.05.067.
- 662 Stahl J., Tolsma PH., Loonen MJJE., Drent RH. 2001. Subordinates explore but dominants profit:
663 resource competition in high Arctic barnacle goose flocks. *Animal behaviour* 61:257–264.
664 DOI: 10.1006/anbe.2000.1564.
- 665 Teichroeb JA., White MMJ., Chapman CA. 2015. Vervet (*Chlorocebus pygerythrus*) Intragroup
666 Spatial Positioning: Dominants Trade-Off Predation Risk for Increased Food Acquisition.
667 *International Journal of Primatology* 36:154–176. DOI: 10.1007/s10764-015-9818-4.
- 668 Theimer TC. 1987. The effect of seed dispersion on the foraging success of dominant and
669 subordinate dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour* 35:1883–1890. DOI:
670 10.1016/S0003-3472(87)80081-7.
- 671 Vahl WK., Lok T., van der Meer J., Piersma T., Weissing FJ. 2005. Spatial clumping of food and
672 social dominance affect interference competition among ruddy turnstones. *Behavioral*
673 *Ecology* 16:834–844. DOI: 10.1093/beheco/ari067.
- 674 Valone TJ. 1989. Group foraging, public information, and patch estimation. *Oikos* 56:357–363.
675 DOI: 10.2307/3565621.

- 676 Valone TJ. 2006. Are animals capable of Bayesian updating? An empirical review. *Oikos*
677 112:252–259. DOI: 10.1111/j.0030-1299.2006.13465.x.
- 678 Valone TJ., Templeton JJ. 2002. Public information for the assessment of quality: a widespread
679 social phenomenon. *Philosophical Transactions of the Royal Society B: Biological Sciences*
680 357:1549–1557. DOI: 10.1098/rstb.2002.1064.
- 681 Vickery WL., Giraldeau L-A., Templeton JJ., Kramer DL., Chapman CA. 1991. Producers,
682 scroungers, and group foraging. *The American Naturalist* 137:847–863. DOI:
683 10.1006/anbe.1996.0014.
- 684 Wiens JA. 1976. Population Responses to Patchy Environments. *Annual Review of Ecology and*
685 *Systematics* 7:81–120. DOI: 10.1146/annurev.es.07.110176.000501.
- 686

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.

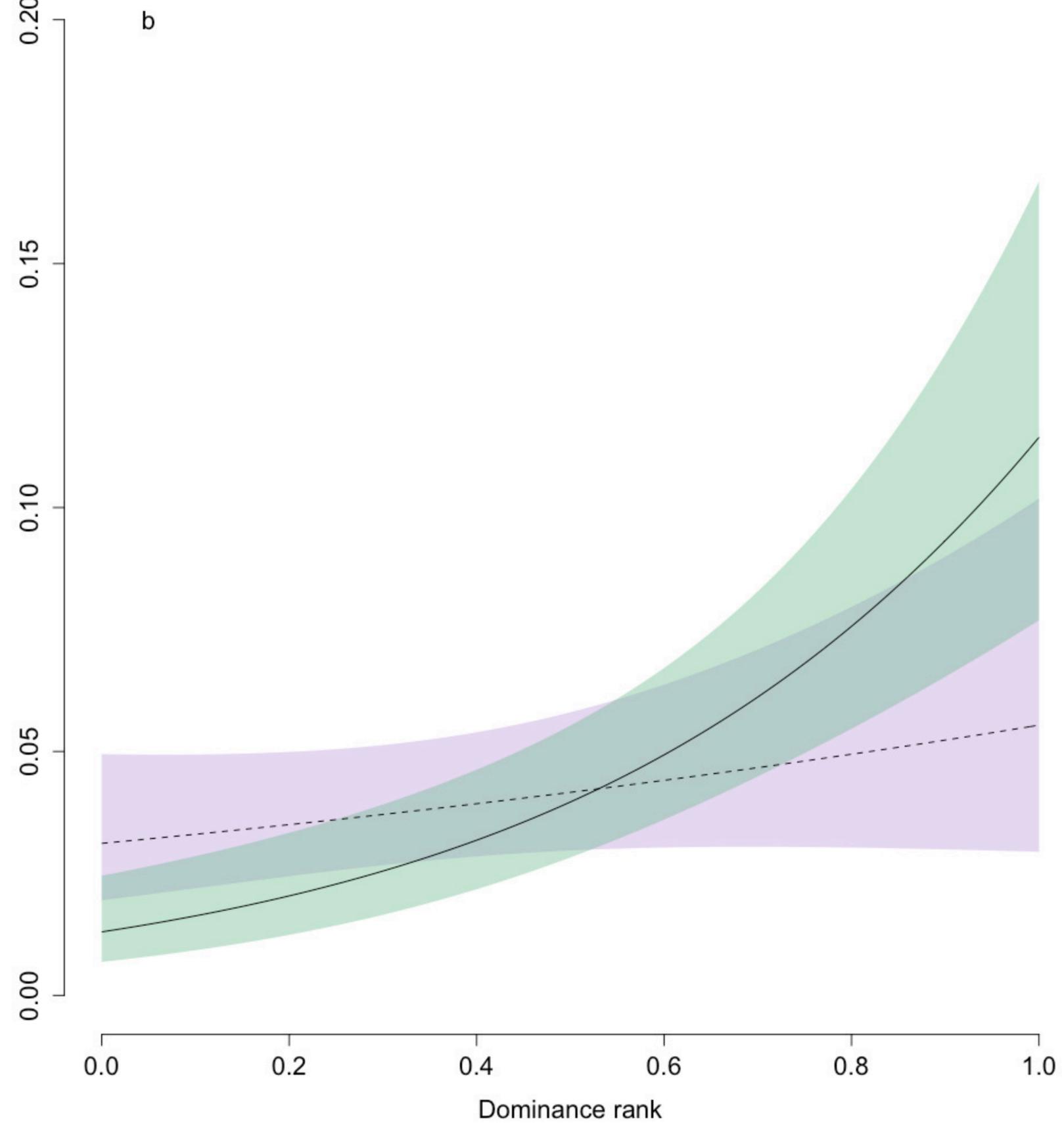
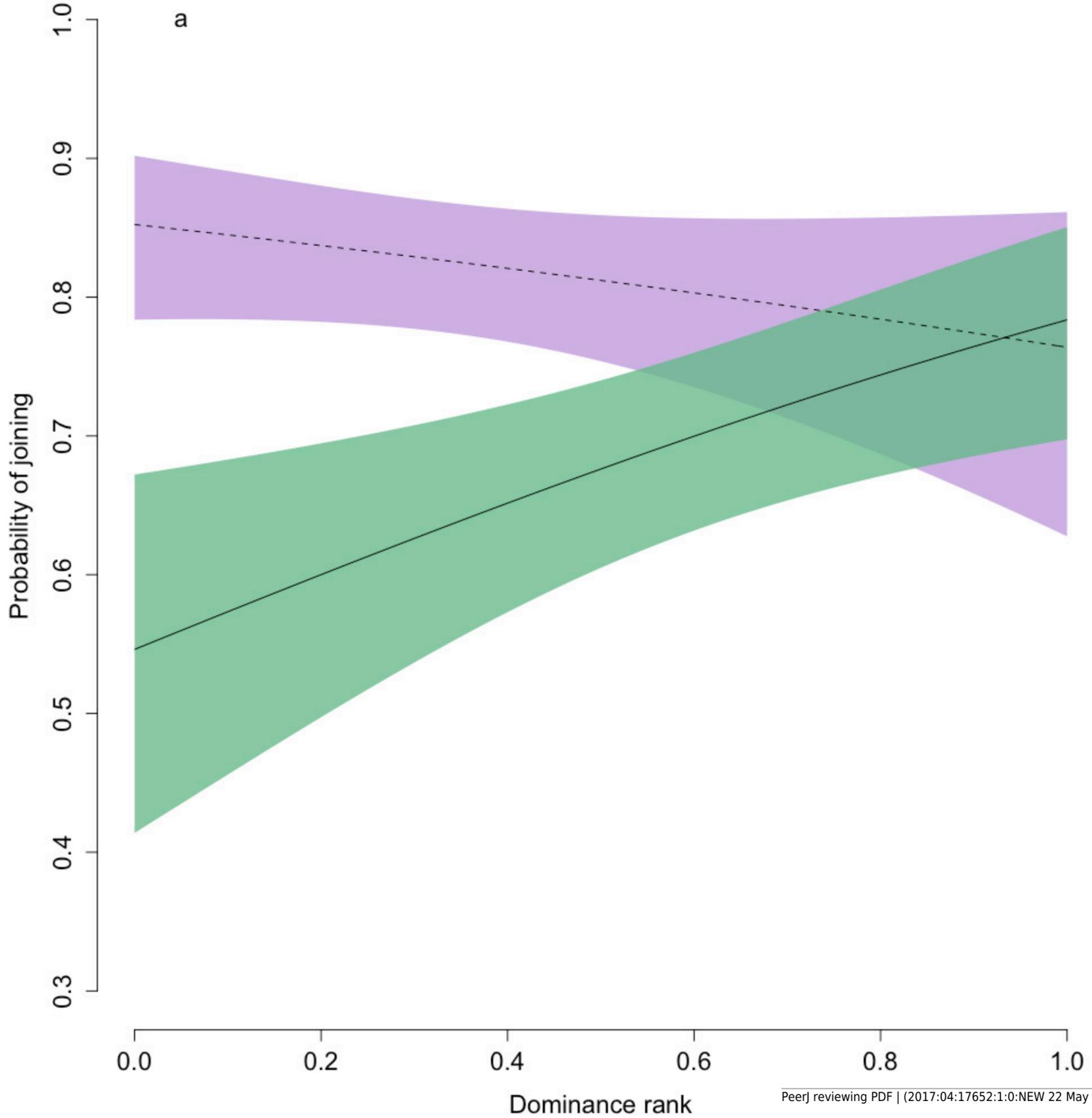


Figure 2 (on next page)

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.

