

## 1 **Title**

2 Biological Markets in Cooperative Breeders: Quantifying Outside Options

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## 13 **Media summary**

14 In many animal societies, only one or a few individuals breed, while others help to raise  
15 their offspring. Traditionally, individuals were thought to help because breeding alone  
16 was their only alternative – an often unfeasible task. However, we now show that paper  
17 wasp helpers have other options: they can start new groups with other partners or join  
18 neighbouring groups where they have good chances of becoming breeders themselves.  
19 Helpers thus have options that give higher evolutionary fitness than breeding alone.  
20 Traditional cooperative theory therefore overestimates the incentives for helping, and  
21 biological market theory, which incorporates partner choice, may be more appropriate.

## 22 **Abstract**

23 A major aim in evolutionary biology is to understand altruistic help and reproductive  
24 partitioning in cooperative societies, where subordinate helpers forego reproduction to  
25 rear dominant breeders' offspring. Traditional models of cooperation in these societies  
26 typically make a key assumption: that the only alternative to staying and helping is  
27 solitary breeding, an often unfeasible task. Using large-scale field experiments on paper  
28 wasps (*Polistes dominula*), we show that individuals have high quality alternative  
29 nesting options available that offer fitness payoffs just as high as their actual chosen  
30 options, far exceeding payoffs from solitary breeding. Furthermore, joiners could not  
31 easily be replaced if they were removed experimentally, suggesting that it may be costly  
32 for dominants to reject them. Our results have implications for expected payoff  
33 distributions for cooperating individuals and suggest that biological market theory,  
34 which incorporates partner choice and competition for partners, is necessary to  
35 understand helping behaviour in societies like *P. dominula*. Traditional models are likely  
36 to overestimate the incentive to stay and help and therefore the amount of help  
37 provided, and may underestimate the size of reproductive concession required to retain  
38 subordinates. These findings are relevant for a wide range of cooperative breeders  
39 where there is dispersal between social groups.

## 40 **Keywords**

41 Social insects, Economics, Partner choice, Competition, Group living, Trade

42

## 43 **Introduction**

44 Altruistic helping behaviour occurs throughout the animal kingdom despite costs to  
45 helpers' direct fitness. In cooperatively breeding animals, subordinates care for, defend  
46 and provision the offspring of dominant breeders, while foregoing or delaying their own  
47 reproduction (1, 2). A range of factors has been identified to explain the evolution and  
48 maintenance of this phenomenon, including both direct fitness benefits, such as  
49 inheritance of the breeding position (3, 4), and indirect fitness benefits obtained  
50 through helping a relative (5, 6). However, there is an increasing awareness in the  
51 literature of the limitations of traditional theoretical models, and a call for more  
52 complex models that more realistically describe the social environment of individuals  
53 (7-12). Specifically, traditional models predicting the level of help and reproductive  
54 skew in cooperative breeders often make a key assumption: that a subordinate helper's  
55 only alternative to staying and helping in its current group is to leave and breed  
56 solitarily (13-18). However, breeding alone is often unfeasible or highly risky (3, 19,  
57 20), leading to the prediction that subordinates should accept a high workload and a  
58 small share or zero part of the reproduction, in order to remain in the group.

59         Recent literature increasingly suggests that in order to correctly estimate the  
60 costs and benefits associated with staying and helping in a group, one must compare the  
61 payoffs of that decision with an individual's true alternative options (7, 8, 11, 21). In  
62 reality, a subordinate's alternative options may include switching to another group or  
63 recruiting other cooperative partners to initiate a new breeding group (11, 20, 22, 23).  
64 If such alternative options could lead to higher fitness payoffs than solitary breeding,  
65 payoff distributions may have been miscalculated in past studies, overestimating the  
66 incentive for subordinates to stay and help. Hence, future studies are encouraged to  
67 include the following: partner choice rather than partner control, where sanctioning of

68 uncooperative partners is replaced by partner switching (12, 23-25); outside options  
69 beyond solitary breeding (9, 10); asymmetric relationships where the exchange of  
70 behaviours is more valuable for one of the parties (21, 26, 27); and N-player  
71 interactions not achievable in traditional 2-player cooperative games (21, 28). These  
72 modifications can be achieved by invoking biological market models (21). Biological  
73 market theory predicts that competition for cooperative partners will affect the value of  
74 commodities exchanged between individuals of different trader classes (9, 10). In  
75 cooperative breeders, subordinates may be seen as effectively exchanging helping  
76 behaviour for group membership (15, 29, 30), and the value of helping behaviour may  
77 therefore be affected by the supply of and demand for help in the market. Subordinates  
78 may be described as 'paying-to-stay' (30-32) or dominants as 'paying-for-help' (33, 34),  
79 depending on which commodity is in focus. For example, when there is competition  
80 among dominants for a limited supply of helpers so that help is in high demand,  
81 dominants may be willing to accept subordinates paying less for group membership  
82 through reducing their work efforts. Similarly, dominants might be willing to pay more  
83 for help by granting a higher share of reproduction to subordinates (9, 10, 22, 33, 34).

84         Several studies of cooperatively breeding mammals (31, 33, 34), fishes (32, 35,  
85 36), birds (30, 37, 38) and insects (22) have found support for the concept that  
86 dominants and subordinates exchange commodities as described above. In the  
87 cooperatively breeding paper wasp, *Polistes dominula*, we previously reported data  
88 consistent with the hypothesis that dominants have to accept a lower payment from  
89 their subordinates when competition for help is increased in the population (22). We  
90 first showed that wasps had outside options and a choice of cooperative partners. We  
91 then experimentally increased the amount of outside options available to subordinates  
92 and found that subordinates, as a result, decreased their work efforts (22). These

93 results suggest that there is a biological market in this species where the supply of  
94 outside options affect the exchange of cooperative behaviours within groups. However,  
95 in order to wholly understand the dynamics between dominants and subordinates, we  
96 need to know not only the number of alternative options available but also their quality.  
97 Only by evaluating the attractiveness of outside options will the behavioural decisions  
98 of cooperative partners be clear. Here, we quantify the outside options available to *P.*  
99 *dominula* wasps and estimate the fitness payoffs associated with these options. We  
100 further evaluate how partner choice may affect the payoff distribution between  
101 cooperative partners, and assess the implications this may have for cooperative theory.

102         The nesting behaviour and social organisation of *P. dominula* is well studied, and  
103 our study sites offer large samples of small groups (8, 22, 39). At these sites, thousands  
104 of mated females from the same generation emerge simultaneously from hibernation in  
105 early spring and found hundreds of nests along cactus hedges (*Opuntia ficus-indica*).  
106 Groups of typically fewer than 10 females and small numbers (~6.4% of all females in  
107 (40)) of solitary breeders rear workers that mature during late spring and early  
108 summer. Here we focus on the pre-worker stage where groups of similar-aged females  
109 live as cooperative breeders. The dominant breeder lays all or most of the eggs, while  
110 subordinates build and expand the nest, forage and help care for the offspring of the  
111 dominant (41). Nest residents often consist of genetically related individuals (sisters  
112 and cousins), but a significant proportion of subordinates are unrelated to the dominant  
113 they are helping (42-44). The chance of inheriting the breeding position or obtaining a  
114 small share of the reproduction has been used to explain the presence of unrelated  
115 helpers in this species: Leadbeater et al (2011) found that the amount of direct fitness  
116 obtained as a subordinate was greater than through solitary breeding (3). However, if  
117 helpers have alternative options available that offer higher fitness payoffs than solitary

118 breeding, the incentive to stay and help in their current groups may previously have  
119 been overestimated.

120 We ask the following questions: i) Do available nesting options include high-  
121 payoff alternatives? Alternative options will affect the predictions of existing models  
122 only if they offer a higher payoff than solitary nesting; ii) Do alternative options differ  
123 from observed choices in ways that should affect direct and indirect fitness, such as  
124 inheritance rank and relatedness to the dominant? We predict that alternative options  
125 are inferior to observed choices: in a biological market, individuals are expected to  
126 assess their options and make the choice that offers the highest payoff (10); iii) Is it  
127 costly for dominants to reject an additional cooperative partner? We expect help to be  
128 in high demand because productivity and group survival increase with the number of  
129 helpers in *P. dominula* (3, 22), so we predict that rejecting a joiner represents a cost to  
130 dominant breeders.

## 131 **Methods**

### 132 **Study species, field site and handling of animals**

133 *Polistes dominula* is a primitively eusocial (cooperatively-breeding) wasp lacking  
134 morphological castes. At our field site, females from the same generation found nests in  
135 early spring after overwintering. The first female offspring to mature in late spring  
136 become workers and those maturing during summer mate and overwinter, to restart  
137 the cycle next spring (3).

138 Experiments were carried out in a rural area in Southern Spain, close to Conil de  
139 la Frontera, Cadiz (N 36°17'10.9" W 6°03'57.8") (3, 22) during two field seasons:  
140 March-May 2013 and 2014. We tagged and numbered a total of ~700 nests: ~475 nests  
141 in two subpopulations in 2013 and ~225 nests in 2014 from one subpopulation (Fig 1,

142 same data as used for ‘the partner choice experiment’ in (22)). We further recorded the  
143 location of all nests along three axis (to nearest 5cm) allowing us to calculate the  
144 distances between nests in a 3D space.

145 Combining the two field seasons, individuals from ~200 of these nests were  
146 collected during early mornings, before sunrise (6.00-7.00). In the laboratory we gave  
147 each wasp a unique code of four coloured dots on her thorax using enamel paints;  
148 measured the length of one of her wings to the nearest 0.1 mm; and obtained a DNA  
149 sample by cutting the tarsus from a middle leg. Tarsus samples were kept in 100%  
150 ethanol at ~4°C until used for genotyping. Wasps were released close to their nests the  
151 same morning before 11.00. When wasps were permanently removed as a part of an  
152 experimental treatment they were either freeze-killed or released at a field site 2.5km  
153 away: none returned to her original site.

#### 154 **Experimental setup**

155 The day after nest residents were marked on a nest, we checked the nest in the evening  
156 for additional, unmarked residents. Any unmarked residents were collected the  
157 following morning and marked as described above. Once all nest residents were  
158 marked, we started daytime and evening censuses. Daytime censuses consisted of 3-4  
159 spot-checks per day (min. 30 min between each census) on sunny days every 2-4 days,  
160 where the presence or absence of nest residents were recorded during the main  
161 foraging period (11.00-17.00). From the daytime censuses we identified the social rank  
162 of each resident in the linear dominance hierarchy: the dominant breeder spends the  
163 most time on the nest while the lowest ranked individual spends the most time away  
164 from the nest foraging (45).

165 In the evenings, nest residents return to their nests for the night. During evening  
166 censuses (18.00-20.00), performed every 2-4 days, we searched focal nests for new

167 joiners. To mark a new joiner with minimal disturbance, we carefully applied a single  
168 pink paint dot to its abdomen while it was on the nest (day 0 of the Joiner Experiment).  
169 We videoed a subset of 21 focal nests on day 1 for three hours during the main foraging  
170 period (11.00-17.00). The following morning (day 2), we caught and marked the joiner  
171 as described above. On day 3 we confirmed the presence of the joiner during an evening  
172 census, so that we could plan to apply treatment the following morning (day 4;  
173 treatment morning). If the joiner was not present on its nest during one of these checks,  
174 we looked for it on the nest for a maximum of three days. If the joiner re-appeared  
175 within this period we continued with the next step of the procedure; if it did not we  
176 resumed normal censuses of the nest.

177         On the morning of treatment in the Joiner Experiment, we applied one of three  
178 treatments ( $N$  treated focal nests = 62): 1) **Joiner's first choice**: This was our control  
179 treatment where the joiner was allowed to stay and no nest residents were removed; 2)  
180 **Joiner's second choice**: We removed the joiner's first nest choice by permanently  
181 removing the nest and all of its residents, while immediately releasing the joiner itself. If  
182 any established residents were absent from the nest, we left the nest *in situ* for a  
183 maximum of 48 hours before removing it, allowing us to attract and remove remaining  
184 residents; 3) **Joiner removal**: We permanently removed the joiner (or both joiners if  
185 two had joined) while releasing all other residents near to the nest.

186         In addition to applying one of the three described treatments, we also recorded  
187 the presence of all residents on focal nests by collecting all wasps on their nest,  
188 recording their IDs, and releasing individuals immediately according to treatment. We  
189 further performed a brood census on each focal nest, which included counting the  
190 number of cells, and categorising the development of brood within each cell. Nest-level  
191 brood values were later summed as follows: small larva (given a value of 1.5), medium



192 larva (2), large larva (3) and pupa (4); a cell without a larva or pupa was assumed to  
193 contain an egg (1).

194 In addition to the Joiner Experiment, we carried out a Subordinate Experiment  
195 similar to Treatment 2 (Joiner's second choice), but using established low-ranking  
196 subordinates, rather than new joiners, from a separate set of nests. In each of 34 nests  
197 that had not received joiners during our observations, we chose one of the lowest  
198 ranking subordinates and released it after removing the nest and the remaining nest  
199 residents, as in the Joiner Experiment, Treatment 2.

200 Following the treatments, we searched for released joiners and subordinates in  
201 all nests in the sub-populations during daytime and evening censuses every 2-4 days.  
202 When a released individual was found on a new host nest with unmarked residents, we  
203 waited 2-3 days and then collected and marked the residents. We also resumed daytime  
204 censuses on all focal nests (including these new host nests) 2-3 days after treatment,  
205 and performed brood census as described above every 10-15 days. We discontinued all  
206 censuses on a nest when its first worker matured.

### 207 **Video analysis**

208 Each video was watched by one of seven people who recorded when nest residents left  
209 and returned to the nest, and all behavioural interactions. Observers were all trained by  
210 one person, who spot-checked for consistency. Behavioural interactions were ranked  
211 according to level of aggressiveness: antennation (given a value of 1), food sharing (2),  
212 and aggression (3; including all more aggressive encounters such as bite, chew and  
213 lunge). Two aggression values were calculated for each individual: the sum of values for  
214 all behaviours initiated and the sum of values for all received behaviours during the full  
215 video recording.

216 Foraging returns brought back to the nest were ranked according to value in the  
217 following way: nothing visible (given a value of 0), nesting material (1), liquid food, as  
218 evidenced by trophallaxing (2), or a solid food ball (3). Foraging return values were  
219 calculated for each individual as the sum of values during the full video recording.

## 220 **Genotyping and relatedness**

221 Protocols were identical to those described previously (22). Briefly, DNA was extracted  
222 from tarsus samples and samples were genotyped at nine microsatellite loci used  
223 previously in studies of the same population (3, 22, 44, 46, 47). Each locus had between  
224 6 and 51 different alleles in our samples (median in 2013 = 13; median in 2014 = 11).  
225 All loci were amplified in a single multiplex reaction using the Qiagen multiplex PCR kit  
226 (Qiagen, Venlo, The Netherlands).

227 Relatedness 5.0.8 software (48) was used to calculate relatedness between  
228 joiners and nest residents as in (22). The Full Sibship Reconstruction procedure in  
229 Kingroup v2 software (44, 49) was used to identify groups of sisters among the nests in  
230 each block (primary hypothesis: haplodiploid sisters; null hypothesis: haplodiploid  
231 cousins)(3). We then counted the number of sisters each resident had in its own nest  
232 and in other nests. Only individuals with at least 6 out of 9 loci scored successfully were  
233 used (median number of successful loci per sample = 9); 1996 out of 2011 wasps were  
234 successfully genotyped.

## 235 **Statistics**

236 All statistical analyses were performed using the statistical software R (50). Whenever  
237 appropriate, non-parametric tests were used, and whenever the effect of more than one  
238 predictor was tested, GLMs (Generalized Linear Models) or GLMMs (Generalized Linear  
239 Mixed Models) were used (51). For count data we used poisson error and tested for  
240 overdispersion: negative binomial error was used if models were overdispersed, and

241 again we tested to ensure these models were no longer overdispersed before  
242 proceeding. For models with continuous data we used a Gaussian error structure and  
243 checked to ensure that residuals were homogenous and normally distributed. Non-  
244 significant predictor variables ( $p > 0.05$ ) were removed from full models in order to  
245 obtain more reliable  $p$ -values for the remaining predictors. When analysing data from  
246 video recordings, we incorporated nest ID and the ID of the person watching the video  
247 as random effects. When analysing aggression and foraging return values we used the  
248 glmmADMB package (52) to build GLMMs with negative binomial error. This package  
249 further allowed us to account for zero-inflation in the aggression models.

## 250 **Results**

### 251 **Joiners' alternative options**

252 We permanently removed the first nest choices of 32 joiners and recovered 25 (78.1%)  
253 of them on their second nesting choices. Of these 25 second-choice joiners, 18 joined  
254 other established nests, 3 initiated new nests with other females, 3 joined nests of  
255 unknown ages, and only a single joiner definitely initiated a new nest alone.

256 Out of 21 second-choice joiners with known fates, 6 (28.6%) became the  
257 dominant breeder on their second-choice nest after joining or initiating it; the  
258 remaining 15 (71.4%) became subordinates. A first-choice joiner became the dominant  
259 breeder on 2 out of 14 control nests (14.3%) after joining. Thus, more joiners tended to  
260 become dominant through their second nest choice than through their first, although  
261 this difference was not significant (soon after joining: Chi-squared with Yates's  
262 correction = 0.33,  $df = 1$ ,  $p = 0.57$ ; at worker maturation: Chi-squared with Yates's  
263 correction = 0.70,  $df = 1$ ,  $p = 0.10$ ).

264 Joiners' second choices were similar to their first choices in terms of other  
265 factors expected to affect fitness payoffs: Firstly, there was no difference between first-  
266 and second-choice joiners in the social rank they obtained after joining, correcting for  
267 group size (Fig 2a; GLM, poisson error;  $y$  = social rank after treatment; main effects:  
268 treatment:  $z = 0.26, p = 0.80$ , group size:  $z = 3.32, p < 0.001$ , interaction between  
269 treatment and group size:  $z = 0.95, p = 0.34, N = 36$ ). Secondly, there was no difference  
270 between first- and second-choice joiners in terms of the joiners' genetic relatedness to  
271 the dominant in the group they joined (comparing first- and second-choice joiners after  
272 treatment: Mann-Whitney U test:  $W = 73, p = 0.64, N = 26$ ; comparing second-choice  
273 joiners' first and second nest choices: Wilcoxon Paired,  $V = 19, p = 0.95, N \text{ pairs} = 8$ ), or  
274 in the number of sisters they had in the group, correcting for group size (Fig 2b; GLM,  
275 negative binomial error;  $y$  = number of sisters after treatment; main effects: first- vs.  
276 second-choice joiners:  $z = 0.038, p = 0.97$ , group size:  $z = 3.31, p < 0.001$ , the interaction  
277 between treatment and group size:  $z = -1.41, p = 0.16, N = 40$ ;  $y$  = number of sisters of  
278 second-choice joiners; main effects: first vs. second choice:  $z = -0.97, p = 0.33$ , group  
279 size:  $z = 3.68, p < 0.001$ , the interaction between choice and group size:  $z = 0.09, p =$   
280  $0.93, N = 22$ ). Thirdly, there was no difference between first-choice joiners, second-  
281 choice joiners and established nest residents in whether they stayed in their groups  
282 until worker maturation or had disappeared by this stage ( $Chi\text{-square} = 1.42, df = 2, p =$   
283  $0.49$ ; first-choice joiners: 14 out of 20 (70.0%); second-choice joiners: 12 out of 23  
284 (52.2%); established nest residents: 84 out of 141 (59.6%) stayed till worker  
285 maturation).

286 New nests of second-choice joiners were mainly located within a couple of  
287 meters of first nest choices (Fig 1; median = 1.21m, mean = 1.93m, max. = 8.9m). Seven  
288 out of 22 (31.8%) second-choice joiners chose the closest nest (of which 5 were

289 established nests and 2 were newly initiated). It was relatively common for wasps to  
290 visit other nests in the population. We spotted 194 of the 1603 marked wasps in the  
291 population (12.1%) on at least two different nests. Wasps visited nests that were  
292 located up to 54.6m away from their original nests, but >95% of them visited within a  
293 5m radius (median distance = 0.9m; mean distance = 2.2m).

#### 294 **Consequences of rejecting a joiner for established nest residents**

295 We removed one or two joiners from each of 16 joiner-removal nests (21 joiners  
296 removed). After treatment, more joiner-removal nests received extra joiners (7 out of  
297 16 nests: 43.8%) than did control nests where joiners were allowed to stay (2 out of 14  
298 nests: 14.3%). However, the difference in number of extra joiners received in the two  
299 treatments was not significant (Fig 3a; Mann-Whitney U test:  $W = 91.5$ ,  $p = 0.37$ ,  $N = 30$ ),  
300 and the extra joiners received were not enough to replace those removed: control nests  
301 received significantly more joiners overall (including focal joiners) than joiner-removal  
302 nests did excluding removed focal joiners (Fig 3b; Mann-Whitney U test:  $W = 169$ ,  $p =$   
303  $0.014$ ,  $N = 30$ ).

304 Original dominants were no more likely to lose their dominant breeding  
305 positions in control nests where joiners were allowed to stay than in joiner-removal  
306 nests. After treatment, the dominant lost her breeding position in 4 out of 13 (30.8%)  
307 control nests and in 4 out of 15 (26.7%) joiner-removal nests (*Chi-square with Yates's*  
308 *Correction* = 0,  $df = 1$ ,  $p = 1$ ). Additionally, established nest residents were no more likely  
309 to leave their nests after a joining event in control compared to joiner-removal nests  
310 (Mann-Whitney U test:  $W = 116.5$ ,  $p = 0.86$ ,  $N$  nests = 30).

311 Nest success, measured as date of worker maturation and as brood development  
312 at worker maturation, was not affected by treatment or by a switch in the dominant  
313 breeder's identity. Only the number of nest residents and brood development at the

314 time of treatment significantly affected brood development at worker maturation (both  
315 effects positive) (GLM,  $y$  = date of worker emergence; main effects: treatment:  $t = -0.50$ ,  
316  $p = 0.78$ , dominance-usurpation:  $t = 1.51$ ,  $p = 0.14$ , group size:  $t = -0.94$ ,  $p = 0.35$ , brood  
317 value at joining:  $t = -1.69$ ,  $p = 0.10$ ;  $y$  = brood value at worker emergence; main effects:  
318 treatment:  $t = 0.45$ ,  $p = 0.62$ , dominance-usurpation:  $t = 0.79$ ,  $p = 0.94$ , group size:  $t =$   
319  $3.59$ ,  $p = 0.0012$ , brood value at joining:  $t = 4.64$ ,  $p < 0.001$ ;  $N$  nests = 55).

### 320 **Behavioural interactions during joining events**

321 New joiners did not spend more time foraging than established subordinates, correcting  
322 for rank (GLMM; Gaussian error;  $y$  = time spent off the nest; main effects: joiner or  
323 subordinate:  $Chi\text{-}sq = 1.63$ ,  $p = 0.20$ , rank:  $Chi\text{-}sq = 95.57$ ,  $p < 0.001$ ). However, new  
324 joiners brought back a higher total value of foraging items than established  
325 subordinates, correcting for time spent foraging. In other words, forage value per time  
326 unit spent foraging was higher for recent joiners than for established subordinates. The  
327 amount of aggression that a joiner received also tended to be positively correlated with  
328 foraging return values, while relatedness between the joiner and the established nest  
329 residents had no effect on foraging returns (GLMM; negative binomial error;  $y$  = total  
330 foraging return value; main effects: joiner or subordinate:  $z = 2.73$ ,  $p = 0.0063$ ,  
331 aggression received:  $z = 1.71$ ,  $p = 0.088$ , time spent off the nest:  $z = 1.75$ ,  $p = 0.080$ ,  
332 average relatedness between joiner and residents:  $z = -1.47$ ,  $p = 0.14$ ). Recent joiners  
333 that later became the dominant breeders on their nests worked less hard during video  
334 recordings than joiners that remained subordinate ( $N = 19$ ;  $y$  = foraging return value  
335 per time unit; *Wilcoxon's*  $W = 8.5$ ,  $p = 0.043$ ).

336 Joiners neither received nor initiated more aggression than other nest residents,  
337 and average relatedness between joiner and residents did not affect aggression levels  
338 (GLMM; negative binomial error;  $y$  = aggression received; main effects: joiner or

339 resident:  $z = 1.41, p = 0.16$ ; number of days after joining:  $z = -0.20, p = 0.84$ ; relatedness  
340 between joiner and residents:  $z = 0.33, p = 0.74$ ; time spent on the nest:  $z = 3.52, p <$   
341  $0.001$ ;  $y =$  aggression initiated; main effects: joiner or resident:  $z = -1.11, p = 0.27$ ,  
342 number of days after joining:  $z = -0.83, p = 0.41$ , relatedness between joiner and  
343 residents:  $z = 0.22, p = 0.82$ , time spent on the nest: initiated:  $z = 10.19, p < 0.001$ ;  $N$   
344 *wasps* = 142,  $N$  *nests* = 21).

### 345 **Established subordinates' alternative options**

346 Of 34 released subordinates, we relocated 18 (52.9%) on their second nesting choices:  
347 10 joined other established nests; 3 initiated a new nest with each other; 4 joined nests  
348 that could have been either established or new; only a single subordinate nested  
349 solitarily (taking over an abandoned nest). As with the second-choice joiners, the  
350 second nesting choices of released low-ranking subordinates were no different than  
351 their first choices with regard to inheritance rank obtained and presence of sisters  
352 (ranks: Wilcoxon paired,  $V = 63.5, p = 0.22, N = 15$ ; presence of sisters: Chi-squared with  
353 Yates's correction = 0,  $df = 1, p = 1$ ). Released subordinates also mainly chose their new  
354 nests within a couple of meters (median = 1.30m; mean = 1.42m; max = 3.37m).

## 355 **Discussion**

### 356 **Joiners had high-payoff alternative options**

357 We quantified the outside options available to cooperatively breeding paper wasps, *P.*  
358 *dominula*, and found that at the time of joining a nest, individuals had alternative  
359 options that offered potentially high fitness payoffs. After we experimentally removed  
360 their first nest choices, joiners' second nesting choices included a >1:4 chance of  
361 obtaining the dominant breeding position in a social group, which is the highest-payoff  
362 possible in this species. This means that outside options offered much greater fitness

363 payoffs than solitary nesting: at our field site, the payoff from solitary nesting is close to  
364 zero due to extremely high nest failure rates (>90% of solitary nests fail (3, 40, 53)).  
365 This result shows clearly that partner choice in *P. dominula* has the potential to affect  
366 payoff distributions in models predicting the amount of help provided by subordinates  
367 (7, 21) or the amount of reproduction that dominants might have to concede to retain  
368 helpers (14, 42, 54). Simply comparing payoffs from observed helping decisions with  
369 those from a default solitary breeding option, as is traditionally done, is likely to greatly  
370 overestimate the relative benefit of staying and helping in the current group. When  
371 high-quality outside options exist, dominants may accept a lower subordinate work  
372 effort than traditional models would predict. Hence, we demonstrate that multiplayer  
373 models, such as those offered by biological market theory, are more appropriate than  
374 traditional models for understanding levels of help in cooperative breeders such as *P.*  
375 *dominula* (7, 9, 21, 22).

### 376 **First and second nest choices offered similar payoffs**

377 Joiners and established subordinates did not necessarily have to settle for inferior  
378 payoff options, compared to their first nesting choice, when forced to make a second  
379 choice, contrary to our predictions. This result suggests that individuals had more than  
380 one relatively high-quality option available in the market. We found that direct fitness  
381 returns associated with the chances of usurping or inheriting the breeding position, as  
382 well as indirect fitness returns from helping a related dominant, were no smaller in  
383 second choices than in first nesting choices. We predicted that joiners should evaluate  
384 their options and choose the one that offered the highest fitness payoff (10, 21, 53).  
385 However, joiners may have insufficient information to make this choice: it is likely  
386 difficult for an individual to evaluate the exact chances of obtaining the breeding  
387 position in all nests in the market, prior to actually joining. Furthermore, there is little



388 evidence that females can discriminate relatedness at the individual level in this species  
389 (39, 44, 55) and thereby preferentially join relatives to maximise inclusive fitness.  
390 Indeed, both joiners and subordinates sometimes chose to join nests without sisters  
391 despite having sisters in nearby nests. These results suggest that joiners chose one of  
392 several options available to them, each offering relatively high payoffs, indicating that  
393 the biological market is large (22).

#### 394 **Rejecting a joiner may be costly for dominant breeders**

395 Experimentally removed joiners could not easily be replaced with new ones, suggesting  
396 that there is not an unlimited pool of potential joiners in the population (as was also  
397 found in *Polistes carolina* (20)). Additionally, nest success increased with the number of  
398 nest residents, substantiating previous findings that larger groups fare better (3, 40)  
399 and that it is in the interest of dominants to accept joiners, particularly related ones, in  
400 order to increase group size. Taken together, these results suggest that, as we predicted,  
401 it may be costly for dominants to reject joiners. Supporting this result, we found that  
402 original dominants were no more likely to lose their dominant breeding positions when  
403 joiners were allowed to stay, compared with when joiners were removed. Hence, by  
404 accepting a joiner, an original dominant does not necessarily incur a cost in terms of an  
405 increased risk of nest usurpation, as she already faces a risk of losing her breeding  
406 position to one of her established subordinates. Allowing joiners to stay also did not  
407 generally make established subordinates more likely to leave.

408         We thus propose that a dominant cannot afford to be too 'choosy' when  
409 presented with potential joiners: it is in her interest to increase group size (3), so long  
410 as the risk of the joiner usurping dominance is not too high. This potentially makes  
411 joiners the 'choosers' in the market (10), so that dominants are effectively competing  
412 with each other to attract a limited supply of joiners (22). Dominants may therefore be

413 prepared to accept a reduced workload from subordinates in order to retain them when  
414 competition for help increases in the population.

#### 415 **Joiners may pay for group membership**

416 Rather than using aggression, joiners may have used appeasement in the form of pay-  
417 to-stay in order to become accepted in their new nests. Within the first few days of  
418 joining, we found that joiners provided higher value forage than other subordinates on  
419 their nests, perhaps to “pay” for acceptance by the group. Furthermore, joiners were not  
420 involved in a disproportionate number of aggressive interactions, contrary to what  
421 would be expected if they were ‘forcing’ their acceptance as new residents. These  
422 results render support for the hypothesis that subordinates trade helping behaviour in  
423 return for group membership (15): when first arriving at a nest, a joiner may need to  
424 prove her worth and convey she does not represent a high risk of usurping the breeding  
425 position (15, 32).

426 An alternative to the general idea that a joiner works in exchange for group  
427 membership is that she works simply because any investment in the nest would directly  
428 benefit her if she later took over the dominant breeding position herself (‘group  
429 augmentation’ (56)). However, our findings do not support the hypothesis that  
430 subordinates are maximising only group augmentation benefits, because joiners that  
431 later became dominants worked *less* hard than those that remained subordinate. This is  
432 consistent with previous findings that group members higher up the hierarchy, and  
433 therefore more likely to inherit the dominant position, in fact work less hard than  
434 lower-ranked subordinates (45).

#### 435 **Sampling costs and prospecting**

436 Given that experimentally presented foreign conspecifics are normally attacked by nest  
437 residents (44), the lack of aggression towards new joiners suggests that residents may

438 have already been familiar with joiners, perhaps through previous visits by joiners to  
439 establish familiarity via 'prospecting behaviour' (11, 57). Individuals in cooperative  
440 species may benefit from maintaining a social network outside their current groups, by  
441 visiting and familiarising themselves with members of other groups. This prospecting  
442 behaviour can provide them with information about whether between-group dispersal  
443 would be beneficial, and maximise their chances of being accepted in the new group,  
444 should they be expelled from their current group, choose to leave or if their nest fails  
445 (11, 57, 58). Indeed, nests fail at high rates in *P. dominula* (3, 40), and prospecting  
446 behaviour may be common: we spotted 12.1% of marked wasps on at least two  
447 different nests. This number is similar to previous studies of the same population  
448 (~16% in (40) and ~14% in (22)).

449         However, prospecting behaviour is likely to be costly (59): visiting other groups  
450 requires time and energy that could otherwise be spent foraging. These costs, called  
451 sampling costs or searching costs in biological market terms (9, 10), are likely to limit  
452 the number of groups a subordinate wasp can maintain in its social network. Second  
453 choice joiners mainly chose options that were nearby. This may partly be because nests  
454 containing genetic relatives tend to be nearby, but greater costs of prospecting further  
455 afield could also contribute. In a scenario where sampling costs are very high, for  
456 example in a very low-density population where maintaining peaceful relationships  
457 with distant neighbouring groups would pose a high risk of predation or great energetic  
458 expenditure, market forces could fail to operate, as there might effectively be no outside  
459 options available (10). Hence, quantifying sampling costs and documenting the actual  
460 social networks that individuals gain through prospecting is an important avenue for  
461 further studies in this system.

## 462 **Conclusion**

### 463 **Invoking biological market models to include outside options**

464 Our key finding is that in a cooperatively breeding paper wasp, *P. dominula*, both new  
465 joiners and established subordinates have alternative nesting options that offer fitness  
466 payoffs comparable to their first nest choices and that are higher than the payoff  
467 through solitary nesting. The existence of multiple options with similar payoffs has  
468 important implications for the conditions that subordinates should accept in their  
469 groups; or in biological market terms, the deal settled on between trading partners. For  
470 example, high-quality outside options will affect the trade value of helping behaviour  
471 and therefore influence how much help subordinates are prepared to provide with  
472 rearing the dominant's offspring (22). Outside options may also determine whether  
473 subordinates should demand a share of the reproduction in return for their services in  
474 species where reproductive concessions are likely to occur (23, 60, 61). Hence, our  
475 findings clearly suggest that biological market models are indeed necessary for  
476 understanding helping behaviour in *P. dominula*. This result is relevant for a wide range  
477 of cooperatively breeding species where successful dispersal amongst groups occurs  
478 (for example cichlids (11), carrion crows (62), dwarf mongooses (60), and baboons  
479 (63)). Unlike traditional models, which assume that a subordinate's only alternative is  
480 solitary breeding, market models allow for partner choice, partner switching and  
481 competition for partners (9, 10). To conclude, traditional cooperative theory and  
482 reproductive skew models are therefore likely to overestimate subordinates' propensity  
483 to stay and help in their group, overestimate the level of help that they provide, and  
484 perhaps underestimate the level of reproductive concession the dominant should offer  
485 her helpers. Future studies should identify and quantify the alternative options

486 available and include these in models predicting the rate of exchange of cooperative  
487 behaviours within groups.

## 488 **Data sharing**

489 All data is made available online via Dryad [doi: 10.5061/dryad.58c8v ]

## 490 **Competing interests**

491 We have no competing interests.

## 492 **Authors' contributions**

493 LG carried out behavioural experiments in the field, analysed the data, participated in  
494 the design of the study and drafted the manuscript; JF designed the study, participated  
495 in conducting field experiments, and helped draft the manuscript. Both authors gave  
496 final approval for publication.

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656

657

658 **Figure Legends**

659

660 **Fig 1 Map of nests and second-choice joiners' moves:** Map of all nests in the three  
661 subpopulations used during two different field season in 2013 (left hand and middle  
662 sections) and 2014 (right hand section). Cactus hedges are indicated in green and nests  
663 as white Xs. Second-choice joiners' first nest choices are indicated in yellow and their  
664 second choices in red, with an arrow connecting the two.

665

666 **Fig 2 Joiners in their first and second nest choices:** Rank obtained by joiners (a) and  
667 the number of sisters (b) in their first-choice (blue) and second-choice nests (red);  
668 points have been slightly jittered along the X-axis. Grey lines indicate the parameter  
669 space boundaries: if dots lie on the horizontal lines, a joiner had become the dominant  
670 breeder, i.e. rank 1, (a) or had zero sisters in its nest (b); if dots lie on the steep lines,  
671 joiners had become the lowest ranked individuals (a) or had only sisters in the group  
672 (b). Stippled lines indicate simple regression lines for first-choice (blue) and second-  
673 choice (red) joiners.

674

675 **Fig 3 Number of joiners in focal nests:** The number of joiners received in first-choice  
676 (control) nests and in joiner-removal nests: (a) The number of extra joiners that arrived  
677 after treatment; (b) The total number of joiners received, including the treatment-  
678 joiners in control nests but excluding them in joiner-removal nest.

679