

1 **Larger group sizes facilitate the emergence and spread of innovations in a group-living bird**

2 **Benjamin J. Ashton<sup>1,2\*</sup>, Alex Thornton<sup>3</sup>, Amanda R. Ridley<sup>1</sup>**

3 <sup>1</sup>Centre for Evolutionary Biology, University of Western Australia, Perth, Australia

4 <sup>2</sup>School of Biological Sciences, University of Bristol, Bristol, United Kingdom

5 <sup>3</sup>Centre for Ecology and Conservation, University of Exeter, Penryn Campus, United Kingdom

6 \*Corresponding author – benjamin.j.ashton@hotmail.co.uk, Life Sciences Building, 24 Tyndall Ave,  
7 Bristol BS8 1TQ

8 **Abstract**

9 The benefits of group living have traditionally been attributed to risk dilution or the efficient  
10 exploitation of resources; individuals in social groups may therefore benefit from access to valuable  
11 information. If sociality facilitates access to information, then individuals in larger groups may be  
12 predicted to solve novel problems faster than individuals in smaller groups. Additionally, larger  
13 group sizes may facilitate the subsequent spread of innovations within animal groups, as has been  
14 proposed for human societies. We presented a novel foraging task (where a food reward could be  
15 accessed by pushing a self-shutting sliding door) to 16 groups of wild, cooperatively breeding  
16 Australian magpies, ranging in size from 2-11 individuals. We found a non-linear decline in the time  
17 taken for the innovative behaviour to emerge with increasing group size, and social information use  
18 facilitated the transmission of novel behaviour, with it spreading more quickly in larger groups  
19 compared to smaller groups. This study provides important evidence for a nonlinear relationship  
20 between group size and the emergence of innovation (and its subsequent transmission), in a wild  
21 population of animals. Further work investigating the scope and strength of group size-innovation  
22 relationships, and the mechanisms underpinning them, will help us understand the potential  
23 advantages of living in larger social groups.

24 **Key words**

25 Animal innovation, group size, pool of competence hypothesis

26 **Introduction**

27 The benefits of group living have been studied extensively for decades (Krause & Ruxton, 2002), and  
28 are often attributed to processes that help animals exploit resources more efficiently (e.g. social  
29 foraging (Galef & Giraldeau, 2001; Giraldeau & Caraco, 2000)), or reduce risks from threats such as  
30 predators (Silk, 2007). More recently, a growing body of evidence is lending support to the  
31 hypothesis that larger group sizes may also facilitate the emergence of innovative solutions to novel  
32 problems (Krause, Ruxton, & Krause, 2010; Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011).

33 Much of the evidence supporting a positive relationship between group size and problem-solving  
34 performance comes from studies on humans (Clément et al., 2013; Laughlin, Hatch, Silver, & Boh,  
35 2006). Evidence of this relationship in nonhuman animals is limited to a handful of studies, and has  
36 produced equivocal results (reviewed by Griffin & Guez (2015)). Some studies report positive effects  
37 of group size (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011), whereas others report negative  
38 effects (Griffin, Lermite, Perea, & Guez, 2013; Overington, Cauchard, Morand-Ferron, & Lefebvre,  
39 2009) or no effect (Thornton & Samson, 2012; Thornton & Malapert, 2009a).

40 A number of potential factors may generate a positive relationship between group size and the  
41 emergence of behavioural innovations. For instance, the presence of more group members may  
42 reduce neophobia and the need to invest in anti-predator vigilance, facilitating the exploitation of  
43 novel foraging resources (Griffin & Guez, 2015; Visalberghi & Addessi, 2000) (but see Stöwe *et*  
44 *al.*(2006)). Alternatively, studies of captive house sparrows (*Passer domesticus* (Liker & Bókony,  
45 2009)) and wild parid flocks (*Parus major* (Morand-Ferron & Quinn, 2011)) have argued in favour of  
46 the “skill pool” or “pool of competence” hypothesis, whereby group size effects on innovation are  
47 driven by greater phenotypic diversity within larger groups (Giraldeau, 1984; Giraldeau & Lefebvre,

48 1986). Larger groups are more likely to have a greater variation of individuals in terms of age,  
49 dominance rank, motor skills and neophobia, all of which have been found to influence innovative  
50 behaviour (Biondi, Bó, & Vassallo, 2010; Griffin & Guez, 2014; Keynan, Ridley, & Lotem, 2015;  
51 Thornton & Samson, 2012). However, the evidence for “pool of competence” effects in wild animal  
52 groups is limited to a single study (Morand-Ferron & Quinn, 2011).

53 In contrast to studies reporting positive associations between group size and innovation, Griffin *et al.*  
54 (2013) and Overington *et al.* (2009) found that larger group sizes inhibit innovative behaviour.  
55 Captive Carib grackles, *Quiscalus lugubris*, were slower to produce innovative solutions to a novel  
56 foraging task when in the presence of conspecifics (Overington *et al.*, 2009). Similarly, the innovative  
57 propensity of wild-caught Indian mynahs, *Acridotheres tristis*, was greater when alone than in the  
58 presence of five conspecifics, or in pairs (Griffin *et al.*, 2013). In addition, group size failed to explain  
59 the likelihood of wild meerkats, *Suricata suricatta*, interacting with (or solving) foraging tasks  
60 (Thornton & Samson, 2012; Thornton & Malapert, 2009a). Likewise, solitary ravens (*Corvus corax*)  
61 were more likely to approach novel objects compared to ravens in dyads or groups (Stöwe *et al.*,  
62 2006). Thus, although large groups may provide individuals with some benefits, increased levels of  
63 competition, scrounging and aggression could also reduce opportunities for innovation as group size  
64 increases (Overington *et al.*, 2009).

65 Although the effect of group size on the emergence of innovative behaviour is poorly understood,  
66 the effect of group size on the subsequent *spread* of novel information has received even less  
67 attention, particularly in wild animal populations. Once an innovative behaviour has emerged, naïve  
68 group members may learn it from experienced conspecifics (Aplin *et al.*, 2015). Evidence for social  
69 learning is well-documented across a wide range of taxa in both captive and wild conditions (for a  
70 comprehensive review see Hoppitt & Laland (2013)). However, the potential effect of group size on  
71 the rate at which novel information spreads through a group is unclear. Evidence from studies on  
72 humans suggests that innovations are transmitted more rapidly and effectively in larger

73 groups(Derex, Beugin, Godelle, & Raymond, 2013; Mithen, 1994); consequently, we predict that  
74 novel information will spread more rapidly in larger groups of non-human animals via social learning.  
75 In this study, we examined the relationship between group size and the emergence and subsequent  
76 spread of innovation in a wild population of colour-ringed and habituated Australian magpies  
77 (Western Australian subspecies *Cracticus tibicen dorsalis*; hereafter referred to as ‘magpies’).  
78 Magpies are large (250-400g) cooperatively breeding passerines that live in territorial groups ranging  
79 from 2-12 adults, in which multiple individuals of both sexes contribute to rearing offspring and  
80 territorial defence (Ashton, Ridley, Edwards, & Thornton, 2018; Edwards, Mitchell, & Ridley, 2015;  
81 Hughes et al., 2003; Kaplan, 2008; Mirville, Kelley, & Ridley, 2016; Pike, Ashton, Morgan, & Ridley,  
82 2019). Unlike other subspecies of Australian magpie, sex can be determined visually in Western  
83 Australian magpies because they are sexually dichromatic(Ashton et al., 2018). We presented a  
84 novel foraging task to magpie groups of differing sizes, whereby a food reward could be accessed by  
85 pushing a self-shutting sliding door either left or right. We predicted that (i) innovations would arise  
86 more rapidly in larger groups, and (ii) innovative behaviour would spread more rapidly in larger  
87 groups, facilitated by social learning.

## 88 **Materials and Methods**

### 89 **Study site & population.**

90 The study took place in the urban grassland areas of Guildford, Western Australia, during the  
91 breeding season from July to December 2014. The study population consists of 16 groups, ranging in  
92 size from two to 11 individuals (excluding fledglings). The study population is habituated to human  
93 presence, allowing detailed behavioural observations (<2m) and the presentation of novel foraging  
94 tasks(Ashton et al., 2018). In 11 out of the 16 groups (hereafter referred to as “core groups”,  $N = 65$   
95 birds), the majority of individuals are ringed, allowing individual identification. The remaining five  
96 groups are either partially ringed or contain no ringed individuals ( $N = 37$  birds). Over the course of

97 the study period all group sizes remained the same throughout the testing period. In order to  
98 determine the size and composition of unringed groups we waited until they were foraging in open  
99 parklands. Multiple trips confirmed stable group size in both ringed and unringed groups. All 16  
100 groups were included in analyses investigating the emergence of innovative behaviour, as individual  
101 identification was not necessary. However, groups containing mainly unringed individuals were  
102 excluded from further analyses investigating the spread and social transmission of innovative  
103 behaviour because individual identity could not be reliably confirmed in experimental trials.

#### 104 **Novel foraging task.**

105 To investigate the emergence of innovative behaviour, we presented 16 groups of magpies with a  
106 novel foraging task, similar to that used on other bird species previously (Aplin et al., 2015). To  
107 determine the role of group size in the natural emergence and spread of innovative behaviour we  
108 did not train specific individuals to act as “demonstrators”, unlike previous experiments (Aplin et al.,  
109 2015; Gunhold, Massen, Schiel, Souto, & Bugnyar, 2014; Gunhold, Whiten, & Bugnyar, 2014;  
110 Thornton & Malapert, 2009b); for example Aplin *et al.*(2014) trained individuals on a specific solving  
111 technique (either pushing left or right). The task consisted of a transparent plastic box containing  
112 grated mozzarella cheese as a food reward (Figure 1). The reward could be obtained by pushing a  
113 self-shutting sliding door either left or right. Elastic bands caused the door to re-set to the central  
114 (closed) position immediately after being released, thus preventing others from scrounging the food  
115 reward accessed by a ‘solver’ individual. To avoid devices being monopolised by a single dominant  
116 individual, we presented two identical devices to each of the 16 groups, in open parkland areas  
117 where they routinely forage. Devices were only presented when all members of the group were  
118 present within 20m, and were placed 2m apart in the middle of an area where the group was  
119 foraging. Each device contained sufficient food such that it did not become depleted during trials. All  
120 experimental trials were carried out as close to sunrise as possible (between 4:30am and 7:00am  
121 according to season). Experimental trials were recorded using a *Sony Handycam* (model HDR-

122 XR260VE), and transcribed via video analysis using the *Cybertracker* program on an *Asus Google*  
123 *Nexus 7* tablet. Of the 11 core groups, each ringed individual's behaviour was transcribed separately  
124 for each experimental trial at each group. All activity around the device was recorded, including time  
125 spent oriented towards the device, whether the bird made contact with the device, whether it  
126 attempted to obtain the food reward (both successful and unsuccessful attempts, i.e. pecking at the  
127 transparent box), and if successful, what direction it pushed the door. Any aggressive and submissive  
128 interactions between individuals during the trial were also recorded. Aggressive actions were  
129 defined as any dominant behaviour directed from one individual to another (e.g., pecking and  
130 chasing behaviour). Submissive behaviours included birds vocally and physically submitting (rolling  
131 onto their backs), as well as retreating from an approaching individual. Since neophobia may play an  
132 important role in the emergence of innovative behaviour, for each trial we also recorded each  
133 individual's latency to make contact with the device after coming within 5m of it. In addition, the  
134 identity of birds observing other individuals interacting with the device (whether they solved it or  
135 not, what direction they pushed the door) was also recorded. Individuals were quantified as  
136 observing if their head was oriented towards an individual interacting with the task, they were  
137 within 10m of the individual, their body was oriented towards the individual, they had an  
138 uninterrupted line of sight, and they were not engaging in any other activities at that time (Samson &  
139 Manser, 2016). 10% of trials were recorded by two people in order to determine inter-rater  
140 reliability of quantifying "observing" ( $N = 22$  novel foraging task trials). Intra-class correlation  
141 coefficients indicated a high level of reliability ( $ICC = 0.982$ ,  $P = <0.001$ ,  $N = 22$  trials). Experimental  
142 trials were terminated after 15 minutes, or when any group member left the trial (i.e. when an  
143 individual that had been interacting with the task moved more than 20m away from either of the  
144 two devices). Each group was presented with the devices until every individual in the group had  
145 learned to access food, up to a maximum of 7 trials, with 24hrs between each presentation (the  
146 number of trials ranged from 1-7, mean  $\pm SE = 3.1 \pm 0.49$ ). The order in which groups were initially  
147 presented with the device was selected randomly. Once initially selected, trials were carried out on

148 consecutive days at each group. To determine if reduction in the need for anti-predator vigilance  
149 may be the cause of a possible relationship between group size and the emergence of innovative  
150 behaviour, we monitored anti-predator behaviour (mobbing of predators, alarm calling, sentinel  
151 duty), but no such behaviour was observed during any experimental trial. In addition, behavioural  
152 focal follows were collected at the study site during the experimental period (20-minute behavioural  
153 activity focals, carried out on all individuals multiple times per week, for further details of focal  
154 follows see Edwards et al. (2015)), and the frequency of antipredator behaviour recorded was very  
155 low (mean  $\pm$  SE =  $0.067 \pm 0.018$  anti-predator events per 20 minute behavioural focal). Australian  
156 magpies are a large passerine with few natural predators(Johnstone & Storr, 2004); it is therefore  
157 unsurprising there were no antipredator behaviours observed during experimental trials.

#### 158 **Ethical Note**

159 All methods were performed in accordance with the University of Western Australia's guidelines and  
160 regulations, and were approved by the University of Western Australia Animal Ethics Office (ref:  
161 RA/3/100/1272).

#### 162 **Statistical analyses.**

##### 163 **Effect of group size on the emergence and spread of innovations.**

164 To determine whether innovative behaviour emerges more rapidly in larger groups we fit a non-  
165 linear, exponential regression between group size and the time taken for innovative behaviour to  
166 emerge (i.e. time until the task was first solved within each group, measured in seconds).

167 Secondly, we used a Cox proportional hazards regression model to investigate the effect of group  
168 size on the time taken for innovative behaviour to spread after initial emergence. A Cox proportional  
169 hazards regression was used so we could account for the fact that some individuals could have learnt  
170 the innovative behaviour if given more time. The response term used was the time taken for each  
171 individual to learn the innovative behaviour after initial emergence within the group (measured in

172 seconds). Following Harrison *et al.* (2018) we adopted a hypothesis-driven modelling approach,  
173 rather than constructing a global model, whereby we carried out a series of models each  
174 investigating the effect of a different ecological variable. Explanatory terms included were; group  
175 size, the number of innovators in the group at the time of solving (multiple innovators are possible in  
176 a group if individuals solved the task without having observed any other individual attempt the task),  
177 the sex ratio of adults in the group, and the number of aggressive and submissive interactions  
178 between individuals during experimental trials. It is also possible solving time might be influenced by  
179 differences in neophobia, so latency to interact with the task was also included as an explanatory  
180 term. We clustered the observations around group identity to account for interdependence in the  
181 data, because solving times within groups might be correlated. The initial innovators were removed  
182 from Cox proportional hazards regression models to ensure that we were only examining the spread  
183 rather than the initial emergence of innovation. We did not include age in analyses as we do not  
184 know the exact fledge date of the majority of adults in the study population, and there were too few  
185 juveniles and fledglings tested ( $N = 7$ ) to include age as a categorical term (adult vs juvenile).

#### 186 **Social transmission of door opening preferences.**

187 To examine whether magpies show any consistent side biases between pushing left or right on the  
188 device, we ran a binomial test on the initial innovators in each group. Only initial innovators were  
189 used in this analysis to control for social information use, which may influence the direction pushed  
190 for subsequent solvers.

191 To determine whether social information use influenced the direction in which observer birds  
192 pushed the door, we ran a GLMM to determine if observers were more likely to push the door in the  
193 same direction as the individual they first observed. The response term used was the direction first  
194 pushed by the solver (binary response term, right=1, left=0), explanatory terms were the direction  
195 pushed by the first individual they observed, sex (of the observer), and group size. Group identity  
196 was included as a random term. Analyses were conducted using IBM SPSS Statistics software



197 (version 22) and the survival package(Therneau, 2015) in R (v.3.1.1, <http://www.r-project.org>) was  
198 used for the Cox proportional hazards regression.

## 199 **Results**

### 200 **Do innovations emerge more rapidly in larger groups?**

201 We recorded a total of 1050 attempts to gain access to the food reward, including pecking and  
202 pushing the door, by 65 individuals across the 11 core groups. Of these 65 birds, 50 were successful  
203 in accessing food (rate of success = 76.92%). Of these 50, 21 were never seen to observe other birds  
204 solving, and so were classed as innovators. The number of innovators per group ranged from 1-4,  
205 mean  $\pm$  SE= 2.18 $\pm$ 0.33, and group size positively correlated with the number of innovators per  
206 group; Spearman's correlation,  $r = 0.637$ ,  $P = 0.035$ ,  $N = 11$ . At the group level, there was a non-  
207 linear decline in the time taken for the innovative behaviour to emerge, with innovative behaviour  
208 emerging more quickly in larger groups (exponential regression,  $r = 0.559$ ,  $P = 0.001$ , AIC = 146.7,  
209 Figure 2). It is worth noting an exponential model fits the data better than a linear model (linear  
210 regression,  $r = 0.428$ ,  $P = 0.006$ , AIC = 172.91  $N = 16$ ). This pattern remained when the data point for  
211 the group size of 2 was removed (exponential regression,  $r = 0.475$ ,  $P = 0.01$ , AIC = 132.85; linear  
212 regression,  $r = 0.395$ ,  $P = 0.01$ , AIC = 146.98).

### 213 **Do innovations spread more rapidly in larger groups?**

214 Following the initial innovation in each group, a Cox proportional hazards model revealed there was  
215 a significant effect of group size on the subsequent spread of innovative behaviour, whereby  
216 innovative behaviour spread more quickly in larger group sizes (Table 1, Figure 3).The number of  
217 innovators at the time of solving did not have a significant influence on the spread of innovative  
218 behaviour. Latency to approach the task and the number of aggressive or submissive interactions  
219 also did not influence the spread of innovative behaviour (Table 1).

### 220 **Does social information use play a role in the spread of innovations?**

221 Of the 11 core groups over all the trials, 44.62% of birds ( $N = 29$ ) solved the task after observing  
222 another individual successfully solve the task, 32.31% of birds ( $N = 21$ ) solved the task having not  
223 observed any individuals interact with the task, and 13.85% of birds ( $N = 9$ ) failed to solve the task. It  
224 was unknown if 9.23% of birds ( $N = 6$ ) solved the task due to them being unringed. When the  
225 innovative behaviour first emerged in groups, innovators were no more likely to push left ( $N = 3$   
226 individual innovators) or right ( $N = 8$ ), suggesting there was no intrinsic, population-level side bias  
227 (binomial test,  $P = 0.227$ ,  $N = 11$ ). However, individuals who solved the task after observing a  
228 successful attempt were significantly more likely to push the door in the same direction as the solver  
229 they first observed, rather than the alternative direction (Table 2). This trend remains when the  
230 initial observation is the door being pushed left ( $N = 7$  out of 8 individuals pushing the same way  
231 [87.5%], binomial test,  $P = 0.07$ ) and right ( $N = 17$  out of 21 individuals pushing the same way  
232 [80.95%], binomial test,  $P = 0.007$ ). The trend for pushing the same way when the initial observation  
233 is left is not significant, however the proportion of individuals pushing the same way is high (higher  
234 than when the initial observation was right), suggesting the lack of a significance may be due to a  
235 small sample size.

## 236 **Discussion**

237 Positive relationships between group size and the emergence of innovative behaviour have been  
238 suggested as a possible benefit of living in larger groups (Giraldeau, 1984). In accordance with this  
239 prediction, we found an asymptotic effect of group size on the time taken to solve the task, with  
240 individuals in larger groups solving a novel foraging task faster than those in smaller groups. The  
241 differences in the time taken to learn the innovative behaviour (and the time taken for the  
242 innovative behaviour to spread), between small and large groups are relatively small compared to  
243 other studies investigating the spread of innovative behaviour (e.g. Liker & Bókony (2009); Aplin et  
244 al. (2014)). However, it is worth noting that although the time periods are small, this is an  
245 experimental study using a relatively simple task. Where problems are more challenging and require

246 greater skill or experience to master, the effect of group size on the emergence and spread of  
247 innovative behaviour might be larger. It is also possible the asymptotic relationship between group  
248 size and the emergence of innovative behaviour was a product of the simplicity of the task. Had the  
249 task been harder, performance may not be bound by quick solving times as it is now, which would  
250 allow larger group sizes to innovate more quickly than medium-sized groups. Such a scenario could  
251 create a linear relationship between group size and the emergence of innovative behaviour. Future  
252 studies may avoid this issue by presenting multiple tasks of varying difficulty, or a single more  
253 difficult task. To our knowledge, only two other studies have reported positive effects of group size  
254 on the emergence of innovative behaviour in the context of novel foraging tasks (Liker & Bókony  
255 (2009) and Morand-Ferron & Quinn (2011); although see the literature on collective decision-  
256 making, e.g. (Sumpter, Krause, James, Couzin, & Ward, 2008)). Our findings thus add to the existing  
257 evidence that group size effects may play a critical role in driving behavioural innovations in wild  
258 populations.

259 In previous research, positive relationships between group size and the emergence of innovative  
260 behaviour have been postulated to result from the “skill pool” effect, where larger groups have  
261 more individuals with a greater range of traits at their disposal, enabling them to solve novel  
262 problems more rapidly (Giraldeau, 1984; Morand-Ferron & Quinn, 2011). However, it remains  
263 possible that an exponential relationship between group size and time taken to innovate could be  
264 generated by statistical probability, without the need to invoke a skill pool explanation. If, for  
265 instance all individuals have an equal, set probability of solving a task at a given time step, then the  
266 decrease in time taken for innovative behaviour to emerge scales exponentially with group size. This  
267 is because the larger the group is, the greater the probability that there will be an individual who will  
268 solve it more quickly than the set probability at the given time-step (Hoppitt *et al.* (2010) make  
269 similar arguments concerning the use of sigmoidal curves as diagnostics of social learning).  
270 Therefore, whilst our current results appear consistent with the predictions of the pool of  
271 competence hypothesis, it is not possible to conclude whether this relationship emerged due to a

272 skill-pool effect, or due to simple statistical probability. To address whether increased phenotypic  
273 diversity per se facilitates the speed or likelihood of innovation, the best approach may be to  
274 compare the emergence of innovative behaviour between groups of the same size with different  
275 compositions of individuals in terms of age, sex, dominance status or personality. Nevertheless,  
276 regardless of the precise mechanism underpinning the effect, our findings still indicate that the rapid  
277 emergence of solutions to novel problems may be a substantial benefit of living in large groups.

278 Explanations other than the skill pool hypothesis have been suggested for the observed relationships  
279 between group size and the emergence of innovative behaviour. For instance, positive relationships  
280 could be the result of an antipredator vigilance effect in larger groups, allowing more time for  
281 exploration and innovative behaviour (Griffin & Guez, 2015). During the course of our experimental  
282 trials we recorded no antipredator behaviour (e.g. mobbing of predators, alarm calling, sentinel  
283 duty), suggesting that anti-predator effects are unlikely to account for the relationship between  
284 group size and the emergence of innovative behaviour observed in Australian magpies. Likewise,  
285 Liker and Bókony (2009) found no evidence of antipredator vigilance on the success rate at  
286 innovative problem solving tasks. It is also possible that indirect effects of group size on neophobia  
287 may drive the group size-innovation relationship. However, latency to contact the task did not  
288 predict performance. Alternatively, the recent finding that Australian magpies from larger groups  
289 have greater general cognitive performance compared to magpies from smaller groups (Ashton et  
290 al., 2018) suggests that cognition may play an important role in the relationship between group size  
291 and the emergence of innovative behaviour. If larger groups are composed of individuals with  
292 greater cognition, and performance on the task is underpinned by cognitive traits, this may explain  
293 faster solving times in larger groups.

294 Conversely, there is also evidence to suggest that larger group sizes can inhibit innovative  
295 behaviours (Griffin et al., 2013; Overington et al., 2009). It has been speculated this may be due to  
296 increased antagonistic behaviour in larger groups (Overington et al., 2009). However, in our study

297 the frequency of aggressive and submissive interactions between individuals at the experimental  
298 device had no effect on the time taken for individuals to learn the innovative behaviour.  
299 Additionally, both Overington *et al.* (2009) and Griffin *et al.* (2013) found aggressive behaviour did  
300 not underpin the reported negative relationships between group size and innovative behaviour. In  
301 combination, this suggests that levels of aggression do not play an important role in the relationship  
302 between group size and the emergence of innovative behaviour, whether this relationship is positive  
303 or negative.

304 The rapid emergence of innovative behaviour in large groups will be particularly beneficial if other  
305 group members can learn from the initial innovator (it is also worth noting that other group  
306 members may innovate themselves). We found that innovative behaviour spread more rapidly in  
307 larger groups, and evidence of side-copying on the task indicates that this was likely facilitated  
308 through social learning. This suggests larger group sizes promote not only the initial emergence of  
309 innovations, but also the subsequent transmission among group members. Theoretical and empirical  
310 research suggests that larger population sizes played a critical role in the accumulation of cultural  
311 knowledge in human societies (Muthukrishna, Shulman, Vasilescu, & Henrich, 2014). Our results  
312 suggest that this may also be the case in group-living nonhuman animals. The positive relationship  
313 between group size and the number of innovators within a group may lead one to hypothesise  
314 multiple innovation events in larger groups may facilitate the spread of innovative behaviour.

315 However, there was no effect of the number of innovators at the time of solving on the spread of  
316 innovative behaviour. Information may spread particularly rapidly in larger groups due to the greater  
317 frequency of social interactions (Mithen, 1994), but of course transmission rates will also be  
318 influenced by the particular structure of social networks (Franz & Nunn, 2009). Investigating the  
319 interplay between social group size and network structure in social transmission dynamics in natural  
320 animal populations is therefore an important priority for future research.

321 In conclusion, our study provides evidence for a positive relationship between group size and  
322 innovation in wild animals. Furthermore, our findings show that, as suggested by studies of human  
323 cultural transmission (Derex et al., 2013; Kempe & Mesoudi, 2014; Mithen, 1994; Muthukrishna et  
324 al., 2014), novel information spreads more rapidly in larger groups. Together, our results provide a  
325 rare link between the emergence and spread of novel information in a social animal in their natural  
326 environment.

### 327 **Author contributions**

328 BJA carried out the fieldwork, carried out statistical analyses, drafted the manuscript and  
329 participated in the design of the study; AT & ARR participated in the design of the study and helped  
330 draft the manuscript. All authors gave final approval.

### 331 **Competing financial interests**

332 We have no competing financial interests.

### 333 **Funding**

334 This work was funded by an ARC Discovery grant awarded to ARR & AT (DP140101921). BJA was  
335 supported by an International Postgraduate Research Scholarship through the University of Western  
336 Australia. AT received additional support from a BBSRC David Phillips Fellowship (BB/H021817/2).

### 337 **Acknowledgements**

338 We thank Eleanor Russell and the late Ian Rowley for giving us access to their life history records of  
339 the Guildford magpie population, and for allowing us to continue on from their work on the  
340 population. We thank Emily Edwards and Margot Oorebeek for help with various aspects of the  
341 fieldwork. We thank Inês Braga Goncalves, Lucy Aplin and Damien Farine for helpful discussion and  
342 comments.

### 343 **References**

- 344 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015).  
345 Experimentally induced innovations lead to persistent culture via conformity in wild birds.  
346 *Nature*, 518, 538–541. <https://doi.org/10.1038/nature13998>
- 347 Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to  
348 group size and affects fitness in Australian magpies. *Nature*, 554, 364–367.  
349 <https://doi.org/10.1038/nature25503>
- 350 Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration,  
351 neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal*  
352 *Cognition*, 13(5), 701–710. <https://doi.org/10.1007/s10071-010-0319-8>
- 353 Clément, R. J. G., Krause, S., von Engelhardt, N., Faria, J. J., Krause, J., & Kurvers, R. H. J. M. (2013).  
354 Collective Cognition in Humans: Groups Outperform Their Best Members in a Sentence  
355 Reconstruction Task. *PLoS ONE*, 8(10), 1–7. <https://doi.org/10.1371/journal.pone.0077943>
- 356 Derex, M., Beugin, M. P., Godelle, B., & Raymond, M. (2013). Experimental evidence for the  
357 influence of group size on cultural complexity. *Nature*, 503(7476), 389–391.  
358 <https://doi.org/10.1038/nature12774>
- 359 Edwards, E. K., Mitchell, N. J., & Ridley, A. R. (2015). The impact of high temperatures on foraging  
360 behaviour and body condition in the Western Australian Magpie *Cracticus tibicen dorsalis*.  
361 *Ostrich*, 86(1–2), 137–144. <https://doi.org/10.2989/00306525.2015.1034219>
- 362 Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social  
363 learning. *Proceedings of the Royal Society B Biological Sciences*, 276(1663), 1829–1836.  
364 <https://doi.org/10.1098/rspb.2008.1824>
- 365 Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal  
366 mechanisms and adaptive functions. *Animal Behaviour*, 61(1), 3–15.

367 <https://doi.org/10.1006/anbe.2000.1557>

368 Giraldeau, L. (1984). The skill pool effect and frequency-dependent learning. *American Naturalist*,  
369 *124*(1), 72–79.

370 Giraldeau, L. A., & Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock  
371 of feral pigeons: a case for the skill pool effect. *Animal Behaviour*, *34*(3), 797–803.  
372 [https://doi.org/10.1016/S0003-3472\(86\)80064-1](https://doi.org/10.1016/S0003-3472(86)80064-1)

373 Giraldeau, L., & Caraco, T. (2000). *Social foraging theory*. Princeton University Press.

374 Griffin, A. S., & Guez, D. (2015). Innovative problem solving in nonhuman animals: the effects of  
375 group size revisited. *Behavioral Ecology*, *26*(3), 722–734.  
376 <https://doi.org/10.1093/beheco/aru238>

377 Griffin, A. S., Lermite, F., Perea, M., & Guez, D. (2013). To innovate or not: contrasting effects of  
378 social groupings on safe and risky foraging in Indian mynahs. *Animal Behaviour*, *86*(6), 1291–  
379 1300. <https://doi.org/10.1016/j.anbehav.2013.09.035>

380 Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms.  
381 *Behavioural Processes*, *109*, 121–134. <https://doi.org/10.1016/j.beproc.2014.08.027>

382 Gunhold, T., Massen, J. J. M., Schiel, N., Souto, A., & Bugnyar, T. (2014). Memory, transmission and  
383 persistence of alternative foraging techniques in wild common marmosets. *Animal Behaviour*,  
384 *91*, 79–91. <https://doi.org/10.1016/j.anbehav.2014.02.023>

385 Gunhold, T., Whiten, A., & Bugnyar, T. (2014). Video demonstrations seed alternative problem-  
386 solving techniques in wild common marmosets. *Biology Letters*, *10*(9), 20140439.  
387 <https://doi.org/10.1098/rsbl.2014.0439>

388 Harrison, X. A., Donaldson, L., Correa-cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D. D., ...  
389 Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in



390 ecology. *PeerJ*, 1–32. <https://doi.org/10.7717/peerj.4794>

391 Hoppitt, W., Kandler, A., Kendal, J. R., & Laland, K. N. (2010). The effect of task structure on diffusion  
392 dynamics: Implications for diffusion curve and network-based analyses. *Learning & Behavior : A*  
393 *Psychonomic Society Publication*, 38(3), 243–251. <https://doi.org/10.3758/LB.38.3.243>

394 Hoppitt, W., & Laland, K. N. (2013). *Social Learning: An introduction to Mechanisms, Methods, and*  
395 *Models*. Princeton University Press.

396 Hughes, J. M., Mather, P. B., Toon, A., Ma, J., Rowley, I., & Russell, E. (2003). High levels of extra-  
397 group paternity in a population of Australian magpies *Gymnorhina tibicen*: evidence from  
398 microsatellite analysis. *Molecular Ecology*, 12(12), 3441–3450. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-294X.2003.01997.x)  
399 [294X.2003.01997.x](https://doi.org/10.1046/j.1365-294X.2003.01997.x)

400 Johnstone, R. E., & Storr, G. M. (2004). *Handbook of Western Australian Birds Volume II – Passerines*.  
401 Western Australian Museum.

402 Kaplan, G. (2008). Alarm calls and referentiality in Australian magpies: between midbrain and  
403 forebrain, can a case be made for complex cognition? *Brain Research Bulletin*, 76(3), 253–263.  
404 <https://doi.org/10.1016/j.brainresbull.2008.02.006>

405 Kempe, M., & Mesoudi, A. (2014). An experimental demonstration of the effect of group size on  
406 cultural accumulation. *Evolution and Human Behavior*, 35(4), 285–290.  
407 <https://doi.org/10.1016/j.evolhumbehav.2014.02.009>

408 Keynan, O., Ridley, A. R., & Lotem, A. (2015). Social foraging strategies and acquisition of novel  
409 foraging skills in cooperatively breeding Arabian babblers. *Behavioral Ecology*, 26(1), 207–214.  
410 <https://doi.org/10.1093/beheco/aru181>

411 Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford University Press.

412 Krause, J., Ruxton, G. D., & Krause, S. (2010). Swarm intelligence in animals and humans. *Trends in*

413 *Ecology and Evolution*, 25(1), 28–34. <https://doi.org/10.1016/j.tree.2009.06.016>

414 Laughlin, P., Hatch, E., Silver, J., & Boh, L. (2006). Groups Perform Better Than the Best Individuals on  
415 Letter-to-Numbers Problems: Effects of Group Size. *Journal of Personality and Social*  
416 *Psychology*, 4(4), 644–651. <https://doi.org/10.1037/0022-3514.90.4.644>

417 Liker, A., & Bókony, V. (2009). Larger groups are more successful in innovative problem solving in  
418 house sparrows. *Proceedings of the National Academy of Sciences of the United States of*  
419 *America*, 106(19), 7893–7898. Retrieved from  
420 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2683070&tool=pmcentrez&rende](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2683070&tool=pmcentrez&rendertype=abstract)  
421 [rtype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2683070&tool=pmcentrez&rendertype=abstract)

422 Mirville, M. O., Kelley, J. L., & Ridley, A. R. (2016). Group size and associative learning in the  
423 Australian magpie (*Cracticus tibicen dorsalis*). *Behavioral Ecology and Sociobiology*, 70(3), 417–  
424 427. <https://doi.org/10.1007/s00265-016-2062-x>

425 Mithen, S. (1994). Technology and Society during the Middle Pleistocene: Hominid Group Size, Social  
426 Learning and Industrial Variability. *Cambridge Archaeological Journal*, 4(01), 3.  
427 <https://doi.org/10.1017/S0959774300000949>

428 Morand-Ferron, J., & Quinn, J. L. (2011). Larger groups of passerines are more efficient problem  
429 solvers in the wild. *Proceedings of the National Academy of Sciences of the United States of*  
430 *America*, 108(38), 15898–15903. <https://doi.org/10.1073/pnas.1111560108>

431 Muthukrishna, M., Shulman, B. W., Vasilescu, V., & Henrich, J. (2014). Sociality influences cultural  
432 complexity. *Proceedings of the Royal Society B Biological Sciences*, 281(1774), 20132511.  
433 <https://doi.org/10.1098/rspb.2013.2511>

434 Overington, S., Cauchard, L., Morand-Ferron, J., & Lefebvre, L. (2009). Innovation in groups: does the  
435 proximity of others facilitate or inhibit performance? *Behaviour*, 146(11), 1543–1564.

436 <https://doi.org/10.1163/156853909X450131>

437 Pike, K. N., Ashton, B. J., Morgan, K. V., & Ridley, A. R. (2019). Social and Individual Factors Influence  
438 Variation in Offspring Care in the Cooperatively Breeding Western Australian Magpie. *Frontiers*  
439 *in Ecology and Evolution*, 7(April), 1–13. <https://doi.org/10.3389/fevo.2019.00092>

440 Samson, J., & Manser, M. B. (2016). Caching in the presence of competitors: Are Cape ground  
441 squirrels (*Xerus inauris*) sensitive to audience attentiveness? *Animal Cognition*, 19, 31–38.  
442 <https://doi.org/10.1002/sml.1.1>)

443 Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of*  
444 *the Royal Society of London. Series B, Biological Sciences*, 362(1480), 539–559.  
445 <https://doi.org/10.1098/rstb.2006.1994>

446 Stöwe, M., Bugnyar, T., Heinrich, B., & Kotrschal, K. (2006). Effects of group size on approach to  
447 novel objects in ravens (*Corvus corax*). *Ethology*, 112(11), 1079–1088.  
448 <https://doi.org/10.1111/j.1439-0310.2006.01273.x>

449 Sumpter, D. J. T., Krause, J., James, R., Couzin, I. D., & Ward, A. J. W. (2008). Consensus Decision  
450 Making by Fish. *Current Biology*, 18(22), 1773–1777. <https://doi.org/10.1016/j.cub.2008.09.064>

451 Therneau, T. (2015). *A package for survival analysis in S*. Retrieved from [https://cran.r-](https://cran.r-project.org/package=survival)  
452 [project.org/package=survival](https://cran.r-project.org/package=survival)

453 Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*,  
454 83(6), 1459–1468. <https://doi.org/10.1016/j.anbehav.2012.03.018>

455 Thornton, A., & Malapert, A. (2009a). Experimental evidence for social transmission of food  
456 acquisition techniques in wild meerkats. *Animal Behaviour*, 78(2), 255–264.  
457 <https://doi.org/10.1016/j.anbehav.2009.04.021>

458 Thornton, A., & Malapert, A. (2009b). The rise and fall of an arbitrary tradition: an experiment with

459 wild meerkats. *Proceedings of the Royal Society B Biological Sciences*, 276(1660), 1269–1276.

460 <https://doi.org/10.1098/rspb.2008.1794>

461 Visalberghi, E., & Addessi, E. (2000). Seeing group members eating a familiar food enhances the

462 acceptance of novel foods in Capuchin Monkeys. *Animal Behaviour*, 60, 69–76.

463 <https://doi.org/10.1006/anbe.2000.1425>

464

## 465 **Tables and Figures**

466

467 **Table 1** Survival models (Cox's proportional hazards regression) for the proportion of group  
468 members that learnt the innovative behaviour.

Variable	±S.E.	Z	P
<b>Group size</b>	<b>0.09</b>	<b>4.41</b>	<b>&lt;0.001</b>
Number of innovators at time of solving	0.18	-1.41	0.158
Number of aggressive and submissive interactions	0.08	-1.09	0.273
Latency to interact	0.003	0.43	0.666
Sex ratio	1.328	1.19	0.233

471

Statistically significant terms in bold. *N* = 54 individuals from 11 groups of 7 different group sizes.

472

473

474

475

476

477

478

479  
480  
481  
482  
483  
484  
485  
486  
487  
488  
489  
490  
491  
492  
493  
494  
495  
496  
497  
498

**Table 2** GLMM model investigating factors affecting the direction first pushed by observers at the device, including the full model set (top) and top set (bottom).

Model	QICc	$\Delta$ QICc
Direction first observed	30.479	0
Basic	40.496	10.017
Group size	42.333	11.854
Sex	42.593	12.114

Parameter	Estimate	Standard error	Confidence interval	P value
Direction first observed	3.393	1.067	1.302, 5.483	0.001

The top set includes models within 2 QICc values of the best model. Group identity was included as a random term.  $N = 29$  individuals.

**Figure 1.** Novel foraging task. Food rewards could be extracted by pushing the self-shutting sliding door either left or right.

**Figure 2.** The time taken for innovative behaviour to emerge (once individuals first interact with the task, seconds) in relation to group size ( $r = 0.559$ ,  $P = 0.001$ ,  $N = 16$ ).

**Figure 3.** Survival curves showing the effect of group size on the spread of innovative behaviour within groups.

499

500 **Figure 1**

501



502

503

504

505

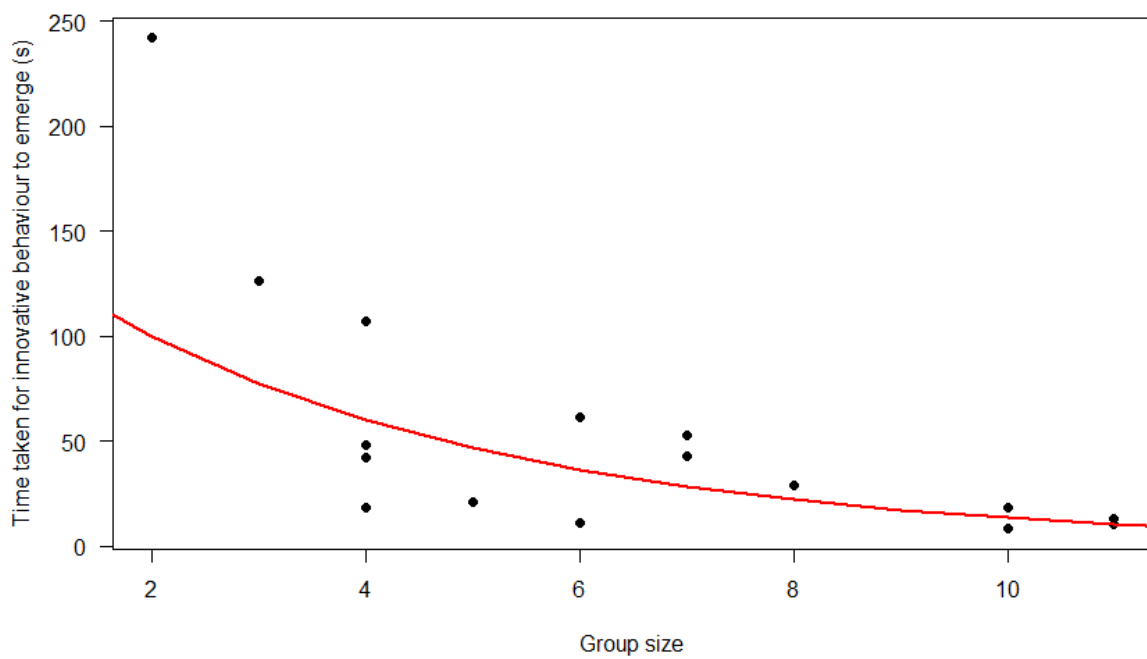
506

507

508

509 **Figure 2**

510



517

518

519

520

521

522 **Figure 3**

523

524

525

526

527

528

529

530

531

532

533

534

535

536

537

538

539

540

