

1 **Early life learning ability predicts adult social structure, with potential implications for**

2 **fitness outcomes in the wild**

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10 Abstract

- 11 1) Social environments influence important ecological processes and can determine how  
12 selection acts on traits. Cognitive abilities can shape these social environments and in turn,  
13 affect individuals' fitness.
- 14 2) To understand how cognitive abilities evolve, we need to understand the complex interplay  
15 between an individual's cognitive abilities, the social environment that they inhabit and the  
16 fitness consequences of these relationships.
- 17 3) We measured the associative learning ability of pheasant chicks, *Phasianus colchicus*, then  
18 released them into the wild where we quantified their social position by observing their  
19 associations at feeding stations and monitored the number of days survived.
- 20 4) We observed disassortative mixing by learning performance at the population level, and  
21 poor learners had more associates than good learners. Learning was beneficial for survival  
22 when focal individuals had fewer than four associates, but survival probability across  
23 learning abilities equalised for individuals with more than four associates.
- 24 5) While the mechanisms underlying these relationships remain to be determined, the patterns  
25 of association exhibited by pheasants at feeders can be predicted by individual variation in  
26 cognitive performances and we suspect these patterns are related to differences in  
27 information use. Critically, these resulting patterns of association have fitness consequences  
28 for individuals that cannot be explained directly by their cognitive ability, but which could  
29 mediate selection on cognition.

30 Introduction

31 Cognitive abilities are critical to how animals behave, yet we understand little about the selective  
32 pressures contributing to their evolution. Reported relationships between individual variation in  
33 performance in cognitive tasks and subsequent (proxy) fitness outcomes are generally straightforward  
34 and positive (Shohet & Watt 2009; Boogert *et al.* 2011; Maille *et al.* 2016; Pasquier & Grüter 2016;  
35 Ashton *et al.* 2018a; Sonnenberg *et al.* 2019), but see for no (Isden *et al.* 2013) or negative (Sewall *et*  
36 *al.* 2013; Madden *et al.* 2018) relationships. There is growing evidence that an individual's  
37 performance in cognitive tasks and perhaps their ability, is contingent on the social environment in  
38 which they have grown (Ashton, Thornton & Ridley 2018b; Ashton *et al.* 2018a), or currently live  
39 (Langley *et al.* 2018b). Simultaneously, the social environment in which an individual lives, or at least  
40 their position within it, may also depend on their cognitive abilities (Wascher *et al.* 2018). For example,  
41 individuals demonstrating good learning abilities are more favourable social (Kulahci, Ghazanfar &  
42 Rubenstein 2018), sexual (Chen *et al.* 2019) or foraging partners (Katsnelson *et al.* 2011). This is  
43 important because the structure of the network and the individual's position within it may affect the  
44 fitness of individuals, with well-connected individuals having greater reproductive success (Silk 2007;  
45 Cameron, Setsaas & Linklater 2009) and longer survival (Stanton & Mann 2012; Ellis *et al.* 2017).  
46 Therefore, if an individual's cognitive abilities determine their social position and this has fitness  
47 consequences, then selection on cognitive traits may be mediated by the social environment and be  
48 frequency-dependent according to the cognitive abilities of others in the population.

49

50 The importance of particular cognitive abilities to an individual's fitness may be dependent on the  
51 structure of the social network that an individual inhabits because social partners influence the  
52 information available to individuals (phenotypic assortment leads to increased information  
53 transmission (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Jones, Aplin, Devost, & Morand-Ferron,  
54 2017; Kulahci *et al.*, 2016) and phenotypic disassortment reduces information transmission, (Carter *et*

55 *al.* 2015)). Thus, individuals may occupy social positions according to their cognitive abilities and so  
56 enhance their access to favourable partners (i.e. the good independent learner if the focal individual  
57 has poor independent learning ability) and/or the number of partners (Aplin & Morand-Ferron, 2017)  
58 to maximise access to the quality and amount of social information. Consequently, the relative  
59 contribution that cognitive abilities make to an individual's fitness may be dependent upon the social  
60 environment that a focal individual inhabits. Therefore, in order to understand how selection acts on  
61 cognition it is necessary to consider both the role that an individual's cognitive ability has in placing  
62 them within their social network and the fitness outcomes accruing to them because of this social  
63 position. Critically, because learning performance can both influence (Wascher *et al.* 2018) and be  
64 influenced by social structure (Langley *et al.* 2018b), a system in which these processes can be  
65 separated is needed.

66

67 Pheasants (*Phasianus colchicus*) are a gregarious species that exhibit variation in learning performance  
68 relating to the social environment. An individual's performance in learning tasks varies depending on  
69 the social environment in which they are tested (Langley *et al.* 2018b) and is related to their social  
70 position, such that higher ranking males exhibit more accurate (Langley *et al.* 2018c) and faster  
71 (Langley *et al.* 2018a) learning performances. The pheasants' social environment is structured with  
72 individuals exhibiting non-random preferential assortment based on sex (Whiteside *et al.*, 2018;  
73 Whiteside *et al.*, 2017). An individual pheasant's cognitive ability can have consequences for their  
74 fitness with individuals that were slow to reverse a learned association being likely to survive for  
75 longer after their release in to the wild (Madden *et al.* 2018). In the UK, pheasants are reared in  
76 captivity prior to release into the wild where they face natural hazards, thus, they can be assayed for  
77 cognitive performance under standardised social group conditions early in life (van Horik *et al.* 2017)  
78 before having the opportunity to interact and develop social ties naturally. This allows us to determine  
79 the role that variation in cognitive ability measured in early life has on shaping later life social position

80 and follow the fate of free-living birds to investigate how these two factors predict survival. We  
81 investigated whether pheasants' social associations at feeding stations in the wild in an area without  
82 any hunting were structured according to learning ability on a visual discrimination foraging task,  
83 assayed during early life. Specifically, we first tested whether individuals assorted (Farine, 2014;  
84 Newman, 2003) according to their early-life learning ability. Learning performances predict later  
85 behavioural strategy (Katsnelson *et al.* 2011) and differences in behavioural strategies lead to mixing  
86 of behavioural phenotypes (Kurvers *et al.* 2010). In the case of pheasants visiting feeders, we expected  
87 that individuals who were poor learners and hence slow to accumulate accurate personal information  
88 may seek to associate with good learners that accumulated information about the location and  
89 profitability of feeding sites. Therefore, we predicted that there would be disassortment by learning  
90 performances at the population level. Second, we tested whether early life learning ability predicted  
91 an individual's later position (individual level assortment and social centrality) within their social  
92 environment. We expected that poor learners would be more disassorted as they would generally  
93 favour knowledgeable individuals (Kulahci *et al.* 2018), whereas for good learners, the extent of  
94 disassortment would not be as strong because they would be more ambivalent in their choice of  
95 partner based on learning ability. We also expected poor learners to have higher social centrality in  
96 order to maximise their access to social information from multiple informed learners regarding  
97 resources, similarly to that observed in great tits (Aplin & Morand-Ferron, 2017). Finally, we tested  
98 whether an individual's cognitive performance or their social position better predicted their chances  
99 of survival. In other gregarious species, individuals most central in their social network survive for  
100 longer (Ellis *et al.* 2017), purportedly because they have access to social information about resources  
101 facilitated by social position. Hence, we'd expect that individuals that are more central in their  
102 networks would survive for longer as pheasants are a gregarious species and more central individuals  
103 will have access to the most social information about feeders. We've previously shown that learning  
104 performance did not directly predict the probability of survival in pheasants (Madden *et al.* 2018), but

105 in that study, we did not consider social position. Therefore, we tested whether the influence that  
106 early life learning performance made to survival was mediated by the social environment.

107 **Methods**

108 **Subjects and housing**

109 This study was conducted from May 2014 – February 2015 at North Wyke Rothamsted Research Farm,  
110 Devon (50°77'N, 3°9'W). Two hundred pheasant chicks were purchased from a commercial game  
111 dealer and placed into one of four identical pens (50 individuals per pen). Each indoor pen (2m x 2m)  
112 consisted of a holding area that was heated and contained perches and saw-dust bedding. This area  
113 was separated from an unheated but sheltered outdoor area (1m x 4m) by a guillotine partition door.  
114 Adjacent to the holding area was a visually isolated testing arena (0.75 m x 0.75 m), divided from the  
115 holding area by a sliding entrance door and connected to the outdoor area by an exit door. At three  
116 weeks old, chicks also had access to an outdoor enclosure (4m x 12m) connected to the sheltered run,  
117 containing perches and branch shelters. Chicks were provided with age-specific chick crumb  
118 (Sportsman game feed) and water *ad libitum* throughout all areas of the pen, except in the testing  
119 arena. Chicks were identifiable by numbered patagial wing tags (Roxan Ltd, Selkirk, U.K). Chicks were  
120 reared in these conditions for 10 weeks while we assayed their cognitive performances.

121

122 **Cognitive testing procedures**

123 Chicks were trained to enter the testing arena individually upon hearing an auditory cue (observer  
124 humming/whistling) from ~2 weeks old. Testing began when chicks were 4 weeks old. During a testing  
125 session, after entering the testing arena the sliding door was closed and individuals could retrieve a  
126 freely available mealworm located on the centre of the task apparatus, thus standardising their  
127 approach to the task. An observer then recorded the chick's interactions with the task. Upon  
128 completion of the task, or if individuals did not participate within 2 minutes, or exhibited signs of stress  
129 (lost-calling, pacing, flapping), they were released into the outside area of the pen via the exit door.  
130 Hence, while each chick entered the testing arena once during a testing session, we could not control  
131 the number of choices they made in each session. There were two testing sessions per day; one in the

132 morning and another in the afternoon on five consecutive days. Birds were tested when they were  
133 five weeks old, having previously all experienced an identical set of tests (see (van Horik & Madden  
134 2016) for details).

135

### 136 **Learning ability**

137 Learning ability was assessed by measuring visual discrimination performances. Foraging grids  
138 containing wells marked with different colour cues are a commonly used paradigm to assess visual  
139 discrimination performances of avian subjects (Boogert *et al.* 2011; Shaw *et al.* 2015; Ashton *et al.*  
140 2018a). Individual pheasants were presented with a square apparatus (20 cm L x 20 cm W x 5cm D),  
141 containing 24 circular wells. A layer of opaque crepe paper covered each well. Chicks had been trained  
142 to peck through the crepe paper that covered wells on the testing apparatus. During testing, half the  
143 wells were encircled with a red ‘#’ shape and contained mealworm food rewards, the other half of the  
144 wells were encircled with a black hexagon and were blocked by a bung, so that the paper could not  
145 be pecked through. The locations of rewarded and unrewarded wells were random and differed  
146 between sessions. A choice was denoted as when a bird pecked at the crepe paper of a well. This  
147 choice was scored as ‘correct’ if the peck was to a rewarded well and scored as ‘incorrect’ if the peck  
148 was to an unrewarded well. Revisits to opened previously rewarded wells were not recorded reliably  
149 and were ignored. We allowed birds to revisit unrewarded wells. We used the number of correct  
150 choices and revisits to unrewarded wells to derive our learning measures for each individual. Once  
151 birds had emptied all rewarded wells or reached two minutes in the testing arena (whichever came  
152 first), the exit door was opened and the test apparatus was removed. We considered an individual’s  
153 first 100 choices (made over 3 to 5 testing sessions) to reflect their learning performance. One  
154 hundred choices provided a balance between improving our estimate of learning performance for an  
155 individual by collecting more choice data and the risk that birds ceasing interacting with the test  
156 apparatus and thus being excluded from the dataset because they did not complete the standardised

157 number of choices. Our learning performance score was the percentage of correct choices of the final  
158 15 choices of this series of 100; this represents how well individuals had learned the affordances of  
159 the task after a set number of choices.

160

161 Of the 64 birds that completed at least 100 choices and were included in the network, individuals  
162 chose the unrewarded cue a median of seven times in their first 15 choices with all birds making at  
163 least one incorrect choice and only one bird making no correct choices during the first period,  
164 indicating that individuals had the opportunity to learn to discriminate between rewarded and  
165 unrewarded visual stimuli. Individuals chose an average of 47.9% ( $\pm 1$  SD = 15.0%) correct wells in their  
166 first 15 choices and this increased to an average of 76.1% ( $\pm 1$  SD = 14.8%) correct wells in the final 15  
167 choices, demonstrating a mean population improvement of 28% correct choices. Sixty one individuals  
168 performed above chance levels (50% correct) in their final task performances (median, IQR: 0.80, 0.67  
169 to 0.87), indicative of learning. There was no significant difference between female and male final  
170 performances ( $t_{62} = 0.03$ ,  $P = 0.97$ ).

171

## 172 **Observing social associations in the wild**

173 In July, when the pheasants were 10 weeks old, they were all released on to the site on the same day,  
174 being placed in an open-topped release-pen  $\sim 4000\text{m}^2$  situated near to the centre of the farm. The  
175 release-pen was surrounded by an electric fence, which excluded terrestrial predators but was  
176 exposed to aerial predation. Pheasants could disperse from the pen at will into the rest of the 250  
177 acre site which contains lowland deciduous woodland, grassland and fen meadow. The site is not  
178 subject to game shooting or predator control and we provided 40 feeders that dispensed wheat as  
179 feed (see Whiteside et al., 2018).

180

181 We used Bushnell Trophy motion-activated cameras to continuously monitor feeders (and  
182 surrounding areas) for use by released pheasants. All images were viewed manually. We recorded the  
183 identity of all birds at a feeder via their wing tag numbers and the time of their attendance from  
184 timestamps on the images. Untagged birds or those whose wing tags could not be seen were excluded  
185 from further analysis.

186

187 We considered associations observed during October for our analyses of social structure because prior  
188 to this (August and September), associations were extremely dense and almost exclusively in the  
189 release pen where birds were predominantly living at unnaturally high densities. By October, birds  
190 had dispersed from the pen and so associated more naturally. By November, many birds were dead,  
191 resulting in low statistical power to investigate social structure but this high mortality also provided  
192 us with sufficient power to conduct survival analyses considering the fates of birds included in social  
193 networks in October. For completeness, we replicated all our analyses for social structures derived  
194 from monthly data collected between November 2014 to February 2015 and the qualitative pattern  
195 does not differ, although falling power made interpreting the effects problematic. In March, we began  
196 trapping adults and housing them in captivity as part of a separate experiment, therefore we ceased  
197 collecting association data.

198

#### 199 **Determining survival of pheasants in the wild**

200 We investigated the fate of released pheasants using three methods. First, we observed their use of  
201 feeding stations. The final day that a pheasant was recorded at a feeder was deemed to be their day  
202 of death. We acknowledge that birds may have left the study site but highlight that of 30 birds which  
203 were radio tagged, only one individual was detected off of the site during the four months (see  
204 (Madden *et al.* 2018)). Generally, the majority of released pheasants remain within 1.6 km of their  
205 release pen (Wilson, Drobney & Hallett 1992). Second, we carried out regular searches of the site,

206 recording birds observed alive and retrieving any carcasses. We conservatively assigned the day of  
207 death as the day that the carcass was found. These searches were conducted twice a week until the  
208 end of the study. Third, in March, we started to catch pheasants, for a new experiment, using funnel  
209 traps baited with wheat. Birds caught were considered alive at the end of the study period.

210

## 211 **Statistical analysis**

### 212 *Association networks*

213 Weighted association networks, based on co-occurrence at feeder sites, were constructed for October  
214 2014 using the *asnipe* package (Farine, 2017). We constructed three networks for this month; a mixed-  
215 sex network containing female and male associations combined, as well as two same-sex networks  
216 (one for female-only associations and one for male-only associations). We considered sexes separately  
217 because at that time of year, they exhibit sexual segregation and this may skew their patterns of  
218 assortment (Whiteside et al., 2018). We used a fixed 600 second sliding time window such that all  
219 birds appearing at a feeder within 10 minutes of one another were considered to be in association  
220 with one another. This gambit of the group approach (assuming that all individuals could associate  
221 with all others in our marked population) was used to generate group by individual matrices  
222 (Whitehead & Dufault 1999), and the strength of association between two individuals was calculated  
223 based on simple ratio indices (Cairns & Schwager 1987). For each network, we calculated assortativity  
224 coefficients (Newman 2003) and their standard errors using a jackknife simulation, implemented by  
225 the *assortnet* package (Farine 2016). ‘Weighted assortativity’ ( $r$ ) is a coefficient that depicts the  
226 proportion of associations that are between similar phenotypes and is deemed to be more robust to  
227 influential and rare events on perceived social structure than assortativity coefficients derived from  
228 binary networks (Farine 2014). The coefficient ranges from 1 (perfectly assorted, i.e. all edges connect  
229 two nodes of the same phenotype) to  $-1$  (perfectly disassortative, i.e. all edges connect two nodes of  
230 different phenotype), whereby values of 0 are neutrally assorted. From each association network we

231 extracted three network metrics for individuals to quantify their social position. The first metric was  
232 an individual's assortment score and the second two metrics were used to indicate social centrality:  
233 'degree', which is the number of associations an individual has, and 'strength' which is the frequency  
234 of associations. The individual assortment score indicates how similar or dissimilar an individual's  
235 social partners are in terms of their cognitive performance. This was generated by deriving the  
236 absolute difference between the cognitive performance scores of each dyad and correlating this  
237 matrix of differences with the matrix of association strengths, using a Spearman's rank correlation.  
238 Like population assortment values, positive values indicate assortment by cognitive performance and  
239 negative values indicate disassortment by cognitive performances. We used General Linear Models  
240 (LM) to investigate whether any of an individual's three network metrics was predicted by their  
241 cognitive performance

242

#### 243 *Survival analysis*

244 To assess whether cognitive performance and/or social position predicted the number of days a bird  
245 survives after release, we used a Cox's proportional hazards model (Kleinbaum & Klein 2012) using  
246 the 'survival' package (Therneau 2015). This analysis copes well with instances in which we do not  
247 know the exact date of death, such as when we find a carcass but are unsure of exactly when the  
248 individual died, as well as unobserved deaths that occur when individuals 'disappear' or deaths that  
249 occur after the study has finished. These data can be censored based on the last sighting. Individuals  
250 that were found dead during the study period were given a censored value of 1 (n = 40) and we also  
251 recorded the number of days before they died. Individuals that were seen alive at the end of the  
252 study period were given a censored value of 0 (n = 61). To prevent overcomplicating our survival  
253 models we included only explanatory variables that were significantly related to each other in the  
254 previous analyses, i.e. degree and learning performance. We constructed a single mixed-sex model  
255 with sex included as an explanatory variable and we also included times observed to control for the

256 different number of times that individuals were seen during the observation period. To investigate  
257 whether social position was more or less important for individuals of different cognitive ability, an  
258 interaction term between learning performance and degree number was included. To ensure the  
259 collinearity between explanatory variables did not inflate the variance of estimated parameters,  
260 variance inflation factors (VIFs) were checked for all models to ensure these were  $< 2$ . For each  
261 model we report the estimated Hazard ratio in mortality risk per unit of each explanatory variable.  
262 We used the 'survfit' function to predict the median number of days survived for a poor (first  
263 quartile) and good (third quartile) learners.

264

#### 265 *Generating null models*

266 Social network data represents relational data that is non-independent, thus violating assumptions of  
267 many statistical approaches. To generate appropriate null models and determine statistical  
268 significance of relationships between network metrics and cognitive performance, we compared the  
269 observed coefficients of each network, to a distribution of expected coefficients, generated from  
270 permutations. Coefficients from relationships involving individual assortment scores were compared  
271 to a distribution of coefficients generated from edge permutations of networks. These edge  
272 permutations maintained the centrality and trait relationship while testing the assortment by trait  
273 relationship. Coefficients from relationships between learning performance and centrality measures  
274 (degree and strength), as well as coefficients from survival models were compared to a distribution of  
275 coefficients generated from data stream permutations. Data stream permutations involve repeatedly  
276 swapping the observations of individuals between groups and this method accounts for potential  
277 sampling biases by keeping the number of observations per individual constant (Croft *et al.* 2011). We  
278 conducted 10000 permutations and 100 'swaps' per permutation. Mixed-sex random networks were  
279 generated while restricting the permutations within day, sex and feeder location in order to maintain  
280 meaningful constraints on the structure of the network based on temporal, spatial or other ecological  
281 factors that potentially shape these structures. We restricted within day to control for death or

282 dispersal of individuals. We restricted within sex because pheasants assort according to sex during the  
283 months of this study (Whiteside et al., 2018). We restricted within location to control for intrinsic  
284 preferences from individuals for specific locations, independent of preferences for foraging partners.  
285 For the same-sex networks we generated random networks while restricting permutations within day  
286 and feeder location.

287 **Results**

288 **Do pheasants socially assort based on their learning performance?**

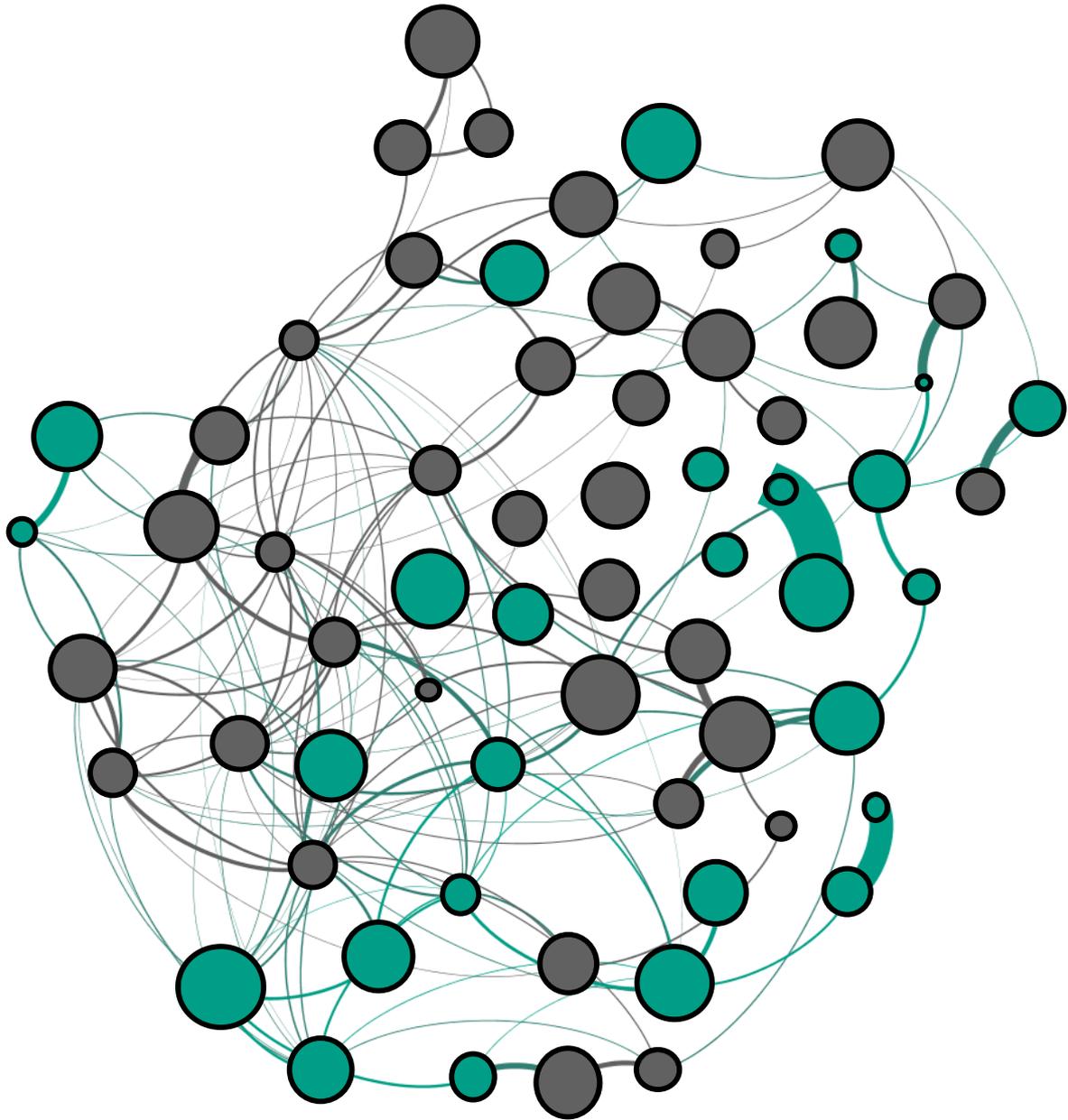
289 There was disassortative mixing by learning performances in both the mixed-sex and female-only  
 290 networks. Pheasants that were more accurate on the visual discrimination task, hereby ‘good  
 291 learners’, were more likely to associate with those that had been less accurate, hereby ‘poor learners’.  
 292 This level of disassortment differed from a distribution of randomly generated coefficients (Table 1;  
 293 Fig. 1). In male-only networks, the assortment coefficient for learning performances were again  
 294 negative, suggesting disassortative mixing but these were not significantly different from random  
 295 (Table 1). For details on visits to feeders from which the networks were constructed, see  
 296 Supplementary Information X.

297

298 **Table 1: Weighted assortment (*r*) by learning performance within mixed-sex and single-sex**  
 299 **networks calculated from associations at feeding stations in the wild by released female and male**  
 300 **pheasants. Values in bold represent significant *p*-values ( $p < 0.05$ ) deduced from comparison of**  
 301 **observed coefficient to expected coefficients (generated from 10,000 data stream permutations)**

	<b>Mixed-sex</b>	<b>Female-only</b>	<b>Male-only</b>
<i>r</i>	-0.304 ± 0.137	-0.497 ± 0.288	-0.154 ± 0.072
	[95% range = -0.300 - -0.241]	[95% range = -0.490 - -0.359]	[95% range = -0.203 - -0.127]
<i>p</i>	<b>0.001</b>	<b>0.001</b>	0.311

302



303

304 **Figure 1: Social associations at feeding stations in the wild for female (green,  $N = 27$ ) and male (grey,**  
305  **$N = 37$ ) pheasants showing disassortative mixing by learning performance. Node size represents %**  
306 **of correct choices on a visual discrimination task, i.e. larger nodes represent higher % correct. Line**  
307 **thickness represents strength of association between nodes.**

308 **Do individuals with different learning performances occupy different social positions?**

309 There was a negative relationship between individual assortment score and learning performance,  
310 suggesting that good learners associated more with individuals less similar to themselves in terms of  
311 learning performance (disassorted), while poor learners were more assorted (mixed-sex and female-  
312 only networks; Table 2, Fig. 1). However, this relationship was not significantly different from a  
313 distribution of randomly generated coefficients. Good and poor learners differed in how central they  
314 were in the mixed-sex network. There was a negative relationship between degree number and  
315 learning performance and this was significantly different from random suggesting that poor learners  
316 had more associates (i.e. higher degree) than good learners. The same negative relationships between  
317 individual assortment and the number of associates with learning performance were seen in male-  
318 only and the female-only networks but were not different from random (Table 2, Fig. 1). The  
319 relationship between learning performance and the number of associates was positive in female-only  
320 networks but this was not different from random (Table 2, Fig. 1). Learning performance was not  
321 related to association strength in either of the single-sex or mixed-sex networks (Table 2).

322 **Table 2: Regression coefficients for the relationship between learning performances and three**  
 323 **measures of social position (individual assortment, degree and the strength of these associations)**  
 324 **from pheasants' associations at feeding stations. Negative relationships indicate that individuals**  
 325 **that were less accurate by the end of testing were: more assorted and had more and stronger**  
 326 **associations. Values in bold represent significant p-values ( $p < 0.05$ ) deduced from comparison of**  
 327 **observed coefficient to expected coefficients (generated from 10,000 data stream or edge**  
 328 **permutations)**

	Mixed-sex			Female only			Male only		
	<i>Assortment</i>	<i>Degree</i>	<i>Strength</i>	<i>Assortment</i>	<i>Degree</i>	<i>Strength</i>	<i>Assortment</i>	<i>Degree</i>	<i>Strength</i>
<i>b</i>	-0.087	-2.420	-0.340	-0.032	1.719	-0.262	-0.542	-11.017	-0.980
<i>p</i>	0.349*	<b>0.030</b>	0.397	0.463*	0.104	0.471	0.252*	0.317	0.144

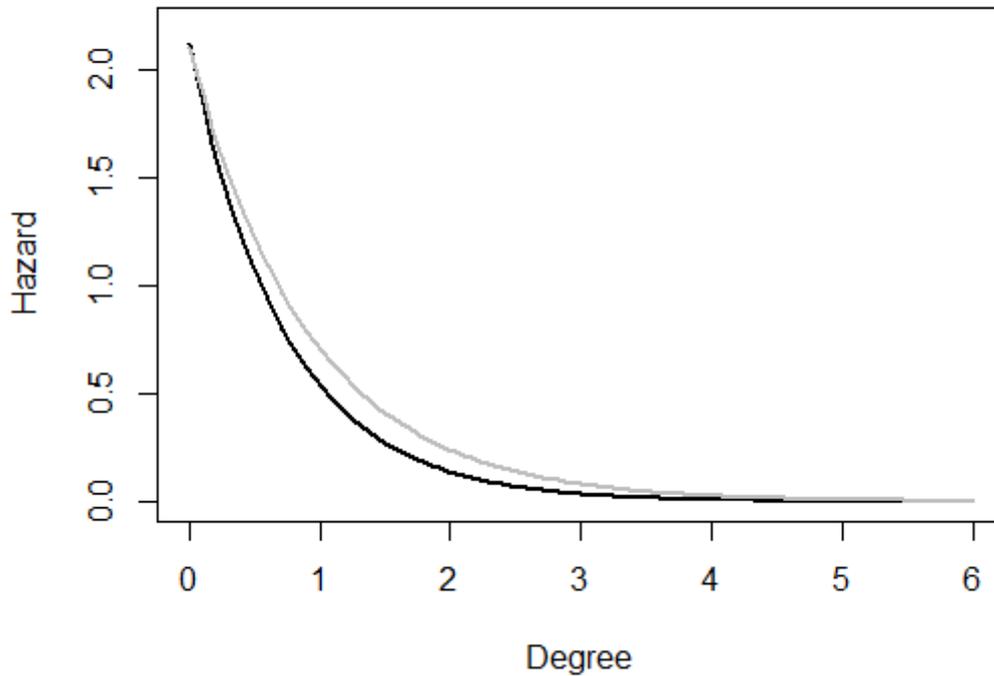
329 \*Distribution of coefficients generated from edge permutations

330

331 **Does an individual's social position or learning performance predict their survival?**

332 In mixed-sex networks there was a significant interaction between learning performance and the  
 333 number of associates on the probability of survival, with good learners that had between one and four  
 334 associates having a slightly lower risk of death than poor learners with the same number of associates,  
 335 but this difference in risk was equalised when individuals had 0 or >4 associates (learning \* degree:  
 336 regression coefficient = -0.008, hazard ratio = 0.993, Lower 95% CI = 0.926, Upper 95% CI = 1.063,  $z =$   
 337  $-0.215$ ,  $n = 60$ ,  $p = 0.040$ ; Fig. 2). The predicted median survival time among pheasants with two  
 338 associates was 87 and 105 days for poor and good learners, respectively. There was no difference in  
 339 hazard risk between the sexes (sex (males): regression coefficient = 0.927, hazard ratio = 2.527, Lower  
 340 95% CI = 1.110, Upper 95% CI = 5.678,  $z = 2.226$ ,  $n = 60$ ,  $p = 0.780$ ). These results controlled for variation

341 in the amount of times that individuals were observed (times observed: regression coefficient = -0.04,  
342 hazard ratio = 0.960, Lower 95% CI = 0.934, Upper 95% CI = 0.983,  $z = -3.221$ ,  $n = 60$ ,  $p = 1.000$ ).



343

344 **Figure 2:** The relationship between degree number and learning performance on the hazard risk of  
345 pheasants (controlling for sex and the number of times observed). The first and third quartiles of the  
346 learning performance distribution represent good (black line) and poor (grey line) learners,  
347 respectively. A hazard ratio greater than 1 indicates an increased risk of death with a change in the  
348 explanatory variable; a hazard ratio of exactly 1 indicates no difference in risk with a change in  
349 explanatory variable; a hazard ratio of  $<1$  indicates a decreasing risk in death with a change in  
350 explanatory variable.

351 **Discussion**

352 Individual variation in learning ability predicts subsequent social structure and the complex interplay  
353 between these factors has consequent survival implications for pheasants. Generally, stronger  
354 associations were observed between individuals of less similar learning performances, indicative of  
355 mixing based on learning performances, and poor learners were more socially central in these  
356 networks. Among individuals with between one and four associates, good learners survived for longer  
357 than poor learners, however, among individuals with none or more than four associates, variation in  
358 learning performances did not influence survival. Our findings highlight that to understand how  
359 cognitive traits may be selected for and thus evolve, it is important to appreciate how these traits both  
360 structure and are distributed within the social environment because an individual's social position  
361 commonly has fitness consequences.

362

363 Our observations support the suggestion that an individual's cognitive ability and their social  
364 environment are not independent (Ashton *et al.* 2018b; Wascher *et al.* 2018). We assessed cognitive  
365 performance under standardised social and environmental conditions, early in life when individuals  
366 had not encountered 75% of the population, and then observed social structures months later. An  
367 individual's learning accuracy, assessed when they were five weeks old, predicted the (number and  
368 type of) individuals they associated with when they were five months old. Because our learning  
369 measure was collected from voluntarily participating birds and we did not exclude revisits to  
370 unrewarded wells, we could not control for inter-choice intervals, standardise the probability of an  
371 individual making a correct choice within or between sessions, or standardise the total number of  
372 rewarded wells presented to each individual (see SI 3). Despite these three issues adding noise to our  
373 learning measure, an individual's learning accuracy, assessed when they were five weeks old,  
374 predicted the (number and type of) individuals they associated with when they were five months old.  
375 Thus, the social structure we observed was not formed prior to the assay of cognitive ability and was

376 unable to exert an influence on their early life cognitive performance. Instead, the social structure  
377 observed later in life may arise because individuals persistently exhibit different learning abilities that  
378 underpin variation in their behavioural strategy (Aplin & Morand-Ferron, 2017; Katsnelson et al.,  
379 2011). Subsequently, these behavioural strategies may bias association patterns. We found support  
380 for our first prediction that there would be non-random mixing leading to disassortment by learning  
381 ability in the population. We suspect that poor learners may behave as ‘scroungers’, relying on social  
382 rather than personal information and accompanying good learners while foraging at feeders. Such  
383 negative assortment based on individual tendency to use personal or social information when locating  
384 food resources is seen in foraging aggregations of geese (Kurvers *et al.* 2010), but contrasts with the  
385 more usually observed positive assortment based on morphological or behavioural features (size:  
386 (Krause, Godin & Brown 1996); consistent behavioural traits (Aplin et al., 2013; Carter et al., 2015;  
387 Croft, Krause, & Darden, 2009; Massen & Koski, 2014). We found some support for our second  
388 prediction that these poor learners would also adopt a more socially central position to maximise their  
389 access to social information (as in (Aplin & Morand-Ferron, 2017)). Poor learners were more socially  
390 central in terms of the number of associates they had, but not in terms of their strength of  
391 associations. This suggests that poor learners associate with many different individuals, rather than  
392 maintain repeated associations with the same individuals. Our third prediction was that there would  
393 be a negative relationship between an individual’s learning ability and their assortment score.  
394 Specifically, we predicted that poor learners would actively choose to associate with good learners  
395 because of the benefits of scrounging available to them. In contrast, good learners would be less  
396 selective in their partners or indeed exert no preference over associates because they thrive using  
397 personal information and do not rely on associate to locate food resources. However, the relationship  
398 between an individual’s learning performance and their level of assortment was not significantly  
399 different from null models.

400

401 The fitness consequences of an individual's social position, specifically the number of associates that  
402 they had, were mediated by the individual's learning performance. Among individuals that had  
403 between one and four associates, those that were good independent learners benefitted more  
404 strongly than poor learners from increased survival chances, indicated by the interaction between  
405 learning performance and the number of associates being significantly different to null models. This  
406 suggests that for individuals with a low number of associates, a greater ability to collect and store  
407 personal information provides individuals with survival benefits. We suspect that when poor learners  
408 that opt to use social information have this few associates, they face the risk of decreased survival  
409 perhaps because the range of good learners that utilise personal information is limited. Why this  
410 pattern is not evident when individuals had no associates (i.e. risk of mortality was equal for learners)  
411 requires further investigation. We suspect that our ability to predict survival for those with no  
412 associates is imperfect because only two individuals had zero associates compared with 10 individuals  
413 with one associate. For individuals with more than four associates, variation in learning ability did not  
414 influence survival. For pheasants, individuals with more associates at feeders have a lowered  
415 predation risk, perhaps due to increased net vigilance by group members (Whiteside, Langley, &  
416 Madden, 2016). Subsequently, poor learners may lower their chances of predation and enhance their  
417 survival by associating with many others and paying the cost of decreased foraging efficiency for the  
418 benefit of improved survival via vigilance. It is unclear why the transition of fitness benefits occurs at  
419 four associates. Whiteside et al., (2016) showed that harems of nearly four individuals provided  
420 optimal benefits from balancing foraging and vigilance and that harems of this size were most  
421 commonly observed in the wild. The Whiteside et al. (2016) findings were derived during the breeding  
422 season, several months after the winter feeding associations that we used, and depended on sex  
423 differences in vigilance behaviour which were not considered in this current study.

424

425 The relationship between learning performance and social position were generally seen in the mixed-  
426 sex and female-only networks, but not in male-only networks. This may be because, in pheasants,  
427 females are the more consistently gregarious sex. During the winter months, males compete for  
428 territories and associations between males at feeding stations are likely to be related to dominance  
429 interactions, such as displays and contests (Mateos & Carranza 1997) for the acquisition of a territory  
430 (Robertson 1997). In contrast, females may share feeding associations as a prelude to the formation  
431 of female groups which collectively visit and sample advertising males during the breeding season.

432

433 Our observations demand further detail if we are to comprehensively understand the evolution of  
434 cognitive abilities within a social context. In order to understand the strength and direction of  
435 selection, we also need a better understanding of the consistency of an individual's social network  
436 position (Aplin et al., 2015) over time and context. Our results are also specific to association networks  
437 at feeding stations, we are therefore unable to generalise our findings to other types of network or  
438 behaviours, such as associations during foraging in open landscapes or during roosting. Exploring how  
439 different types of networks are structured according to cognitive traits within the same individuals  
440 would be an interesting avenue for future research as this would highlight the contexts in which these  
441 traits are, or are not, important for shaping social behaviour and inducing differential fitness  
442 consequences. We have yet to demonstrate the mechanisms by which assortment based on early life  
443 cognitive performance arises. Social preferences (specifically preferences for same or different sex  
444 associates) may arise early in life for pheasants (Whiteside et al., 2017) and patterns of association  
445 vary over their lifetime (Whiteside et al., 2018). One productive approach would be to understand  
446 how learning ability manifests in individual's foraging and social behaviour and the cues to others that  
447 this may provide.

448

449 Our findings demonstrate that an individual's social position later in life is a consequence of their early  
450 life learning performance and that both factors affect their survival chances. In a previous study, our  
451 failure to incorporate social structure into analysis may explain why we did not find a significant  
452 relationship between learning performance and survival (Madden *et al.* 2018). Therefore, we suggest  
453 that the fitness consequences of an individual's cognitive ability is modulated by the social  
454 environment that the individual constructs and lives in. This influences how selection acts on such  
455 individual differences in cognitive ability and means that simple relationships between cognitive  
456 ability and fitness may be confounded by the social environment. This can lead to frequency-  
457 dependent mechanisms in which an individual's fitness depends on its social environment (e.g.  
458 (Dubois, Giraldeau & Reale 2012)). Considering cognitive traits in the context of social structure is  
459 helpful because currently most studies suggest strong positive selection for specific (Smith *et al.* 2015;  
460 Maille *et al.* 2016; Sonnenberg *et al.* 2019) or general (Ashton *et al.* 2018a) cognitive abilities. Strong  
461 directional selection implies that traits should rapidly reach fixation or undergo continued  
462 exaggeration such that species might be expected to exhibit uniform/or extremely high specific or  
463 general cognitive abilities. This is seldom observed. The mediating effects of the social environment  
464 revealed in this study means that the direct relationship is perturbed and the fitness benefits and costs  
465 of particular cognitive abilities are contingent on the social context in which the individual lives.

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474

475 **Authors' contributions**

476 E.J.G.L conceived and designed the study with J.R.M.; E.J.G.L., J.O.v.H., M.A.W. and  
477 C.E.B. collected the data; E.J.G.L. and M.N.W. carried out the analyses; E.J.G.L. drafted the  
478 manuscript; J.O.v.H, M.A.W., C.E.B., M.N.W. and J.R.M. commented on the manuscript. All authors  
479 gave final approval for publication.

480

481 **Data accessibility**

482 The datasets supporting this article are available from the Dryad Digital Repository:

483 <https://doi.org/10.5061/dryad.k3j9kd53x>

484

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615

616 **SI 1 - Learning performances**

617 **SI 2 - Descriptive statistics for association networks**

618 ○ **Table S1: Descriptive statistics for association networks of pheasants at artificial**  
619 **feeders**

620 **SI 3 - Confounds of our learning measure**

621 **SI 4 - R code**

622

---

623 **SI 1 - Learning performances**

624 Of the 64 birds that completed at least 100 choices and were included in the association networks,  
625 individuals chose the unrewarded cue a median of seven times in their first 15 choices with all birds  
626 making at least one incorrect choice and only one bird making no correct choices during the first  
627 session, indicating that individuals had the opportunity to learn to discriminate between rewarded  
628 and unrewarded visual stimuli. Individuals chose an average of 47.9% ( $\pm 1SD = 15.0\%$ ) correct wells in  
629 their first 15 choices and this increased to an average of 76.1% ( $\pm 1SD = 14.8\%$ ) correct wells in the  
630 final 15 choices, demonstrating a mean population improvement of 28% correct choices. Sixty one  
631 individuals performed above chance levels (50% correct) in their final task performances (median, IQR:  
632 0.80, 0.67 to 0.87), indicative of learning. There was no significant difference between female and  
633 male final performances ( $t_{62} = 0.03$ ,  $P = 0.97$ ).

634

635 **SI 2 - Descriptive statistics for association networks**

636 We recorded 3416 visits across 40 feeding stations from 101 marked pheasants during October 2014  
637 (Table S1). Individuals were observed a mean  $\pm$  se  $34.66 \pm 9.15$  times. In the mixed-sex network there  
638 was a mean association strength of 0.38 and a mean degree of 9. There was a significant correlation  
639 between the strength and degree of associations (Spearman's correlation:  $r_s = 0.787$ ,  $n = 101$ ,  $p <$   
640  $0.001$ ).

641

642 **Table S1: Descriptive statistics for social networks generated from associations at feeding stations**  
643 **by female and male pheasants, in mixed-sex and same-sex networks. The table shows the total**  
644 **number of individuals per network, the number of groups (gambit-of-the-group approach), number**  
645 **of individuals within each network to complete the learning task and the number of individuals that**  
646 **we could obtain an individual assortment score for, based on the focal individual and their**  
647 **associates learning performances.**

	Mixed-sex	Female-only	Male-only
<b>Individuals <math>n</math></b>	101	53	48
<b>Groups <math>n</math></b>	3500	1262	2838
<b>Learning <math>n</math></b>	64	27	37
<b>Assortment <math>n</math></b>	60	19	34

648

649

650 **SI 3 - Confounds of our learning measure**

651 We highlight two potential problems with our measure of learning ability. First, the probability of  
652 making successive correct choices in a given session was not standardised. Within a session, once a  
653 bird made a correct choice, this well was opened and was removed from the possible options.  
654 Therefore, with each successive correct choice, the probability of making the next correct choice was  
655 lowered. For example, the probability of making a correct first choice is 0.5 (12/24 wells) and this  
656 decreases to a probability of 0.48 (11/23 wells) of making the second correct choice, due to one  
657 opened correct well and 12 unchanged incorrect wells. Second, individuals differed in the number of  
658 sessions taken to reach 100 choices. Incorrect wells were blocked and visually unchanged if selected  
659 (i.e. not opened), this meant that birds could make multiple incorrect choices in a given session and  
660 therefore individuals varied in their experience with the apparatus. Birds included in this study made  
661 a median of 21 choices per pokebox apparatus (IQ range 12-28). Learning measures were derived from  
662 birds that experienced a median of 5 pokeboxes (IQ range 4-7). By not standardising the availability of  
663 rewarded wells within or between individuals from choice-to-choice or the inter-choice intervals  
664 within sessions, we suspect that our learning measure is noisy. Because we could not ensure  
665 standardisation, we were concerned that birds experiencing fewer pokeboxes would have less  
666 opportunity to learn and hence we expected them to exhibit lower learning performance. Therefore,  
667 we explicitly tested this relationship. Contrary to our expectations, we found that birds which  
668 experienced fewer poke boxes actually exhibited greater learning performance ( $R_s = -0.39$ ,  $n = 62$ ,  $P =$   
669  $0.0019$ ). Because birds could have no prior knowledge of how many pokeboxes they would be able to  
670 experience, we cannot conceive of a mechanism by which our failure to standardise testing conditions  
671 introduced bias in learning performance, although we acknowledge that such imperfect testing  
672 conditions undoubtedly added noise to our measure. However, as all individuals had made incorrect  
673 choices by their second session (see SI 1 - Learning performances), we argue that individuals had the  
674 opportunity to learn the discrimination and the decreasing probability of correct choices reduces the  
675 influence that chance has on final learning performances. Nevertheless, we suggest that our measure  
676 of learning be interpreted with caution.

```

677 SI 3 - R code
678 #####
679 ##### Population-level assortment coefficients #####
680 #####
681 # P-value function #
682 pval<-function(a,b){
683   p<-(1-(sum(b<a)/length(b)))
684   bigger<-sum(b<a);smaller<-sum(b>a)
685   if(bigger>smaller)p<-(1-(bigger/length(b))) else{p<-(1-(smaller/length(b)))}
686   p}
687
688 # Load in data
689 data<-read.csv("Feeder photo data_asnipe.csv",header=T) # Mixed-sex network #
690 data<-read.csv("Feeder photo data_asnipe_FEMALES ONLY.csv",header=T) # Female-only
691 #
692 data<-read.csv("Feeder photo data_asnipe_MALES ONLY.csv",header=T) # Male-only #
693
694 attach(data)
695 summary(data)
696
697 library("asnipe")
698
699 # A time window approach to calculate group co-memberships
700 Oct_group_by_ind<-get_associations_points_tw(data, time_window = 600, which_days =
701 62:93, which_locations = NULL)
702
703 # split the resulting list
704 gbi <- Oct_group_by_ind[[1]]
705 times <- Oct_group_by_ind[[2]]
706 locations <- Oct_group_by_ind[[3]]
707
708 # get network
709 Oct_network<-get_network(gbi)
710

```

```

711 # Add attributes to network
712 atts<-read.csv("Chick 2014 attributes.csv",header=T)
713 Sex=as.character(atts$Sex[match(colnames(gbi),atts$Bird)]) # if using mixed-sex network
714 Shapef=(atts$Shape.final[match(colnames(gbi),atts$Bird)])
715 Shapef = as.numeric(as.character(Shapef))
716 Oct_network = Oct_network[!is.na(Shapef),!is.na(Shapef)]
717 Shapef_no.na = Shapef[!is.na(Shapef)]
718
719 # Assortment coefficient #####
720 library(assortnet)
721 assort_obs = assortment.continuous(Oct_network, Shapef_no.na, weighted = TRUE, SE =
722 TRUE, M = 1)
723 assort_obs
724
725 # Permutations - compare observed to null networks
726 network <- get_network(gbi, data_format="GBI", association_index="SRI", times=times,
727 locations=locations)
728
729 # Permute the network, constricting within day, sex and location (remove sex if using same-
730 sex networks)
731 network_perm <- network_permutation(gbi, data_format="GBI", association_matrix=network,
732 times=times, days=floor(times/3600), identities = colnames(gbi), within_day=TRUE,
733 permutations=10000, returns = 100, classes = Sex, within_class = TRUE, locations = locations,
734 within_location = T)
735 network_perm = network_perm[,!is.na(Shapef),!is.na(Shapef)] #subset to individuals with
736 score
737
738 # Permuted coefficients
739 coef.perm = apply(network_perm, 1, function(x)
740 assortment.continuous(x,Shapef_no.na,weighted=T,SE=F)$r)
741 coef.obs = assort_obs$r
742 hist(coef.perm, breaks=100)
743 abline(v=assort_obs$r,col="red")
744
745 # p value
746 pval(coef.obs,coef.perm)
747

```

```

748 #####
749 ##### Social position ~ Learning performances #####
750 #####
751 # Individual assortment function #####
752 get_ind_assortment = function(assoc_matrix, sim_matrix){
753   N = nrow(assoc_matrix) # no. of individuals
754   ind_assort = rep(NA,N) # empty vector to hold assortment values
755   for(i in 1:N){
756     ind_assort[i] = cor(assoc_matrix[i,-i], sim_matrix[i,-i], method = "spearman") # correlation
757     between association matrix (excluding themselves/ the diagonal)
758   } # and their row of similarity matrix
759   return(ind_assort)
760 }
761
762 pval<-function(a,b){
763   p<-(1-(sum(b<a)/length(b)))
764   bigger<-sum(b<a);smaller<-sum(b>a)
765   if(bigger>smaller)p<-(1-(bigger/length(b))) else{p<-(1-(smaller/length(b)))}
766   p}
767
768 # Function for edge perm #####
769 lrew.degcont<-function(am){
770   a<-graph.adjacency(am,"undirected",weighted=T)
771   b<-rewire(a,keeping_degseq(niter=round(ecount(a))))
772   E(b)$weight <- sample(E(a)$weight)
773   am.p<-as.matrix(as_adj(b,attr="weight"))
774   am.p}
775
776 # get network
777 Oct_network<-get_network(gbi)
778
779 # Attach attributes
780 atts<-read.csv("Chick 2014 attributes_all birds2.csv",header=T)
781 Sex=as.character(atts$Sex[match(colnames(gbi),atts$Bird)])

```

```

782 Bird=as.character(atts$Bird[match(colnames(gbi),atts$Bird)])
783 Shapef=as.numeric(atts$Shape.final[match(colnames(gbi),atts$Bird)])           #Learning
784 performances
785
786 # Remove/ignore NAs
787 Oct_network = Oct_network[!is.na(Shapef),!is.na(Shapef)]
788 Shapef_no.na = Shapef[!is.na(Shapef)]
789
790 # Build similarity matrix of learning score (assortment scores)
791 sim = -as.matrix(dist(Shapef_no.na))
792
793 # Get assortment scores and attach to network
794 shapef_ass<-get_ind_assortment(Oct_network,sim)
795
796 # Individual assortment ~ Learning: Observed #####
797 coef.obs = lm(shapef_ass ~ Shapef_no.na)$coefficients[2]
798 coef.obs
799 model<-lm(shapef_ass ~ Shapef_no.na)
800
801 # Randomization
802 coef.r <- matrix(nrow = 1000, ncol = 2)
803 for(i in 1:1000){
804   e.perm<-lrew.degcont(Oct_network) #do permutation
805   shapef_ass.r<-get_ind_assortment(e.perm,sim) #recalculate individual assortment
806   coef.r[i,] <- coef(lm(shapef_ass.r ~ Shapef_no.na)) #get the randomized coefficient
807 }
808
809 # Plot
810 par(mfrow = c(1,1))
811 plot(shapef_ass ~ Shapef_no.na, pch = 16, ylab = "Individual Assortment Score", xlab =
812 "Learning Score")
813 abline(lm(shapef_ass ~ Shapef_no.na))
814 hist(coef.r[,2],col="black",breaks=100, xlab = "Coefficient Value", main = "")
815 abline(v = coef.obs, col = "red")

```

```

816
817 # p value
818 pval(coef.obs,coef.r)
819
820 # Strength and degree #####
821 # Correlation between degree and strength
822 strength = rowSums(network)
823 degree = rowSums(ifelse(network>0,1,0))
824 cor.test(strength,degree,method="spearman")
825
826 # Permute the network
827 network_perm <- network_permutation(gbi, data_format="GBI", association_matrix=network,
828 times=times, days=floor(times/3600), identities = colnames(gbi),within_day=TRUE,
829 permutations=10000, returns =100,locations = locations, within_location = T,classes =
830 Sex,within_class = TRUE)
831
832 # Attach learning performances
833 Shapef=(atts$Shape.final[match(colnames(gbi),atts$Bird)])
834 Shapef = as.numeric(as.character(Shapef))
835
836 # Degree strength ~ Learning #####
837 coef.obs = lm(colSums(network) ~ Shapef)$coefficients[2]
838 coef.obs
839
840 # Extract coeffs from permuted networks and plot
841 coef.perm = apply(network_perm, 1, function(x)lm(colSums(x) ~ Shapef)$coefficients[2])
842
843 # Plot
844 hist(coef.perm,breaks=100,main="Strength~Learning",xlab="Coefficients")
845 abline(v = coef.obs, col = "red")
846
847 # p value
848 pval(coef.obs,coef.perm)
849 plot(coef.perm,type="l")
850

```

```

851 # Degree number ~ Learning #####
852 coef.obs = lm(colSums(ifelse(network>0,1,0)) ~ Shapef)$coefficients[2]
853 coef.obs
854
855 coef.perm = apply(network_perm, 1, function(x)lm(colSums(ifelse(x>0,1,0)) ~
856 Shapef)$coefficients[2])
857
858 # Plot
859 hist(coef.perm,breaks=100,main=" Degree~Learning",xlab="Coefficients")
860 abline(v = coef.obs, col = "red")
861
862 # p value
863 pval(coef.obs,coef.perm)
864
865 #####
866 ##### Survival models #####
867 #####
868 library(asnipe)
869 library(survival)
870
871 # Association (feeder) data and survival data
872 feeder_data<-read.csv("Feeder photo data_asnipe.csv",header=T)
873 dframe1<-read.csv("Oct_Survival_SN_CP_mixedsex_network.csv",header=T)
874 dframe1 <- dframe1[!is.na(dframe1$Bird),] #get rid of NA rows
875 head(feeder_data)
876
877 Oct_group_by_ind<-get_associations_points_tw(feeder_data, time_window = 600,
878 which_days = 62:93, which_locations = NULL)
879
880 gbi <- Oct_group_by_ind[[1]] #the group-by-individual matrix
881 dates <- Oct_group_by_ind[[2]] #the dates (now properly returned by the asnipe function)
882 locations <- Oct_group_by_ind[[3]] #the locations (also now correct)
883
884 id <- colnames(gbi) #the IDs in the gbi

```

```

885 net <-get_network(gbi) #final SRI network
886 id <- colnames(net) #the IDs in the network
887 sex <- dframe1$Sex[match(id,dframe1$Bird)] #get the sexes of birds in the network
888
889 dframe1$learning <- scale (dframe1$Shape.final, scale=TRUE, center=TRUE)
890 dframe1$num <- colSums(net>0)[match(as.character(dframe1$Bird),id)] #get the degree from
891 the original network, matching bird ID to the names in the network
892 dframe1$str <- colSums(net)[match(as.character(dframe1$Bird),id)] #get the strength from
893 the original network, matching bird ID to the names in the network
894
895 # Control for number of days observed
896 alldays = feeder_data[feeder_data$Date>=62&feeder_data$Date<=93,]
897 dframe1<-subset(dframe1, (!is.na(dframe1$Shape.final)))
898 nrow(alldays)
899
900 R= nrow(dframe1)
901 dframe1$days.obsd = numeric(R)
902 dframe1$times.observed = numeric(R)
903 for(i in 1:R){
904   bird = dframe1$Bird[i]
905   bird.october = alldays[alldays$ID == bird,]
906   october.bird.days = unique(bird.october$Date)
907   dframe1$days.obsd[i] = length(october.bird.days)
908   dframe1$times.observed[i] = nrow(bird.october)
909 }
910 dframe1$days.obsd
911 dframe1$times.observed
912 head(dframe1)
913
914 dframe1$Sex <- ifelse(dframe1$Sex == "m",1,0) #change this to numeric (female is intercept,
915 male = 1)
916
917 # Survival model: Observed coefficients
918 orig_model <- coxph(Surv(Death,Censored) ~ learning * num + Sex + times.observed, data =
919 dframe1) #fit your original survival model. This can change however you want, but needs to
920 match the structure of the model you fit to the permutations

```

```

921 orig_coef <- coef(orig_model) #save the coefficients
922 summary(orig_model)
923
924 # Survival model: Permuted coefficients
925 net_perm <-
926 network_permutation(gbi,within_day=T,days=dates,within_location=T,locations=locations,ret
927 urns = 100, permutations = 10000) #10,000 permutations, 100 flips per permutation,
928 constrained within day and location
929
930 #for each permuted network, recalculate degree and re-run the survival model, and then pull
931 out the coefficients
932 perm_coef <- apply(net_perm,1,function(x){
933
934   dframe1$num.p <- colSums(x>0)[match(as.character(dframe1$Bird),id)] #save the
935   permuted degree values and line them up with your bird IDs
936   perm_model <- coxph(Surv(Death,Censored) ~ learning * num.p + Sex + times.observed,
937   data = dframe1) #fit a permuted model (same as original but with permuted degree)
938   coef(perm_model)
939
940 })
941
942 # p value
943 permutation_pval <- sapply(1:length(coef(orig_model)),function(x){
944
945   min( c(mean(perm_coef[x,] >= orig_coef[x]), mean(perm_coef[x,] <= orig_coef[x])) )*2
946
947 })
948
949 # Put in a table
950 surv_table <- as.data.frame(summary(orig_model)$coefficients)
951 surv_table$P_Perm <- permutation_pval
952 surv_table
953
954 # Hazard plot #####
955 names(dframe1)

```

```

956 orig_model <- coxph(Surv(Death,Censored) ~ Shape.final * num + Sex + times.observed, data
957 = dframe1) #fit your original survival model.
958 summary(orig_model)
959 orig_coef <- coef(orig_model) #save the coefficients
960 orig_coef
961 poor_learn <- quantile(dframe1$Shape.final,0.25,na.rm=T)
962 good_learn <- quantile(dframe1$Shape.final,0.75,na.rm=T)
963 hist(dframe1$num)
964 curve(exp(orig_coef[5]*x + good_learn*orig_coef[1]*x + good_learn*orig_coef[2] +
965 good_learn*orig_coef[3] + good_learn*orig_coef[4]),xlim=c(0,6), ylab = "Hazard", xlab =
966 "Degree", ylim = c(0,2.2), col = "black", lwd = 2) #plot the first curve
967 curve(exp(orig_coef[5]*x + poor_learn*orig_coef[1]*x + poor_learn*orig_coef[2]+
968 good_learn*orig_coef[3] + good_learn*orig_coef[4]),add=T, col = "grey",lwd=2) #second
969 curve
970

```