

1 **Facilitative effects of social partners on Java sparrow activity**

2
3 Juan Zhang ^a, Andrew J. King ^{b, c}, Ines Fürtbauer ^{b, c}, Yan-Wen Wang ^a, Ya-Qi He ^a,
4 Zhi-Wei Zhang ^a, Dong-Mei Wan ^a, Jiang-Xia Yin ^{a, *}

5
6 ^a *School of Life Sciences, Liaoning University, Shenyang, Liaoning, China*

7 ^b *Department of Biosciences, College of Science, Swansea University, Swansea, U.K.*

8 ^c *Institute for Communities and Wildlife in Africa, Department of Biological Sciences,*
9 *University of Cape Town, Cape Town, South Africa*

10
11 * Author for correspondence:

12 Dr. Jiang-Xia Yin.

13 School of Life Sciences, Liaoning University, 110036 Shenyang, Liaoning, China

14 E-mail address: xia0615@126.com

15
16 Declarations of interest: none

17 18 **Abstract**

19
20 Group-living animals can affect each other's behaviour, causing changes in the rate or
21 type of behaviours performed (social facilitation), or convergence in behaviour to that
22 displayed by the majority of neighbours (social conformity). Facilitation and
23 conformity effects can act to reduce direct competition and/or enable social
24 coordination, and the degree to which individuals can affect each other's behaviour
25 can depend upon the identities and traits of those interacting. To investigate the effect
26 of social partners on individual behaviour, we studied the activity of Java sparrows
27 (*Lonchura oryzivora*) in three contexts (alone, in the presence of three males, or in the
28 presence of three females) and in two conditions (novel environment and novel object
29 tests). A significant proportion of variation in bird activity across trials was attributed
30 to variation among individuals, indicating a personality trait. However, activity varied
31 systematically according to whether birds were tested alone or in the presence of
32 companions. We found that irrespective of the focal bird's sex, individuals were more
33 active in a social context compared to when alone, and this effect was greatest when
34 focal birds were in the presence of male companions. Overall, our findings
35 demonstrate facilitative effects of social partners on Java sparrow activity, and the
36 magnitude of this effect depends on the sex of companions. These results therefore
37 support the hypothesis that social isolation causes behavioural inhibition (which may
38 be caused by increased perception of risk), and future studies should carefully assess
39 the ecological and evolutionary consequences for the emergence of social facilitation,
40 inhibition or conformity across different species and contexts.

41
42 *Key words:* activity, *Lonchura oryzivora*, personality, sex difference, social context

43

44 **Introduction**

45

46 Consistent individual differences have been described in a wide variety of species and
47 taxa (see Gosling, 2001; Wolf & Weissing, 2012; for reviews). Such inter-individual
48 differences in behaviour can affect how individuals cope with environmental variation
49 (e.g. Wolf & Weissing, 2012) and ultimately determine individual survival and
50 reproductive output (e.g. Smith & Blumstein, 2008). For example, a meta-analysis of
51 published animal personality studies has found ‘bolder’ males tend to have higher
52 reproductive success than ‘shyer’ males, but at a greater cost of a shorter life span
53 (Smith & Blumstein, 2008). Consistent inter-individual differences in behaviour can
54 therefore have important consequences for species ecology and evolution (Dall,
55 Houston, & McNamara, 2004; Sih, Bell, Johnson, & Ziemba, 2004), impacting space
56 and habitat use (e.g. Duckworth, 2006), disease and information transmission
57 dynamics (Krause, James, & Croft, 2010), species interactions (e.g. Schreiber, Bürger,
58 & Bolnick, 2011), and community structure (e.g. Post, Palkovacs, Schielke, &
59 Dodson, 2008).

60 Animal personality can be studied by observer rating (Itoh, 2002) or by coding of
61 behaviour (Watters & Powell, 2011). Observer rating is a relatively subjective
62 measure that relies on the impression of animal made by experience; in contrast,
63 coding behaviour is a more objective evaluation technique that directly observes and
64 records animal behaviour (Watters & Powell, 2011) that can indicate presence of
65 personality traits (see Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; for
66 reviews). For example, novel environment tests are often used to measure individual's
67 exploration-avoidance and activity.

68 However, a growing body of evidence suggests that the expression of individual
69 personality can differ depending on whether individuals are on their own or in the
70 presence of companions (Webster & Ward, 2011). For example, social birds such as
71 common ravens (*Corvus corax*) and carrion crows (*Corvus corone*, *Corvus cornix*)
72 interact more with novel objects in a social context (Miller, Bugnyar, Pölzl, & Schwab,
73 2015), but common ravens are quicker to approach novel objects when tested alone
74 (Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006). Similarly, house sparrows (*Passer
75 domesticus*) are more active in a social context (Tuliozi, Fracasso, Hoi, & Griggio,
76 2018), but zebra finches (*Taeniopygia guttata*) are bolder in a foraging experiment
77 when alone compared to when in a flock (Kerman, Miller, & Sewall, 2018).

78 How individuals affect each other's behaviour may also depend upon the identities
79 of those interacting (conformity). Experiments with Gouldian finch (*Erythrura
80 gouldiae*), for instance, show that birds adjusted their behaviour according to the
81 personality of their social partner: where birds were paired with a more exploratory or
82 more risk-taking partner, they themselves became more exploratory or more
83 risk-taking than when they were tested alone, and vice versa (King, Williams, &
84 Mettke-Hofmann, 2015). Despite growing evidence for specific individuals or
85 behavioural types can have moderating effects upon others personality across species
86 and contexts (e.g. Webster & Ward, 2011; King, Williams, & Mettke-Hofmann, 2015;
87 Fürtbauer & Fry, 2018), if and how adjustments in behaviour differ according to the

88 sex of conspecifics is not well understood, but may be important for several reasons.
89 For example, males and females can differ in their specific personality traits (e.g.
90 male house sparrows have shorter latencies to forage than females: Tuliozi, Fracasso,
91 Hoi, & Griggio, 2018) and personality traits can be an indicator for individual quality
92 (e.g. Zann, 1996; Schuett & Dall, 2009). Therefore, any change in individuals' rate or
93 type of behaviour when with others (social facilitation), or convergence in behaviour
94 to that displayed by the majority of neighbours (social conformity) may differ
95 according to the sexes of interacting individuals (Schuett, Dall, & Royle, 2011; David,
96 Pinxten, Martens, & Eens, 2015).

97 We sought to investigate the effect of same- or opposite-sex social partners on the
98 expression of individual behaviour in the Java sparrow (*Lonchura oryzivora*). The
99 Java sparrow is a small, highly social, passerine bird species (Islam, 1997) resident in
100 Java and Indonesia which feeds mainly on grain and other seeds (Islam, 1997) and
101 displays sexual dimorphism and elaborate courtship (Soma & Iwama, 2017). To
102 investigate the potential moderating effects of conspecifics upon Java sparrow activity,
103 we measured the behaviour of birds in three contexts (alone, in the presence of three
104 females, or in the presence of three males) and two conditions (novel environment and
105 novel object tests). This allowed us to test if and how social companion presence and
106 sex may influence activity levels of focal birds when repeatedly tested in behavioural
107 assays in different contexts that are commonly used in personality researches (Toms,
108 Echevarria, & Jouandot, 2010; Carter, Feeney, Marshall, Cowlshaw, & Heinsohn,
109 2013; Perals, Griffin, Bartomeus, & Sol, 2017; Huang, Kerman, Sieving, & Mary,
110 2016). First, to confirm that our measure of activity represents a personality trait, we
111 tested for within-individual consistency and among-individual differences in activity
112 across all trials (Dingemanse & Dochtermann, 2013; Fürtbauer, Pond, Heistermann,
113 & King, 2015). Next, if social isolation causes behavioural inhibition due to increased
114 perception of risk (Krause & Ruxton, 2002; Webster & Ward, 2011), we expected that
115 focal birds should systematically alter their activity levels, and tested whether birds
116 become more active in the presence of companions, compared to when alone. Finally,
117 we tested whether birds would show greater changes in activity in the presence of the
118 opposite-sex companions compared to same-sex companions due to potentially
119 greater between-sex differences in activity (Ruckstuhl, 1998; Ruckstuhl & Kokko,
120 2002) and enhanced social facilitation effects related to sexual behaviour and
121 courtship between the sexes (e.g. Evans & Marler, 1994).

122

123 **Methods**

124

125 *Ethical Note*

126 All procedures involving animals were carried out in accordance with the Policy on
127 the Care and Use of Animals, approved by the Ethical Committee, Center of
128 Zoological Evolution and Systematic Zoological Museum of China, School of Life
129 Sciences, Liaoning University (EC-LNU 20170150). We adhered to the ASAB/ABS
130 Guidelines for the use of animals. Birds were checked daily for health and injuries
131 and none were observed.

132 *Study Species and Housing*

133 Java sparrows were obtained from a registered pet shop in Shenyang, Liaoning, China
134 in March 2018. All birds were bred in farms in Dalian, Liaoning, and were kept in
135 family groups (cage size 31 × 52 × 41 cm). After being fledging (15-20 days after
136 hatched), birds were transported to pet shops and kept singly (cage size 25 × 25 × 25
137 cm). Study subjects were purchased at 20-25 days after hatching and were housed
138 singly (cage size 35 × 30 × 25 cm) in the same keeping room for several months
139 before testing in the laboratory (see below). Birds could see and hear each other in the
140 keeping room but had no physical contact. Birds had full-spectrum light on a 14:10 h
141 light:dark cycle, and the temperature was controlled at 25 °C. Each housing cage
142 contained one feeder, one drinker, two perches, and a nest-box. Birds were fed millet
143 seed, grit, fresh vegetables and water ad libitum. Birds were checked daily for health
144 and injuries.

145

146 *Behavioural Trials*

147 We conducted behavioural trials with $N = 13$ females and $N = 25$ males in a separate
148 test laboratory. Trials were undertaken during the morning, within 5 h of sunrise, and
149 on each test day between 10-20 focal birds were observed. Birds underwent
150 behavioural trials twice, three weeks apart (Mainwaring, Beal, & Hartley, 2011).
151 During the first test day birds were observed in the novel environment test, and during
152 the second day birds were observed in the novel object test. During each test day,
153 focal individuals were observed in three contexts (alone, in the presence of three
154 females, or in the presence of three males). The order of the three contexts was
155 randomized to control for order effects. Focal bird testing order was also randomized.
156 On each test day, three male and three female birds were randomly selected from $N =$
157 44 birds housed in the same keeping room for use as companion birds in social
158 context trials. The companion birds were placed in a space separated from the focal
159 bird by wire mesh. Thus, companion birds and focal birds had visual and auditory
160 contact, but no physical contact. Companion birds were not used as focal birds and
161 had no prior physical interactions with focal birds. Details of the set-up used in novel
162 environment and novel object tests are given below.

163

164 *Novel environment*

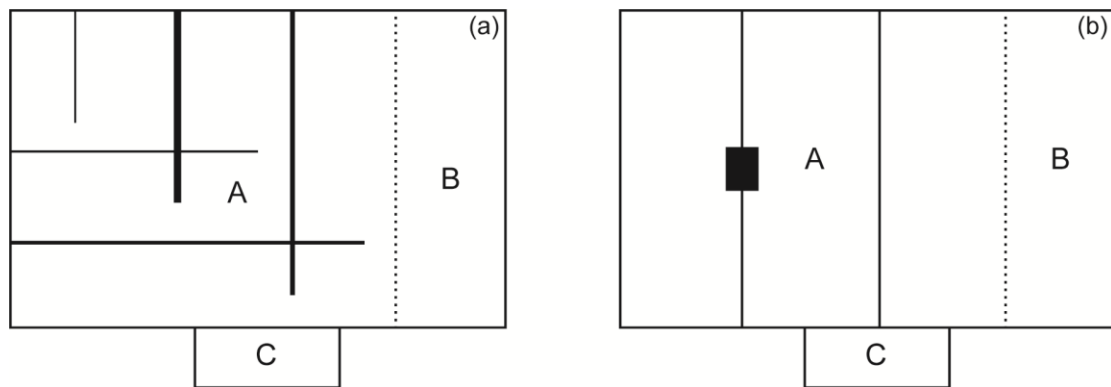
165 We used an experimental aviary (60 × 43 × 40 cm) with five perches with different
166 lengths and heights which were randomly positioned for each trial. The aviary was
167 divided into a small introductory space, a test space, and a companion space (Fig. 1a).
168 Both the test space and the companion space had a feeder and a drinker. The focal bird
169 was placed in the introductory space with the sliding door open to freely enter the test
170 space. The sliding door was closed after the bird entered the test space; this was taken
171 as the start time for the trial.

172

173 *Novel object*

174 For novel object tests we used the same experimental aviary (60 × 43 × 40 cm) as for
175 the novel environment test, but provided two perches of same length and height, and a

176 feeder and a drinker placed on the ground between the two perches (Fig. 1b). An
177 orange doll (13 × 7 × 3 cm) was fixed on one of the perches as the novel object. We
178 chose to use the same novel object in all three contexts (alone, in the presence of three
179 female companions, in the presence of three male companions) since previous studies
180 show the colour, size and structure of novel objects can have large differences on bird
181 behaviour (Wells, 2009; Mastrota & Mench, 1995; Huber-Eicher & Wechsler, 1998;
182 McKenna, Sharifi, & Gerken, 2019) and our goal was to examine the effect of social
183 context on behaviour rather than response to novelty *per se*. Neither the companion
184 birds nor the focal birds were exposed to the novel environment or novel object prior
185 to testing.
186



187

188

189 **Figure 1.** Schematic diagram of (a) novel environment test aviary and (b) novel object test aviary.
190 The dashed line represents a wire mesh, section A, B and C represent the test space, companion
191 space, and introductory space, respectively. In the novel environment aviary, the solid lines of
192 different thickness and length represent five perches of different lengths and heights. In the novel
193 object aviary, the two solid lines represent perches and the black square represent the novel object.

194

195 *Activity measure*

196 During trials we recorded the total number of flights and hops focal birds made over a
197 10-minute period as a measure of activity. Recordings were made using an HP F860
198 video recorder at a distance of 3 m from the test space while one operator sat in the
199 test laboratory (Naguib et al., 2013). Using video playbacks, we video noted the total
200 number of flights and hops, and all tests and video noting of activity was undertaken
201 by one observer (JZ). Flight was defined as a movement from one perch to another,
202 and hop was the movement from one end of a perch to the other (Dingemanse, Both,
203 Drent, van Oers, & van Noordwijk, 2002).

204

205 *Statistical Analyses*

206 Data on flight and hop counts were $\ln(x+1)$ transformed for analyses to meet the
207 assumptions of our statistical models. We tested for differences in activity levels in the
208 novel environment and novel object tests (since habituation might have played a role
209 in the activity levels for the latter) using paired-sample *T*-tests, and tested for
210 repeatability of bird activity across trials by calculating average measures intra-class

211 correlation coefficients (ICCs) and 95% confidence intervals (CIs) using SPSS v. 21.0.
 212 We used Linear Mixed Models (LMMs) fitted in R (R Development Core
 213 Team, 2019), package lme4 (Bates, Maechler, Bolker, & Walker, 2015) to assess
 214 whether context (alone, male companions, female companions) and focal bird sex
 215 (male, female), predicted variation in activity levels. We tested for an interaction
 216 between context and sex in line with our predictions and fitted bird ID as random
 217 intercept in our models to control for individual differences and repeated observations.
 218 Model fits were checked by visual inspection of quantile-quantile plots of model
 219 residuals versus the predictor.

220

221 RESULTS

222

223 *Repeatability of Activity*

224 A significant proportion of observed variation in the sample across the six behavioural
 225 trials could be attributed to variation among individuals (ICC (CI) = 0.267
 226 (0.144-0.430), F -test_{37, 185} = 3.191, P < 0.001). Activity levels were similar in the
 227 novel environment and novel object tests (Paired-sample T -test: alone: t_{37} = -1.411, P
 228 = 0.167; female companions: t_{37} = -1.332, P = 0.191; male companions: t_{37} = 1.056, P
 229 = 0.298) suggesting condition did not affect activity.

230

231 **Table 1.** Results from linear mixed models (LMMs) testing the effects of context, focal bird sex,
 232 and potential sex*context interaction on focal bird activity in novel environment and novel object
 233 trials.

Model and Effects	<i>df</i>	<i>F</i> -value	<i>P</i>
Novel environment			
Context (alone, female companions, male companions)	2	21.625	<0.001
Sex (male, female)	1	0.588	0.448
Sex*Context	2	1.988	0.144
Novel object			
Context (alone, female companions, male companions)	2	9.734	<0.001
Sex (male, female)	1	1.754	0.194
Sex*Context	2	0.035	0.965

234 Focal bird activity (x) expressed as $(\ln(x+1))$. N = 38. Degrees of freedom (*df*), *F*-statistic, and
 235 *P*-values are given; see main text for results of comparisons within categories.

236

237 *Activity and Novel Environment*

238 Bird activity in the novel environment did not differ according to focal bird sex and
 239 was significantly greater when focal birds were in the presence of female companions
 240 compared to when alone (LMM: Estimate \pm SE = 0.901 \pm 0.272, t = 3.313, P = 0.001;
 241 Table 1, Fig. 2) and male companions compared to when alone (LMM: Estimate \pm SE
 242 = 1.682 \pm 0.272, t = 6.184, P < 0.001; Table 1, Fig. 2). We found no interaction
 243 between sex of the focal bird (male, female) and context (alone, female companion,
 244 male companion) on activity levels (Table 1, Fig. 2). Given the inter-individual
 245 variation in focal bird activity observed, we included bird identity as a random effect

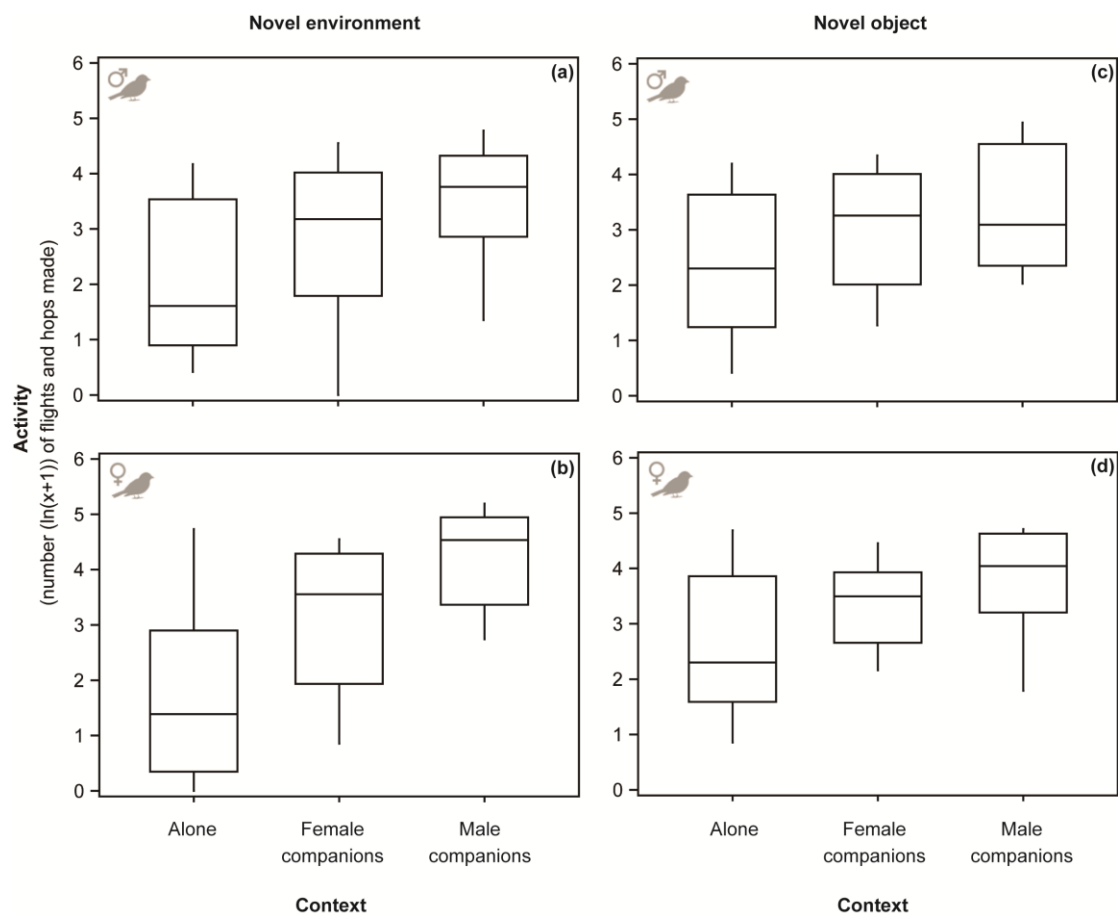
246 and this improved model fit (AIC 403.03 versus 398.24; log-likelihood ratio test: X_1^2
247 = 6.793, $P = 0.009$).

248

249 *Activity and Novel Object*

250 Bird activity when presented with a novel object did not differ according to focal bird
251 sex and was significantly greater when focal birds were in the presence of female
252 companions compared to when alone (LMM: Estimate \pm SE = 0.747 ± 0.244 , $t =$
253 3.061 , $P = 0.003$; Table 1, Fig. 2) and male companions compared to when alone
254 (LMM: Estimate \pm SE = 1.106 ± 0.244 , $t = 4.530$, $P < 0.001$; Table 1, Fig. 2). We
255 found no interaction between sex of the focal bird (male, female) and context (alone,
256 female companion, male companion) on activity levels (Table 1, Fig. 2). Given the
257 inter-individual variation in focal bird activity observed, we included bird identity as a
258 random effect and this produced a comparable model (AIC 369.9 versus 364.69; log-
259 likelihood ratio test: $X_1^2 = 6.793$, $P = 0.096$).

260



261

262

263 **Figure 2.** Bird activity (total number of flights and hops) when tested alone, in the presence of
264 three females, or in the presence of three males, in a novel environment (a, b), and when presented
265 with a novel object (c, d), for male (a, c) and female (b, d) focal birds. Counts (x) are expressed as
266 $(\ln(x+1))$. The box plots show the median and 25th and 75th percentiles. The whiskers show the
267 lower and upper extremes.

268

269 **DISCUSSION**

270

271 We examined the activity of Java sparrows in a novel environment and in the presence
272 of a novel object, testing focal birds alone, in the presence of three male companions,
273 or in the presence of three female companions. We found consistent inter-individual
274 differences in activity, no overall sex-differences in behaviour of focal birds across
275 contexts, and higher activity levels in the presence of companions. We discuss each of
276 these main findings in turn.

277 The within-individual consistency and among-individual differences in activity we
278 observed indicate our activity measure represents a personality trait, in line with
279 previous work (Kluen, Kuhn, Kempnaers, & Brommer, 2012; Devost, Jones,
280 Cauchoix, Montreuil-Spencer, & Morand-Ferron, 2016). To limit any possible
281 carryover effects of social conditions prior to behavioural testing on personality
282 (Webster & Ward, 2011), we housed all birds alone prior to testing. However, this can
283 also affect behavioural expression during tests. For example, Shams et al. (2017)
284 found zebrafish (*Danio rerio*) show increased locomotion and decreased shoaling
285 during open-field tests following social isolation, and Jolles et al. (2016) found that
286 recent social conditions (either housed solitarily, solitarily part of the time or socially
287 in groups) affected the short-term repeatability of three spined stickleback
288 (*Gasterosteus aculeatus*) behaviour, with solitary housed individuals showing higher
289 repeatability. We therefore suggest, future work should further investigate the effects
290 of prior social experience upon behavioural expression and consider carefully any
291 order effects.

292 We did not find support for our prediction that focal birds would show increased
293 activity levels in opposite-sex pairs (Ruckstuhl, 1998; Ruckstuhl & Kokko, 2002;
294 Evans & Marler, 1994). We made this prediction on the basis that competitive and
295 cooperative behaviours vary within and between the sexes (Wiley & Poston, 1996;
296 Wong & Candolin, 2005; Song et al., 2016) and sex-differences in specific behaviours
297 are common across bird species (e.g. zebra finches: Mainwaring, Beal, & Hartley,
298 2011; house sparrows: Ensminger & Westneat, 2012; Tuliozi, Fracasso, Hoi, &
299 Griggio, 2018). Instead, we found a similar increase in activity for both male and
300 female focal birds in the presence of the same-sex and opposite-sex companions. This
301 finding could be explained by our use of three companions during tests. In previous
302 work studies have tended to explore changes in the behaviour of individuals when
303 tested alone and in dyads (e.g. van Oers, Klunder, & Drent, 2005; Fürtbauer & Fry,
304 2018; King, Williams, & Mettke-Hofmann, 2015). Here, our use of a larger number of
305 conspecifics may result in individuals increasing their activity levels to the most
306 active individual or average activity of the group (Webster & Ward, 2011), and thus
307 potentially mask any specific sex-mediated changes in activity patterns that may be
308 expressed and observable in dyads. Indeed, this is in line with our finding that both
309 males and females tended to show higher activity in the presence of companions.

310 We also found that both male and female focal birds tended to show greater activity
311 when in the presence of male companions compared to female companions. Islam
312 (1997) found male Java sparrows to be more active than females, and so it is possible

313 that three male companions were on average more active than three female
314 companions, and thus elicited greater activity from focal birds. However, we did not
315 find that male focal birds were more active than female focal birds when they were
316 tested singly (or in any of our contexts) suggesting an absence of sex-differences in
317 activity in our study population. However, we cannot rule-out higher male companion
318 activity levels driving the patterns we observed because we have no information about
319 the personalities of companions or their behaviour during trials. We are therefore
320 designing future experiments to investigate this further.

321 Overall, our results demonstrate that social context can facilitate the expression of
322 individual activity in the Java sparrow, with focal birds being more active in the
323 presence of conspecifics (especially males). These results therefore support the
324 hypothesis that social isolation causes behavioural inhibition (which may be caused
325 by increased perception of risk). In the laboratory, future experiments should
326 investigate (i) the effect of social contexts prior to testing and (ii) the presence of
327 flocks with natural composition (e.g. larger mixed-sex groups) on the activity of
328 individuals to fully understand the behavioural outcomes we report here. In the wild,
329 future studies should assess the ecological relevance of facilitative effects of social
330 partners on Java sparrow activity. For example, it will be useful to investigate how
331 individual personalities affect group activity and if social facilitation provides a
332 behavioural mechanism for altering group phenotypic composition (Farine, Montiglio,
333 & Spiegel, 2015). Specifically, we would predict that social facilitation of activity
334 could enhance coordination and cohesion of large mobile flocks in the wild, but that
335 there would also be constraints on the degree to which individuals are able to change
336 their behaviours (i.e. their behavioural plasticity). This may result in association by
337 phenotype (here, activity levels) that would decrease individual heterogeneity within
338 groups, and increase it between groups.

339

340 **Acknowledgements**

341 We thank the staff of the key laboratory of Animal Resource and Epidemic Disease
342 Prevention in Liaoning Province for assistance with laboratory work. We also thank
343 Animal Behaviour Editor Claudia Wascher, Xiaotao Lü, and two anonymous Referees
344 for improving our manuscript, and Layla King for support. This work was supported
345 by Doctoral Scientific Research Foundation of Liaoning (20170520179), Shenyang
346 Science and Technology Bureau (18-013-0-04), and Liaoning natural fund guidance
347 plan (2019-ZD-0196). Authors declare no conflict of interests.

348

349 **Author contributions**

350 JXY, DMW, and JZ designed the experiment. JZ, YWW, YQH, and ZWZ performed
351 the data collection. JZ, AJK and IF conducted the analyses. JZ, JXY, AJK, and IF
352 wrote the manuscript with feedback from all co-authors

353

354 **References**

355 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models
356 using lme4. *Journal of Statistical Software*, 67, 1–48.

357 Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013). Animal
358 personality: what are behavioural ecologists measuring? *Biological Reviews*, 88(2), 465–475.

359 Dall, S. R., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality:
360 consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739.

361 David, M., Pinxten, R., Martens, T., & Eens, M. (2015). Exploration behavior and parental effort
362 in wild great tits: partners matter. *Behavioral Ecology and Sociobiology*, 69(7), 1085–1095.

363 Devost, I., Jones, T. B., Cauchoix, M., Montreuil-Spencer, C., & Morand-Ferron, J. (2016).
364 Personality does not predict social dominance in wild groups of black-capped chickadees.
365 *Animal Behaviour*, 122, 67–76.

366 Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002).
367 Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal*
368 *Behaviour*, 64(6), 929–938.

369 Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour:
370 mixed- effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54.

371 Duckworth, R. A. (2006). Aggressive behaviour affects selection on morphology by influencing
372 settlement patterns in a passerine bird. *Proceedings of the Royal Society B: Biological*
373 *Sciences*, 273(1595), 1789–1795.

374 Ensminger, A. L., & Westneat, D. F. (2012). Individual and Sex Differences in Habituation and
375 Neophobia in House Sparrows (*Passer domesticus*). *Ethology*, 118(11), 1085–1095.

376 Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus*
377 *gallus*: their relationships to food availability, courtship and social facilitation. *Animal*
378 *Behaviour*, 47(5), 1159–1170.

379 Farine, D. R., Montiglio, P. O., & Spiegel, O. (2015). From individuals to groups and back: the
380 evolutionary implications of group phenotypic composition. *Trends in Ecology & Evolution*,
381 30(10), 609–621.

382 Fürtbauer, I., Pond, A., Heistermann, M., & King, A. J. (2015). Personality, plasticity and
383 predation: linking endocrine and behavioural reaction norms in stickleback fish. *Functional*
384 *Ecology*, 29(7), 931–940.

385 Fürtbauer, I., & Fry, A. (2018). Social conformity in solitary crabs, *Carcinus maenas*, is driven by
386 individual differences in behavioural plasticity. *Animal Behaviour*, 135, 131–137.

387 Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal
388 research? *Psychological Bulletin*, 127(1), 45.

389 Huang, P., Kerman, K., Sieving, K. E., & Mary, C. M. S. (2016). Evaluating the
390 novel-environment test for measurement of exploration by bird species. *Journal of Ethology*,
391 34(1), 45–51.

392 Huber-Eicher, B. E. A. T., & Wechsler B. (1998). The effect of quality and availability of foraging
393 materials on feather pecking in laying hen chicks. *Animal Behaviour*, 55(4), 861–873.

394 Islam, K. (1997). Java Sparrow (*Padda oryzivora*). *The Birds of North America*, (304), 12.

395 Itoh, K. (2002). Personality research with non-human primates: Theoretical formulation and
396 methods. *Primates*, 43(3), 249–261.

397 Jolles, J. W., Taylor, B. A., & Manica, A. (2016). Recent social conditions affect boldness
398 repeatability in individual sticklebacks. *Animal Behaviour*, 112, 139–145.

399 Kerman, K., Miller, L., & Sewall, K. (2018). The effect of social context on measures of boldness:
400 Zebra finches (*Taeniopygia guttata*) are bolder when housed individually. *Behavioural*

401 *Processes*, 157, 18–23.

402 King, A. J., Williams, L. J., & Mettke-Hofmann, C. (2015). The effects of social conformity on
403 Gouldian finch personality. *Animal Behaviour*, 99, 25–31.

404 Kluen, E., Kuhn, S., Kempnaers, B., & Brommer, J. E. (2012). A simple cage test captures
405 intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal*
406 *Behaviour*, 84(1), 279.

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

408 Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks.
409 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4099–
410 4106.

411 Mainwaring, M. C., Beal, J. L., & Hartley, I. R. (2011). Zebra finches are bolder in an asocial,
412 rather than social, context. *Behavioural Processes*, 87(2), 171–175.

413 Mastrota, N. F., & Mench, J. A. (1995). Colour avoidance in northern bobwhites: effects of age,
414 sex and previous experience. *Animal Behaviour*, 50(2), 519–526.

415 McKenna, L., Sharifi, A. R., & Gerken, M. (2019). Behavioural and cardiac responses towards
416 different novel objects in juvenile female and male pigs (*Sus scrofa*). *Applied Animal*
417 *Behaviour Science*, 215, 13–20.

418 Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in
419 common ravens and carrion crows during development and across social context. *Behavioral*
420 *Ecology and Sociobiology*, 69(7), 1209–1220.

421 Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P., & Waas, J. R. (2013). Noise
422 annoys: effects of noise on breeding great tits depend on personality but not on noise
423 characteristics. *Animal Behaviour*, 85(5), 949–956.

424 Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: what does
425 it really tell us about animal personality? *Animal Behaviour*, 123, 69–79.

426 Post, D. M., Palkovacs, E. P., Schielke, E. G., & Dodson, S. I. (2008). Intraspecific variation in a
427 predator affects community structure and cascading trophic interactions. *Ecology*, 89(7),
428 2019–2032.

429 R Development Core Team. (2019). *R: A language and environment for statistical computing*.
430 Vienna, Austria: R Foundation for Statistical Computing.

431 Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal*
432 *Behaviour*, 56(1), 99–106.

433 Ruckstuhl, K. E., & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of
434 group size, activity budgets and synchrony. *Animal Behaviour*, 64(6), 909–914.

435 Schreiber, S. J., Bürger, R., & Bolnick, D. I. (2011). The community effects of phenotypic and
436 genetic variation within a predator population. *Ecology*, 92(8), 1582–1593.

437 Schuett, W., & Dall, S. R. (2009). Sex differences, social context and personality in zebra finches,
438 *Taeniopygia guttata*. *Animal Behaviour*, 77(5), 1041–1050.

439 Schuett, W., Dall, S. R., & Royle, N. J. (2011). Pairs of zebra finches with similar ‘personalities’
440 make better parents. *Animal Behaviour*, 81(3), 609–618.

441 Shams, S., Amlani, S., Buske, C., Chatterjee, D., & Gerlai, R. (2017). Developmental social
442 isolation affects adult behavior, social interaction, and dopamine metabolite levels in zebrafish.
443 *Developmental Psychobiology*, 60(1), 43–56.

444 Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative

445 overview. *The Quarterly Review of Biology*, 79(3), 241–277.

446 Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis.
447 *Behavioral Ecology*, 19(2), 448–455.

448 Soma, M., & Iwama, M. (2017). Mating success follows duet dancing in the Java sparrow. *PLoS*
449 *One*, 12(3), e0172655.

450 Song, Z., Lou, Y., Hu, Y., Deng, Q., Gao, W., & Zhang, K. (2016). Local resource competition
451 affects sex allocation in a bird: experimental evidence. *Animal Behaviour*, 121, 157–162.

452 Stöwe, M., Bugnyar, T., Heinrich, B., & Kotrschal, K. (2006). Effects of group size on approach to
453 novel objects in ravens (*Corvus corax*). *Ethology*, 112(11), 1079–1088.

454 Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A methodological review of
455 personality-related studies in fish: focus on the shy-bold axis of behavior. *International*
456 *Journal of Comparative Psychology*, 23(1).

457 Tuliozi, B., Fracasso, G., Hoi, H., & Griggio, M. (2018). House sparrows' (*Passer domesticus*)
458 behaviour in a novel environment is modulated by social context and familiarity in a
459 sex-specific manner. *Frontiers in Zoology*, 15(1), 16.

460 van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: risk-taking
461 behavior in a social and a nonsocial situation. *Behavioral Ecology*, 16(4), 716–723.

462 Watters, J. V., & Powell, D. M. (2011). Measuring animal personality for use in population
463 management in zoos: suggested methods and rationale. *Zoo Biology*, 31(1), 1–12.

464 Webster, M. M., & Ward, A. J. (2011). Personality and social context. *Biological Reviews*, 86(4),
465 759–773.

466 Wells, D. L. (2009). Sensory stimulation as environmental enrichment for captive animals: a
467 review. *Applied Animal Behaviour Science*, 118(1–2), 1–11.

468 Wiley, R. H., & Poston, J. (1996). Perspective: indirect mate choice, competition for mates, and
469 coevolution of the sexes. *Evolution*, 50(4), 1371–1381.

470 Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution.
471 *Trends in Ecology & Evolution*, 27(8), 452–461.

472 Wong, B. B., & Candolin, U. (2005). How is female mate choice affected by male competition?
473 *Biological Reviews*, 80(4), 559–571.

474 Zann, R. A. (1996). *The zebra finch: a synthesis of field and laboratory studies* (Vol. 5). Oxford
475 University Press.