Varietas delectat: groups with diverse personalities mitigate physiological stress in a songbird

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AUTHORS' CONTRIBUTIONS

C.I.V., A.F., and Z.Ba. conceived and designed the study. C.I.V., A.F., P.L.P., O.G., J.P., and Z.Be. performed research. C.I.V., J.P., O.G., and Á.Z.L. contributed new reagents/analytic tools. C.I.V., A.F., and Z.Ba. analysed data. C.I.V., A.F., and Z.Ba. drafted the manuscript with major input from Á.Z.L. and P.L.P. All authors contributed revisions and approved the final version of the manuscript. The authors declare no conflict of interest.

ABSTRACT

Social groups often consist of diverse phenotypes, including personality types. Social selection theory hypothesizes that group composition (i.e. social environment) influences the performance of group members. However, this hypothesis remains experimentally unexplored, and it is still contentious whether a homogeneous or a diversely composed group (i.e. social heterosis) is more beneficial to the individual. We experimentally formed groups of house sparrows with high and low diversity of personality, and found that their physiological state (body condition, physiological stress, and oxidative stress) improved with increasing group-level diversity of personality. These findings demonstrate that group composition affects the condition of group members and individuals benefit from social heterosis (i.e. associating with a diverse set of behavioural types). This aspect of the social life can play a key role in the evolutionary coexistence of different personalities in nature and has implications for human teams and animal welfare.

Keywords

Affiliation, exploratory behaviour, group composition, health, *Passer domesticus*, personality, social environment, social evolution, social heterosis.

38 **INTRODUCTION**

39 Social groups were once considered aggregates of similar individuals, but more recently are
40 viewed as a mixture of members with diverse phenotypes (Farine *et al.* 2015). Variation within
41 group can occur in morphology (e.g. size), behavioural traits (e.g. reactive and proactive
42 behavioural types (Sih *et al.* 2004)), or social roles (e.g. leaders/followers in human teams (King
43 *et al.* 2009), or producers/scroungers in sparrow flocks (Fülöp *et al.* 2019)). Group composition
44 has implications for emergent group-level processes such as decision-making, which ultimately
45 drive group functioning (reviewed in (Aplin *et al.* 2014; Farine *et al.* 2015)). Ethnic diversity can,
46 for instance, have a positive effect on research teams' scientific performance (AlShebli *et al.*
47 2018).

48 Personality, the consistent among-individual differences in behavioural phenotype (Réale
49 *et al.* 2007), has strong relevance for social life (Webster & Ward 2011). Social groups can
50 largely differ in their personality composition (Farine *et al.* 2015). Groups' personality
51 composition can have effects at both the level of group as a whole ('upstream effects') and the
52 level of individual group members ('downstream effects'). The group-level consequences of
53 groups' personality composition have mostly been assessed in human teams (van Knippenberg &
54 Schippers 2007; Dyer *et al.* 2009b), where personality composition may affect team performance,
55 albeit in an inconsistent manner (Barrick *et al.* 1998; Halfhill *et al.* 2005; Stewart 2006). In non-
56 human organisms, upstream effects of personality composition have been shown to influence
57 within-group social network structure, collective behaviour, and group performance (Sih &
58 Watters 2005; Dyer *et al.* 2009a; Aplin *et al.* 2014; Bengston & Jandt 2014; Brown & Irving
59 2014). Although individual-level aspects of sociality, e.g. rank in the dominance hierarchy, have
60 been shown to influence the state of individual members (reviewed by (Sapolsky 2005; Creel *et*

61 *al.* 2013)), the downstream effects of group composition on individual state is surprisingly little
62 scrutinised (Farine *et al.* 2015). This happens despite that social selection theory postulates that
63 the fitness of an individual is contingent upon the phenotype of those with whom it affiliates (i.e.
64 social environment; (Wolf *et al.* 1999; Sih & Watters 2005)).

65 Health state can have a strong influence on the individual's performance (Kelly &
66 Vitousek 2017) and, at the same time, is moulded by changes of individual's social environment
67 (Creel *et al.* 2013). Therefore, it is reasonable to assume that physiological condition (e.g. body
68 condition, stress physiology, oxidative stress, and immune capacity) of group members is also
69 influenced downstream by the personality composition of their group. Correlative studies on
70 human work teams found that age and gender composition can be associated with subjective self-
71 reported health impairment (Wegge *et al.* 2008), but human studies with experimental
72 manipulation of group composition and actual health measurements are still lacking. Earlier
73 animal studies only assessed how individuals' position within the social structure (e.g. rank in
74 dominance hierarchy, an individual-level social attribute) affected their health or physiology
75 (reviewed by (Sapolsky 2005; Creel *et al.* 2013)). No experimental study on animals, however,
76 tested directly whether group phenotypic composition (a group-level social attribute) affects the
77 stress level and health state of group members.

78 We conducted an experimental study to explore whether manipulated personality
79 composition of groups *per se* or in interaction with individual personality type affects the
80 physiological condition of group members. Given that diverse groups might have advantages for
81 group functioning, we predicted that individuals in groups with more diverse personality
82 composition would improve their physiological condition as compared with individuals in groups
83 with more homogeneous personality composition. In this case, improved physiological condition

of group members is a legacy of being part of a diversely composed and better functioning group and each group member shares this legacy. We do not know whether this potential benefit is indeed uniform for each member. Alternatively, some members might harvest more the benefits of better group-level functioning to the detriment of other group members. We assessed this prediction by testing whether personality diversity of the groups interact with individual personality type to influence physiological condition. A significant interaction might suggest that individuals that either match or mismatch the group's personality composition benefit more than other group members do.

METHODS

Study protocol

The study is based on a large sample of 240 house sparrows. We captured 40 sparrows (1:1 sex ratio) per each of the six study replicates. These 40 birds were divided into four treatment groups (see below) consisting of 10 birds each, which yielded 24 social groups for the entire study (four treatment groups per study replicate × six study replicates). The study timeline was identical in each study replicate as follows. Upon capture (day 0), birds were marked with an aluminium ring, and their sex and body mass was recorded. Then they were housed in indoor aviaries for 18 days at the Campus of Babeș-Bolyai University, Cluj-Napoca, Romania. On days 5–7, we recorded exploratory behaviour as a well-established and ecologically relevant axis of personality (Wolf & Weissing 2012) following the novel environment test of Dingemanse and co-authors (Dingemanse *et al.* 2002). At day 9, we measured the body mass and tarsus length of the birds, and took pre-treatment blood sample. Then the birds were allocated according to an *a priori*

defined protocol into one of four social treatment groups of 10 birds each: ‘random’ (random subsample of birds of a given replicate), ‘low exploratory’ (only birds with low exploratory scores), ‘high exploratory’ (only birds with high scores), and ‘variable’ (mixture of birds with either low or high scores). To further characterise the birds’ social environment, we calculated the Shannon diversity index of exploratory behaviour for each group by dividing exploration values into 10 ordered categories of roughly equal sizes. The social treatment period lasted nine days until day 18, when we measured again the body mass and took a second blood sample to measure the post-treatment physiological condition. Physiological state was characterised by measuring the within-individual change in body condition (scaled body mass index, SMI), heterophil-to-lymphocyte (H/L) ratio (an indicator of glucocorticoid-mediated stress response; (Davis *et al.* 2008)), oxidative stress (damage to lipids – malondialdehyde concentration, MDA), and innate immune capacity (natural antibodies – agglutination score; complement system – lysis score). Within-individual change in physiological condition was computed as the difference between the post-treatment and pre-treatment values. We provide a more detailed description of study timeline, captivity conditions, measurement of exploratory behaviour, assignment to social treatment groups, blood sampling and physiological measurement methods in the *SI Appendix*.

None of the birds died during the study and all of them were released at the site of capture in good health on day 18. The study complies with the ethical guidelines of the Babeș-Bolyai University (permit no. 30792) and the European laws regarding animal welfare, and adheres to the ASAB guidelines for the use of animals in behavioural research.

Statistical procedures

128 Malondialdehyde level was log-transformed to normalize its distribution. Changes in each
129 physiological trait during the social treatment period were analysed in separate models as
130 dependent variables. These change variables were calculated by subtracting the pre-treatment
131 values from the post-treatment values. Exception from this are the scores of haemagglutination
132 and haemolysis that were highly zero-inflated. Therefore, we converted these variables into
133 binary variables (0 for absence and 1 for presence of agglutination or lysis), and scored the
134 change during treatment at a 4-point scale by considering all four possible transitions: 0 for 1 →
135 0 transition ("immune depression"); 1 for 0 → 0 transition ("stable weak immunity"); 2 for 1 →
136 1 transition ("stable good immunity"); 3 for 0 → 1 transition ("immunity improvement").

137 The explanatory variables were the same in all models as follows: sex and social
138 treatment were set as fixed factors with two and four levels, respectively, and individual
139 exploratory score as a continuous predictor with log(x+1)-transformation. In addition, all second-
140 order interactions between the three explanatory variables were also tested. Study replicate (six
141 levels) and group ID (24 levels) nested within study replicate were entered as random factors.
142 Within each model, the continuous response variables (i.e. body condition, heterophil-to-
143 lymphocyte ratio and malondialdehyde concentration) and exploration score were Z-transformed
144 to zero mean and unit standard deviation (Schielzeth 2010). We used linear mixed-effects models
145 with normal error distribution (LMMs; 'lmer' function of the R package 'lme4' (Bates *et al.*
146 2015)) for change in body condition, heterophil-to-lymphocyte ratio and malondialdehyde, while
147 we used cumulative link models (CLMMs; 'clmm' function of the R package 'ordinal'
148 (Christensen 2015)) for change in agglutination and lysis scores. The assumption of homogeneity
149 of variances among treatment groups were met for each response variable of the LMM models
150 (Levene test, all $P > 0.22$). We assessed the fulfilment of model assumptions by graphical

151 diagnosis; all assumptions were met for each model. Each model was simplified to obtain
152 minimal adequate models (MAMs) containing only significant main effects or their interactions
153 by sequentially dropping predictors with non-significant ($P > 0.05$) effects using the 'drop1' R
154 function. Table 1 presents the type II Anova results of MAMs, while Table S2 presents the
155 parameter estimates of both the full models and the MAMs.

156 To assess the relationships between groups' Shannon diversity of personality and changes
157 in physiological state, we computed the group-level mean of change in physiological variables
158 for each of the 24 groups by averaging the 10 group members' physiological change values.
159 These relationships were tested using LMMs with normal error distribution. In all models, the
160 group-level mean of change in physiological parameter was entered as dependent variable,
161 groups' Shannon diversity of exploration as a continuous predictor, and study replicate was
162 entered as a random factor. Both the dependent variables and the exploration diversity values
163 were Z-transformed. For all the statistical models the reported significance levels were calculated
164 using type II Wald Chi-square tests using the 'Anova' and 'Anova.clmm' functions of the R
165 packages 'car' (Fox & Weisberg 2011) and 'RVAideMemoire' (Hervé 2019), respectively.

166

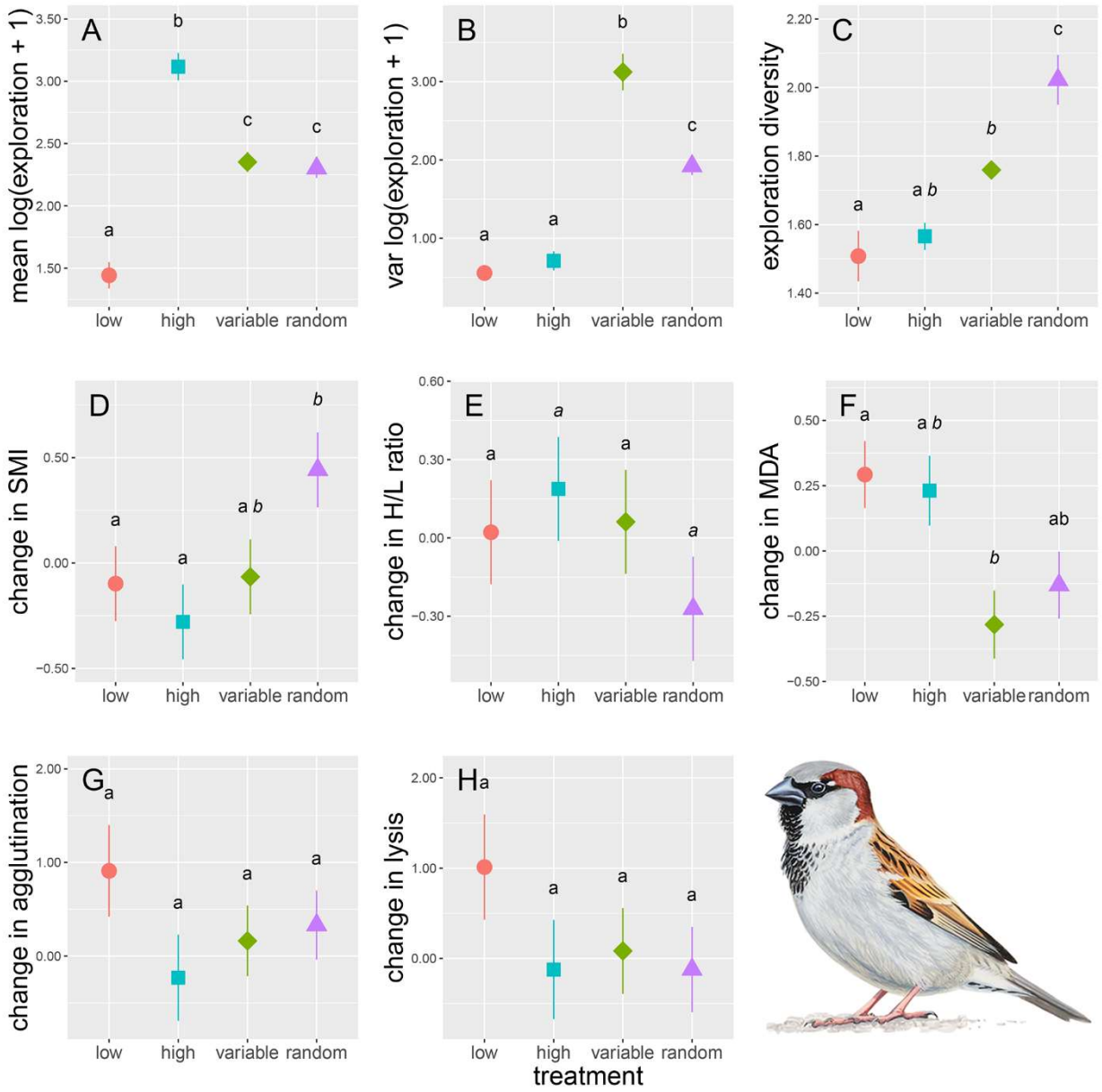
167 **RESULTS**

168 The groups in the four experimental treatments differed in the mean, variance and Shannon
169 diversity index of their personality composition (Fig. 1A–C; statistics in Social treatment section
170 of Materials and Methods in *SI Appendix*). Treatment groups also clearly differed in within-
171 individual change in body condition (Fig. 1D), heterophil-to-lymphocyte ratio (Fig. 1E) and
172 oxidative stress (damage to lipids – malondialdehyde concentration; Fig. 1F), but not in change in

173 the activity of constitutive innate immunity (natural antibodies – agglutination score, and
174 complement system – lysis score; Fig. 1G and Fig. 1H) (Table 1). The differences in
175 physiological condition among treatment groups (Fig. 1D–F) are mostly congruent with the
176 group differences in personality diversity (cf. Fig. 1C) rather than with the mean or variance of
177 personality of the groups (cf. Fig. 1A–B). Individuals' personality was not associated with the
178 change in physiological condition by itself, but it was in interaction with social treatment in case
179 of agglutination and lysis: changes in agglutination scores increased with exploration in the low
180 exploratory groups, while changes in lysis scores decreased with exploration in the random
181 groups (Table 1; see also additional results in *SI Appendix* and Table S2).

182

183 **Figure 1** Behavioural and physiological differences among the social treatment groups.
184 Treatment groups differ according to (A) mean, (B) variance and (C) Shannon diversity index of
185 personality (i.e. exploration score), change in (D) body condition (SMI), (E) heterophil-to-
186 lymphocyte ratio (H/L ratio, an indicator of glucocorticoid-mediated stress response), (F)
187 oxidative damage to lipids (i.e. malondialdehyde, MDA), and (G–H) constitutive immune
188 capacity, as expressed through agglutination score (G) and lysis score (H). Means ± SEM are
189 shown; raw data on panels A–C and model-predicted values on panels D–H. Different lowercase
190 letters denote significant differences ($P \leq 0.05$), while similar but italicized letters denote
191 marginal differences ($P < 0.1$) between social treatment groups based on pairwise comparisons
192 with Tukey-adjusted *P*-values. Male house sparrow drawing credit: Márton Zsoldos.



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194 **Table 1** Minimal adequate models containing predictors of changes in individual physiological
195 state of house sparrows during the social treatment period. Statistically significant effects are
196 marked in bold. SMI – Scaled Mass Index (body condition), H/L – heterophil-to-lymphocyte
197 ratio (indicator of glucocorticoid-mediated stress response), MDA – malondialdehyde (oxidative
198 damage to lipids), S – sex, T – social treatment, EB – exploratory behaviour.

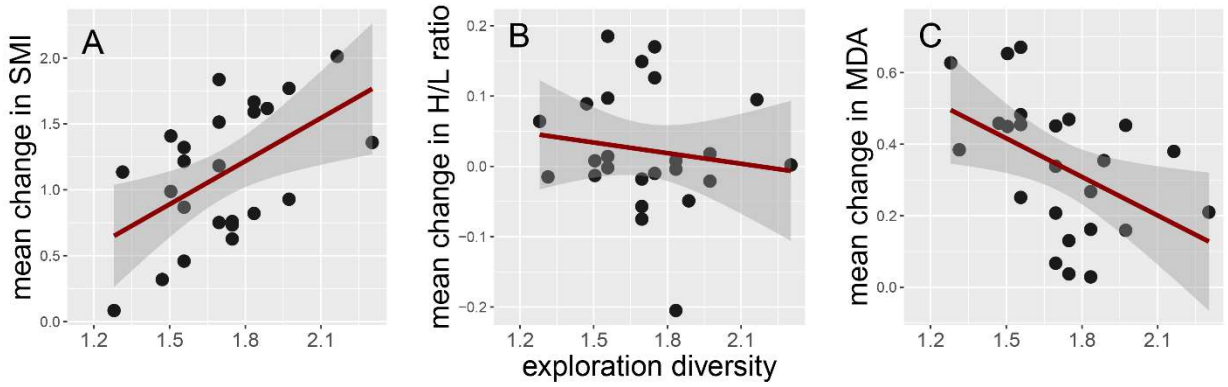
Response	Predictor	χ^2	df	*P*
SMI	S	6.52	1	**0.011**
	T	17.15	3	**< 0.001**
H/L	T	7.94	3	**0.047**
MDA	S	0.13	1	0.719
	T	13.34	3	**0.004**
	S × T	8.35	3	**0.039**
Agglutination	T	0.32	3	0.955
	EB	0.05	1	0.831
	T × EB	9.53	3	**0.023**
Lysis	T	1.13	3	0.770
	EB	1.78	1	0.182
	T × EB	10.74	3	**0.013**

To assess the role of personality diversity of experimental social groups, we tested whether the calculated Shannon diversity predicts the physiological responses to social treatment. Because the Shannon diversity index is a group-level metric (i.e. one value for a 10 birds group, hence 24 values in total), we computed the group-level mean of within-individual change in each physiological trait by averaging the change values of the 10 birds per group and assessed their association with groups' Shannon diversity of personality. We found that in groups with higher personality diversity body condition increased more (β = 0.515, SE = 0.152, t = 3.380, P < 0.001;

207 Fig. 2A), while heterophil-to-lymphocyte ratio (β = –0.279, SE = 0.128, t = 2.174, P = 0.030; Fig.
208 2B) and oxidative damage to lipids (i.e. malondialdehyde; β = –0.464, SE = 0.189, t = 2.457, P =
209 0.014; Fig. 2C) became lower. Mean change in agglutination and lysis scores were not related to
210 group personality diversity (agglutination: β = 0.058, SE = 0.188, t = 0.310, P = 0.757; lysis: β =
211 –0.034, SE = 0.131, t = 0.263, P = 0.792).

212

213 **Figure 2** Physiological condition improved in social groups with diverse personalities.
214 Relationships between personality diversity in social groups of house sparrows and mean change
215 in (A) body condition (SMI), (B) heterophil-to-lymphocyte (H/L) ratio, and (C) oxidative damage
216 to lipids (MDA) during the social treatment period. Dots are group-level means, regression lines
217 are model-predicted slopes with 95% confidence intervals (shaded area).



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219

220 **DISCUSSION**

221 In the realm of human psychology, it is a long-standing debate whether uniformly or diversely
222 composed teams perform better (Barrick *et al.* 1998; Stewart 2006), but nothing has been known
223 about whether group composition affects the physiological condition of group members either in

224 humans or other animals. Here we showed that "variety is delighting," as condition improved,
225 and levels of glucocorticoid-mediated stress response and oxidative stress was lower for house
226 sparrows living in a social environment with diverse personalities. Therefore, living in social
227 groups with diverse composition provides benefits in terms of reduced physiological stress and
228 superior health state. The finding of no significant interactions between social treatment and
229 individual's exploration, at least in cases of improved physiological variables, suggests that all
230 individuals in diverse groups enjoy the benefits.

231 Diverse groups provide more opportunities for specialization (Bergmüller & Taborsky
232 2010; Farine *et al.* 2015) and are more likely to host keystone individuals, which are influential
233 individuals with disproportionately large effect on other group members and/or overall group
234 functioning (Modlmeier *et al.* 2014). Both role specialization and keystone individuals can lead
235 to superior group-level performance (upstream effect). Indeed, great tit affiliations consisting of
236 diverse personalities show the most effective coordinated action when exploring a habitat patch
237 (Aplin *et al.* 2014). Note that the group compositions simulated in this modelling study (Aplin *et*
238 *al.* 2014) are highly similar to our experimental setup. Similarly, a mixture of shy and bold fish
239 can be advantageous in reducing the trade-off between exploring novel foraging tasks and
240 antipredator vigilance (Dyer *et al.* 2009a). The minority of keystone individuals can also
241 substantially affect group-level behaviour and performance (Brown & Irving 2014). These group-
242 level advantages of diversely composed groups can bring about higher individual performance
243 (downstream effect) in terms of either fitness or condition (Bengston & Jandt 2014) by reducing
244 stress exposure and ultimately leaving group members in better physiological condition. Note
245 that we found a positive effect of social diversity on health in a set-up where food was unlimited.
246 This suggests that this benefit of diversity might arise because of the innate working of the group

247 (e.g. the type and intensity of interactions between members) rather than being the consequence
248 of more obvious benefits like improved foraging success, habitat exploration, defence against
249 predators, and decision-making. Therefore, preference for bonding with dissimilar individuals
250 (i.e. heterophily), and in turn, the better health state of individuals in diverse groups might
251 reinforce the improved group-level outcomes creating a positive feedback loop (Seebacher &
252 Krause 2017) between group-level and individual-level performances. Such a feedback loop can
253 then drive the evolutionary maintenance of heterophily (Pruitt & Riechert 2011).

254 Consistency of personality traits places a constraint on individuals because one is either
255 more reactive (shy, neophobic, less exploratory, less aggressive) or more proactive (bold, novelty
256 seeking, more exploratory, more aggressive) (Sih *et al.* 2004). However, if different personalities
257 affiliate, they can share mutual benefits; a concept termed social heterosis (Nonacs & Kapheim
258 2007). Social heterosis in associations of dissimilar personalities thus can explain why
259 behavioural (and genetic) diversity can evolutionarily persist (Nonacs & Kapheim 2007).
260 Negative frequency-dependent selection is another evolutionary explanation for the existence of
261 behavioural polymorphisms (producers–scroungers, hawks–doves, and leaders–followers), and
262 has been shown to maintain diversity in group personality composition (Pruitt & Riechert 2009).
263 Our results provide a physiological mechanism that could also be responsible for the evolutionary
264 maintenance of behavioural diversity in social groups. Behavioural diversity is a requisite for the
265 evolution of leadership (Johnstone & Manica 2011), cooperation (McNamara *et al.* 2004), and
266 social responsiveness, which in turn is necessary for the evolution of personality (Wolf *et al.*
267 2011). Our findings, thus, bring helpful insight into the study of social evolution, which is a
268 fundamental question in biology and has implications for human work teams in particular and for
269 human society in general. Although the role of group composition in human team performance is

still contentious (van Knippenberg & Schippers 2007), there is some evidence showing that heterophily is advantageous in project groups that are less stable in time and are engaged in creative tasks, but disadvantageous in production groups that are stable in time and are engaged in routine tasks (Stewart 2006). If humans also may gain health benefits from belonging to a diversely composed team as sparrows do, the fact that homophily is still the rule of thumb in humans (McPherson *et al.* 2001) poses a challenge on the health benefits of heterophily, and thus deserves more attention.

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SI Appendix

METHODS

Study protocol

The study is based on a large sample of 240 house sparrows. We caught 40 sparrows during each study replicate (1:1 sex ratio). Sparrows were caught with mist nets at a cattle farm near Bălcaciu village, central Transylvania, Romania (46°11'N, 24°3'E) during six capture sessions (9 November 2014, 5 December 2014, 5 January 2015, 23 January 2015, 10 February 2015, and 28 February 2015). Upon capture (day 0), birds were marked with an aluminium ring, and their sex and body mass (± 0.1 g) was recorded. The birds were transported to the Campus of the Babeș-Bolyai University, Cluj-Napoca (46°46'N, 23°33'E) and housed in indoor aviaries for 18 days.

Study timeline

The study timeline was the same for all six replicates. We let the birds to habituate to captivity on the day of capture (day 0) and the next two days (days 1–2). They were housed in four indoor aviary rooms (3 m length × 2 m width × 2.5 m height) in which the birds were distributed randomly in groups of equal sizes (10 birds in each room). The aviary rooms were visually separated from each other. To assess the exploratory behaviour of birds in a novel environment, we first transferred them into individual cages in the morning of day 3 and let them to habituate for two days (days 3–4), then tested for exploration on days 5–7 (see below the details). Day 8 was a resting day. At day 9, we measured the body mass and tarsus length (± 0.01 mm) of the birds, and took the pre-treatment blood sample (150–200 µL; see below the methods). Then the

403 birds were allocated according to an *a priori* defined protocol into one of four social treatment
404 groups of 10 birds each (see below). These four social groups of 10 birds in each of the six study
405 replicates were housed in the same four adjacent aviary rooms as mentioned above. Each social
406 group had an even or quasi-even sex ratio (Table S1). There was no significant difference in sex
407 ratio between the treatment groups in any of the study replicates (χ^2 test, all $P > 0.362$). The
408 social treatment period lasted nine days until day 18, when we measured again the body mass and
409 took a second blood sample to measure the post-treatment physiological condition. On the same
410 day, we released the birds at the site of capture.

411

412 **Table S1.** Sex ratio as shown by the sample sizes per each sex (F – female, M – male) per each
413 experimental group per each study replicate. Each group was formed by 10 birds during each
414 study replicate totalling 40 birds per study replicate and 240 birds for the entire study.

	Social treatment group							
	random		variable		low		high	
	F	M	F	M	F	M	F	M
replicate #1	4	6	5	5	6	4	5	5
replicate #2	6	4	6	4	4	6	4	6
replicate #3	5	5	3	7	7	3	5	5
replicate #4	5	5	3	7	7	3	5	5
replicate #5	7	3	4	6	5	5	4	6

replicate #6	7	3	4	6	5	5	4	6

415

416 **Housing and ethical note**

417 Birds were transported within max. 4 h from capture into aviaries. To increase the sparrow's
418 comfort, aviaries were enriched with several perches and one nest box per bird for resting, hiding
419 and roosting, and a water tank was full-time available for bathing. The artificial photoperiod was
420 identical to the natural day–night cycle throughout. Birds were fed *ad libitum* with a seed mixture
421 consisting of ground corn, barley, millet and sunflower, and this diet was supplemented with one
422 grated boiled egg per aviary room every other day (Pap *et al.* 2008; Vágási *et al.* 2010). Fresh
423 drinking water was provided on a daily basis. None of the birds died during the study and all of
424 them were released at the site of capture in good health.

425

426 **Exploratory behaviour**

427 When transferred into individual cages (day 3), birds were randomly ordered from 1 to 40 and
428 split into three clusters (first 13, next 14, and last 13 birds). Their exploration test was performed
429 according to this 1–40 order on days 5–7 (one cluster was tested each day). We recorded
430 exploratory behaviour as a well-established axis of personality following the novel environment
431 test of Dingemanse and co-authors (Dingemanse *et al.* 2002). Sparrows were deprived of food
432 and water for 1 h before the novel environment test started. Their cage was moved to the test
433 room 10 min before the test run and was covered with a dark curtain, so birds were left to calm
434 down in complete darkness and quietness before the test run. The birds entered the test room
435 from their cage through a sliding door after being startled by knocking the wall of the cage, but

436 without being handled or seeing any person. They were tested alone by spending 10 min in the
437 test room (3 m length × 2 m width × 2 m height) that contained four artificial wooden trees with
438 four branches each and arranged symmetrically within the test room. Exploratory behaviour was
439 video recorded through a one-way window with a hand-held video camera (Panasonic HC-V510)
440 between 09:00 and 16:00 (schedule of the test runs: 09:00, 09:30, 10:00, 10:30, 11:00, 11:30,
441 12:00, 12:30, 13:00, 13:30, 14:00, 14:30, 15:00, and 15:30) by the same person (A.F.).
442 Exploratory score is the total number of hops (performed either on the trees or on the ground) and
443 flights during the 10-min test. The exploratory behaviour was scored by the same person (Z.Be.).

444 An additional set of 40 birds that were not involved in the social experiment were
445 assessed thrice for their exploratory behaviour in the same novel environment as the 240
446 experimental birds in order to verify whether this behavioural trait is consistent in time, a
447 prerequisite of personality traits. The timeline and housing condition for these 40 birds were
448 identical with those 240 birds that were involved in the six study replicates (i.e. they were housed
449 under the same conditions and spent the same number of days before the first test and between
450 the consecutive tests). Consistency of the exploratory behaviour was measured by calculating
451 individual repeatability (i.e. separating variation in exploratory score into a within-individual and
452 an among-individuals component) using a linear mixed-effects model (R package 'rptR' (Stoffel
453 *et al.* 2017)) as per Nakagawa and Schielzeth (Nakagawa & Schielzeth 2010). Exploration score
454 was first log-transformed and then Z-transformed (i.e. scaled to mean = 0 and standard deviation
455 = 1; (Schielzeth 2010)). We first built a full model in which exploration score was the dependent
456 variable with sex (male/female), exploration test repeat (first/second/third), aviary room (from
457 one to four) where the birds were kept between test repeats, and their second-order interaction
458 were entered as potential confounding fixed effects, and individual's ID, test day (three test days;

459 see above), and the novel environment test order (1–40) nested within test day were entered as
460 random factors. The minimal model was obtained by sequentially dropping all the non-significant
461 fixed predictors from the full model until only significant effects remained. Individuals were
462 significantly consistent in their exploratory behaviour across the three exploration test repeats in
463 both the full model and minimal model (full model: $R = 0.472$, SE = 0.097, 95% confidence
464 interval = 0.316–0.691, $P < 0.001$; minimal model: $R = 0.416$, SE = 0.100, 95% confidence
465 interval = 0.199–0.589, $P < 0.001$).

466

467 **Social treatment**

468 The social treatment consisted of creating four groups that differed in personality composition:
469 'random' (random subsample of birds of a given replicate), 'high variance' (mixture of birds with
470 either low or high exploration scores), 'low exploratory' (only birds with low scores), and 'high
471 exploratory' (only birds with high scores). For this, we first ranked the 40 birds of each study
472 replicate according to their exploration score in an increasing order (i.e. rank #1 is the least
473 exploratory bird). The 'random' group was set up by forming 10 quartets along this rank order
474 (i.e. first quartet consisting of birds ranking #1–4 and the last quartet of birds ranking #37–40),
475 randomizing the order within each quartet, and then choosing the first bird from each quartet. The
476 'high variance' group was set up by reordering the remaining 30 birds, forming 15 duos along
477 this rank order, randomizing the order of birds within each duo, and choosing the first bird from
478 the first five and the last five duos. The remaining 20 birds were reordered once again and the
479 first 10 birds along this exploration rank order formed the 'low exploratory' group, while the last
480 10 birds formed the 'high exploratory' group. The goodness of this protocol was *a priori* assessed
481 by generating 40 random exploration scores with uniform, normal or exponential distribution.

482 The group formation protocol worked for each of the three distribution types as the four groups
483 the protocol created differed both according to mean and to variance of exploration scores.

484 Social treatment protocol successfully created differences in the mean, variance and
485 Shannon diversity index of exploration score (personality) among groups (Fig. 1). The mean
486 exploratory score was smallest in the low exploratory group, intermediate in the random and
487 variable groups, and largest in the high exploratory group (ANOVA, $F = 18.87$, df = 3,236, $P <$
488 0.001) (Fig. 1A). Variance was lower in the low and high exploratory groups than in the random
489 and variable groups ($F = 16.21$, df = 1,238, $P < 0.001$) (Fig. 1B). Comparing the latter two
490 groups, variance was lower in the random group than the variable group ($F = 10.04$, df = 1,118, P
491 $= 0.002$) (Fig. 1B), which shows that the random group is an even sample of the entire range of
492 exploratory behaviour, while the variable group is in fact a mixture of low exploratory and high
493 exploratory groups in equal proportion. Indeed, opposite to the exploration score variance, the
494 Shannon diversity index computed for each social group of 10 sparrows (24 groups in total; four
495 treatment groups per study replicate × six study replicates) was highest in the random group, was
496 intermediate in the variable group, and lowest in the low and high exploratory groups (treatment
497 group effect: $\chi^2 = 68.118$, df = 3, $P < 0.001$; random vs. variable: $P = 0.008$) (Fig. 1C).

498

499 **Blood sampling**

500 Blood samples were collected on day 9 and day 18 to assess the physiological state of sparrows
501 before and after the social treatment period, respectively. Blood samples were collected into
502 heparinized capillaries by puncturing the brachial vein with insulin syringe. A drop of blood was
503 smeared onto a microscope slide for counting leucocytes. The capillaries with blood samples

504 were stored in dark cooling boxes at 4°C for max. 4 h until centrifuged (5 min at 6200 *g*) to
505 separate the plasma and erythrocyte fractions. Plasma was partitioned into aliquots for each
506 physiological parameter and all aliquots were stored at –50°C until the laboratory assay took
507 place.

508

509 **Physiological parameters**

510 We measured the following five parameters to describe the physiological state of the birds. First,
511 we computed a size-corrected body mass index to characterize the individuals' body condition
512 (i.e. the relative amount of energy stores in the form of muscle and fat). For this, we used the
513 Scaled Mass Index (Peig & Green 2009) (for details, see (Vágási *et al.* 2012)). Second, 50
514 leukocytes were counted from blood smears by G.O. (for details, see (Pap *et al.* 2011, 2015)).
515 Heterophil-to-lymphocyte ratio was used as an indicator of glucocorticoid-mediated stress
516 response (Davis *et al.* 2008). Because all the leukocytes were heterophils on some smears,
517 heterophil-to-lymphocyte ratio was calculated as heterophils / (heterophils + lymphocytes); thus,
518 a value close to 1 indicates higher physiological stress. Third, oxidative stress was assessed by
519 J.P. and C.I.V. by measuring the amount of oxidative damage to cell membrane phospholipids
520 via the plasma concentration of malondialdehyde, a toxic intermediate of oxidative lipid
521 decomposition (for details, see (Bókony *et al.* 2014)). Fourth, the level of natural antibodies
522 (agglutination score) and the activity of the complement system (lysis score) as two associated
523 measures of the constitutive innate immune system was assessed by J.P. and C.I.V. via a
524 haemagglutination–haemolysis assay (Matson *et al.* 2005) (for details, see (Pap *et al.* 2010)).
525 Higher scores mean that the immune system constituents of the plasma can agglutinate or lyse
526 foreign red blood cells at lower concentration (i.e. indicate better immune capacity).

527

528 **ADDITIONAL RESULTS**

529 Individual's exploration score had no clear association with the change in physiological condition
530 either alone or in interaction with social treatment (Table 1; see Table S2 for full models).
531 Exceptions are the cases of change in natural antibody level (i.e. agglutination score) that was
532 positively associated with personality in the low exploratory group (β = 0.893, SE = 0.351, z =
533 2.547, P = 0.011), but not in other groups (all P > 0.05), and the change in complement activity
534 (i.e. lysis score) that was negatively associated with personality in the random group (β = –0.693,
535 SE = 0.217, z = 3.188, P = 0.001), but not in other groups (all P > 0.05).

536

537 **Table S2.** Parameter estimates of full models containing all the predictors of changes in
538 individual physiological state of house sparrows during the social treatment period. Parameter
539 estimates of minimal adequate models are also shown besides the corresponding full models.
540 Statistically significant effects are marked in bold. (a) SMI – Scaled Mass Index (body
541 condition), (b) H/L – heterophil-to-lymphocyte ratio (indicator of physiological stress), (c) MDA
542 – malondialdehyde (oxidative damage to lipids), (e) Agglutination – level of natural antibodies,
543 (f) Lysis – activity of the complement system. Predictors: HVG – high variance group
544 (experimental group with high exploratory behaviour variance), HEG – high exploratory group
545 (experimental group of birds with high exploratory behaviour), LEG – low exploratory group
546 (experimental group of birds with low exploratory behaviour), S – sex (F – female is the
547 reference level), EB – exploratory behaviour, REP – study replication, T – social treatment. For
548 random effects, σ^2 is the residual variance, while τ_{00} is the variance explained by random factors.

(a) SMI

	Full model			Min. adequate model		
Fixed effects	*β*	SE	*t*	*β*	SE	*t*
Intercept	0.336	0.23	1.458	0.595	0.19	3.134
HVG	–0.257	0.258	0.996	–0.508	0.183	2.768
HEG	–0.524	0.293	1.792	–0.721	0.183	3.94
LEG	0.113	0.306	0.37	–0.54	0.182	2.958
S (F)	0.165	0.245	0.675	–0.305	0.12	2.553
EB	0.137	0.143	0.957			
HVG × S	–0.418	0.354	1.179			
HEG × S	–0.509	0.351	1.451			
LEG × S	–0.758	0.355	2.134			
HVG × EB	–0.142	0.159	0.894			
HEG × EB	–0.03	0.232	0.129			
LEG × EB	0.184	0.251	0.735			
S × EB	0.069	0.14	0.488			
Random effects						
σ^2	0.82			0.84		

τ_{00}	0.02 $_{REP:T}$; 0.09 $_{REP}$	0.02 $_{REP:T}$; 0.09 $_{REP}$
N	6 REP; 4 T	6 REP; 4 T
Observations	240	240
Marg. R^2; Cond. R^2	0.118; 0.231	0.086; 0.188

(b) H/L

	Full model			Min. adequate model		
Fixed effects	*β*	SE	*t*	*β*	SE	*t*
Intercept	–0.43	0.244	1.765	–0.271	0.199	1.362
HVG	0.299	0.248	1.208	0.333	0.169	1.972
HEG	0.454	0.285	1.59	0.459	0.169	2.72
LEG	0.362	0.3	1.209	0.293	0.169	1.736
S (F)	0.259	0.251	1.034			
EB	0.157	0.147	1.066			
HVG × S	0.145	0.363	0.4			
HEG × S	–0.033	0.36	0.092			
LEG × S	–0.177	0.364	0.486			
HVG × EB	–0.08	0.163	0.493			

HEG × EB	–0.016	0.237	0.069			
LEG × EB	–0.16	0.256	0.625			
S × EB	–0.104	0.144	0.722			
Random effects						
σ^2	0.87			0.85		
τ_{00}	$0.00_{REP:T}$; 0.15_{REP}			$0.00_{REP:T}$; 0.15_{REP}		
N	6 REP; 4 T			6 REP; 4 T		
Observations	240			240		
Marg. R^2; Cond. R^2	0.054; NA			0.032; NA		

(c) MDA

	Full model			Min. adequate model		
Fixed effects	*β*	SE	*t*	*β*	SE	*t*
Intercept	0.015	0.196	0.074	0.008	0.191	0.042
HVG	–0.403	0.262	1.538	–0.409	0.253	1.615
HEG	–0.028	0.301	0.092	–0.07	0.257	0.272
LEG	0.519	0.315	1.648	0.441	0.27	1.636
S (F)	–0.302	0.262	1.152	–0.278	0.254	1.094

EB	–0.025	0.156	0.164			
HVG × S	0.478	0.382	1.252	0.517	0.362	1.428
HEG × S	0.904	0.385	2.349	0.864	0.367	2.355
LEG × S	–0.054	0.382	0.142	–0.035	0.359	0.098
HVG × EB	–0.002	0.174	0.013			
HEG × EB	–0.045	0.256	0.175			
LEG × EB	0.174	0.269	0.645			
S × EB	–0.089	0.154	0.578			
Random effects						
σ^2	0.95			0.94		
τ_{00}	$0.00_{REP:T}$; 0.00_{REP}			$0.00_{REP:T}$; 0.00_{REP}		
N	6 REP; 4 T			6 REP; 4 T		
Observations	231			231		
Marg. R^2; Cond. R^2	0.091; NA			0.088; NA		

(d) Agglutination

	Full model			Min. adequate model		
Fixed effects	*β*	SE	*t*	*β*	SE	*t*

HVG	0.884	0.56	0.22	0.844	0.426	0.399
HEG	0.433	0.644	1.299	0.565	0.504	1.133
LEG	1.859	0.656	0.945	1.758	0.523	1.079
S (F)	1.021	0.503	0.041			
EB	0.757	0.302	0.923	0.747	0.255	1.147
HVG × S	0.887	0.766	0.157			
HEG × S	1.641	0.748	0.662			
LEG × S	0.912	0.742	0.124			
HVG × EB	1.08	0.343	0.223	1.099	0.327	0.289
HEG × EB	2.443	0.519	1.722	2.241	0.505	1.597
LEG × EB	4.359	0.557	2.644	4.332	0.549	2.672
S × EB	0.975	0.311	0.081			
Random effects						
σ^2	3.29			3.29		
τ_{00}	0.17 $_{REP:T}$; 0.30 $_{REP}$			0.17 $_{REP:T}$; 0.29 $_{REP}$		
N	6 REP; 4 T			6 REP; 4 T		
Observations	237			237		
Marg. R^2; Cond. R^2	0.049; 0.167			0.045; 0.162		

556

557 (e) Lysis

	Full model			Min. adequate model		
Fixed effects	*β*	SE	*t*	*β*	SE	*t*
HVG	1.416	0.575	0.605	1.217	0.402	0.488
HEG	0.678	0.684	0.568	0.991	0.489	0.019
LEG	3.358	0.69	1.756	3.053	0.523	2.136
S (F)	0.868	0.582	0.242			
EB	0.462	0.339	2.28	0.392	0.293	3.188
HVG × S	0.61	0.848	0.583			
HEG × S	2.188	0.859	0.912			
LEG × S	1.006	0.829	0.007			
HVG × EB	2.357	0.383	2.237	2.535	0.369	2.52
HEG × EB	2.455	0.569	1.578	2.318	0.542	1.551
LEG × EB	6.73	0.638	2.99	5.759	0.622	2.816
S × EB	0.677	0.34	1.151			
Random effects						
σ^2	3.29			3.29		

τ_{00}	$0.00_{REP:T}$; 0.89_{REP}	$0.00_{REP:T}$; 0.86_{REP}
N	6 REP; 4 T	6 REP; 4 T
Observations	237	237
Marg. R^2; Cond. R^2	0.108; NA	0.090; NA

558

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