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16 **SUMMARY**

17   While there are now a number of theoretical models predicting how

18consistent individual differences in behaviour may be generated and

19maintained, so far, there are few empirical tests. The social niche

20specialization hypothesis predicts that repeated social interactions among

21individuals may generate among-individual differences and reinforce within-

22individual consistency through positive feedback mechanisms. Here we test

23this hypothesis using groups of the social spider, *Stegodyphus mimosarum*,

24that differ in their level of familiarity. In support of the social niche

25specialization hypothesis, individuals in groups of spiders that were more

26familiar with each other showed greater repeatable among-individual

27variation in behaviour. Additionally, individuals that were more familiar with

28each other exhibited lower within-individual variation in behaviour, providing

29one of the first examples of how the social environment can influence

30behavioural consistency. Our study demonstrates the potential for the social

31environment to generate and reinforce consistent individual differences in

32behaviour and provides a potentially general mechanism to explain this type

33of behavioural variation in animals with stable social groups.

34

INTRODUCTION

36

37   A fundamental goal in the field of the animal personality literature is to
38understand the mechanisms responsible for generating and maintaining
39consistent individual differences in behaviour. While there are now a number
40of well-developed theoretical models predicting potential causal mechanisms
41(reviewed in [1-3]), thus far empirical tests of these predictions are
42extraordinarily few (but see [4-6]). In order to fully explain the presence of
43consistent individual differences in behaviour, or personalities, a potential
44mechanism would need to address the two key aspects of personality:
45among-individual variation in behaviour and within-individual consistency
46over time. A recent hypothesis termed the social niche specialization
47hypothesis predicts that the social environment may play a key role in both
48promoting individual differentiation and individual consistency [7, 8].

49   The social niche specialization hypothesis predicts that when a group
50of individuals interacts repeatedly, it can be beneficial for them to develop
51"social niches" [7, 8]. These social niches provide a way to reduce
52competition among individuals and increase individual payoffs. First, by
53differentiating their behaviour from each other individuals can reduce direct
54competition with group mates [6, 9]. This type of niche specialization has
55been well established in ecology, where the presence of competing
56conspecifics can generate diet specializations among individuals [10, 11] and

57the social niche specialization hypothesis expands this concept beyond the

58foraging context. The presence of among-individual variation in behaviour

59can increase colony productivity [12] and individual reproduction [13] within

60social groups, supporting the prediction that social niches can enhance

61individual fitness and colony success.

62   Once among-individual differences in behaviour are established, the

63social niche specialization hypothesis predicts that they will be reinforced

64thereby generating within-individual consistency in behaviour [7, 8].

65Predictability in behaviour might increase successful interactions among

66individuals which can be especially important in stable social groups [1, 14].

67Within-individual consistency could also be generated if changing behaviour

68is too costly or if positive feedback mechanisms such as learning reinforce an

69individual's likelihood to repeat the behaviour [15, 16]. Therefore, the social

70niche specialization hypothesis addresses both aspects of animal personality

71by predicting that groups of individuals that have repeatedly interacted,

72should exhibit greater among-individual variation and lower within-individual

73variation in behaviour. Stated another way, familiar groups of individuals

74should exhibit stronger personalities.

75   While the development of social niches is theoretically possible in any

76group of repeatedly interacting individuals, these niches will likely be

77strongest when group membership is stable. When group turnover is low,

78individuals can more easily maintain the same social niche. For example,

79several studies have shown that individual birds will maintain consistent

80foraging behaviours when in the same social group [17, 18]. However, when

81the social context changes, frequently so will individual behaviour [17, 19].

82In particular, a recent study demonstrated that social interactions did not

83strengthen personalities in threespined sticklebacks, even when group

84membership was experimentally maintained [20]. However, in the wild,

85sticklebacks maintain fairly fluid groups with high turnover [21, 22].

86Therefore, it seems likely that social niche specialization holds the potential

87to be a more powerful mechanism in groups with stable membership where

88repeated interactions among individuals are frequent. Here we test the key

89prediction of the social niche specialization hypothesis that familiarity among

90group members should generate individual personalities using the social

91spider *Stegodyphus mimosarum.* Social spiders of the genus *Stegodyphus*

92offer a superb model to evaluate the social niche specialization hypothesis

93because the dispersal tendency of this species is extraordinarily low, and

94thus, persistent social interactions among colony members are a common

95feature in this species. Specifically, we compared the strength of consistent

96individual differences in behaviour in groups of spiders that had lived

97together for differing amounts of time, i.e. were more or less familiar with

98each other. We measured two ecologically relevant behaviours in this

99species: response to a simulated predator attack and response to a

100simulated prey encounter. Variation in these behaviours might influence task

101differentiation such as prey capture and colony defence as has been found in

102other species (e.g. [12, 23, 24]). If repeated social interactions generate

103social niches, we predicted that among-individual variation in behaviour

104would increase and within-individual variation would decrease with the

105amount of time the group had been together.

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108**METHODS**

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110**Collection and Laboratory Maintenance**

111	*Stegodyphus mimosarum* live in multi-female colonies ranging from 1-

1122000 members throughout eastern Africa [25, 26]. Their webs are composed

113of two structures: a two-dimensional capture web and a dense three-

114dimensional retreat composed of a series of silken tunnels. Spiders reside

115within their retreat for the majority of the day, and only emerge in response

116to prey or at night in order to repair their capture web. Females cooperate

117together in colony maintenance tasks including collective web maintenance

118and defence, cooperative prey capture, and alloparental care [27]

119	Ten colonies of *S. mimosarum* were collected in the town of Bela-Bela

120(24°53′S 28°17′E) in Limpopo, South Africa in November 2012. Colonies were

121collected by knocking down their capture webs, trimming off colonies'

122supporting foliage, and placing the colony in a cloth pillow case. Colonies

123were then transported to laboratory at the University of Pittsburgh, USA.

124Colonies were sorted in laboratory and their colony size (1-700 spiders) was

125determined. Eight of the largest colonies (400-600 individuals) were selected

126for use in our study. From each of these colonies we haphazardly selected 48

127females for inclusion in our studies. Assignment of females to different

128treatments groups was determined randomly using a random number

129generator in Excel (Microsoft 2010). Prior to being assigned to a treatment,

130females were housed individually in 2-oz deli cups that contained a dome of

131poultry wiring to facilitate web construction. Females were maintained in

132isolation for four weeks prior to the start of our experiment and sustained on

133an *ad libitum* diet of size-matched two-week old crickets.

134

135

136**Manipulation of Familiarity**

137   In order to observe how repeated social interactions influenced among-

138and within-individual behavioural variation, we manipulated the amount of

139time groups of spiders lived together. We generated 64 experimental

140colonies of 6 individuals and each colony was assigned to one of two

141familiarity treatments: control colonies (N=32 colonies) where familiarity was

142maintained throughout the experiment, and mixed colonies where familiarity

143changed over the experiment. Altogether the familiarity treatment ran for

144five weeks, and within each treatment, each colony was exposed to a social

145disturbance after either one, two, three or four weeks (N=8 groups per social

146disturbance per treatment). So for example, colonies that experienced a

147social disturbance after one week were then left undisturbed for four weeks

148and would have longer to become familiar with each other than colonies that

149were disturbed after four weeks. By varying the time of the social

150disturbance we could investigate how the length of social familiarity

151influenced individual behavioural variation. The social disturbance involved

152all of the members being removed from the colony and then being placed

153into a new container with all the same individuals (control treatment), or with

154new and unfamiliar individuals (mixed treatment).Colonies in the mixed

155treatment were reassembled using individuals from the same source colony

156that had not previously interacted. Therefore, individuals in the control and

157mixed colonies both experienced the same disturbance, but only the identity

158of the individuals in the mixed colonies was altered; any differences between

159the control and mixed colonies we could attribute to differences in familiarity

160among colony members.

161   We used a split-design where each of our eight source colonies were

162used to establish one replicate of each of our eight treatment combinations

163(mixed and control colonies at one, two, three and four weeks since social

164disturbance). Relatedness among individuals is known to influence social

165spider behaviour [28, 29] and this design ensured that all source colonies

166equally contributed to all treatment groups. Therefore, if relatedness among

167individuals was more influential on behaviour than familiarity, we would

168expect to see no differences between the control and mixed colonies. All

169experimental colonies were housed in 1.5L clear, plastic deli cups which

170contained a concave-up dome of poultry wiring to facilitate web construction.

171Lids were covered with a 1mm x 1mm screen which allowed ample airflow

172and low humidity levels. Colonies were kept on a maintenance diet of *ad*

173*libitum* six-week old crickets once weekly. To ensure successful prey capture,

174crickets were immobilized prior to being place in colonies' capture webs.

175After the social disturbance, all individuals were rehoused within a new 1.5L

176container with chicken wire. All colonies resumed normal feeding behaviour

177within three days of the social disturbance. At the end of our five week

178experiment, all colonies were disassembled, individuals were isolated back

179into 2-oz deli cups, and their personality types were repeatedly assayed daily

180for the next ten days in two ecological contexts.

181

182**Personality Assay: Boldness towards Predators**

183   This assay was designed to measure how quickly an individual

184recovered from a potential predator attack. Variation among individuals in

185this behaviour could be influential in determining individual specializations

186within the nest on tasks such as colony defence [12, 23, 24] and is a known

187determinant of division of labour and collective behaviour in this species.

188Boldness-shyness assays were initiated by removing spiders from their home

189containers and placing them within a rectangular enclosure (13.5 cm x 13

190cm x 3.5 cm). Spiders were permitted 60 sec to acclimate before applying

191two rapid jets of air to the dorsal, anterior part of the animal from

192approximately 10 cm away, using an infant ear-cleaning bulb. This stimulus

193universally elicited a huddle response from *S. mimosarum,* and resembles

194the rapid approach of an avian predator [23, 30]. As our measure of

195boldness, we recorded the individual's latency to resume movement

196following the huddle response. Five boldness assays (one per day) were

197completed on each spider beginning 24 hours after the end of the familiarity

198treatments. After completing their assays spiders were returned to their

199home containers.

200

201**Personality Assay: Tendency to Attack Prey**

202   This assay was designed to measure how quickly an individual

203attacked a simulated prey item; a behaviour that is likely important in

204determining foraging task specializations within a colony [12, 23, 24]. We

205staged prey capture events in spiders' home containers and noted whether

206they attacked a prey stimulus or not. Using a simulated prey item allowed us

207to standardize the prey escape cues each spider was exposed to. Trials were

208initiated by removing the lid to spider's container and placing a 1.5 cm x 1.5

209cm piece of printer paper in the spider's capture web. We then provided

210spiders 2 minutes acclimation time before administering a vibratory

211stimulus. We subsequently vibrated the paper using a portable, handheld

212vibratory device (FunFactory, Minivibe Bubbles). A thin aluminium wire

213extended from the end of the vibrator and made contact with the paper,

214which resulting in the paper flittering back and forth within the capture web

215similar to Lepidopteran prey. We vibrated the paper for a total of ten

216minutes, or until the spiders emerged and bit the paper. For this behavioural

217assay we recorded a binary response of whether the spider approached and

218attacked the stimulus within the ten minute timeframe or not. . Prey capture

219assays started 24h after individuals had completed their boldness assays.

220This ensured that individuals had enough time to construct rudimentary

221capture webs and retreats within their home containers. Prey capture assays

222were implemented daily for five days.

223

224

225**Data analysis**

226   In order to ease analysis and interpretation of our data, we first

227inverted our measure of boldness: latency to resume movement after a

228huddle response. To do this, we subtracted each individual's latency from

229the maximum time of ten minutes (600 seconds). Therefore, individuals with

230higher boldness scores were considered more "bold," i.e. they resumed

231movement more quickly after the huddle response, compared to individuals

232with lower boldness scores which were considered more "shy". The resulting

233boldness scores were non-Gaussian distributed and best approximated a

234Poisson error distribution which we used for all further analyses. Attack

235tendency was a binary variable and we used a categorical (yes/no) error

236distribution for all analyses.

237   We first tested for the main effects of familiarity treatment (mixed

238versus control) and time since social disturbance (one, two, three, four

239weeks) on each of our behavioural measures. We ran a separate generalized

240linear mixed model for each behaviour including familiarity treatment, time

241since social disturbance and their interaction as fixed effects. We also

242included individual, experimental colony and source colony as random

243effects to account for the non-independence of our behavioural measures.

244There was no significant variation among experimental or source colonies

245and so we subsequently removed these effects from further analyses.

246   Our primary research question was to determine whether increasing

247familiarity among colony mates increased consistent individual differences in

248behaviour. To test this we compared the among- and within-individual

249variation components of each behaviour in each of our treatment

250combinations. However, it is important to note that because of its binary

251nature, it is impossible to directly estimate the within-individual (residual)

252variance in attack tendency. We ran a separate model for each behaviour in

253each familiarity treatment (control versus mixed) at each time point (weeks

254since social disturbance) including individual as a random effect. We then

255used these variance components to estimate repeatability as the proportion

256of total variation attributable to among-individual variation. We corrected all

257repeatability estimates as appropriate for each behaviour's distribution

258(Poisson with additive overdispersion for boldness, binary for attack

259tendency; [31]). We did not include any other fixed or random effects, such

260as experimental colony, source colony or body size, as these factors only

261varied between, not within, individuals and any variance attributable to

262these factors would remain in the within-individual (residual) variance

263providing a conservative repeatability estimate [32]. Additionally, in

264 preliminary analyses we found that these effects had no significant or

265 consistent effect on either behaviour nor accounted for any significant

266 portion of behavioural variation (data not shown). Therefore all repeatability

267 estimates reported here can be considered "non-adjusted" and should be

268 more broadly generalizable [31]. We used generalized linear mixed models

269 with Markov Chain Monte Carlo estimation for all analyses. MCMC is a

270 Bayesian statistical method that is powerful for fitting non-Gaussian

271 distributions and partitioning variance among random effects [32, 33].   We

272 used MCMCglmm [33] in R 2.15 (http://www.r-project.org/) which returns

273 95% credibility intervals for both fixed and random effects. If the 95% CI's of

274 two variance estimates did not overlap, we interpreted this as evidence that

275 the estimates are significantly different from each other. Throughout we

276 used non-informative proper priors [33] appropriate for the relative error

277 distributions (Poisson for boldness; categorical for attack latency) and

278 preliminary analyses indicated that our results were not sensitive to changes

279 in prior settings (data not shown). We ensured convergence and adequate

280 chain mixing by comparing the posterior distributions and auto-correlation

281 plots of five independent chains with 500,000 iterations, a 1,000 burn-in

282 period and thinning every 100 iterations for each model.

283

284   **RESULTS**

285

286   The average boldness score across all individuals was 216 ± 5.3 (±

287stn. error), meaning that individuals resumed moving after the huddle

288response after 383 seconds. While there was no main effect of familiarity

289treatment (treatment effect: -0.97, 95% CI: [-2.99, 1.16]) there was a

290significant effect of time since social disturbance (time effect: -0.56 [-1.16, -

2910.03]).   Groups that had been together longer tended to be shyer than

292groups that had recently been disturbed (Figure 1a). This effect did not

293differ between the two colony types (colony x time interaction: -0.31 [-0.56,

2941.02]).

295   Across both treatments and all time periods, attacks on a simulated

296prey item occurred in 25% of all trials This proportion did not differ between

297colony types (colony effect: -0.008 [-1.13, 1.25]) or across time (time effect: -

2980.11 [-0.42, 0.22]; colony x time interaction: 0.15 [-0.30, 0.58]; Figure 1b).

299   We found evidence for consistent individual differences in both

300boldness and attack tendency in both familiarity treatments (Figure 2, Table

3011). In support of the social niche specialization hypothesis, the repeatability

302of boldness was significantly higher in the control colonies compared to the

303mixed colonies at all time points, except when the colonies had not been

304disturbed for four weeks. Importantly, this increase in repeatability was

305driven by lower within-individual variation in boldness in the control colonies

306compared to the mixed colonies. This means that individuals in the control

307colonies exhibited more consistent behaviour at all time points compared to

308individuals in the mixed colonies. Additionally, the among-individual

309variation and therefore repeatability of boldness significantly increased the

310longer a group had been together regardless of whether it was a control or

311mixed colony. After not being disturbed for four weeks, individuals in the

312mixed colonies achieved similar among- and within-individual variation as

313those in the control colonies. In contrast, the repeatability of attack

314tendency remained at a similar level in both familiarity treatments across all

315time periods (Table 1)

316

317   **DISCUSSION**

318

319   The field of animal personality currently seeks potentially generalizable

320mechanisms that can generate and maintain consistent individual

321differences in behaviour. The social niche specialization hypothesis offers

322one such mechanism. The social niche specialization hypothesis posits that

323individuals will develop social niches as a result of living within a stable

324social group. In support of this view, we demonstrated here that consistent

325individual differences in boldness behaviour increased in the social spider *S.*

326*mimosarum* the longer that individuals remained in a stable social group.

327   We recovered evidence that social niches for boldness behaviour

328developed as a result of familiarity among colony mates. Control colonies all

329experienced a social disturbance but were placed back with their original

330familiar colony mates. If social group familiarity is a key driver of

331repeatability, we would expect to see stronger personalities in these

332individuals as compared to the mixed colonies, regardless of when the social

333disturbance occurred. As predicted, the repeatability estimates of boldness

334were significantly higher in the control colonies than mixed colonies at all

335time points, except when the colonies had not been disturbed for four weeks.

336This increase in repeatability was driven by lower within-individual variation

337in the control colonies. Individuals became more consistent in their

338behaviour the longer they had spent with a social group, supporting the

339hypothesis that repeated social interactions can increase the benefits of

340predictable behaviour [7, 8]. Our data suggest that, at least in this species,

341four weeks of repeated social interactions are needed to fully establish social

342niches. While several studies have now investigated how different ecological

343factors influence among-individual variation in behaviour [4-6, 11], fewer

344have investigated how these factors generate individual consistency in

345behaviour (but see [19, 34]). Our study demonstrates that the stability of

346the social environment may be especially influential in generating and even

347reinforcing individual differences once they appear. A promising next step

348will be to test whether colonies composed of behaviourally consistent

349(predictable) members perform better than colonies of unpredictable

350individuals.

351   While we found evidence for increased social niches in boldness with

352longer group fidelity, we found no such pattern for individuals' tendency to

353attack. Repeatabilities in attack tendency were similar regardless of the

354familiarity treatment or the time since the social disturbance. The overall

355low attack rates (attacks only occurred in ~25% of all trials) and distribution

356of the data (it is impossible to directly estimate the within-individual variance

357in a binary variable) likely reduced our ability to partition the behavioural

358variance. Granted, it is possible that our simulated prey was not as realistic

359as we hoped; however, this interpretation is at odds with the findings of

360other studies on other social *Stegodyphus* that used identical methods [23].

361Another explanation may be that attack tendency is more strongly

362influenced by genetic or un- (or slowly-) changing state variables, such as

363body size [35, 36]. While we found no evidence that body size influenced

364attack tendency in *S. mimosarum* (data not shown), it remains that some

365other unmeasured state variable may influence this particular behaviour. It

366is also possible that among-individual variation in this particular behaviour is

367not as important as variation in boldness in familiar groups; other studies

368have found relatedness to be the most influential determinant of foraging

369efficiency in some social spiders [28, 29]. Consistent with this view, [12]

370found that colony productivity increased with within-colony variation in some

371aspects of behaviour (brood care and exploration) but not others

372(aggressiveness). Boldness has already been implicated as an important

373determinant of task differentiation in other *Stegodyphus* species [23, 24] and

374our data support the finding that among-individual differences in boldness

375are a particularly important element of social organization in social

376*Stegodyphus*.

377   Social niche specialization may be a particularly powerful mechanism
378for generating social organization in societies where individuals exhibit group
379fidelity, such as our spiders. In contrast, it may be difficult for evolutionary
380processes to select for the proper mix of personalities in groups where
381membership changes with each generation. This may help to explain why a
382previous study on sticklebacks recovered no evidence that repeated social
383interactions increased among-individual variation or within-individual
384consistency in behaviour [20]. Because, sticklebacks form large schools in
385the wild, and while certain pairs are found together more often than chance
386would predict [21], school membership is generally fluid [21, 22]. We argue
387that in these types of groups, the formation of social niches will be difficult
388since individuals are constantly interacting with new individuals (e.g. [37]).
389Instead we expect that more plastic behaviour would be beneficial. In
390contrast, repeated social interactions in more stable societies may provide a
391mechanism by which individual sense gaps in their societies' workforce and
392fill them, i.e., via shifts in personality. In other words, simple mechanisms
393such as positive feedback loops throughout development may, over time,
394permit the adaptive differentiation of individuals' personalities and (perhaps)
395their social roles. Such simple feedback loops have been implicated in
396numerous studies on social insect societies and manifest behaviourally as
397individual differences in task performance thresholds ([38, 39]but see [40]).
398Here we studied how repeated social interactions among individuals in a
399social group influences behavioural variation, but another potential scenario

400where social niches might be important is in species with long-term mating

401partnerships [14]. An exciting area for future research would be to

402investigate how the number of stable social partners influences the

403development of social niches.

404

405**Conclusions**

406   The presence of consistent individual differences in behaviour have

407sparked so much interest in part because they have the potential to impact

408any number of evolutionary and ecological processes. And, while studies

409documenting the presence of personalities in animals continue to grow, we

410still know little about the factors responsible for their existence. Here we

411show that living in stable social groups has the potential to generate and

412maintain consistent individual differences in behaviour. Individuals that were

413from groups that were more familiar with each other exhibited greater

414among-individual variation and within-individual consistency in behaviour.

415Many species form social groups, suggesting that the development of social

416niches may allow individuals to increase their own fitness by enhancing their

417fit with their (social) environment.   However, stability of group membership

418can vary dramatically among species and populations and we urge that more

419studies explore the potency of group fidelity to drive the generation and

420maintenance of individual differences in key functional traits, such as

421behaviour.

422

423   **ACKNOWLEDGEMENTS**

REFERENCES

[1] Dall, S.R., Houston, A.I. & McNamara, J.M. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* **7**, 734-739. (doi:10.1111/j.1461-0248.2004.00618.x).

[2] Dingemanse, N.J. & Wolf, M. 2010 Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3947-3958. (doi:10.1098/rstb.2010.0221).

[3] Wolf, M. & Weissing, F.J. 2010 An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3959-3968. (doi:10.1098/rstb.2010.0215).

[4] Mathot, K.J., van den Hout, P.J., Piersma, T., Kempenaers, B., Réale, D. & Dingemanse, N.J. 2011 Disentangling the roles of frequency-vs. state-dependence in generating individual differences in behavioural plasticity. *Ecology Letters* **14**, 1254-1262. (doi:10.1111/j.1461-0248.2011.01698.x).

[5] Nicolaus, M., Tinbergen, J.M., Bouwman, K.M., Michler, S.P., Ubels, R., Both, C., Kempenaers, B. & Dingemanse, N.J. 2012 Experimental

449   evidence for adaptive personalities in a wild passerine bird.

450   *Proceedings of the Royal Society B: Biological Sciences* **279**, 4885-

451   4892. (doi:10.1098/rspb.2012.1936).

452

453 [6] Laskowski, K.L. & Bell, A.M. 2013 Competition avoidance drives individual

454   differences in response to a changing food resource in sticklebacks.

455   *Ecology Letters*. (doi:10.1111/ele.12105).

456

457 [7] Bergmüller, R. & Taborsky, M. 2010 Animal personality due to social niche

458   specialisation. *Trends in Ecology & Evolution* **25**, 504-511.

459   (doi:10.1016/j.tree.2010.06.012).

460

461 [8] Montiglio, P.-O., Ferrari, C. & Réale, D. 2013 Social niche specialization

462   under constraints: personality, social interactions and environmental

463   heterogeneity. *Philosophical Transactions of the Royal Society B:*

464   *Biological Sciences* **368**. (doi:10.1098/rstb.2012.0343).

465

466 [9] Ravigné, V., Dieckmann, U. & Olivieri, I. 2009 Live where you thrive: joint

467   evolution of habitat choice and local adaptation facilitates

468   specialization and promotes diversity. *The American Naturalist* **174**,

469   E141-E169. (doi:10.1086/605369).

470

471 [10] Svanbäck, R. & Bolnick, D.I. 2007 Intraspecific competition drives

472 increased resource use diversity within a natural population.

473 *Proceedings of the Royal Society B: Biological Sciences* **274**, 839-844.

474 (doi:10.1098/rspb.2006.0198).

475

476 [11] Araújo, M.S., Bolnick, D.I. & Layman, C.A. 2011 The ecological causes of

477 individual specialisation. *Ecology Letters* **14**, 948-958.

478 (doi:10.1111/j.1461-0248.2011.01662.x).

479 [12] Modlmeier, A.P., Liebmann, J.E. & Foitzik, S. 2012 Diverse societies are

480 more productive: a lesson from ants. *Proceedings of the Royal Society*

481 *B: Biological Sciences* **279**, 2142-2150. (doi:10.1098/rspb.2011.2376).

482

483 [13] Pruitt, J.N. & Riechert, S.E. 2011 How within-group behavioural variation

484 and task efficiency enhance fitness in a social group. *Proceedings of*

485 *the Royal Society B: Biological Sciences* **278**, 1209-1215. (doi:10.1098/

486 rspb.2010.1700).

487

488 [14] Schuett, W., Tregenza, T. & Dall, S.R. 2010 Sexual selection and animal

489 personality. *Biological Reviews* **85**, 217-246.

490

491 [15] Harcourt, J.L., Ang, T.Z., Sweetman, G., Johnstone, R.A. & Manica, A.

492 2009 Social feedback and the emergence of leaders and followers.

493 *Current Biology* **19**, 248-252. (doi:10.1016/j.cub.2008.12.051).

494

495 [16] Wolf, M., Van Doorn, G.S. & Weissing, F.J. 2008 Evolutionary emergence

496   of responsive and unresponsive personalities. *Proceedings of the*

497   *National Academy of Sciences* **105**, 15825-15830.

498   (doi:10.1073/pnas.0805473105).

499

500 [17] Morand-Ferron, J., Wu, G.-M. & Giraldeau, L.-A. 2011 Persistent

501   individual differences in tactic use in a producer–scrounger game are

502   group dependent. *Animal Behaviour* **82**, 811-816.

503

504 [18] Beauchamp, G. 2001 Consistency and flexibility in the scrounging

505   behaviour of zebra finches. *Canadian journal of zoology* **79**, 540-544.

506

507 [19] Favati, A., Leimar, O., Radesäter, T. & Løvlie, H. 2014 Social status and

508   personality: stability in social state can promote consistency of

509   behavioural responses. *Proceedings of the Royal Society B: Biological*

510   *Sciences* **281**, 20132531. (doi:10.1098/rspb.2013.2531).

511

512 [20] Laskowski, K.L. & Bell, A. in press Strong personalities, not social niches,

513   drive individual differences in social behaviour in sticklebacks. *Animal*

514   *Behaviour*.

515

516 [21] Ward, A.J., Botham, M.S., Hoare, D.J., James, R., Broom, M., Godin, J.-G.J. & Krause, J. 2002 Association patterns and shoal fidelity in the three–spined stickleback. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**, 2451-2455. (doi:10.1098/rspb.2002.2169).

520

521 [22] Croft, D., James, R., Ward, A., Botham, M., Mawdsley, D. & Krause, J. 2005 Assortative interactions and social networks in fish. *Oecologia* **143**, 211-219. (doi:10.1007/s00442-004-1796-8).

524

525 [23] Grinsted, L., Pruitt, J.N., Settepani, V. & Bilde, T. 2013 Individual personalities shape task differentiation in a social spider. *Proceedings of the Royal Society B: Biological Sciences* **280**. (doi:10.1098/rspb.2013.1407).

529 [24] Keiser, C.N., Jones, D.K., Modlmeier, A.P. & Pruitt, J.N. in press Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. *Behavioral Ecology and Sociobiology*.

533

534 [25] Seibt, U. & Wickler, W. 1988 Bionomics and social structure of 'family spiders' of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae), Goethe Universität.

538

539[26] Crouch, T. & Lubin, Y. 2000 Effects of climate and prey availability on

540   foraging in a social spider, Stegodyphus mimosarum (Araneae,

541   Eresidae). *Journal of Arachnology* **28**, 158-168. (doi:10.1636/0161-

542   8202(2000)028[0158:EOCAPA]2.0.CO;2).

543

544[27] Lubin, Y. & Bilde, T. 2007 The evolution of sociality in spiders. *Advances*

545   *in the Study of Behaviour* **37**, 83-145. (doi:10.1016/S0065-

546   3454(07)37003-4).

547

548[28] Ruch, J., Heinrich, L., Bilde, T. & Schneider, J.M. 2009 Relatedness

549   facilitates cooperation in the subsocial spider, Stegodyphus

550   tentoriicola. *BMC evolutionary biology* **9**, 257. (doi:10.1186/1471-2148-

551   9-257).

552

553[29] Schneider, J.M. & Bilde, T. 2008 Benefits of cooperation with genetic kin

554   in a subsocial spider. *Proceedings of the National Academy of Sciences*

555   **105**, 10843-10846. (doi:10.1073/pnas.0804126105).

556

557[30] Riechert, S.E. & Hedrick, A.V. 1990 Levels of predation and genetically

558   based anti-predator behaviour in the spider, *Agelenopsis aperta*.

559   *Animal Behaviour* **40**, 679-687. (doi:10.1016/S0003-3472(05)80697-9).

560

561[31] Nakagawa, S. & Schielzeth, H. 2010 Repeatability for Gaussian and non-

562   Gaussian data: a practical guide for biologists. *Biological Reviews* **85**,

563   935-956. (doi:10.1111/j.1469-185X.2010.00141.x).

564

565[32] Dingemanse, N.J. & Dochtermann, N.A. 2013 Quantifying individual

566   variation in behaviour: mixed-effect modelling approaches. *Journal of*

567   *Animal Ecology* **82**, 39-54. (doi:10.1111/1365-2656.12013).

568

569[33] Hadfield, J.D. 2010 MCMC methods for multi-response generalized linear

570   mixed models: the MCMCglmm R package. *Journal of Statistical*

571   *Software* **33**, 1-22.

572

573[34] Arnold, C. & Taborsky, B. 2010 Social experience in early ontogeny has

574   lasting effects on social skills in cooperatively breeding cichlids. *Animal*

575   *Behaviour* **79**, 621-630. (doi:10.1016/j.anbehav.2009.12.008).

576

577[35] Pitcher, T.J. 1986 Functions of shoaling behaviour in teleosts. In *The*

578   *behaviour of teleost fishes* (pp. 294-337), Springer.

579

580[36] Biro, P.A. & Stamps, J.A. 2010 Do consistent individual differences in

581   metabolic rate promote consistent individual differences in behavior?

582   *Trends in Ecology & Evolution* **25**, 653-659.

583   (doi:10.1016/j.tree.2010.08.003).

584

585 [37] Cote, J., Fogarty, S. & Sih, A. 2012 Individual sociability and choosiness

586   between shoal types. *Animal Behaviour* **83**, 1469-1476.

587   (doi:10.1016/j.anbehav.2012.03.019).

588

589 [38] Beshers, S.N. & Fewell, J.H. 2001 Models of division of labor in social

590   insects. *Annual review of entomology* **46**, 413-440.

591

592 [39] Myerscough, M. & Oldroyd, B. 2004 Simulation models of the role of

593   genetic variability in social insect task allocation. *Insectes Sociaux* **51**,

594   146-152. (doi:0.1007/s00040-003-0713-1).

595

596 [40] Jandt, J.M. & Dornhaus, A. 2014 Bumblebee response thresholds and

597   body size: does worker diversity increase colony performance? *Animal*

598   *Behaviour* **87**, 97-106. (doi:10.1016/j.anbehav.2013.10.017).

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602**Table 1.** Variance component (among- and within-individual) and 603repeatability estimates of boldness and attack behaviours in control and 604mixed colonies that experienced a social disturbance one, two, three, or four 605weeks ago. The within-individual variance could not be estimated for the 606binary variable of attack tendency (see methods for details). Numbers in [] 607indicate 95% credibility intervals.

608

|	**Time since social disturbance**			
	One week	Two weeks	Three weeks	Four weeks
	Boldness			
Control colonies				
Among	6.87 [3.94, 11.49]	21.80 [11.90, 36.32]	15.11 [9.12, 29.53]	23.41 [13.03, 46.33]
Within	4.45 [3.51, 6.06]	3.52 [2.64, 4.79]	2.61 [2.00, 3.64]	4.95 [3.61, 7.22]
R	0.62 [0.47, 0.73]	0.86 [0.78, 0.92]	0.86 [0.79, 0.93]	0.83 [0.73, 0.91]
Mixed colonies				
Among	4.12 [0.78, 10.30]	0.05 [0, 7.05]	11.93 [6.24, 21.52]	21.75 [11.22, 42.17]
Within	19.31 [14.47, 27.03]	23.58 [16.68, 33.20]	12.01 [8.82, 16.33]	9.91 [7.12, 13.69]
R	0.16 [0.05, 0.36]	0.002 [0, 0.24]	0.54 [0.35, 0.66]	0.74 [0.56, 0.82]
	Attack tendency			
Control colonies				
Among	1.40 [0.39, 4.85]	1.73 [0.32, 5.00]	6.26 [2.16, 18.37]	2.02 [0.21, 6.24]
R	0.32 [0.12, 0.56]	0.35 [0.12, 0.56]	0.70 [0.42, 0.85]	0.32 [0.11, 0.62]
Mixed colonies				
Among	2.88 [0.84, 7.45]	3.14 [0.94, 8.73]	4.30 [1.46, 13.15]	3.31 [1.23, 8.68]
R	0.45 [0.22, 0.66]	0.50 [0.23, 0.70]	0.55 [0.34, 0.78]	0.50 [0.26, 0.70]

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611   **FIGURE LEGENDS**

612

613**Figure 1.** Average (± stn. error) boldness scores (a.) and proportion of prey

614attacks (b.) in the mixed and control colonies that experienced a social

615disturbance one, two, three, or four weeks ago.

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617**Figure 2.** Among-individual (a.), within-individual (b.), and the resulting

618repeatability estimate (c.) in boldness scores in the mixed and control

619colonies that experienced a social disturbance one, two, three or four weeks

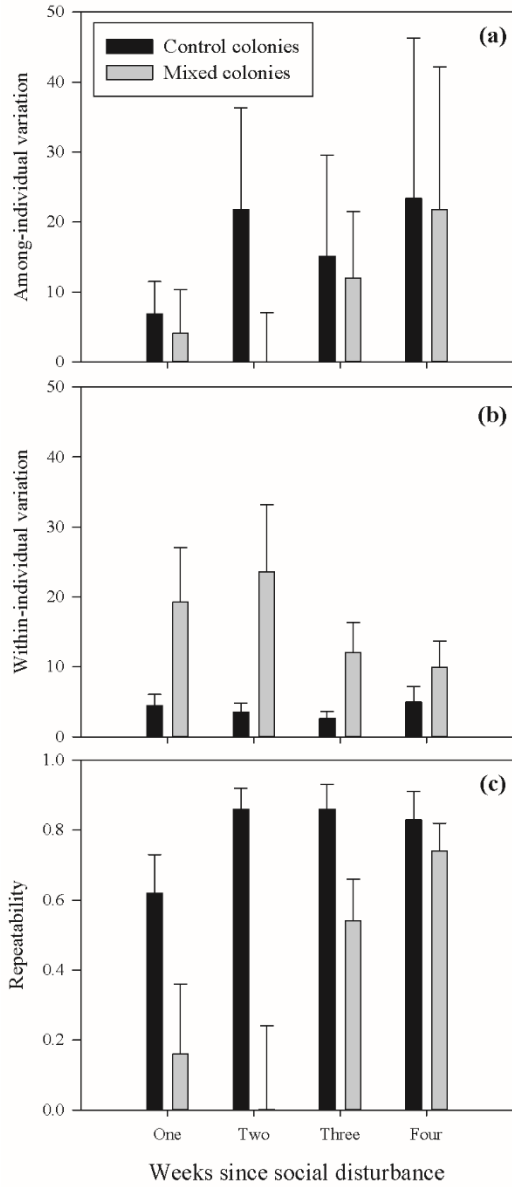620ago. Error bars represent the 95% CI for each estimate.

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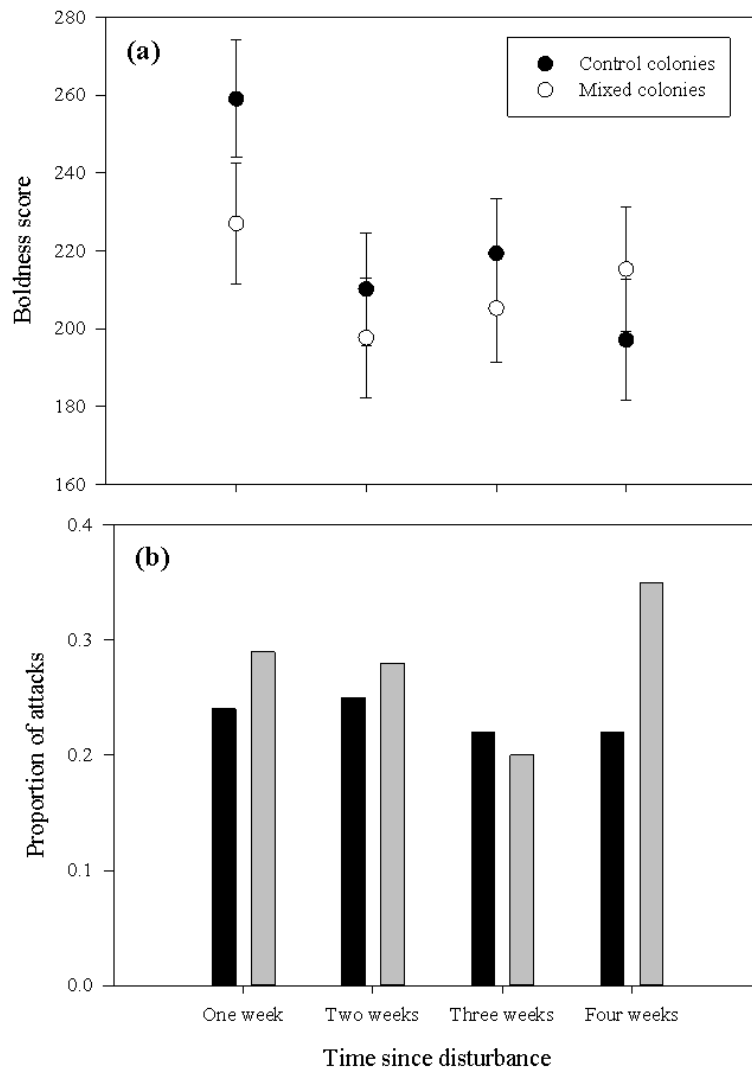
Figure 1.

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628**Figure 2.**
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