Personality predicts the propensity for social learning in a wild primate

Social learning can play a critical role in the reproduction and survival of social animals. Individual differences in the propensity for social learning are therefore likely to have important fitness consequences. We asked whether personality might underpin such individual variation in a wild population of chacma baboons (*Papio ursinus*). We used two field experiments in which individuals had the opportunity to learn how to solve a task from an experienced conspecific demonstrator: exploitation of a novel food and a hidden item of known food. We investigated whether the (1) time spent watching a demonstrator and (2) changes in task-solving behaviour after watching a demonstrator were related to personality. We found that both boldness and anxiety influenced individual performance in social learning. Specifically, bolder and more anxious animals were more likely to show a greater improvement in task solving after watching a demonstrator. In addition, there was also evidence that the acquisition of social information was not always correlated with its use. These findings present new insights into the costs and benefits of different personality types, and have important implications for the evolution of social learning.

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INTRODUCTION

Individuals can acquire information either through interacting with their environment directly—personal information—or through observing the behaviour of other individuals —social information (Dall et al. 2005). Personal information can be costly and time consuming to collect (Laland 2004). For social animals, social information provides an alternative to gathering costly personal information, potentially facilitating the acquisition of information about when, where and how to get food, where to travel and remain, whom to choose as a mate, and which predators to avoid (Giraldeau et al. 2002; Reader & Biro 2010). Social learning—where an individual changes its behaviour after observing another—allows the rapid dissemination of novel information among group members, and has also been widely implicated in the formation of tradition and cultures within species (Whiten 2000; Castro & Toro 2004). On the other hand, social learning can be conceived as a form of 'information parasitism' and can be maladaptive if information rapidly becomes outdated (Laland 2004). Nonetheless individual differences in innovation and social learning abilities remain largely overlooked (Thornton & Lukas 2012). This is surprising, as an understanding of individual variation in social learning is likely to be necessary for predicting the formation and persistence of traditions and culture within groups, and the individual fitness advantages of personal versus social information use (Thornton & Lukas 2012).

Animal personality refers to between-individual differences in behaviour that persist through time (Sih et al. 2004). Evidence for personality-related individual differences in information use (Kurvers et al. 2010; Carter et al. 2013) suggests personality may also explain individual differences in social learning (Marchetti & Drent 2000). This may occur at two different steps in the social learning process, when (1) a

36 subset of individuals initially gathers personal information about a novel situation and (2)

37 this subset—the 'demonstrators'—provide other individuals with the opportunity to then

38 gather and use social information about the novel situation from them. In the first step,

39 for individuals to exploit a novel food or solve a novel task they must interact with it for

40 long enough to obtain sufficient personal information about it (Seferta et al. 2001;

41 Thornton & Samson 2012). Individual variation in responses to novel stimuli are

42 frequently used to differentiate individuals by two personality traits, namely boldness and

43 exploration (Carter et al. 2012b). Those animals that are less bold, i.e. shyer, or less

44 explorative of novelty, i.e. 'neophobic', individuals (Réale et al. 2007; Carter et al. 2012c)

45 tend to be less willing to interact with a novel food or task and are thus less able to

46 acquire the personal information necessary to solve the problem (but see Cole & Quinn

47 2011). For example, neophobic myna (*Acridotheres tristis*) are less likely to solve

48 innovation tasks than neophilic myna (see also Coleman et al. 2005; Toxopeus et al.

49 2005; Sol et al. 2011). In the second step, those animals that are less willing or able to

50 gather personal information may be more likely to use social information. For instance,

51 where individuals seek to exploit a novel food or solve a novel task, bolder individuals

52 may do so directly because they are willing to gain personal information about it, and

53 subsequently become demonstrators for shyer individuals who may be more likely to

54 attend to, and act upon, social information (Kurvers et al. 2010).

55   We investigated the relationship between animal personality and social learning

56 in wild chacma baboons (*Papio ursinus*). Baboons present an ideal system to explore

57 such individual differences, since they are highly social, live in stable groups, and social

58 learning has previously been documented among infants and juveniles (Whiten 2000). In

59 addition, individual baboons in our study population vary consistently in two unrelated

60 personality traits, boldness and anxiety, that are repeatable over a three-year period and

61 for which all individuals in the study groups have been assayed up to six times (Carter et

62 al. 2012c). We use the term 'boldness' to refer to an individual's response to a novel

63 food, where bolder individuals spend more time inspecting a novel food; and 'anxiety' for

64 an individual's response to a threatening stimulus, where more anxious individuals show

65 a stronger fear response towards, and spend more time investigating, a threat (Carter et

66 al. 2012c). Though threat responses can also be used to describe boldness, we have

67 previously found no evidence that our threat presentation test measures boldness in this

68 species (for further details, see Carter et al. 2012c).

69   To test our hypothesis that personality traits (boldness, anxiety) influence

70 individual propensity for social learning, we performed two types of field experiments in

71 which social learning to solve a task could occur: exploitation of a novel food

72 (experiment NF) and a hidden food (HF). We investigated whether (Q1) propensity to

73 solve the tasks using personal information alone, (Q2) time spent collecting social

74 information (watching a demonstrator solve the tasks), and (Q3) social learning, i.e.

75 changes in task-solving behaviour after exposure to a demonstrator, were related to the

76 baboons' boldness or anxiety. Thus we addressed three questions with two experiments

77 for two personality traits that could influence social learning.

78   We had several predictions in line with our questions. First, we predicted that

79 bolder baboons would be more likely to 'solve' the hidden food task as bolder

80 individuals are more willing to interact with a novel food (Carter et al. 2012a) (Prediction

81 1 for boldness: $P1_{HF}b$). We further predicted that there would be no relationship between

82 anxiety and the propensity to solve the hidden food task as anxiety is unrelated to

83 boldness in this species (Carter et al. 2012c) and anxious individuals are otherwise no

84 more likely to interact with a novel food than calm individuals (P1$_{HF}$a). Second, regarding

85 whether an individual would collect social information, we predicted that more anxious

86 baboons would spend more time watching the demonstrator than calmer baboons, in

87 both the novel food and hidden food tasks, as anxious baboons attend to a threatening

88 stimulus for longer than calm baboons (Carter et al. 2012c) (P2$_{NF,HF}$a). We further

89 predicted that shyer baboons would spend more time watching a demonstrator than

90 bolder baboons in both tasks as shy geese attend to social information more than bold

91 geese (Kurvers et al. 2010) (P2$_{NF,HF}$b). Finally, regarding whether individuals differed in

92 their propensity for social learning in the novel food and hidden food tasks, we predicted

93 that more anxious individuals (P3$_{NF,HF}$a) would show greater social learning than calmer

94 baboons, as anxious individuals were predicted to attend to social information more than

95 calm baboons (P2$_{NF,HF}$a above). Similarly, we predicted that shyer individuals (P3$_{NF,HF}$b)

96 would show greater social learning than bold baboons in both tasks, as shy individuals

97 were predicted to attend to social information more than bold baboons (P2$_{NF,HF}$b above).

98 **MATERIALS AND METHOD**

99 *Study area and species*

100 We studied the chacma baboons over three years, from May to November 2009, May to

101 October 2010 and June to September 2011 at Tsaobis Leopard Park, Namibia (15☐

102 45'E, 22☐ 23'S). Two groups of baboons (n = 44, 31 in 2009) have been habituated to

103 the presence of observers at close range and are individually recognisable. We collected

104 data annually from 57 adult, subadult and juvenile baboons (we did not test individuals

105 who were dependent young in 2009) over the 2009 to 2011 period. Individuals were

106   assigned to age classes (juvenile/adult) on the basis of canine eruption in males and

107   menarche in females (after which they were considered adult). Age (years) was

108   estimated from a combination of known birth dates and dental patterns of tooth eruption

109   and wear (Huchard et al. 2009). Individual ranks were assessed through dominance

110   interactions that were recorded during focal observations and *ad libitum* using Matman

111   1.1.4 (Noldus Information Technology 2003). Hierarchies in both troops were strongly

112   linear in all years (in 2010, for example, Landau's corrected linearity index: $h'_{larger\ troop}$ =

113   0.71, $h'_{smaller\ troop}$ = 0.82, $p < 0.001$ in both). Rank was expressed as a relative rank (which

114   controls for group size), calculated from absolute ranks for each baboon using the

115   formula $1-[(1-r)/(1-n)]$ where r is the individual's absolute rank and n is the group size of

116   the individual.

117   *Personality assessments*

118   Boldness and anxiety were assessed using an experimental approach in 2009,

119   2010 and 2011 (for further details, see Carter et al. 2012a; Carter et al. 2012c).

120   Boldness was assessed by scoring responses to a novel food, while anxiety was

121   assessed by scoring responses to a venomous snake (Carter et al. 2012c). In all cases,

122   individuals were presented with a stimulus when they were alone and moving between

123   food patches. The stimuli were presented on the edges of game trails and paths

124   regularly used by the baboons. All experiments were filmed to facilitate data extraction

125   (Panasonic SDR-SW20, Kadoma Osaka, Japan; see movie files in Carter et al. 2012c).

126   Stimuli for the boldness experiments consisted of novel food items which included

127   hard-boiled eggs with the shell on or removed, or a small egg-shaped bread roll, all of

128 which were dyed red or green (Moir's food dye), in 2009; semi-dried eighths of apple or

129 pear, dyed red, in 2010; and eighths of an orange or equivalent-sized pieces of butternut

130 squash in 2011. Any naïve individual that saw another individual interacting with a novel

131 food was presented with a different novel food when they were tested. We recorded the

132 latency in seconds (s) to approach the food item on detection (if the food item was not

133 approached, the individual was given the maximum value of 150 s; individuals that did

134 not detect the item were subsequently re-tested), the time spent inspecting the food item

135 (s; the time between approaching the food item and the end of the experiment, either

136 leaving or eating the item), and the time spent handling the food item (s; the time spent

137 touching the food item). Fifty-eight, fifty-four and fifty baboons received novel food

138 presentations in 2009, 2010 and 2011, respectively (mean and median number of

139 presentations = 2.8, 3.0; range = 1-3 presentations).

140   The stimulus for the anxiety experiments was a taxidermic puff adder *Bitis*

141 *arietans*. We recorded as binary responses whether an individual approached,

142 vocalised, performed a self-directed behaviour, bared its teeth, flagged its tail, stopped

143 and backed away (see Carter et al. 2012c for details). If more than one baboon saw the

144 stimulus during a given presentation, we extracted data for both of the individuals if the

145 second individual did not respond to the reaction of the first individual (and in one case

146 third individual). A baboon was recorded as responding to another individual if it looked

147 in the direction of and/or approached the individual who initially saw the stimulus. In

148 total, we completed 153 snake presentations to 57 baboons over 2009 to 2011 (mean

149 and median number of presentations = 2.7, 3.0; range = 1-6 presentations).

150   As both boldness and anxiety have been shown to be repeatable across years (*r*

151 = 0.26, 0.34, respectively) (Carter et al. 2012c), we used a composite score for each trait

152   from trait values collected over three years (see Carter et al. 2012c). Boldness and

153   anxiety are independent in this species, thus a bolder baboon is equally likely to be as

154   anxious as a shyer baboon (Carter et al. 2012c).

155   *Social learning experiments*

156   From 2009 to 2011, we performed two types of experiment designed to assess

157   differences in social learning in baboons: a novel food experiment and a hidden food

158   experiment. In both cases, we attempted to adopt a 'test – learn (via a demonstrator) –

159   re-test' experimental design. The experiments were run concurrently to limit order

160   effects. All experiments were filmed to facilitate data extraction, and the baboons'

161   identities and activities were dictated to the camera (Panasonic SDR-SW20, Kadoma

162   Osaka, Japan; see Supplemental Video 1). The study population in 2010 comprised 21

163   male and 34 female baboons who were on average (mean) 8.2 years old (range: 4-21),

164   had a relative rank of 0.5 (0-1), inspected the novel food on average for 20 s (0-120)

165   with an mean boldness score of 0.46 (-3.90-1.47) (note that low values represent

166   individuals that inspected the food for longer, such that high scores indicate shyer

167   animals) and an average anxiety score of -0.02 (-0.22-0.53) (where high scores indicate

168   more anxious animals).

169   Novel food experiments

170   The 'test' stage of the novel food experiments was also our assay for boldness (see

171   above). Thus, solitary individuals were presented with a novel food while moving

172 between natural food patches. In the majority of cases, the test subjects only briefly

173 inspected the food and failed to eat it (Carter et al. 2012a). In the 'learn' stage, the same

174 individuals were subsequently given the opportunity to watch an experienced

175 demonstrator with the same novel food. The demonstrator was an individual who had

176 encountered the novel food at least once before, and had consumed at least part of it on

177 the last encounter. We achieved this by presenting a novel food item to small subgroups

178 (two-five baboons within 5 m of one another) that included a randomly-chosen

179 demonstrator. We recorded the identities of any additional baboons that came within 5 m

180 of the demonstrator (and could therefore watch the demonstrator) and the duration that

181 the (potential) observers watched the demonstrator (seconds). Watching the

182 demonstrator was defined as an individual directing its gaze towards the demonstrator.

183 The difference in dominance ranks between the observers and the demonstrator was

184 also recorded.

185   In the final 're-test' stage, we subsequently presented the non-demonstrators with

186 the novel food again, under the same conditions as in the initial test stage (i.e. while

187 each was solitary and moving between food patches). All observers were tested after

188 their 'learn' trial, but could also have been observers in others' 'learn' trials subsequently

189 (as we could not control subgroup formation). If the non-demonstrators had learned from

190 watching the demonstrator, we expected their responses to the novel food to differ from

191 that previously observed. Specifically, we expected shy and anxious individuals'

192 handling time, which positively correlates with the probability of eating the novel food

193 (Carter et al. 2012a), to increase on the 're-test' trial compared to the initial trial, while

194 bold and calm individuals' behaviour would not change (Table 1).

195   As a control, we also re-tested a subset of baboons that did not have the

196   opportunity to watch a demonstrator and therefore could only change their responses to

197   the 'novel' food through further personal experience. The 'social learning of novel food'

198   experiment was carried out on 16 subjects in 2010; the control trials were carried out on

199   23 subjects between 2009 and 2011. The demonstrators for this experiment comprised 6

200   male and 7 female baboons who were on average 6.8 years old, had a relative rank of

201   0.58, inspected the novel food on the first presentation on average for 51 s with an

202   average boldness of -1.17 and an average anxiety of 0.05. The focal subjects for this

203   experiment comprised 13 male and 19 female baboons who were on average 7.6 years

204   old, had a relative rank of 0.48, inspected the novel food on the first presentation on

205   average for 19 s with an average boldness of 0.15 and an average anxiety of -0.01.

206   Hidden food experiments

207   In the hidden food experiment, the subjects were presented with a hidden-food task

208   whilst they were moving with other baboons between food patches. The hidden-food

209   task consisted of an empty, opaque 1 L UHT milk tetrapack that had been rinsed

210   thoroughly and dried. One corner of the top of the tetrapack had been cut off to let the

211   milk out, and the other corner unfolded so that the top, short end of the tetrapack was no

212   longer flat. Fifteen to twenty dried maize kernels – a highly preferred food for the

213   baboons – were placed in the tetrapack. Since the tetrapack was opaque, the baboons

214   had to interact closely with it to find the food inside. We doubt that the baboons could

215   smell the maize kernels, but if they could they would have had to interact intimately with

216   the stimulus to do so. Individuals could discover the food by tipping the tetrapack upside

217   down, or ripping the tetrapack open.

218   During the presentations we recorded the following information: the identities of

219   the baboons that came within 5 m of the stimulus when there was no 'demonstrator',

220   and thus had an opportunity to obtain personal information about the stimulus; the

221   identities of the baboons that interacted with the stimulus, defined as approaching to

222   smell, touch or handle the tetrapack, and whether they solved the task, defined as

223   eating any food from the tetrapack; the identities of the baboons that came within 5 m of

224   a demonstrator, i.e. an individual interacting with the stimulus; and whether they

225   watched the demonstrator, defined as looking in the direction of the demonstrator while

226   stationary, or not, which was defined as not looking in the direction of the demonstrator,

227   or glancing at the demonstrator but not stopping to watch, while at this proximity. The

228   difference in dominance rank between each demonstrator and observer was also

229   recorded.

230   We encountered two unanticipated difficulties with this series of experiments.

231   First, subordinates occasionally moved away carrying the stimulus when they were

232   approached by dominants. In these cases, the experimenter followed the baboon with

233   the stimulus but did not record the 'watching' durations of the observers, as these were

234   unlikely to be accurate. Second, because individuals moved with the task through the

235   troop as it was foraging, it was impossible to present the task to particular individuals in

236   a particular order. Individuals were thus sometimes able to experience a 'learn' trial

237   before a 'test' trial, and we were unable to systematically achieve the more controlled

238   test — learn — re-test experiments of the novel food task. Further, we were unable to

239   control the number of times an individual was tested with or without a demonstrator.

240   However, this situation is more likely to reflect the natural opportunities for social

241   learning than our more controlled test — learn — re-test paradigm, and we have

242 therefore included this series of experiments in our analyses. In this case, for each

243 individual, we recorded three possible trial presentation numbers that reflect the different

244 types of information that they could acquire: the cumulative presentation number

245 (cumulative total social and personal information), the number of presentations with a

246 demonstrator (cumulative social information) and the number of presentations without a

247 demonstrator (cumulative personal information).

248   Because we retrieved a task after it had been solved, no baboons could have had

249 a 'learn' presentation (with a demonstrator) and a 're-test' presentation (without a

250 demonstrator) in the same trial. That is, no individuals could watch a demonstrator and

251 then subsequently interact with an unsolved task, though some individuals did interact

252 with parts of the task that were ripped off and dropped by the demonstrator before the

253 experimenter could retrieve them. Individual baboons experienced the task with a

254 demonstrator a median of 3 times (inter-quartile range (IQR) = 2-5, range = 1-11 times)

255 and without a demonstrator a median of 2 times (IQR = 1-3, range = 1-9 times), and in

256 total (either with a demonstrator or without) a median of 5 times (IQR = 1-3, range = 1-

257 16 times) with a mean interval of 3.30 ± 0.47 days (range = 0-52 days) between trials.

258 We performed a total of 243 baboon-trials to 45 baboons with 18 demonstrators who

259 were demonstrators for a median of 5.5 individuals (IQR = 4-15.5, range = 1-25

260 individuals). The demonstrators for this experiment comprised 11 male and 6 females

261 (and one infant) who were on average 6 years old, had a relative rank of 0.64, with an

262 average boldness of 0.33 and an average anxiety of 0.06. The focal subjects for this

263 experiment comprised 19 male and 22 female baboons who were on average 7.5 years

264 old, had a relative rank of 0.54, with an average boldness of 0.44 and an average

265 anxiety of -0.03.

266 We confirm that we have adhered to the Guidelines for the Use of Animal Behaviour for

267 Research and Teaching (*Anim. Behav.* 2003. **65**, 249-255). Our experimental protocols

268 were assessed and approved by the Ethics Committee of the Zoological Society of

269 London (BPE/052). Our study was approved by the Ministry of Environment and Tourism

270 in Namibia (Research/Collecting Permits 1379/2009, 1486/2010, and 1486/2011).

271 *Statistical analyses*

272 General modelling approach

273 All data were analysed using (generalised) linear mixed effects models (LMEs or

274 GLMMs), fitted in the R environment ([R Development Core Team 2011](#)). Unless

275 otherwise specified below, all models started with all fixed and random effects, and fixed

276 effects were sequentially dropped (from least significant terms first) until a minimal

277 model was obtained that included only those effects which explained a significant

278 amount of the variation in the model. Each dropped term was added to the minimal

279 (final) model to check that it remained non-significant. Significance of terms was

280 determined by *p*-values (all effects with a *p*-value ≤ 0.05 were retained in the models).

281 Full models included the following fixed effects: boldness, anxiety, sex (factor: male or

282 female), age class (factor: juvenile or adult), and rank (continuous variable: standardised

283 between 0 and 1 within each troop). We also included the rank difference between the

284 test subject and the demonstrator in those models investigating whether or not the

285 subject watched the demonstrator (continuous variable; see models 2 described below).

286 Finally, we included presentation number as a fixed effect in all hidden food task models

287 as individuals were exposed to the stimuli on multiple occasions in this experiment. In all

288 models, we included test subject identity and troop identity (to control for repeated

289 measures) as random effects. The latter was further crossed with demonstrator identity

290 in those models investigating whether or not the test subjects watched a demonstrator

291 (models 2). All Gaussian models' residuals were normally distributed, and there were no

292 covariances > 0.40 between fixed effects.

293 Novel food experiments

294 We did not analyse which individuals initially solved the novel food task (Q1), since the

295 processing and consumption of the novel food was the basis of our boldness assay. We

296 thus first investigated whether individuals of different personality types spent longer

297 watching a demonstrator (Q2, predictions 2a and b, i.e. $P2_{NF}$a and b). Using data

298 obtained from the novel food experiments when a demonstrator was interacting with the

299 food (n = 54 baboon-trials with 36 baboons observing 14 demonstrators), we analysed

300 the time the baboons spent watching the demonstrator (s) with a Poisson error structure

301 (model 2, novel food: $m2_{NF}$).

302 Next (Q3), we investigated whether individuals of different personality types were

303 more or less likely to change their behaviour, i.e. learn, after being exposed to social

304 information via a demonstrator (predictions 3a and b, i.e. $P3_{NF}$a and b). We investigated

305 whether the baboons were more likely to increase their handling time of a novel food

306 after watching a demonstrator, and whether this depended on boldness or anxiety, by

307 investigating whether there was a three-way interaction between the personality trait, the

308 presentation ('test' or 're-test'), and the treatment (control or treatment) (models 3_{NF};

309   control: n = 58 paired presentations to 23 baboons over 2009-2011, treatment: n = 32

310   paired presentations to 16 baboons in 2010). However, as we could not concurrently

311   investigate a three-way interaction between both boldness and anxiety due to

312   overparameterization, we performed two models, one for each of the personality traits

313   ($m3_{NF}$ a and b).

314   Hidden food experiments

315   First (Q1), we investigated whether personality predicted whether individuals found food

316   in the hidden food experiment (i.e. solved the task; see predictions $P1_{HF}$a and b). We

317   analysed whether an individual managed to solve the hidden-food task if it had an

318   opportunity to do so (i.e. obtain food from it, binary 1/0; n = 80 occasions when a baboon

319   interacted with the tetrapack, involving 33 different baboons) using a GLMM with a

320   binomial error structure (model 1, hidden food experiment: $m1_{HF}$). As previously

321   mentioned, few individuals had the opportunity to interact with the task without

322   previously having seen a demonstrator interacting with the task; consequently, this

323   analysis cannot distinguish between task-solving due to 'innovation' or social learning

324   (but see Results).

325   Next, we investigated whether individuals of different personality types were more

326   likely to watch a demonstrator (Q2, predictions $P2_{HF}$a and b) using data obtained from

327   the hidden-food experiments with a demonstrator. We analysed whether individuals

328   watched the demonstrator or not (n = 163 baboon-trials with 41 baboons observing 14

329   demonstrators), using a binomial error structure (model 2_{HF}).

330   Finally, we investigated whether the baboons were more likely to increase their

331   response to the hidden-food stimulus after watching a demonstrator, and whether this

332   depended on boldness or anxiety by investigating whether there was an interaction

333   between either of these traits and the presentation number (Q3, predictions $P3_{HF}a$ and

334   b). In this case, we categorised the subjects' responses on a five-point scale, coded 0-4

335   in order of increasing response to the stimulus, as: ignore, the individual walked within 5

336   m of the stimulus without showing a response; look, the individual walked or stopped

337   within 5 m of the stimulus and look towards it; smell, the individual approached the

338   stimulus and bend to smell it; handle, the individual approached the stimulus and picked

339   it up; or eat, the individual obtained food from the stimulus. As the models' residuals

340   were normally distributed when analysed with a Gaussian error, we used linear mixed

341   effects models to model the data (models 3_{HF}) rather than generalised linear mixed

342   models for ordinal data. Due to the design of the hidden food task, subjects varied in the

343   number of presentations they had experienced. To allow for this variation, we ran three

344   models with different predictors: the cumulative number of all presentations (total

345   exposure), the cumulative number of 'test' presentations without a demonstrator, and the

346   cumulative number of 'learn' presentations with a demonstrator. We used backward

347   model selection on all three models, each including one of the different cumulative

348   presentation numbers (total, personal and social information presentations) and then

349   compared with a log likelihood ratio test which of the three minimal models best

350   explained the data, which included 80 baboon-trials to 33 individuals.

351   **RESULTS**

352 The minimal models for all analyses described below are provided in Table 1, and a

353 summary of our findings with regard to our predictions is provided in Table 2. In addition

354 to the results we present below regarding personality, it is notable that age class had an

355 effect on many of the variables that we investigated (Table 1). In all cases, there was a

356 positive effect of being juvenile on our measured variables: juveniles solved the hidden

357 task more often ($m1_{HF}$), spent longer watching a demonstrator ($m2_{NF}$), and showed

358 evidence for greater social learning than adults: juveniles handled the novel food for

359 longer after watching a demonstrator ($m3_{NF}a$), and showed greater responses to (and

360 improvement in, see Supplemental File 1) the hidden food task ($m3_{HF}$). Few other

361 variables had such a consistent effect on our measurements (Table 1).

362 Novel food experiments

363 We assessed individual variation in the time spent observing demonstrators manipulate

364 the novel food (Q2). We found no evidence that shyer baboons were more attentive

365 observers, contrary to $P2_{NF}b$. Further, in contrast to $P2_{NF}a$, calmer baboons spent more

366 time watching demonstrators interacting with a novel food, after accounting for the

367 subject's age and rank ($m2_{NF:}$ $\beta \pm$ s.e. $= -2.79 \pm 0.51$, $t = -2.01$, Fig. 1).

368 Next, we assessed the evidence for social learning, and individual variation in

369 social learning arising from personality differences. In the case of novel foods, we

370 achieved this by analysing the food handling time in the 're-test' conditions both for

371 those baboons that either had no exposure to a demonstrator after the initial test (the

372 control group) and for those that did (the experimental group). In both the models for

373 anxiety (a) and boldness (b) (models 3_{NF} a and b), the three-way interaction was

374 significant (3_{NF}a: $\beta \pm$ s.e. = 7.66 $\pm$ 3.04, z = 2.52, p = 0.01; 3_{NF}b: $\beta \pm$ s.e. = -0.68 $\pm$ 0.08, z

375 = -8.67, p < 0.001). Overall, in the control groups, individuals spent less time handling

376 the novel food when re-tested, and both bolder and more anxious individuals showed a

377 greater decline in handling time when re-tested (Table 1; Fig. 2a, c). In the treatment

378 groups, individuals showed the opposite response—handling times tended to increase

379 when re-tested—and bolder and more anxious individuals showed higher handling times

380 than shyer and calmer individuals, respectively (models 3_{NF} a and b, Table 1; Fig 2b, d).

381 Although calmer individuals also showed higher handling times in the second

382 presentation after watching a demonstrator, this reflected a non-significant 1.4-fold

383 increase in handling time in comparison to the 2.7-fold increase in more anxious

384 individuals. Thus, bolder and more anxious animals showed social learning after

385 exposure to a demonstrator (contrary to P3$_{NF}$b, but in support of P3$_{NF}$a, respectively).

386 Hidden food experiments

387 In our assessment of individual propensity for task-solving (Q1), we found that bolder

388 baboons were more likely to obtain food from the hidden food experiment ($\beta \pm$ s.e. =

389 -0.85 $\pm$ 0.32, z = -2.63, p = 0.008), after accounting for differences in age (model 1,

390 Table 1; Fig. 3), in support of P1$_{HF}$b. Anxiety, however, had no effect on task-solving, in

391 support of P1$_{HF}$a (model 1: $\beta \pm$ s.e. = -0.28 $\pm$ 0.72, z = -0.40, p = 0.69).

392 We then assessed individual variation in the probability of observing the

393 demonstrators (Q2). We found no evidence that shyer or more anxious baboons were

394 more likely to watch an individual manipulate the hidden food task, contrary to P2$_{HF}$b and

395 a respectively (Table 1, m2$_{HF}$).

396   Finally, we assessed the evidence for social learning by analysing the intensity of

397   the response to the stimulus in relation to the number of prior total, social or personal

398   presentations. We found no evidence for an interaction between any of the presentation

399   numbers and either personality trait; in all cases the minimal model was the same

400   (model 3_{HF}). Thus, while bolder animals continued to be better at solving the hidden food

401   task (as observed in m1), we found no evidence that either shyer or more anxious

402   individuals showed improved responses with more prior experience, contrary to

403   predictions 3_{HF}b and 3_{HF}a respectively.

DISCUSSION

405   Our results strongly suggest that personality predicts social learning propensity in wild

406   baboons. In a field experiment in which individuals had the opportunity to learn about a

407   novel food from an experienced demonstrator, both bolder and more anxious individuals

408   increased their handling time of the novel food if they had had an opportunity for social

409   learning. Below we address those predictions that were not supported before focussing

410   on three important issues emerging from our study that have implications not only for

411   understanding social learning in the wild (van de Waal & Bshary 2011), but also for

412   individual differences in cognitive abilities (Thornton & Lukas 2012) and the formation of

413   traditions and culture in animal groups (Whiten 2000).

414   Contrary to expectation, we found no effect of boldness on time spent watching a

415   demonstrator. These results differ from those of Kurvers *et al*. (2010) which suggested

416   that shy individuals used social information more than bold individuals, but this

417   discrepancy may be explained by differences between studies in the familiarity of the

418   study subjects with the experimental challenge (see below). However, our finding that

419   bold individuals were more likely to solve the hidden food task confirms previous

420   research showing an increase in task-solving success when individuals are less

421   neophobic (Seferta et al. 2001; Webster & Lefebvre 2001). Our failure to find a

422   comparable improvement in task solving after watching a demonstrator for the hidden

423   food experiment is unexpected, but may reflect the fact that the task contained a highly

424   preferred food, and individuals may be limited by their rank in their access to the task.

425   That is, individuals may have acquired the social information necessary to solve the

426   task, but were unable or unwilling to access the task due to their lower rank. Though we

427   do not have the resolution of data to test this explicitly, we discuss this possibility further

428   below.

429   Three important issues emerged from our study. First, an individual's ability or

430   interest in collecting social information does not necessarily correlate with its ability or

431   interest in using social information. This observation arises from our findings that bolder

432   and more anxious individuals showed a greater improvement than shyer and calmer

433   individuals in their response to a novel food after watching a demonstrator, despite the

434   fact that there was no effect of boldness on the time spent watching a demonstrator, and

435   calmer individuals were more attentive than more anxious individuals. Three possible

436   explanations could be considered for these results: that (i) a mechanism other than

437   watching a demonstrator is responsible for social learning in baboons, (ii) baboons need

438   little time to acquire sufficient social information to subsequently change their behaviour,

439   or (iii) as mentioned above, the acquisition of social information is not always correlated

440   with its use. The first explanation is unlikely, since the task is a visual one and baboons

441 are strongly visual animals. It therefore seems probable that the second or third

442 explanations are most likely, and these need not be mutually exclusive.

443   Social learning mechanisms such as stimulus enhancement, where the behaviour

444 or presence of a demonstrator attracts the attention of a naïve individual (Brown &

445 Laland 2003), may quickly result in a behavioural change in naïve individuals without the

446 detailed and lengthy observation assumed necessary in processes such as imitation. As

447 such, the baboons could learn that an object is worth investigating in more detail in the

448 future in the time it takes to identify the object that a demonstrator is manipulating, as

449 may be the case in our study. Further, it may be that bold individuals show greater social

450 learning not necessarily because they are 'better' at collecting or processing social

451 information, but because they are generally more willing to interact with a novel task.

452 This, coupled with the rapid social learning through stimulus enhancement we posit to

453 be possible in this study, may result in bolder individuals showing greater social learning.

454 In support of this interpretation, in the novel food control trials, bold baboons decreased

455 their handling time of the novel food but this handling time still exceeded that of shy

456 individuals on their first presentations. This may also explain why our findings differ to

457 those of Kurvers *et al.* (2010), as the authors of that study habituated the study subjects

458 to the experimental arena prior to testing. In both cases (our study, and Kurvers *et al.*'s

459 study), individual variation in response to novel tasks is related to personality, but not

460 necessarily an individual's ability to collect and process social information. The fact that

461 some individuals may be too shy or anxious to interact with a novel task, despite having

462 the information or ability to do so, may have wide implications. For example, an

463 individual's cognitive performance may be systematically underestimated if it is unwilling,

464 but still able, to solve a task, which may hinder studies interested in the fitness

465 advantages and evolution of cognitive performance. Future studies could assess this

466 effect experimentally by testing study animals of different boldness with varying degrees

467 of habituation to a test apparatus. Our interpretation would lead to the prediction that

468 bolder individuals should outperform shyer individuals under low habituation regimes,

469 but that performance may be more equal when the task is no longer threatening.

470   Second, the identity of demonstrators may be important. In both our experiments,

471 many of our initial demonstrators were bold. In the novel food experiment, this was

472 inevitable, as our definition of boldness precluded individuals that did not eat the novel

473 food. However, it also transpired that those individuals that solved the hidden food task

474 were more likely to be bold, though we note that the boldness and anxiety of the

475 demonstrators was, overall, not particularly different to the boldness and anxiety of the

476 population (see summary statistics reported in the methods Methods for these groups).

477 As these experiments were not designed to address this particular question and thus the

478 sample of demonstrators is limited, we have not analysed these data here. However,

479 previous research has suggested that the characteristics of a demonstrator may affect

480 whether an observer gathers or uses social information from them or not (termed

481 'directed social learning': Coussi-Korbel & Fragaszy 1995; Laland 2004). For instance,

482 wild vervet monkeys (*Chlorocebus aethiops*) are more likely to attend to the social

483 information provided by the philopatric sex (females) (van de Waal et al. 2010). It

484 remains to be established whether the personality of the demonstrator might be

485 important, but it seems possible that it may play a role. For example, slow explorers are

486 more thorough at exploring novel environments (Careau et al. 2009) and may therefore

487 be better informed about the location of resources. Although it is difficult to anticipate

488 how demonstrator boldness might affect audience attentiveness and social learning in

489 baboons, we can consider its correlates. Specifically, while sex is unrelated to boldness

490 in our population, there is an effect of age: juvenile baboons are bolder than adults

491 (unpublished data). Since this led to a strong representation of juvenile animals among

492 the demonstrators (10 juvenile, 4 adult demonstrators), and adults may attend less

493 closely to juveniles (only vertical transmission of social information has been

494 documented in this species: (Camberfort 1981)), it is possible that the adults in our

495 sample might have shown lower levels of attentiveness and social learning than would

496 have been observed with adult-only demonstrators.

497   Finally, an important aspect of our study that we did not anticipate was the

498 difficulty of testing certain individuals in the presence of a demonstrator. While we

499 endeavoured to provide all individuals with the opportunity to watch a demonstrator for

500 both tasks, it was not possible to find a situation in which certain individuals were

501 foraging in sufficiently close proximity to potential demonstrators for this to occur (Sih &

502 Del Giudice 2012). In great tits (*Parus major*), slow exploring birds showed higher

503 attraction to unknown conspecifics than fast explorers (Carere et al. 2001) suggesting

504 that personality may influence sociability and thus opportunities to learn from others in

505 some species. Further, in guppies (*Poecilia reticulata*), an individual's social network is

506 related to its personality: individuals associated assortatively according to behavioural

507 type, and shy fish had more and stronger network connections than bold fish (Croft et al.

508 2009). An individual's social network is thus likely to affect which individuals can supply

509 social information, and thus the flow of information through a group (Voelkl & Noë 2008;

510 Sih et al. 2009; Claidiére et al. 2013). If similar personality-related patterning among the

511 social networks of baboons occurs, it may be impossible for some individuals to obtain

512 social information about a novel food or task as they may have only weak associations

513 with demonstrators. Together with the preceding points, it thus appears possible that

514 personality could affect social learning, and hence the formation of culture in animal

515 groups, through a combination of mechanisms. These include not only the differential

516 collection of social information, as we have shown in this study, but also the differential

517 application of social information, directed social learning, and assortative social bonds.

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Personality predicts the propensity for social learning in a wild primate Factors affecting task solving propensity (Q1), the attention given to a demonstrator (Q2), and social learning (Q3) in wild chacma baboons for two experiments (novel foo

Significance of fixed terms was determined by t- and p-values for GLMMs (<0.05) and z-values for LMEs ($\geq$2.00), and random terms by a log-likelihood ratio test. The reference categories are: adult (for Age class), female (for Sex), test (for Test) and control (for Condition).

Experiment	Question	Response	N_{obs}, N_{ind}, ($N_{demonstrators}$)	Deviance	Term	β	S.E/S.D.	*test statistic*[a]	*p*
Novel food	2	Time spent watching demonstrator (s)	54, 36, (14)	180.5	Intercept	2.59	0.52	5.02	
					Anxiety	-2.79	0.51	-2.01	
					Age class: juvenile	1.75	0.40	4.36	
					Rank	-1.74	0.72	-2.43	
					Random: Baboon	0.00	0.00	0.00	1.00
					Random: Troop	1.68	0.51	0.75	0.39
					Random: Demonstrator	0.00	0.00	0.06	0.81
	3 (boldness)	Time handling food (s)	90, 32	1206.00	Intercept	1.00	0.47	2.11	< 0.03
					Test: re-test	-0.78	0.08	-9.57	< 0.001
					Boldness	-1.91	0.51	-3.77	< 0.001
					Condition: treatment	0.17	0.16	-1.09	0.28
					Test: re-test * Boldness	-0.14	0.05	-2.69	0.007
					Test: re-test * Condition: treatment	0.84	0.10	8.58	< 0.001
					Boldness * Condition: treatment	-0.20	0.25	-0.79	0.43
					Test: re-test * Boldness * Condition: treatment	-0.68	0.08	-8.67	< 0.001
					Random: Baboon	5.99	2.45	3090.90	< 0.001
					Random: Troop	0.00	0.00	0.00	1.00

						Estimate	SE		p
	3 (anxiety)	Time handling food (s)	90, 32	1301.00	Intercept	1.00	0.87	1.15	0.25
					Test: re-test	-0.88	0.09	-9.98	< 0.001
					Anxiety	16.11	5.89	2.73	0.006
					Condition: treatment	-0.03	0.08	-0.31	0.75
					Age class: juvenile	3.61	1.05	3.43	< 0.001
					Test: re-test * Anxiety	-11.95	3.02	-3.96	< 0.001
					Test: re-test * Condition: treatment	1.75	0.10	16.70	< 0.001
					Anxiety * Condition: treatment	-8.03	3.73	-2.15	0.03
					Test: re-test * Anxiety * Condition: treatment	7.66	3.04	2.52	0.01
					Random: Baboon	7.49	0.87	3430.00	< 0.001
					Random: Troop	0.34	0.58	0.10	0.75
Hidden food	1	Probability of eating food (0/1)	80, 33	64.09	Intercept	-2.40	1.38	-0.74	0.08
					Age class: juvenile	2.57	1.02	2.52	0.01
					Boldness	-0.85	0.32	-2.63	0.008
					Random: Baboon	0.00	0.00	0.00	1.00
					Random: Troop	2.03	1.43	3.85	0.05
	2	Watch (0/1)	163, 41, (18)	180.5	Intercept	-0.69	0.37	-1.85	0.06
					Presentation number	0.21	0.08	2.82	0.005
					Rank	-2.01	0.68	-2.97	0.003

				difference				
				Random: Baboon	1.04	1.02	5.50	0.02
				Random: Troop	0.00	0.00	0.00	1.00
				Random: Demonstrator	0.06	0.24	0.06	0.80
3	Response (levels 0-4)	80, 33	208.40	Intercept	1.85	0.69	2.70	
				Boldness	-0.29	0.10	-2.81	
				Age class: juvenile	1.34	0.22	6.04	
				Random: Baboon	0.06	0.25	7.29	0.007
				Random: Troop	0.85	0.92	0.00	1.00

The questions tested, experiments conducted, data and models used to test the predictions, and whether we found support for our predictions or not (outlined briefly here).

Predictions highlighted in bold show that we found support for these in our models. Note that this may indicate that there was not a significant relationship. Predictions for which we did not find support but found the opposite trend are in bold and italicized. 'N/A' is listed for both boldness and anxiety effects in the novel food experiment under Question 1. This is because, in the case of boldness, this experiment was also our assay for boldness, and in the case of anxiety, previous work has demonstrated that anxiety is unrelated to boldness (and hence performance in the novel food experiment) in this species (Carter et al. 2012c).

| | | | | | Prediction and whether it was supported | |
| | | | | |---|---|
Question	Test	Experiment	Data analysed	Model	Anxiety	Boldness
1	Propensity to solve the task	Novel food	N/A		N/A	N/A
		Hidden food	Whether the baboon ate food from the task or not (0/1)	m1	**P1a: calm-anxious animals unlikely to differ** **YES**	**P1b: bold animals are likely to solve** **YES**
2	Watching a demonstrator	Novel food	Time (s) spent watching a demonstrator	m2nf	*P2a: anxious animals will be more attentive* *No, calmer individuals were more attentive*	P2b: shy animals will be more attentive NO (neither)
		Hidden food	Whether the baboon watched a demonstrator or not (0/1)	m2hf	P2a: anxious animals will be more attentive No (neither)	P2b: shy animals will be more attentive NO (neither)
3	Change in task-solving behaviour after watching a demonstrator	Novel food	Time spent handling the novel food (s) after treatment/control	m3nf	**P3a: anxious animals will show greater improvement** **YES**	*P3b: shy animals will show greater improvement* *NO, bold individuals improved.*
		Hidden food	Level of interaction with the hidden food container (levels 0-4)	Model set 3hf	P3a: anxious animals will show greater improvement NO (neither)	P3b: shy animals will show greater improvement NO (neither)

Figure 1

Personality predicts the propensity for social learning in a wild primate The times that individuals spent watching a demonstrator manipulate a novel food

The average time anxious and calm juvenile and adult baboons spent watching a demonstrator (s) interact with a novel food (n = 54 trials). Plotted are the means and standard errors for the raw data; note that though the data are presented as categories (split at the mean of the trait for the population) they were analysed as continuous variables.
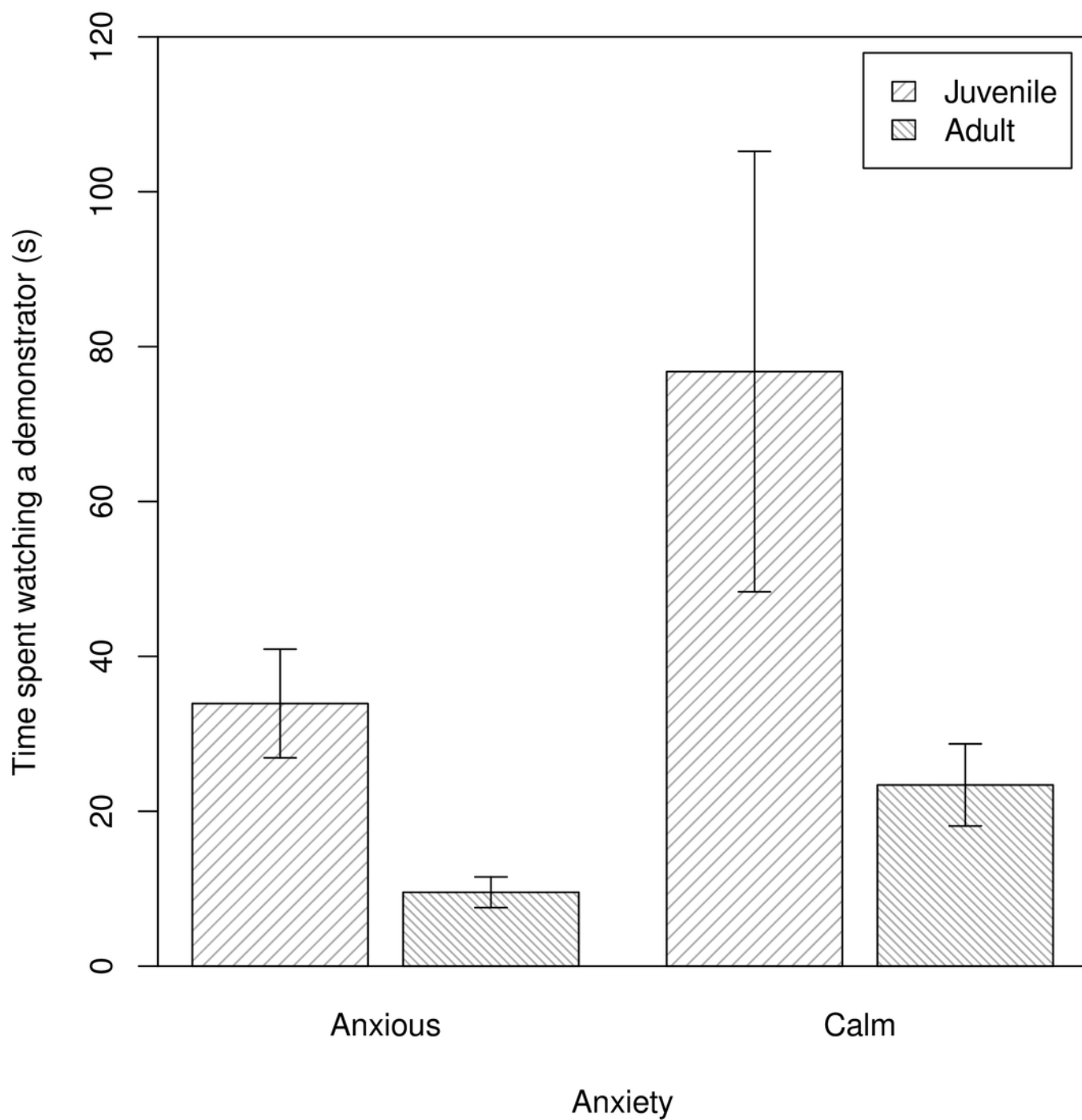
Figure 2

Personality predicts the propensity for social learning in a wild primate Individual responses to a novel food after an opportunity for social learning

The average time that bold and shy (a, b) and anxious and calm (c, d) baboons handled the novel food on their first interaction with it (pres. 1) and on their second interaction with it (pres. 2) either without being exposed to a demonstrator (a, c) or after being exposed to a demonstrator (b, d) (n = 45 trials). Plotted are the means and standard errors for the raw data; note that though the data are presented as categories (split at the mean of the trait for the population) they were analysed as continuous variables.
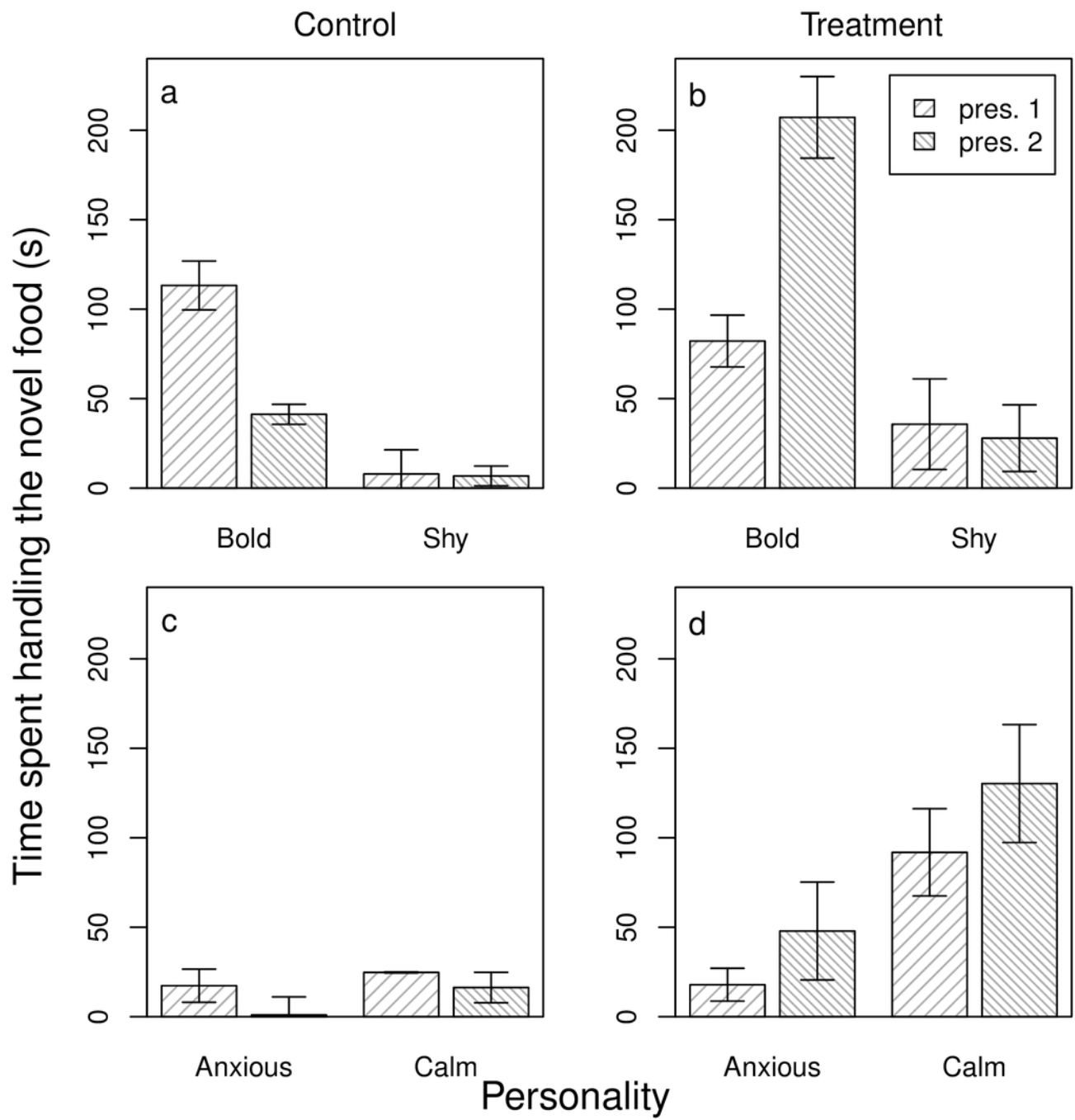
Figure 3

Personality predicts the propensity for social learning in a wild primate The proportions of individuals that solved the task

Differences in proportions of adult and juvenile bold and shy baboons that 'solved' the hidden food task by obtaining and eating food from the box (n = 80). Plotted are the means and standard errors for the raw data; note that though the data are presented as categories (split at the mean of the trait for the population) they were analysed as continuous variables.