

1

2

3 *May 2018*

Ethology

4

5 **Innovation as part of a wider behavioural syndrome in the guppy:**
6 **the effect of sex and body size**

7 Monica Anderson Berdal^{1,2*}, Gunilla Rosenqvist¹, & Jonathan Wright¹

8 ¹Center for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science
9 and Technology (NTNU), Norway

10 ²Department of Biological Sciences, North Dakota State University, USA

11

12 **Running headline:** Personality and Innovation in Guppies

13 **Acknowledgements**

14 We thank Anne-Lise Haugdahl Humstad and Henriette Vaageland for helping out with the
15 experimental set-up and data collection. We would also like to thank Øystein Hjorthol
16 Opedal and Endre Grüner Ofstad for their help with the statistical analysis, and Ned
17 Dochtermann and Niels Dingemanse for helpful comments on an earlier version of this
18 work. This work was partly supported by the Research Council of Norway through its
19 Centres of Excellence funding scheme, project number 223257.

20 **Abstract**

21 Recent work on animal personalities has shown that individuals within populations often
22 differ consistently in various types of behaviour, and that many of these behaviours correlate
23 among individuals to form behavioural syndromes. Individuals of certain species have also
24 been shown to differ in their rate of behavioural innovation in arriving at novel solutions to
25 new and existing problems (e.g. mazes, novel foods). Here we investigate whether behaviours
26 traditionally studied in personality research are correlated with individual rates of innovation
27 as part of a wider behavioural syndrome. Guppies (*Poecilia reticulata*) of both sexes from
28 three different wild population sources were assessed: (i) exploration of an open area; (ii)
29 speed through a three-dimensional maze; (iii) investigation of a novel object; and (iv)
30 attraction to a novel food. The covariance structure (syndrome structure) was examined using
31 structural equation modelling. The best model separated behaviours relating to activity in all
32 contexts from rates of exploration/investigation and innovation. Innovative behaviour
33 (utilizing new food and moving through a novel area) in these fish therefore forms part of the
34 same syndrome as the traditional shy-bold continuum (exploration of an open area and
35 investigation of a novel object) found in many animal personality studies. There were no clear
36 differences in innovation or syndrome structure between the sexes, or between the three
37 different populations. However, body size was implicated as part of the behavioural
38 syndrome structure, and because body size is highly correlated with age in guppies this
39 suggests that individual behavioural differences in personality/innovation in guppies may
40 largely be driven by developmental state.

41 **Keywords:** animal personality, behavioural syndromes, behavioural flexibility, habituation,
42 maze exploration, developmental state

43 **Introduction**

44 Animals are often faced with novel environments and contexts and must respond to these
45 challenges with new or modified behavioural solutions to cope with the new conditions
46 (Reader and Laland 2003b). This is known as innovation and has been defined by Ramsey et
47 al. (2007) as “...the process that generates in an individual a novel learned behaviour that is
48 not simply a consequence of social learning or environmental induction”. This separates the
49 origin of a new behaviour from the social spread of the behaviour through a population, i.e.
50 via cultural transmission (Hoppitt and Laland 2013). Innovation is widespread throughout
51 many taxa (Reader and Laland 2003b), but it is not clear whether and why individuals differ
52 in their propensity to innovate. In addition, what behaviours are considered as innovative
53 seems to vary across different areas of study. Several studies of innovation in primates and
54 birds often includes tasks that demands a higher level of cognition, such as tool use and
55 solving man-made physical puzzles (Goodall 1964, Rutz and St Clair 2012). However, ‘simpler’
56 tasks, such as learning to utilize a new food source (without the use of tools), is also
57 considered an innovative behaviour. This includes milk bottle top opening by blue tits,
58 *Cyanistes caeruleus*, (Fisher and Hinde 1949), and ring-tailed lemurs (*Lemur catta*) learning
59 to reach water by dipping their tails in a lake and then licking the water off their tail, thereby
60 avoiding predators on the ground and in the water (Hosey et al. 1997). In this study, we
61 consider any new or modified behaviour used in a novel context as innovative behaviours.

62 Research on animal personalities has shown that individuals within the same population show
63 consistent differences in behaviour, and that these differences are maintained across
64 environmental contexts (Réale et al. 2010a, Carere and Maestripietri 2013). Individual
65 differences in a range of different behaviours have also been shown to covary among

66 individuals in what are known as 'behavioural syndromes' (Réale et al. 2010a). For example,
67 bolder individuals tend to be more aggressive than shy individuals, and more exploratory
68 individuals are often more active than less exploratory individuals (Riechert and Hedrick 1993,
69 Verbeek et al. 1996). If individuals consistently differ in their rate of innovation, innovative
70 behaviours should also be considered as a personality trait (in the broad sense, Réale et al.
71 2010a). This has been shown in both great tits (*Parus major*) and blue tits (*Cyanistes*
72 *caeruleus*), where individuals differed consistently in their ability to solved different artificial
73 foraging tasks (Morand-Ferron et al. 2011). Innovation could also possibly be linked to
74 individual differences in other behaviours traditionally studied in personality research, such
75 as boldness and neophilia (Reader and Laland 2003b). A link between behavioural type and
76 cognitive type has already been discussed by Sih and Del Giudice (2012), specifically regarding
77 the idea of a speed-accuracy trade-off in foraging. In addition, innovative behaviours involve
78 novel contexts not before experienced by an individual, and so innovation might have risks
79 and/or costs associated with it. This could include increased predation risk, the risk of
80 consuming hazardous foods (Reader and Laland 2003b) and reduced efficiency when utilizing
81 familiar resources. Therefore, bold or more risk-taking individuals might be more innovative
82 than shy or less risk-taking individuals, because they approach and investigate unfamiliar
83 resources at a higher rate (Reader and Laland 2003b, Sih and Del Giudice 2012, Griffin et al.
84 2015). Such individuals will experience more novel situations in which new and flexible
85 behaviour might be useful and carry some adaptive advantage. However, slower, more
86 thoroughly exploring individuals tend to gather more information about their surroundings,
87 and to show greater flexibility in their behaviour (Guillette et al. 2011, Mathot et al. 2012).
88 Thus, whilst bold individuals might be more likely to be the innovators, it is the shy individuals
89 that seem best suited to the task of social learning needed for the cultural transmission of

90 successful innovative behaviours (Reader and Laland 2003b). Although there have been
91 several studies investigating when an individual should copy others (Templeton and Giraldeau
92 1995), and when to rely on private vs. public information (van Bergen et al. 2004), few studies
93 have investigated whether some individuals are more prone to solve problems while other
94 individuals are more prone to copy behaviours, leading to the spread of the new behaviour
95 through the population. In addition, few studies have investigated if there is a link between
96 traditional animal personalities and information use (but see Harcourt et al. 2010). However,
97 there have been studies showing a link between boldness and flexibility of behaviours.
98 Guillette et al. (2009) found that bolder and more exploratory black-capped chickadees
99 (*Poecile atricapillus*) that enter a novel environment faster were also quicker to learn in an
100 acoustic discrimination task, here used as a measure of cognition, as compared with shyer
101 individuals. However, fast-exploring birds have also been shown to be less flexible in a
102 reversal test, where they learned the change between cue and reward slower compared with
103 slow-exploring individual (Guillette et al. 2011). Similarly, a study of Indian mynas
104 (*Acridotheres tristis*) found that more innovative individuals – here measured as time to
105 complete an extractive foraging task – were slower to change their behaviour when there was
106 a change in the significance of the food cue (Griffin et al. 2013). This is consistent with other
107 studies showing that bold proactive individuals are less flexible than shy reactive individuals
108 (Benus et al. 1988, Verbeek et al. 1994). In addition, dominant individuals might be more
109 aggressive than subordinates, and as such they could afford to be less innovative and thus
110 avoid any inherent risks, and instead use their social access to limited resources to take
111 advantage of the discoveries by low-ranking individuals in something akin to a producer-
112 scrounger game (Katzir 1982, Liker and Barta 2002). However, there have been very few

113 studies explicitly on the link between performance in personality assays and tests of
114 innovation (but see: Matzel et al. 2006, Light et al. 2008).

115 Many studies of animal personality are methodologically quite similar to studies investigating
116 innovation. Boldness is often measured as the time an animal takes to emerge from a refuge
117 or the latency before approaching a novel object (Verbeek et al. 1994, Niemela et al. 2012).
118 Approaching a novel area, object or food is therefore equivalent to tests of neophobia versus
119 neophilia, an important component of innovation (Webster and Lefebvre 2001, Reader and
120 Laland 2003b). In a study by Dingemanse et al. (2007) on three-spined sticklebacks
121 (*Gasterosteus aculeatus*), the response to novel food was classified as an exploratory
122 behaviour, which is very similar to tests in much of the literature concerning innovative
123 behaviour, i.e. the ability to utilize a novel food sources (Reader and Laland 2003b).
124 Conversely, many studies on innovation may represent equally good studies of animal
125 personality behaviours. For example, in a study by (Laland and Reader 1999a), innovation was
126 measured as the latency before guppies (*Poecilia reticulata*) went through a maze, where on
127 the other side they were presented with a novel food. Individuals that were able to figure out
128 the maze fastest and ate the novel food first were classified as more innovative than the
129 slower individuals. However, they could just as easily have been classified as bolder or more
130 exploratory individuals, or just more active. Thus, measures of innovation appear to be
131 confounded or to covary with several aspects of other behaviours currently studied in the
132 context of animal personality. Research is clearly needed that investigates the role of such
133 innovative behaviours in the context of animal personality assays, therefore making it
134 possible to examine the structure of possibly wider behavioural syndromes of individual
135 boldness versus shyness.

136 In this study, we investigate behavioural syndrome structures in guppies, specifically to see
137 whether innovative behaviours are part of a wider behavioural syndrome involving aspects of
138 the bold-shy personality continuum. We only investigated innovative behaviours as defined
139 above, however, and not the social transmission of the behaviour through a population. The
140 guppy is an ideal study organism in this regard, because innovation rate has already been
141 well-studied (Laland and Reader 1999a, b, Reader and Laland 2000), which makes it easier to
142 link innovation to any wider bold-shy behavioural syndrome of the type detected in guppies
143 (Smith and Blumstein 2010), and other small fish species in aquarium studies (e.g.
144 Dingemanse et al. 2007). Individuals with higher activity levels were predicted to explore
145 faster and to be more innovative in novel tasks than less active individuals. Irrespective of
146 activity levels, we also predict that bolder individuals showing more neophilic behaviours in
147 novel environments and situations will tend to show higher rates of innovation. We also
148 tested whether sex, body size and population of origin had an effect on the expression of
149 these different behaviours. In a study by Laland and Reader (1999b), it was shown that female
150 guppies were significantly more innovative than males. The authors suggested that this might
151 be due to skewed parental investment, which is exclusively female in guppies, and this is
152 supported by evidence that size has a greater effect on fecundity in females than in males
153 (Laland and Van Bergen 2003). Females in our study were therefore expected to be more
154 exploratory and innovative than the males. Laland and Reader (1999a) also showed that state-
155 dependence can affect innovative behaviour in guppies, because individuals with higher
156 hunger levels were more innovative than individuals with a lower hunger level. In guppies,
157 like most fish with indeterminate growth, body size correlates significantly with age, and
158 during scramble competition younger, smaller individuals are expected to be less competitive.
159 Indeed, latency before completion of a novel foraging task has been shown to be shorter for

160 younger compared to older male guppies (Laland and Reader 1999b). Smaller, younger
161 individuals should therefore be more exploratory and innovative in general compared to
162 larger individuals, since their lower competitive ability should increase their hunger and
163 motivation for searching for new food sources (Laland and Reader 1999a).

164 **Methods**

165 **Study species**

166 Guppies are small freshwater fish found in rivers and lakes on tropical islands in the general
167 area of the Caribbean. The guppies used in this experiment were laboratory-reared at NTNU
168 Norway, but originated from wild stocks from three rivers in Trinidad: Paria (10°47'N,
169 61°15'W); Campo (10°41'N, 61°13'W); and Quare (10°39'N, 61°12'W). Approximately 500
170 individuals were collected from each river, and the three populations have been kept
171 separated in six large aquaria (two per population, 400-500 l), approved by the Norwegian
172 Animal Research Authority (licence number 7). The Paria population was collected in 1991,
173 while the Campo and Quare populations were collected in 1998. Predation pressure was low
174 in both the Paria and Campo rivers, but high in the Quare river (Endler and Houde 1995,
175 Pélabon et al. 2013). The lab populations have not been exposed to predators during the last
176 20 years, and any selection due to the regular captive environment is expected to be the same
177 for all three populations. Among-population differences are therefore considered to have a
178 historical genetic basis. The guppies were maintained on a 09:00-21:00 light-dark cycle at 25°C
179 and were fed daily with dry flakes and freshly hatched brine shrimps (*Artemia nauplii*).

180 **Experimental setup**

181 In this study, each individual guppy was run through four behavioural tests: (i) exploration of
182 a novel arena, (ii) three-dimensional maze solving, and introduction to both (iii) a novel object
183 and (iv) a novel food. Activity level was measured in each test. Most innovative behaviours in
184 animals involve consummation of new food items, or inventing a new way to better process
185 already known food items (Reader and Laland 2003b). It therefore seemed appropriate to
186 include a novel food (iv) as one of our innovation tests. In addition, in (ii) we wanted to mimic

187 the innovative assays involving a maze carried out by Laland and Reader (1999a), as these
188 behaviours have already shown clear differences between the sexes. Exploration, activity and
189 boldness to novel arenas and objects are behaviours traditionally used in the animal
190 personality literature (e.g. Dingemanse et al. 2007), and (i) and (iii) were therefore chosen as
191 such standard tests that would allow us to link them with any individual differences in
192 innovative behaviours. The dataset contained 19 males and 19 females from each of the three
193 populations, adding up to a total of 114 individuals.

194 One male and one female guppy were randomly selected from each of the three populations
195 and placed together in small isolation tanks (22x14.5x14 cm) in the same room as the
196 experiment was conducted – one for each population – where they were food deprived for
197 seven days prior to the experiment. Laland and Reader (1999b) showed that hunger level
198 affected the innovation rate of male guppies, where hungrier individuals were more
199 innovative (i.e. moved faster through a maze apparatus). By properly food depriving the
200 guppies, hunger level was effectively standardized across all individuals, controlling out any
201 differences in behaviour caused by contrasting hunger levels among individuals. We also
202 hoped that this would increase motivation for approaching and eating the novel food, as well
203 as activity in general by increasing the need to search for food. There were no deaths during
204 or after the experiment, indicating that the food deprivation did not harm the guppies during
205 the course of the experiment. Guppies of different body sizes were selected to ensure enough
206 variation to estimate any effect of body size on the different behaviours. Since there is a
207 strong correlation between body size and age in guppies (Reznick et al. 1996), we have
208 included a wide age range in our subjects and some of the guppies included here might even
209 have been considered juveniles.

210 Male and female guppies from each population were randomly assigned to one of six
211 experimental tanks (see Fig.1), where individuals were run separately through each of the
212 four behavioural assays. Above each tank there was a mounted camera that recorded the
213 movements of the fish. The walls of the tanks were covered in black plastic to keep individuals
214 visually isolated from each other. Individuals were first placed in acclimation cages at one end
215 of the tank where they were allowed ten minutes to settle prior to the start of the trial (Fig.
216 1). After the acclimation period, the fish was gently encouraged to leave the cage, and the
217 door was closed behind them to prevent re-entry. This was done to ensure that all guppies
218 had the same amount of time to explore the tank, and thus avoid any issues arising from
219 individual differences in acclimation time versus exploration time among fish. The guppies
220 were (i) given 30 minutes to explore the open area before the maze door was raised, and they
221 were gently encouraged to enter the maze using a small landing net drawn slowly through
222 the water. The fish did not seem to be affected by this procedure, as their swimming speed
223 did not increase markedly at the time or immediately following. Again, this procedure was
224 carried out to avoid any individually determined differences in the time available to different
225 fish to explore the maze. The maze door was then closed, and the guppies had (ii) 30 minutes
226 to get to the end of the 3-dimensional maze. There was no food reward or hiding place at the
227 end of the maze, hence the maze only represented innovation in terms of moving in a novel
228 way through a novel environmental set-up (Laland and Reader 1999a). After the 30 minutes
229 in the maze, the guppies were removed from the maze with a landing net and transferred
230 back into the main exploration area where they were (iii) presented with a novel object (an
231 aquarium decoration), which had been placed in the middle of the exploration area; 10 cm
232 from the maze wall (see Fig.1). After 15 minutes the novel object was removed, and the
233 guppies were presented with (iv) salmon food in a glass bowl, which was a novel food for

234 these populations. The glass bowl had been placed in the tank before the start of the trial and
235 was therefore part of the novel environmental in (i), and thus should not have represented a
236 novel object in itself during (iv). The novel food was placed in the middle of the tank, 10 cm
237 from where the novel object had been, as indicated in Fig.1.

238 We measured body size after the guppies had completed all four behavioural trials. The
239 guppies were sedated in ice water at 8°C and photographed individually with a 1cm ruler next
240 to them, before being put back into their isolation tanks where they recovered immediately.
241 Body length was measured on the digitized image using tpsDIG, where landmarks were placed
242 on the tip of the nose and the back of the tail (tail fin not included) and the distance assessed
243 relative to landmarks placed on the ruler.

244 37 guppies ate the salmon food, meaning that it was perceived as a possible food source. The
245 (i) exploration of the new area and (iii) of the novel object can here be seen as traditional
246 personality tests of exploration and boldness respectively (Sih et al. 2004), while (ii) the maze
247 and (iv) the novel food represents innovative behaviours (Laland and Reader 1999a).
248 Alternatively, the (i) exploration test and (ii) the maze can be seen as spatial tests, while
249 approach of the (iii) novel object and (iv) novel food can be seen as non-spatial tests. Guppies
250 from different predatory regimes have been shown to differ in their exploratory strategies
251 (Burns and Rodd 2008), with guppies living in high predator environments using more time to
252 decide which chambers to explore in a maze, while guppies in low predatory environment
253 made faster but less accurate decisions. Behaviours used in exploring an open field versus a
254 maze might therefore be more strongly correlated with each other than with behaviours used
255 in the approach of a novel object or a novel food item.

256 Video analysis

257 All experiments were recorded using Sony high-resolution colour CCD cameras (model
258 NC1381W) mounted above each of the six experimental tanks. Cameras were connected to
259 H-264 Portable Mini Video Surveillance Recorders from LUPUS TEC (Recording resolution and
260 frame rate: 704x576@25 FPS, 352x280@25 FPS (PAL)) on a 16 MbScanDisk memory card.

261 Data recording started within 30 seconds of fish release from the acclimation cage, at the
262 point when the surface water was sufficiently still to allow observations. To quantify the
263 recorded data of (i) the exploration of a new area and (ii) the maze, twenty-four squares were
264 drawn on a transparent sheet and placed over the monitor screen for both trials (see Fig.S1).

265 Most individuals explored all 24 squares, making results on the number of new squares
266 explored highly skewed to the maximum possible number. However, because not all
267 individuals completed the assays, time to completion would also not fully represent all of the
268 individual variation measured in these assays, because it would not differentiate between
269 individuals that did and did not explore all of the squares. This problem of partial completion
270 of the task was also the case for the other three assays, and the count and timing
271 measurements for the different assays were therefore converted into rates (squares per time)
272 prior to statistical analysis in order to capture all aspects of individual variation in behaviour.

273 Exploration was quantified as the time an individual used to explore the total number of new
274 squares divided by the total number of new squares explored. This created a rate
275 representing the time used to enter/explore each square, where a low value indicates fast
276 exploration. Speed through the maze was assessed by measuring the maximum distance
277 reached by counting number of steps (12 steps in total with 2 squares per step; Fig.S1) each
278 guppy moved through the maze. A ratio with time to reach the maximum point in the maze

279 divided by maximum point (step) reached was created to represent a rate of movement
280 through the maze. Investigation of both the novel object and the novel food was quantified
281 by how close the guppies got to the item, and the time taken to reach this distance. This was
282 done by drawing 5 concentric circles 1 cm apart on a new transparent sheet placed on the
283 monitor around the novel object and novel food (Fig.S1). If the guppies did not enter any of
284 the circles, they were given a score of one, while if they crossed the first circle they were
285 scored with a value of two, and so on to the innermost circle where they were scored a value
286 of six. Again, a ratio with time to reach minimum distance divided by minimum distance reach
287 was created to represent the rate of approach towards the novel object and the novel food.
288 Activity was measured in all four trials (i-iv) as the total number of squares visited in the first,
289 middle and last 5 minutes of each trial. In the novel object trial it was measured for the first,
290 middle and last 3 minutes, and the data were scaled up to equivalent values for 5 minutes for
291 comparison in the other activity measures. Also, the smaller square sizes in the maze (see
292 Fig.S1) required further correction for activity during the maze trial to allow comparison with
293 spatial activity in the main tank area. In this way, the activity level in terms of distance
294 travelled per time period was equalized across the different types of assays.

295 **Statistical analysis**

296 All the statistical analyses were carried out in R, version 3.1.1 (R Development Core Team
297 2015). Activity measures were square-root transformed prior to all statistical analyses to
298 satisfy the assumption of normality.

299 Univariate ANCOVAs were carried out separately on all the eight behavioural variables (i.e.
300 rate of exploration (i), speed through the 3-dimensional maze (ii), approach of both novel
301 object (iii) and novel food (iv), and on activity measures for all four trials) to see if there were

302 any mean differences between the three populations, sexes or any effect of body sizes, or
303 their interactions. Full models with all interactions are presented in all cases. Experimenter
304 identity (which of the two experimenters conducted the experiment), observer identity
305 (which of the two experimenters analysed the videos) and tank identity were added as fixed
306 effects to all the models, but subsequently removed from all results presented as they were
307 shown to have no systematic effects. Mixed effect models were also used to calculate short-
308 term repeatability for activity, as well as to investigate the habituation in activity level across
309 the trials (see Supplementary materials).

310 Bivariate correlations between the eight different behavioural variables (i.e. the four rates
311 and the four activity measures) were calculated using Pearson's correlation coefficients. This
312 correlation matrix was produced for the overall results, and for the two sexes separately (see
313 Tables S5, S7 and S8). To then study the wider structure of these covariances between the
314 different behaviour variables, structural equation modelling (SEM) was carried out using the
315 correlation matrix in the lavaan package in R. Seven hypothesized covariance structures were
316 proposed with different underlying latent variables (Fig.2 and Fig.3).

317 After running the first four hypotheses (Fig.2), we found no difference in ability to explain the
318 data, suggesting that none of these models (H1-H3) really captured the actual patterns of
319 covariance. For example, we know that there was a high across-trial individual repeatability
320 (Table S1) and strong correlations between all the activity variables (Table S5), and that the
321 rate variables seemed correlated (in the non-spatial latent variable in H3). Therefore,
322 exploratory principal component analyses (PCA's) were conducted to investigate possible
323 syndrome structures not yet considered. The PCA's were run without a rotation and with a
324 varimax rotation. A standard PCA adds principal components (PC) where there is most

325 variation left orthogonal to the previous PC, while a varimax rotation rotates all PCs to find
326 the structure that explains the most variation. Both versions of the PCA's were therefore run
327 to better investigate the covariation structure of the data. From these results three new *a*
328 *posteri* hypothetical models were constructed and tested in SEM, as presented in Fig.3.

329 SEM results were ranked according to the Akaike information criterion (AIC), and the best
330 model was used to further explore any structural differences caused by the different sexes
331 and populations, and to see if there was any influence of body size. The best model was run
332 separately for each sex and population, with both free parameters and with parameters
333 constrained to the factor loadings of the opposite sex or the two other populations
334 (Dingemanse et al. 2010). The best model was also run with body size covarying or not with
335 the latent variables to see if it was implicated in the behavioural syndrome. AIC values were
336 again used to see which of these models provided the best fit.

337 **Results**

338 Univariate tests of the variances in each behavioural variable

339 There were very few significant effects of population, sex or body size on the average levels
340 of each of the eight behavioural response variables, especially given the number of tests
341 (Table 1, Fig.4). In the novel food test, males did have a higher activity level than females, and
342 smaller individuals were somewhat more active than larger ones, but the interaction term
343 shows that this effect was largely restricted to females with their larger range of body sizes
344 (Table 1; Fig.S3). Population had no significant effect on any of the measured behaviours.

345 Activity level was highly individually repeatable across the assays in both sexes and all three
346 populations, even with the inclusion of the maze trial (total $R = 0.50$ (0.456-0.537); Table S1).
347 However, this is repeatability across contexts and is only short-term repeatability, which
348 might explain why it is perhaps higher than any true repeatability in activity assessed using
349 the same assay or context over a sufficiently long period of different days or months (Bell et
350 al. 2009).

351 Non-rotated and varimax rotated PCAs

352 PCAs were conducted to further investigate the co-variance structure between the eight
353 behaviour variables. These were done without a rotation (Table 2) and with a varimax rotation
354 (Table 3). In the un-rotated PCA, all the activity variables in addition to rate during the novel
355 food test dropped out in the first principal component (PC), while all the other rates dropped
356 out in PC2. These were the only significant PC's (eigenvalue >1) with eigenvalue 3.33 and 1.38
357 respectively. In the varimax rotated PCA, all the activity measurements dropped out as PC1,

358 while the rates dropped out singularly as PC2-PC5. Only the first PC was significant though,
359 with an eigenvalue of 1.97.

360 SEM of covariance patterns between the behavioural variables

361 To investigate the structure of the behavioural syndrome, seven SEM models were compared
362 (see Methods, Figs. 2 & 3). The H0 hypothesis, where none of the observed variables
363 correlate, had the worst fit (see Table 4), which indicates that there is some sort of syndrome
364 involving these variables. However, there were no meaningful differences between H1 (all
365 behaviours correlate), H2 (personality vs. innovation) and H3 (spatial vs. non-spatial) – see
366 Fig.2, which is why we included three new models based on the results from the PCA (see
367 Methods). Of these, H5 (activity vs. rate) emerged as clearly the best model (Fig.5a), with H4
368 (activity driven) and H6 (only activity) actually having higher AIC scores than H1-3 (Table 4).
369 This suggests that the rates of exploration/innovation were not simply driven by the activity
370 level during the different assays, but that the rate variable in themselves constitute a separate
371 set of covariances captured by the second latent variable, which then covaries with the latent
372 variable containing the activity measures (Fig.5a). The factor loadings for activity in H5 are
373 higher than those for the rate variables, indicating that activity has a stronger effect within
374 the syndrome, although H5 does allow us to conclude that there was a separate lesser
375 covariance within the rate variables as well. The covariance between the latent variables is
376 negative, as expected, since more active individuals were more likely to complete the tasks
377 faster, such as explore the new area or get through the maze (note that lower rates refer to
378 a faster completion of a trial). All loadings for the rate variables were positive, thus bolder
379 and more exploratory individuals were also more innovative. There were no significant

380 differences in the syndrome structure for this model between the sexes or between the three
381 populations (see supplementary materials; Table S6, S7 and S8).

382

383 Including body size as part of the activity syndrome of the best model (H5) gave the best fit
384 (Table 5, Fig.5b). However, because the ΔAIC value is less than 2, it does not have better fit
385 than models where body size is part of the rate latent variable or linked to both latent
386 variables. However, it is better than H5 with only the variance term for body size included in
387 the model ($\Delta AIC > 2$), indicating that body size covaried with the behavioural syndrome
388 structure in the guppies in some way. Body size had a negative factor loading (see Fig.5b),
389 which confirms the effects seen above (Table 1, Fig.S3). Smaller individuals were more active
390 than larger individuals, suggesting that the behavioural syndrome identified here may be
391 condition-dependent in terms of differences in the level of individual indeterminate growth
392 and/or development.

393 **Discussion**

394 In this study, we show that innovative behaviours covary with traditional personality
395 behaviours as part of a wider behavioural syndrome in guppies. Since the best model
396 including activity and rates as separate latent variables (H5) had a better fit than a model with
397 covariances in only activity (H6), it is clear that covariation between the
398 exploration/investigation rates also contributed to the syndrome, and that they were not
399 merely driven by their covariance with levels of activity within the same test (i.e. model H4,
400 see Fig.3). The innovative behaviours (maze solving and exploitation of novel food) and
401 classical behaviours measured in studies of animal personality (exploration and boldness
402 towards a novel object) did not divide into separate latent variables (model H2, see Fig.2). It
403 therefore seems that the classification of the innovation versus classical animal personality
404 behaviours in this way might be an artificial construct arising from the different research
405 traditions (e.g. see the different books: Reader and Laland 2003a, Carere and Maestriperi
406 2013). Approaching a novel object and novel food might not be any different in any
407 fundamental way for the guppies, even though they could be categorized by different groups
408 of researchers as boldness versus innovation behaviours, respectively. Thus, the innovative
409 behaviours we measured (i.e. the maze and novel food trials) might not necessarily have been
410 'innovation' behaviours at all, and might just reflect differences in boldness and shyness in
411 the exploration of novelty. However, these assays were specifically chosen because they are
412 similar to tests that have previously been used to measure innovation for guppies in studies
413 by Laland and Reader (1999a). As previously mentioned, the utilization of a novel food is the
414 most common form of innovative behaviour and has become a focus of many studies in this
415 area (Reader and Laland 2003a). Since the exploration/investigation rate variables here

416 constitute a single latent variable, and all the loadings for the rates were positive, this
417 suggests that this variation could be driven by individual differences in curiosity,
418 neophilia/neophobia, boldness and hence a tendency to innovate. This therefore suggests
419 that individuals that explore faster are also in general more bold and innovative. The negative
420 correlation between the latent variables for activity and rates also indicates that more active
421 individuals finished the different tasks quicker than less active individuals (as mentioned
422 above, a lower rate score refers to fast completion of the tasks), showing that bolder and
423 more innovative individuals were also more active.

424 Population and sex had no effect on the behavioural syndrome structure. These guppies have
425 been in captivity for over 20 years, and they have not been under any specific selection
426 pressure, such as predation or food limitation, during this time. Dingemanse et al. (2007)
427 showed that three-spine sticklebacks living in predator-free environments had weaker
428 syndrome structures compared with sticklebacks that lived in areas with predators. Predation
429 pressure is the main difference between our guppy populations in their original sites, where
430 predator fish were absent in Paria and Campo, whereas Quare experienced high predation
431 risk (Reznick et al. 1996, Pélabon et al. 2013), and behavioural differences between wild guppy
432 populations due to difference in predation pressure have been shown previously (e.g. Burns
433 and Rodd 2008, Harris et al. 2010). The lack of any predator pressure on all the three
434 populations over many generations in captivity might therefore have reduced such
435 behavioural differences among these populations. In other animals, captive strains can exhibit
436 substantial changes in behaviour after only a few generations (Smith and Blumstein 2008,
437 Williams and Hoffman 2009, Larsen et al. 2011, Bolstad et al. 2012). It is therefore problematic

438 to come to any firm conclusions regarding our comparisons between the decedents of these
439 three natural populations.

440 From the univariate analysis, no effect of sex was found on the exploration/investigation rate
441 variables, including anything that could be described as innovation. However, there were
442 some differences between the sexes in activity levels, which interestingly involved larger
443 females being *less* active than males (that showed no effect of body size over their smaller
444 range of body sizes; Fig.S3), and the effect was especially clear in the context of a novel food.
445 Female fitness depends more in longevity since larger, and thus older, females produce more
446 offspring. In addition, females can store sperm and do not necessarily need to seek out males
447 to produce more broods (Reznick and Yang 1993). Males, on the other hand, constantly need
448 to seek out new mates to increase their reproductive outcome as females are the choosy sex,
449 and thus perhaps males have to take more risks (Houde 1988). Female guppies caught in the
450 wild show more cautious behaviour when emerging from a shelter, as compared to males
451 (Harris et al. 2010). In our study, the guppies were not allowed to emerge from the shelter by
452 their own accord, but the lower activity level in females might reflect their more cautious
453 nature in this new environment. In addition, female guppies tend to spend more time in
454 shoals than males (Magurran et al. 1992), and the females in our study might therefore have
455 been more affected by the separation from the rest of the shoal than the males were,
456 resulting in their relatively lower activity levels. Boldness has been shown to correlate with
457 sociality in female guppies (Trompf and Brown 2014), and this might explain our results in
458 terms of differences we find in solitary assays of activity and exploration between the sexes.
459 However, these arguments are hard to reconcile with published work on innovation in this
460 species (Laland and Reader 1999a, b, Laland and Van Bergen 2003). Namely, we found none

461 of the predicted sex differences in innovation found in these previous studies. One reason for
462 the contrasting results here versus accounts in the published literature concerning both
463 population and sex differences in guppy behaviour could be due to the different origins and
464 holding conditions of the fish used in the different labs. It is therefore hard to interpret these
465 sorts of results from different aquarium studies of different populations that have been
466 domesticated for varying periods of time, with or without more or less natural selective
467 forces. This has been shown in another model species in behavioural studies, the zebra finch
468 (*Taeniopygia guttata*), where domesticated populations were found to differ significantly
469 from the wild population in many important aspects of their behaviour, and also from each
470 other (Forstmeier et al. 2007). Clearly, more standardised comparisons of this type are
471 needed, and behavioural studies like this should preferably be carried out on exclusively
472 recently wild-caught populations or captive populations of known selective differences to be
473 able to draw any ecological or evolutionary conclusions.

474 Body size was part of the syndrome structure, where smaller individuals were more active
475 than larger individuals. Among-individual differences in body size might therefore have been
476 driving the whole behavioural syndrome in this study system. The univariate tests also
477 reflected this effect of body size on activity, but mostly in females with their larger range of
478 body sizes. Males were significantly more active than females, and not simply due to their
479 smaller size compared with females. All of these effects were most obvious in the novel food
480 trial, which was the only trial that involved food being present, clearly suggesting a foraging
481 context for these differences. Body size is expected to be an important factor for female
482 fecundity (Reznick and Yang 1993), which might cause smaller females to search more for
483 food and thus be more active than both males and larger females. Because body size was

484 fixed over the timescale of the experiment, and highly correlated with age in guppies (Reznick
485 et al. 1996), activity level might be driven by the relative developmental state of the
486 individual. Smaller fish might need to search more for new sources of food, either due to more
487 energy needed for growth or lower competitive ability around already discovered foods. To
488 show that the behaviours here reflect animal personalities, repeated measures must be taken
489 at different developmental states, in order to show individual behavioural consistency over a
490 longer time period independent of developmental state. In this way, it might also be possible
491 to examine whether differences in individual growth rates affect the syndrome structure we
492 identified here. Individuals with a more rapid growth might be expected to take more risks in
493 the form of exploration and innovation, as part of a 'pace-of-life' syndrome where fast-
494 growing individuals live fast and die young (Réale et al. 2010b).

495 **Conclusions**

496 For our guppy populations, the behavioural syndrome structure was a mixture of personality
497 and innovation behaviours, with no biological basis for this dichotomy in behaviours apart
498 from their respective research traditions. Classifying behaviours as innovation and animal
499 personalities might therefore be arbitrary, and reconciling these two fields might be beneficial
500 for a better understanding of how different aspects of animal behaviour is integrated.

501 The lack of any effects of both sex and population in behaviours, where they have been shown
502 to differ in earlier studies, indicates the difficulty in obtaining consistent results when
503 comparing traits between different domesticated populations. In addition, most of the
504 natural selection pressures that might have been responsible for any patterns in these
505 behaviours might have been weakened or removed entirely from such long-term
506 domesticated populations. It is therefore challenging to find firm answers to predictions
507 based on the ecology of the original wild habitat for such long-term captive populations. We
508 suggest that future experiments of this type should be conducted on wild-caught populations,
509 where populations where the natural selection pressures are known, and then tested in a
510 laboratorial set-up where it is possible to control for any confounding (e.g. social) effects on
511 behavioural variation within and between individuals.

512 Body size appeared to be part of the behavioural syndrome here, and we therefore suggest
513 that differences in individual developmental state might actually drive the whole syndrome
514 documented here. To get a better understanding of how developmental state affects activity
515 levels, repeated behavioural measures would be required for the same individuals in different
516 developmental states. This could also be used to see if there is any particular developmental
517 state when innovative behaviours are more important in creating individual differences,

518 either because more food resources are needed at that point due to rapid growth (or
519 reproduction), or just because smaller, younger individuals have lower competitive abilities
520 and need to innovate and find their own food resources. By following individuals over a longer
521 period of time it might also be possible to record individual differences due to contrasting
522 early life experiences. For instance, how food availability during early development affects
523 mean levels of behaviour and wider syndrome structures, and this could confirm if our results
524 here are part of a wider pace-of-life syndrome (sensu Réale et al. 2010b).

525 In conclusion, behaviours across different areas of study, such as innovation and cognitive
526 problem-solving, should be added to the animal personality research to get a better picture
527 of how behaviours across a wider range of adaptive contexts are integrated. In addition, such
528 studies of wider behavioural syndromes should be carried out on wild populations under
529 natural selection, as well as across different developmental timeframes to get a better
530 understanding of the origins behind the structure of behavioural syndromes.

- 532 Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis.
533 *Animal Behaviour* **77**:771-783.
- 534 Benus, R. F., J. M. Koolhaas, and G. A. Van Oortmerssen. 1988. Aggression and adaptation to the
535 light-dark cycle: Role of intrinsic and extrinsic control. *Physiology & Behavior* **43**:131-137.
- 536 Bolstad, G. H., C. Pelabon, L. K. Larsen, I. A. Fleming, Å. Viken, and G. Rosenqvist. 2012. The effect of
537 purging on sexually selected traits through antagonistic pleiotropy with survival. *Ecology and*
538 *Evolution* **2**:1181-1194.
- 539 Burns, J. G. and F. H. Rodd. 2008. Hastiness, brain size and predation regime affect the performance
540 of wild guppies in a spatial memory task. *Animal Behaviour* **76**:911-922.
- 541 Carere, C. and D. Maestriperi. 2013. *Animal personalities: behavior, physiology, and evolution.*
542 University of Chicago Press.
- 543 Dingemanse, N. J., N. A. Dochtermann, and J. Wright. 2010. A method for exploring the structure of
544 behavioural syndromes to allow formal comparison within and between data sets. *Animal*
545 *Behaviour* **79**:439-450.
- 546 Dingemanse, N. J., J. Wright, A. J. N. Kazem, D. K. Thomas, R. Hickling, and N. Dawnay. 2007.
547 Behavioural syndromes differ predictably between 12 populations of three-spined
548 stickleback. *Journal of Animal Ecology* **76**:1128-1138.
- 549 Endler, J. A. and A. E. Houde. 1995. Geographic variation in female preferences for male traits in
550 *Poecilia reticulata*. *Evolution* **49**:456-468.
- 551 Fisher, J. and R. A. Hinde. 1949. The opening of milk bottles by birds. *British Birds* **42**:347-357.
- 552 Forstmeier, W., G. Segelbacher, J. C. Mueller, and B. Kempenaers. 2007. Genetic variation and
553 differentiation in captive and wild zebra finches (*Taeniopygia guttata*). *Molecular Ecology*
554 **16**:4039-4050.
- 555 Goodall, J. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*
556 **201**:1264.
- 557 Griffin, A. S., D. Guez, F. Lermite, and M. Patience. 2013. Tracking changing environments:
558 innovators are fast, but not flexible learners. *Plos One* **8**:e84907.
- 559 Griffin, A. S., L. M. Guillette, and S. D. Healy. 2015. Cognition and personality: an analysis of an
560 emerging field. *Trends in Ecology & Evolution* **30**:207-214.
- 561 Guillette, L. M., A. R. Reddon, M. Hoeschele, and C. B. Sturdy. 2011. Sometimes slower is better:
562 slow-exploring birds are more sensitive to changes in a vocal discrimination task.
563 *Proceedings of the Royal Society of London B: Biological Sciences* **278**:767-773.
- 564 Guillette, L. M., A. R. Reddon, P. L. Hurd, and C. B. Sturdy. 2009. Exploration of a novel space is
565 associated with individual differences in learning speed in black-capped chickadees, *Poecile*
566 *atricapillus*. *Behavioural Processes* **82**:265-270.
- 567 Harcourt, J. L., S. Biau, R. Johnstone, and A. Manica. 2010. Boldness and Information Use in Three-
568 Spined Sticklebacks. *Ethology* **116**:440-447.
- 569 Harris, S., I. W. Ramnarine, H. G. Smith, and L. B. Pettersson. 2010. Picking personalities apart:
570 estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia*
571 *reticulata*. *Oikos* **119**:1711-1718.
- 572 Hoppitt, W. and K. N. Laland. 2013. *Social learning: an introduction to mechanisms, methods, and*
573 *models.* Princeton University Press.
- 574 Hosey, G. R., M. Jacques, and A. Pitts. 1997. Drinking from tails: social learning of a novel behaviour
575 in a group of ring-tailed lemurs (*Lemur catta*). *Primates* **38**:415-422.
- 576 Houde, A. E. 1988. The effects of female choice and male male competition on the mating success of
577 male guppies. *Animal Behaviour* **36**:888-896.
- 578 Katzir, G. 1982. Relationships between social structure and response to novelty in captive jackdaws,
579 *Corvus monedula* L., I. Response to novel space. *Behaviour* **81**:231-263.

580 Laland, K. N. and S. M. Reader. 1999a. Foraging innovation in the guppy. *Animal Behaviour* **57**:331-
581 340.

582 Laland, K. N. and S. M. Reader. 1999b. Foraging innovation is inversely related to competitive ability
583 in male but not in female guppies. *Behavioral Ecology* **10**:270-274.

584 Laland, K. N. and Y. Van Bergen. 2003. Experimental studies of innovation in the guppy.

585 Larsen, L. K., C. Pelabon, G. Bolstad, Å. Viken, I. Fleming, and G. Rosenqvist. 2011. Temporal change
586 in inbreeding depression in life-history traits in captive populations of guppy (*Poecilia*
587 *reticulata*): evidence for purging? *Journal of Evolutionary Biology* **24**:823-834.

588 Light, K. R., S. Kolata, G. Hale, H. Grossman, and L. D. Matzel. 2008. Up-regulation of exploratory
589 tendencies does not enhance general learning abilities in juvenile or young-adult outbred
590 mice. *Neurobiology of Learning and Memory* **90**:317-329.

591 Liker, A. and Z. Barta. 2002. The effects of dominance on social foraging tactic use in house sparrows.
592 *Behaviour* **139**:1061-1076.

593 Magurran, A., B. Seghers, G. Carvalho, and P. Shaw. 1992. Behavioural consequences of an artificial
594 introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-
595 predator behaviour in the wild. *Proceedings of the Royal Society of London B: Biological*
596 *Sciences* **248**:117-122.

597 Mathot, K. J., J. Wright, B. Kempenaers, and N. Dingemanse. 2012. Adaptive strategies for managing
598 uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*
599 **121**:1009-1020.

600 Matzel, L. D., D. A. Townsend, H. Grossman, Y. R. Han, G. Hale, M. Zappulla, K. Light, and S. Kolata.
601 2006. Exploration in outbred mice covaries with general learning abilities irrespective of
602 stress reactivity, emotionality, and physical attributes. *Neurobiology of Learning and*
603 *Memory* **86**:228-240.

604 Morand-Ferron, J., E. F. Cole, J. E. Rawles, and J. L. Quinn. 2011. Who are the innovators? A field
605 experiment with 2 passerine species. *Behavioral Ecology* **22**:1241-1248.

606 Niemela, P. T., A. Vainikka, A. V. Hedrick, and R. Kortet. 2012. Integrating behaviour with life history:
607 boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology* **26**:450-
608 456.

609 Pélabon, C., G. H. Bolstad, C. K. Egset, J. M. Cheverud, M. Pavlicev, and G. Rosenqvist. 2013. On the
610 relationship between ontogenetic and static allometry. *The American Naturalist* **181**:195-
611 212.

612 Ramsey, G., M. L. Bastian, and C. van Schaik. 2007. Animal innovation defined and operationalized.
613 *Behavioral and Brain Sciences* **30**:393-+.

614 Reader, S. M. and K. N. Laland. 2000. Diffusion of foraging innovations in the guppy. *Animal*
615 *Behaviour* **60**:175-180.

616 Reader, S. M. and K. N. Laland. 2003a. *Animal innovation*. Oxford University Press Oxford.

617 Reader, S. M. and K. N. Laland. 2003b. *Animal innovation: an introduction*. Oxford University Press
618 Oxford.

619 Réale, D., N. J. Dingemanse, A. J. Kazem, and J. Wright. 2010a. Evolutionary and ecological
620 approaches to the study of personality. *The Royal Society*.

621 Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010b.
622 Personality and the emergence of the pace-of-life syndrome concept at the population level.
623 *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**:4051-
624 4063.

625 Reznick, D. and A. P. Yang. 1993. The influence of fluctuating resources on life history: patterns of
626 allocation and plasticity in female guppies. *Ecology* **74**:2011-2019.

627 Reznick, D. N., M. J. Butler IV, F. H. Rodd, and P. Ross. 1996. Life-history evolution in guppies
628 (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection.
629 *Evolution*:1651-1660.

630 Riechert, S. E. and A. V. Hedrick. 1993. A test for correlations among fitness-linked behavioural traits
631 in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour* **46**:669-675.
632 Rutz, C. and J. J. H. St Clair. 2012. The evolutionary origins and ecological context of tool use in New
633 Caledonian crows. *Behavioural Processes* **89**:153-165.
634 Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary
635 overview. *Trends in Ecology & Evolution* **19**:372-378.
636 Sih, A. and M. Del Giudice. 2012. Linking behavioural syndromes and cognition: a behavioural
637 ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*
638 **367**:2762-2772.
639 Smith, B. R. and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis.
640 *Behavioral Ecology* **19**:448-455.
641 Smith, B. R. and D. T. Blumstein. 2010. Behavioral types as predictors of survival in Trinidadian
642 guppies (*Poecilia reticulata*). *Behavioral Ecology* **21**:919-926.
643 Team, R. D. C. 2015. R: A language and environment for statistical computing. R Foundation for
644 Statistical Computing, Vienna, Austria.
645 Templeton, J. J. and L.-A. Giraldeau. 1995. Patch assessment in foraging flocks of European starlings:
646 evidence for the use of public information. *Behavioral Ecology* **6**:65-72.
647 Trompf, L. and C. Brown. 2014. Personality affects learning and trade-offs between private and social
648 information in guppies, *Poecilia reticulata*. *Animal Behaviour* **88**:99-106.
649 van Bergen, Y., I. Coolen, and K. N. Laland. 2004. Nine-spined sticklebacks exploit the most reliable
650 source when public and private information conflict. *Proceedings of the Royal Society B:*
651 *Biological Sciences* **271**:957.
652 Verbeek, M. E., A. Boon, and P. J. Drent. 1996. Exploration, aggressive behaviour and dominance in
653 pair-wise confrontations of juvenile male great tits. *Behaviour* **133**:945-963.
654 Verbeek, M. E., P. J. Drent, and P. R. Wiepkema. 1994. Consistent individual differences in early
655 exploratory behaviour of male great tits. *Animal Behaviour* **48**:1113-1121.
656 Webster, S. J. and L. Lefebvre. 2001. Problem solving and neophobia in a columbiform–passeriform
657 assemblage in Barbados. *Animal Behaviour* **62**:23-32.
658 Williams, S. E. and E. A. Hoffman. 2009. Minimizing genetic adaptation in captive breeding programs:
659 a review. *Biological Conservation* **142**:2388-2400.

660

661

662 **Table 1.** The effect of sex, population, body size and their interactions on the eight behaviour
663 variables: **(a)** activity movement (*_act*) and **(b)** rates of exploration/innovation (*_rate*) in the four trials:
664 exploration (*expl_*), maze (*maze_*), novel object (*no_*) and novel food (*nf_*). See text for details.
665 Because of the number of tests, significant effects were set to $p < 0.01$, and are shown in bold, while
666 the standard significant effects ($p < 0.05$) are outlined by borders. The effect degrees of freedom are
667 given for each parameter, and the error degrees of freedom was 102 in all models.

| (a) Activities | | | | | | | | | |
|-----------------------|----------|------|----------|------|--------|------|--------|------|--------------|
| | expl_act | | maze_act | | no_act | | nf_act | | |
| | d.f. | F | P | F | P | F | P | F | P |
| Pop | 2 | 1.14 | 0.324 | 1.32 | 0.272 | 0.85 | 0.429 | 1.77 | 0.175 |
| Sex | 1 | 4.90 | 0.029 | 3.74 | 0.056 | 0.73 | 0.395 | 7.42 | 0.008 |
| Size | 1 | 5.02 | 0.027 | 3.53 | 0.063 | 3.55 | 0.062 | 8.05 | 0.005 |
| Pop:sex | 2 | 1.28 | 0.284 | 0.67 | 0.512 | 0.16 | 0.856 | 1.51 | 0.226 |
| Pop:size | 2 | 0.48 | 0.618 | 0.54 | 0.585 | 0.26 | 0.775 | 1.14 | 0.323 |
| Sex:size | 1 | 4.72 | 0.032 | 3.76 | 0.055 | 0.63 | 0.430 | 7.19 | 0.009 |
| Pop:sex:size | 2 | 1.32 | 0.272 | 0.64 | 0.531 | 0.13 | 0.874 | 1.27 | 0.284 |

| (b) Rates | | | | | | | | | |
|------------------|-----------|------|-----------|------|---------|------|---------|------|-------|
| | expl_rate | | maze_rate | | no_rate | | nf_rate | | |
| | d.f. | F | P | F | P | F | P | F | P |
| Pop | 2 | 1.85 | 0.163 | 0.18 | 0.836 | 0.79 | 0.455 | 1.62 | 0.203 |
| Sex | 1 | 0.99 | 0.321 | 6.74 | 0.012 | 0.86 | 0.357 | 0.08 | 0.773 |
| Size | 1 | 0.16 | 0.693 | 0.01 | 0.937 | 0.88 | 0.351 | 0.43 | 0.512 |
| Pop:sex | 2 | 0.02 | 0.979 | 3.92 | 0.023 | 2.28 | 0.108 | 0.83 | 0.438 |
| Pop:size | 2 | 1.71 | 0.187 | 0.24 | 0.788 | 0.47 | 0.626 | 1.56 | 0.215 |
| Sex:size | 1 | 1.21 | 0.273 | 5.98 | 0.016 | 0.63 | 0.428 | 0.15 | 0.695 |
| Pop:sex:size | 2 | 0.06 | 0.939 | 3.71 | 0.028 | 2.24 | 0.111 | 0.70 | 0.501 |

668 **Table 2.** Results from the un-rotation PCA. Eigenvalues and the proportion of the variance explained
 669 are given for all the PCs, in addition to the loadings for each variable within these PCs. Strong loadings
 670 (> 0.30) are shown in bold.

| | PC1 | PC2 | PC3 |
|------------------------|--------------|--------------|--------------|
| Eigenvalue | 3.33 | 1.38 | 0.96 |
| Proportion of variance | 0.42 | 0.17 | 0.12 |
| Cumulative variance | 0.42 | 0.59 | 0.71 |
| expl_act | 0.84 | 0.05 | 0.05 |
| expl_rate | -0.18 | 0.58 | 0.61 |
| maze_act | 0.83 | 0.18 | 0.24 |
| maze_rate | -0.14 | -0.71 | -0.38 |
| no_act | 0.89 | 0.15 | -0.02 |
| no_rate | -0.18 | 0.65 | -0.37 |
| nf_act | 0.91 | 0.12 | 0.01 |
| nf_rate | -0.49 | 0.23 | 0.49 |

671

672 **Table 3.** Results from the PCA with a varimax rotation. Eigenvalues and the proportion of the variance
 673 explained are given for all the PCs, in addition to the loadings for each variable within these PCs. Strong
 674 loadings (> 0.30) are shown in bold.

| | PC1 | PC2 | PC3 | PC4 | PC5 |
|------------------------|-------------|-------------|-------------|-------------|-------------|
| Eigenvalue | 1.97 | 1.03 | 1.01 | 1.01 | 1.00 |
| Proportion of variance | 0.25 | 0.13 | 0.13 | 0.13 | 0.13 |
| Cumulative variance | 0.25 | 0.38 | 0.51 | 0.64 | 0.77 |
| expl_act | 0.42 | -0.15 | -0.04 | -0.04 | -0.05 |
| expl_rate | -0.05 | 0.08 | 0.09 | 0.99 | 0.05 |
| maze_act | 0.49 | -0.07 | -0.09 | 0.04 | 0.01 |
| maze_rate | 0.01 | 0.03 | 0.98 | 0.09 | 0.13 |
| no_act | 0.91 | -0.16 | 0.05 | -0.05 | -0.06 |
| no_rate | -0.05 | 0.05 | 0.13 | 0.05 | 0.99 |
| nf_act | 0.83 | -0.15 | -0.03 | -0.06 | -0.02 |
| nf_rate | -0.17 | 0.97 | 0.03 | 0.09 | 0.05 |

675

676 **Table 4.** Comparison of the seven SEM models (see Fig.2 and 3) using AIC values, where K is the
677 number of parameters estimated. The H5 (activity vs. rates) has a better fit than the other models
678 ($\Delta AIC > 2$).

| Model | Name | K | AIC | ΔAIC |
|--------------|---------------------------|----------|------------|--------------------------------|
| H5 | Activity vs. rates | 17 | 2283.92 | 0.00 |
| H3 | Spatial vs.non-spatial | 17 | 2287.59 | 3.67 |
| H1 | All correlates | 16 | 2287.68 | 3.76 |
| H2 | Personality vs.innovation | 17 | 2289.59 | 5.67 |
| H6 | Only activity | 12 | 2298.15 | 14.23 |
| H4 | Activity driven | 16 | 2300.85 | 16.93 |
| H0 | No correlations | 8 | 2596.11 | 312.19 |

679

680 **Table 5.** Further SEM comparisons using just the best model (H5 – activity vs. rate - see Fig.5) was
 681 done to see if body size had any effect on the syndrome structure, using AIC values, where K is the
 682 number of parameters estimated. Body size was included in the best model (H5 – activity vs. rate) as
 683 a variance term with either no covariance with any of the latent variables or as part of either the
 684 activity syndrome or the rate syndrome, or both. The model with the best fit is the one where body
 685 size is included as part of the ‘activity syndrome’ (see Fig.5b), and this model is better than the ‘no
 686 body size syndrome’ model where only the variance term for body size is included. It is, however, not
 687 better than when body size is added as part of the ‘rate syndrome’ or ‘both syndromes’.

| Model | K | AIC | ΔAIC |
|-----------------------|----------|------------|-------------|
| Activity syndrome | 19 | 2606.22 | 0.00 |
| Rate syndrome | 19 | 2607.00 | 0.78 |
| Both syndromes | 20 | 2608.00 | 1.78 |
| No body size syndrome | 18 | 2608.43 | 2.21 |

688

689 **Figure 1.** Tank set-up without the black plastic covering the walls. The tank was 61x25x24.5 cm, and
690 water was filled up to 18 cm, similar to the tank size used by Laland and Reader (1999a; 1999b). The
691 maze (on the right-hand side of the tank) consisted of two partitions that ran across the width of the
692 tank 10 cm apart, with small square holes (6x6 cm) at the bottom at opposite corners. Between these
693 two partitions and between the inner partition and the glass wall, four additional partitions were
694 fitted. The first and the third additional partitions were mounted 4 cm above the ground, while the
695 second and fourth were 5 cm and 8 cm from the ground up, respectively, creating a 3-dimensional
696 maze. In the novel arena (on the left-hand side of the tank), the white spot indicates the position of
697 the novel object, while the grey spot indicates the position for the novel food. These locations were
698 indicated during the trials by dark grey and light grey tape on the top of the glass wall. The box to the
699 far left indicates the acclimation cage – see the text for more details. The maze door, not included in
700 this figure, consisted of a plate placed over the hole in the first partition of the maze shown at the
701 front of the tank (see Fig.S1 for a view from above).

702 **Figure 2.** Causal diagrams of the four original hypotheses (H0-H3): (a) model H0 (with no arrows active)
703 where there is no covariance between any of the variables, and model H1 (arrows active) where all
704 variables covaries into one behavioural syndrome; and (b) model H2 (solid arrows active) where
705 traditional personality behaviours and innovative behaviours constitute two separate latent variables,
706 and model H3 (dashed arrows active) where spatial and non-spatial behaviours constitute two
707 separate latent variables. Doubled-headed arrows between latent variables indicate covariance
708 allowed between them. 'act' indicates activity level measured in all trials, 'Expl' indicates exploration
709 in trial 1, whilst 'NO' indicates novel object and 'NF' novel food.

710 **Figure 3.** Causal diagrams for the three additional models inspired from the results of PCA (Table 2
711 and 3): (a) model H4 where activity constitutes a latent variable, but activity correlates with the rate
712 variable within the same test, hence activity within each trial drives the syndrome; and (b) model H5
713 (all arrows active; based on the un-rotated PCA) where activities and rates constitute two separate

714 latent variables, and H6 (only solid arrows active; based on the varimax rotated PCA) with only activity
715 as a latent variable, and the rates only added as variance terms. 'act' indicates activity level measured
716 in all trials, 'Expl' indicates exploration in trial 1, whilst 'NO' indicates novel object and 'NF' novel food.

717 **Figure 4.** Mean \pm SE for the two sexes in all three populations for: **(a)** activity during the exploration
718 trial (number of squares visited); **(b)** exploration rate (time to explore new squares divided by
719 number of new squares visited); **(c)** exploration of the maze (time to get to maximum point divided
720 by maximum point reached); **(d)** approach to the novel object (time to reach minimum distance to
721 the novel object divided by minimum distance reached); and **(e)** approach to the novel food (time to
722 reach minimum distance to the novel food divided by minimum distance reached). The activity
723 measurements (the total number of squares visited in the first, middle and last 5 minutes) for the
724 maze, the novel object, and the novel food trials were all qualitatively similar to the exploration trial
725 results in (a) and are therefore not shown here for reasons of brevity. See Methods for more
726 information on each measure.

727 **Figure 5.** The best model (H5 - activity vs. rate) with factor loadings (one-headed arrows) and error
728 variance of the observed variables (squares) that is left unexplained by the latent variable (circles).
729 The double-headed arrow between the latent variables show the correlation between them: **(a)**
730 without body size (as in Table 4); and **(b)** body size included in the latent variable for activity (as in
731 Table 5). Negative factor loadings for body size shows that smaller individuals were more active than
732 larger individuals.

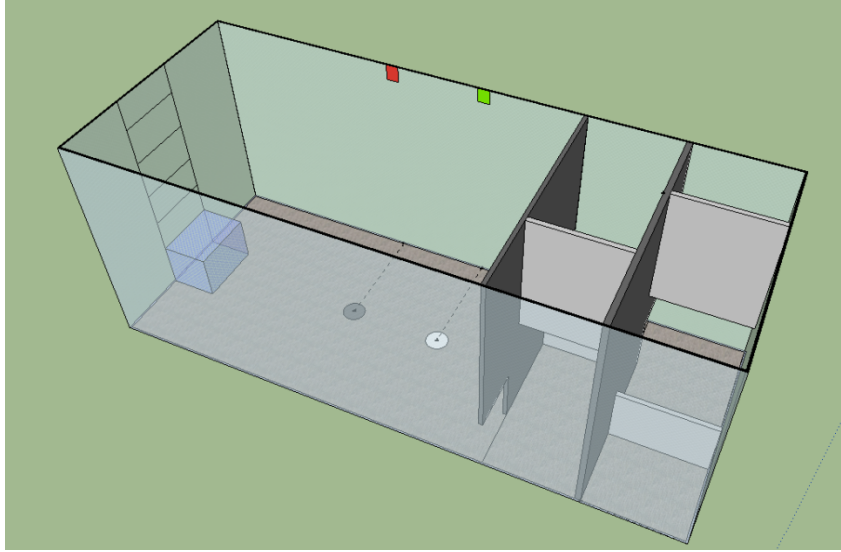


Figure 1.

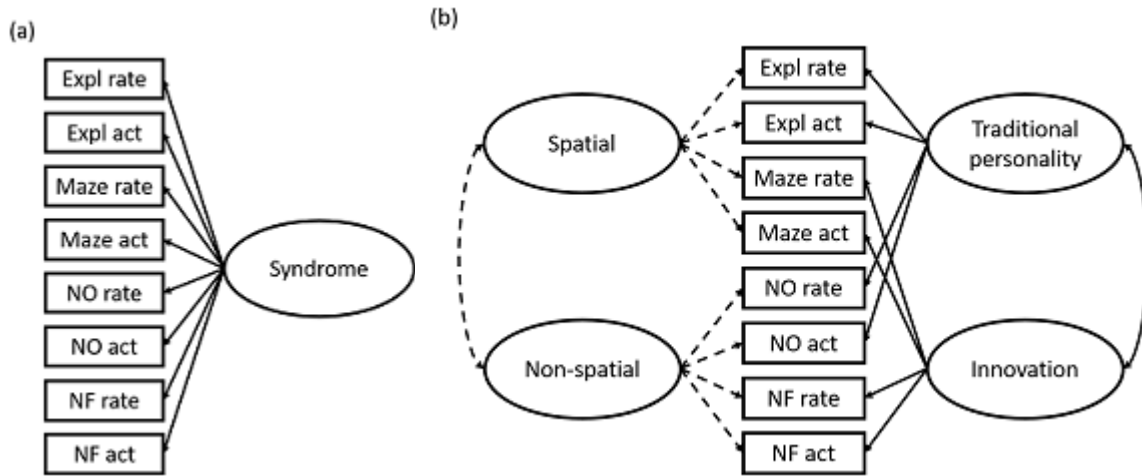


Figure 2.

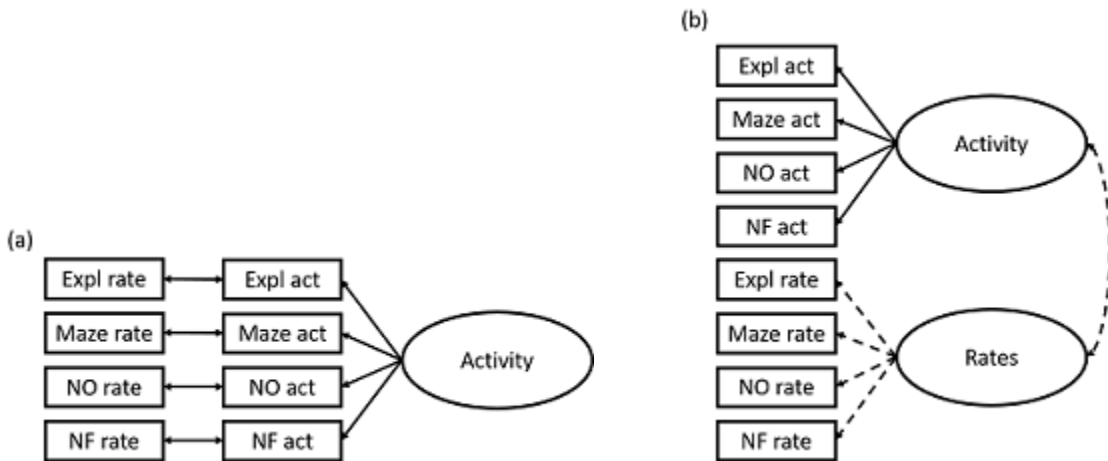


Figure 3

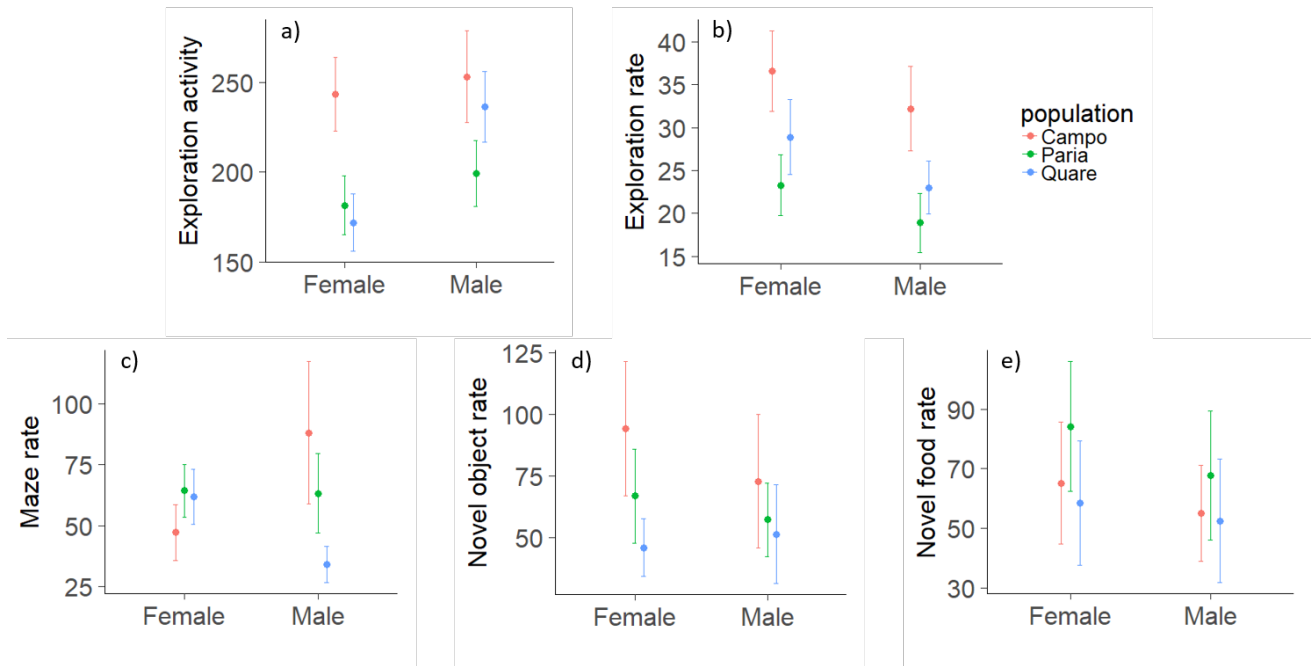


Figure 4.

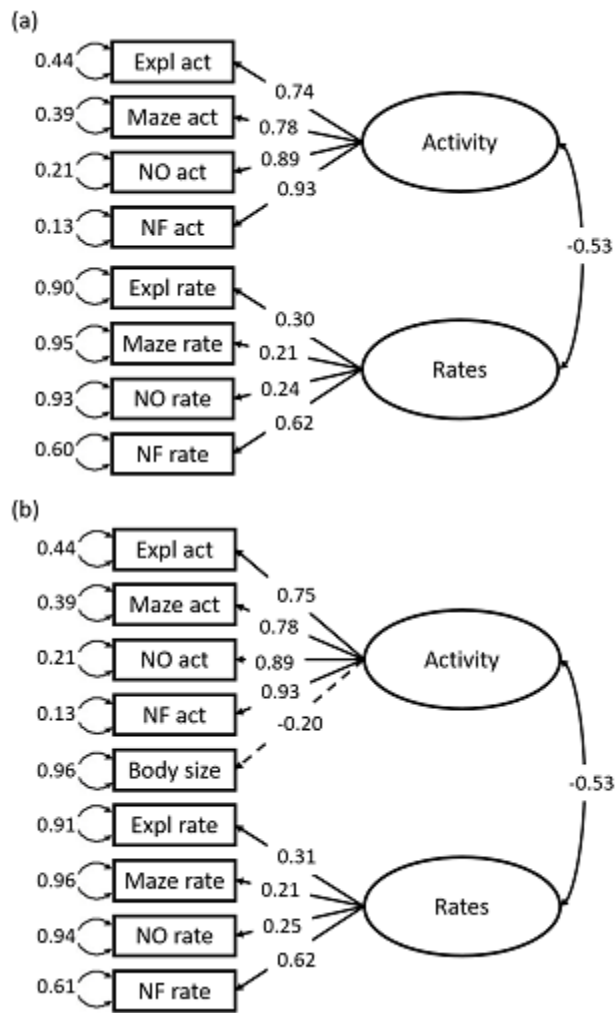
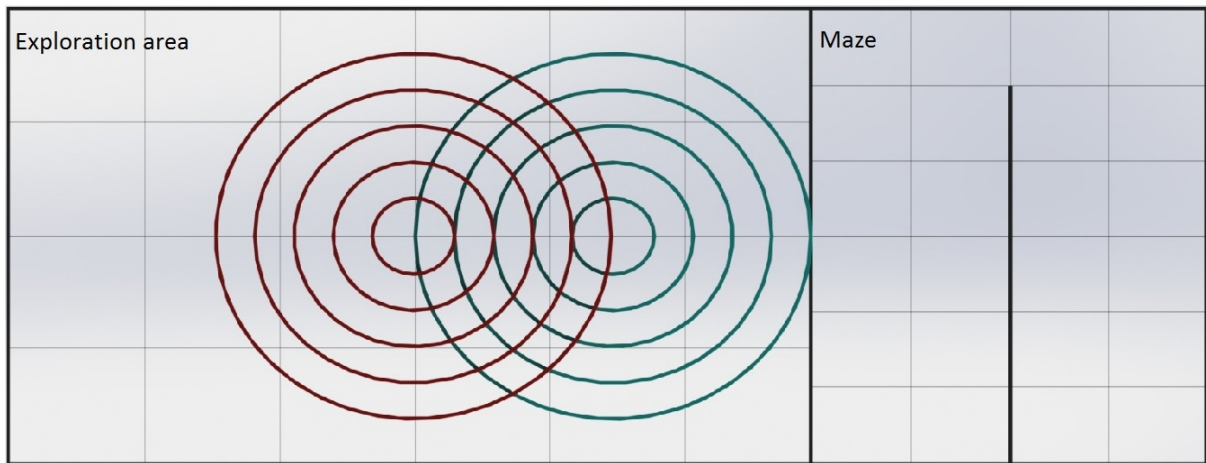


Figure 5.

1 Supplementary materials

2



3

4 **Figure S1.** The tank seen from above with the grids for the video analysis. Both the exploration area

5 and the maze were divided into 24 squares to measure activity and exploration. The maze is also

6 divided into 12 steps (2 squares per step) to measure the maximum distance reached by each guppy.

7 Concentric circles were placed over both the novel object and the novel food to measure approach.

8 The blue rings show the novel object and the red rings show the novel food.

9 Repeatability and Habituation Analyses

10 Although our design did not include true repeated measures, because activity was measured
11 repeatedly throughout the four trials it was possible to assess the individual repeatability over
12 the short period of the test, as well as any habituation effects over time. In both the
13 repeatability and habituation mixed effect models, fish identity was added as a random effect.
14 In addition, both models were run with and without the maze trial included, since the maze
15 represents a somewhat different environment, possibly confounding any effects of both
16 repeatability and habituation on activity. The first, middle and last 5 minutes measures of
17 activity in each trial were used test for habituation (i.e. a reduction in activity over time) and
18 an additional short-term repeatability within each trial for this behaviour. A mixed-effect
19 model in the rpt2 package was used to estimate repeatability with confidence intervals. The
20 twelve different periods of activity measurement (three times from each of the four
21 treatments) were added as a fixed effect to control for any difference in activity level due to
22 the different test conditions and for any habituation over time. Parametric boot-strapping
23 based on model estimates was then used to derive a distribution of repeatability estimates
24 (Table S1). In the habituation model, the twelve periods were instead added to this model as
25 continuous 'time' covariate to see how the activity level changed systematically over time,
26 while the four different tests (i-iv) were added as a factor. Sex and body size were also added
27 as fixed effects to see if they affected rates of habituation (Table S2). The degrees of freedom
28 and appropriate p-values were calculated with a Satterthwaite approximation. The full model
29 contained a lot of non-significant interactions (Table S3), so a model simplification procedure
30 based on p-values and AIC-values was performed (see Forstmeier and Schielzeth 2011; Table
31 S4).

32 **Table S1.** Repeatability (R) in individual activity calculated for combinations of the different
 33 populations and sexes for the 12 repeats (3 time intervals for each of the 4 trials). Since the maze is a
 34 somewhat different environment, the results are shown with and without the maze data included.
 35 The confidence intervals (CI) are provided in brackets.

| Population | Sex | R (CI) with maze | R (CI) without maze |
|-------------------|------------|-------------------------|----------------------------|
| Paria | Both | 0.516 (0.433-0.577) | 0.526 (0.438-0.601) |
| Paria | Male | 0.545 (0.430-0.622) | 0.543 (0.408-0.641) |
| Paria | Female | 0.480 (0.358-0.575) | 0.498 (0.361-0.606) |
| Campo | Both | 0.450 (0.362-0.527) | 0.516 (0.423-0.597) |
| Campo | Male | 0.503 (0.388-0.604) | 0.555 (0.434-0.656) |
| Campo | Female | 0.386 (0.265-0.496) | 0.467 (0.339-0.581) |
| Quare | Both | 0.427 (0.340-0.499) | 0.443 (0.346-0.530) |
| Quare | Male | 0.424 (0.292-0.533) | 0.460 (0.309-0.576) |
| Quare | Female | 0.429 (0.311-0.538) | 0.390 (0.242-0.528) |
| All | Male | 0.518 (0.452-0.570) | 0.543 (0.472-0.603) |
| All | Female | 0.475 (0.409-0.526) | 0.498 (0.418-0.565) |
| All | Both | 0.501 (0.456-0.537) | 0.527 (0.477-0.568) |

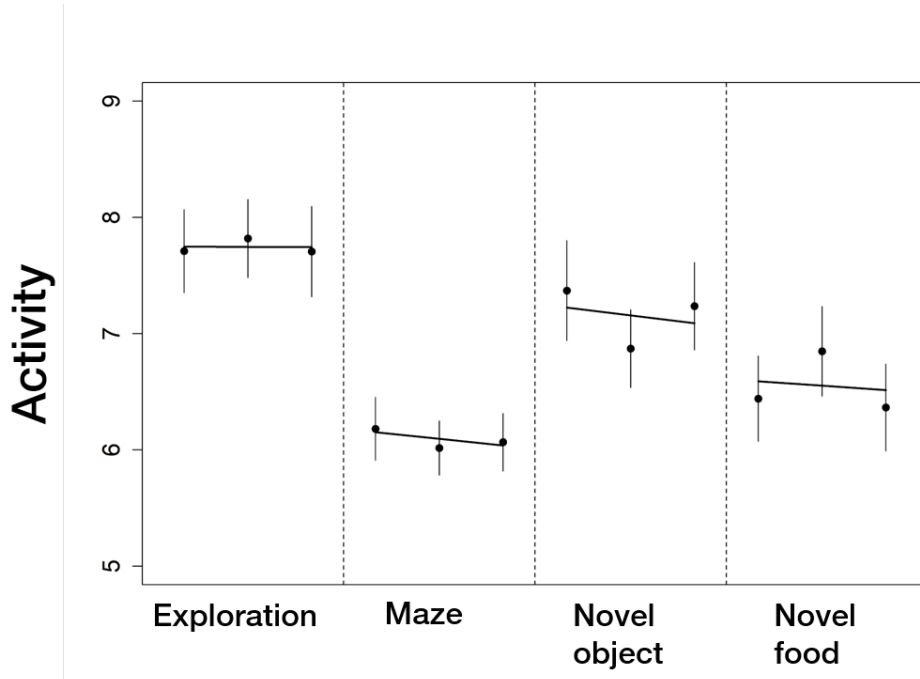
36

37

38 **Table S2.** Habituation in the activity measures including trial (exploration, maze, novel object and
 39 novel food), time within each trial, body size, sex and all the two-way interactions (see Table S3 for
 40 the full model). Since the maze represented a somewhat different environment, results are shown for
 41 models with and without the maze data included. Effect and error degrees of freedom are given.
 42 Because of the number of tests, significant effects were set to $p < 0.01$, and are shown in bold, while
 43 the standard significant effects ($p < 0.05$) are outlined by borders.

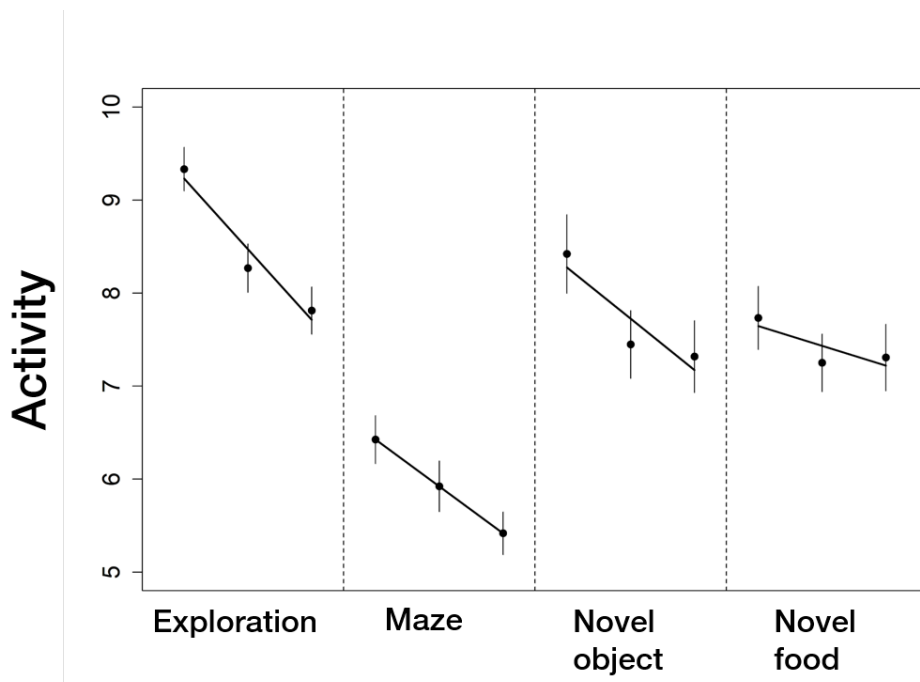
| Variables | With maze | | | Without maze | | |
|-----------|-----------|-------|------------------|--------------|-------|------------------|
| | df | F | p | df | F | p |
| Test | 3, 1239 | 7.44 | <0.001 | 2, 901 | 4.95 | 0.007 |
| Time | 1, 1239 | 20.26 | <0.001 | 1, 901 | 14.04 | <0.001 |
| Size | 1, 823 | 7.32 | 0.007 | 1, 867 | 5.91 | 0.02 |
| Sex | 1, 138 | 7.67 | 0.006 | 1, 149 | 6.76 | 0.01 |
| Test:Time | 3, 1239 | 0.85 | 0.47 | 2, 901 | 1.16 | 0.31 |
| Test:Size | 3, 1239 | 6.82 | <0.001 | 2, 901 | 5.68 | 0.004 |
| Test:Sex | 3, 1239 | 0.79 | 0.50 | 2, 901 | 0.55 | 0.58 |
| Time:Size | 1, 1239 | 14.23 | <0.001 | 1, 901 | 9.91 | 0.002 |
| Time:Sex | 1, 1239 | 1.76 | 0.18 | 1, 901 | 0.95 | 0.33 |
| Size:Sex | 1, 110 | 6.47 | 0.01 | 1, 110 | 6.22 | 0.01 |

45 (a)



46

47 (b)



48

49 **Figure S2.** Change in activity level within and between the four different trials over time for **(a)** large
50 individuals (> median) and; **(b)** small fish (< median). The slope is not significantly different between
51 the different trials (see Table S2).

52

53 **Table S3.** Results from the full habituation model with test, time, body size and sex and all the
54 interactions as fixed effects, and fish identity as a random effect. Both the effect degrees of freedom
55 and the error degrees of freedom are given in each case. Because of the number of tests, significant
56 effects were set to $p < 0.01$, and are shown in bold, while the standard significant effects ($p < 0.05$)
57 are outlined by borders. Most of the moderately significant effects of the three-way interactions
58 disappeared when the four-way interaction was removed. The sample size was 1368 for the models
59 including the maze and 1026 for the model without the maze.

| Variables | With maze | | | Without maze | | |
|--------------------|-----------|-------|------------------|--------------|-------|------------------|
| | df | F | p | df | F | p |
| Test | 3, 1226 | 5.48 | 0.03 | 2, 892 | 1.06 | 0.35 |
| Time | 1, 1226 | 23.85 | <0.001 | 1, 892 | 19.99 | <0.001 |
| Size | 1, 1291 | 5.15 | 0.02 | 1, 1001 | 4.16 | 0.04 |
| Sex | 1, 1291 | 0.08 | 0.77 | 1, 1001 | 0.26 | 0.61 |
| Test:Time | 3, 1226 | 0.40 | 0.81 | 2, 892 | 3.62 | 0.03 |
| Test:Size | 3, 1226 | 0.48 | 0.75 | 2, 892 | 0.86 | 0.42 |
| Test:Sex | 3, 1226 | 0.51 | 0.67 | 2, 892 | 5.44 | 0.02 |
| Time:Size | 1, 1226 | 17.98 | <0.001 | 1, 892 | 15.85 | <0.001 |
| Time:Sex | 1, 1226 | 3.29 | 0.04 | 1, 892 | 5.44 | 0.02 |
| Size:Sex | 1, 1260 | 0.81 | 0.44 | 1, 1001 | 0.32 | 0.57 |
| Test:Time:Size | 3, 1226 | 2.60 | 0.05 | 2, 892 | 3.17 | 0.04 |
| Test:Time:Sex | 3, 1226 | 0.04 | 0.84 | 2, 892 | 1.24 | 0.29 |
| Test:Size:Sex | 3, 1226 | 0.001 | 0.98 | 2, 892 | 0.34 | 0.71 |
| Time:Size:Sex | 1, 1226 | 5.27 | 0.02 | 1, 892 | 6.31 | 0.01 |
| Test:Time:Size:sex | 3, 1226 | 1.64 | 0.18 | 2, 892 | 1.52 | 0.22 |

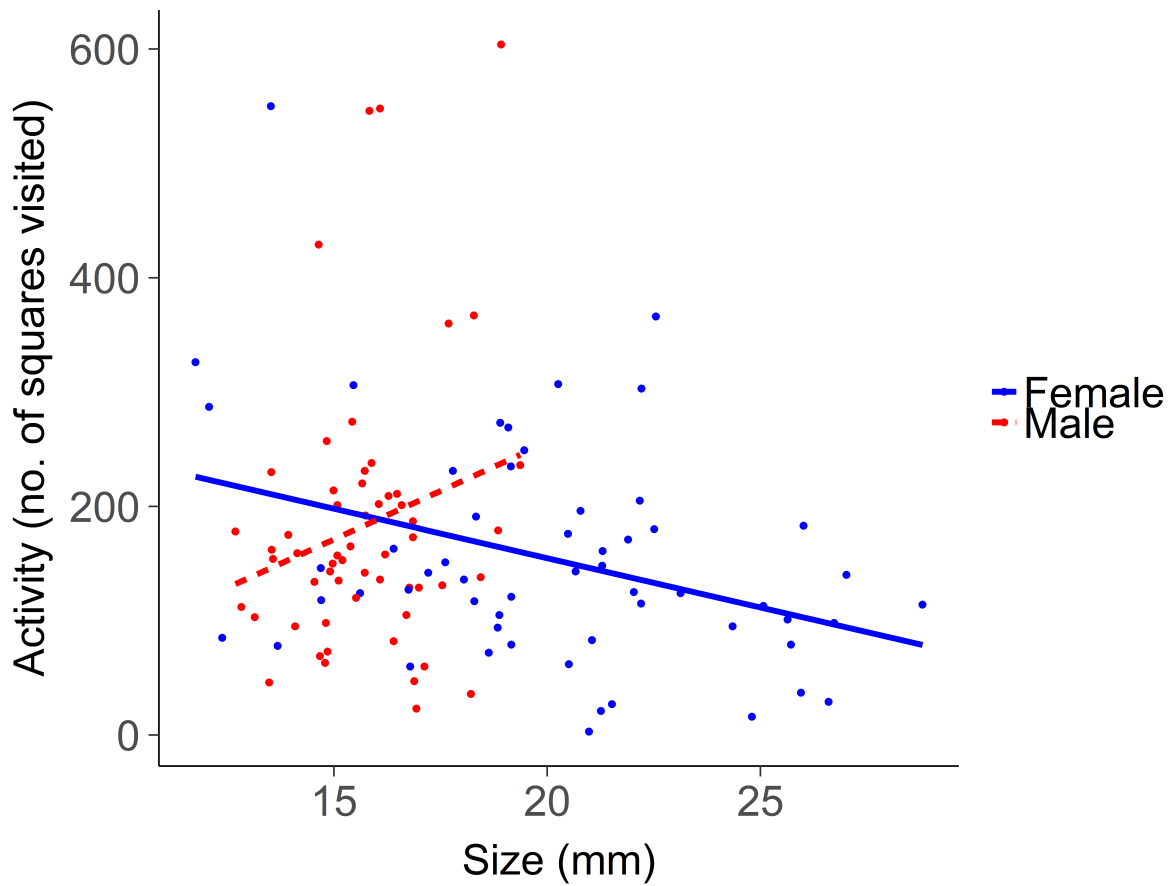
61 **Table S4.** Comparison of the habituation models, both with and without the maze. The full model
 62 (Model 1) contains all interactions; Model 2 contains all the two – and three-way interactions; Model
 63 3 contains all the two-way interactions in addition to the three-way interaction between time, size
 64 and sex, since this was shown to be significant in Model 2 ($F_{1,1229} = 5.26$, $p = 0.02$); and Model 4 contains
 65 only the two-way interactions (see text for more information). The three-way interaction between
 66 time, test and size was not significant in Model 3 ($F_{1,1238} = 2.46$, $p = 0.12$). Due to parsimony, Model 4
 67 was presented in this study (see Table S2). K is the number of parameters estimated.

| Model | With maze | | | Without maze | | |
|---------|-----------|---------|--------------|--------------|---------|--------------|
| | K | AIC | Δ AIC | K | AIC | Δ AIC |
| Model 4 | 21 | 5796.89 | 0.00 | 17 | 4487.36 | 0.00 |
| Model 3 | 22 | 5803.19 | 6.30 | 18 | 4494.38 | 7.02 |
| Model 2 | 31 | 5831.00 | 24.11 | 24 | 4507.74 | 20.38 |
| Model 1 | 34 | 5838.19 | 41.30 | 26 | 4512.40 | 25.04 |

68 **Table S5.** Pair-wise correlations between the eight behavioural variables. The significant correlations
 69 are marked in bold, while correlations within the same tests are in frames.

| | Exploration | | Maze | | Novel object | | Novel food | |
|------------------------------|-------------|-------------------|------------------------------------|--------------------------------|------------------------------------|------------------------------------|------------------------------------|-------------------------------------|
| | Activity | Rate | Activity | Rate | Activity | Rate | Activity | Rate |
| Exploration activity | 1 | r=-0.10 p=0.31 | r=0.63 p<0.001 | r=-0.09 p=0.33 | r=0.66 p<0.001 | r=-0.11 p=0.24 | r=0.68 p<0.001 | r=-0.34 p<0.001 |
| Exploration rate | | 1 | r=0.02 p=0.87 | r=0.19 p=0.04 | r=-0.11 p=0.25 | r=0.12 p=0.21 | r=-0.12 p=0.19 | r=0.19 p=0.05 |
| Maze activity | | | 1 | r=-0.13 p=0.16 | r=0.68 p<0.001 | r=-0.03 p=0.76 | r=0.73 p<0.001 | r=-0.22 p=0.02 |
| Maze rate | | | | 1 | r=0.03 p=0.77 | r=0.27 p<0.001 | r=-0.05 p=0.57 | r=0.07 p=0.43 |
| Novel object activity | | | | | 1 | r=-0.12 p=0.21 | r=0.83 p<0.001 | r=-0.35 p<0.001 |
| Novel object rate | | | | | | 1 | r=-0.08 p=0.38 | r=0.11 p=0.23 |
| Novel food activity | | | | | | | 1 | r=-0.34 p<0.001 |
| Novel food rate | | | | | | | | 1 |

70



72

73 **Figure S3.** Activity level (quantified as the mean number of squares visited) during the novel food test

74 regressed against body size for females (blue dots and line, $y = -8.62x + 327.27$) and males (red dots

75 and line, $y = 16.94x - 82.81$).

76 Structural Equation Modelling

77 For both the Campo and Quare populations, the models with free parameters had the highest
 78 AIC value (see Table S6) meaning that the factor loadings from the other populations could
 79 explain the (co-)variance just as well as freely estimated parameters. For the Paria population,
 80 however, the model with free parameters had the best fit, but was hardly distinguishable
 81 from when it was constrained with the parameters for Quare. Thus, it appears that there were
 82 no significant differences in syndrome structure between any of the three populations.

83 **Table S6.** A comparison for the three populations between model H5 (activity vs. rate) with free
 84 parameters and parameters constrained to the factor loading of the two other populations. K is the
 85 number of parameters estimated.

| | Paria | | Campo | | Quare | |
|-----------------------------------|-------|--------|-------|--------|-------|--------|
| | K | AIC | K | AIC | K | AIC |
| Free parameters | 17 | 742.54 | 17 | 788.47 | 17 | 783.18 |
| Constrained parameters (Paria) | - | - | 11 | 789.20 | 11 | 777.64 |
| Constrained parameters (Campo) | 11 | 757.13 | - | - | 11 | 779.83 |
| Constrained parameters (Quare) | 11 | 742.81 | 11 | 785.49 | - | - |

87 When H5 (activity vs. rates) was run separately for the two sexes, the model would not
88 converge properly for the male subset, thus it was not possible to compare the syndrome
89 structure between the two sexes for the best model. Given that the sample sizes for the two
90 sexes was the same, it might well be that it is a difference in the co-variance matrices that
91 enables us to run H5 for females but not for males. When looking at the correlation matrices
92 for the two sexes we can see that the correlations for some of the rates are somewhat lower
93 in males than in females (see Table S7 and S8 respectively), and these low correlations could
94 suggest a different structure, and might also cause the model to collapse when run on the
95 subset for males. The comparison of males and females was possible for the H6 model (only
96 activity), where the models with free parameters had higher AIC values (1139.59 for males
97 and 1176.76 for females) than the models with constrained parameters (1136.93 for males
98 and 1173.29 for females) for both sexes, thus no difference in syndrome structure in activity
99 between males and females.

100 **Table S7.** Pair-wise correlations between the 8 behavioural variables for males. The significant
 101 correlations are marked in bold, while correlations within the same tests are in frames.

| | Exploration | | Maze | | Novel object | | Novel food | |
|------------------------------|-------------|-------------------|------------------------------------|-------------------|------------------------------------|------------------------------------|------------------------------------|-------------------------------------|
| | Activity | Rate | Activity | Rate | Activity | Rate | Activity | Rate |
| Exploration activity | 1 | r=-0.01 p=0.93 | r=0.70 p<0.001 | r=-0.02 p=0.84 | r=0.66 p<0.001 | r=-0.23 p=0.01 | r=0.72 p<0.001 | r=-0.33 p<0.001 |
| Exploration rate | | 1 | r=0.10 p=0.27 | r=0.15 p=0.10 | r=-0.04 p=0.69 | r=-0.02 p=0.83 | r=-0.09 p=0.33 | r=0.16 p=0.09 |
| Maze activity | | | 1 | r=0.04 p=0.62 | r=0.71 p<0.001 | r=-0.04 p=0.71 | r=0.79 p<0.001 | r=-0.20 p=0.04 |
| Maze rate | | | | 1 | r=0.16 p=0.09 | r=0.36 p<0.001 | r=0.04 p=0.69 | r=0.01 p=0.89 |
| Novel object activity | | | | | 1 | r=-0.13 p=0.18 | r=0.83 p<0.001 | r=-0.36 p<0.001 |
| Novel object rate | | | | | | 1 | r=-0.07 p=0.48 | r=0.39 p<0.001 |
| Novel food activity | | | | | | | 1 | r=-0.33 p<0.001 |
| Novel food rate | | | | | | | | 1 |

103 **Table S8.** Pair-wise correlations between the 8 behavioural variables for females. The significant
 104 correlations are marked in bold, while correlations within the same tests are in frames.

| | Exploration | | Maze | | Novel object | | Novel food | |
|------------------------------|-------------|-------------------|------------------------------------|-------------------------------------|------------------------------------|--------------------------------|------------------------------------|-------------------------------------|
| | Activity | Rate | Activity | Rate | Activity | Rate | Activity | Rate |
| Exploration activity | 1 | r=-0.15 p=0.12 | r=0.56 p<0.001 | r=-0.27 p=0.004 | r=0.63 p<0.001 | r=0.05 p=0.61 | r=0.61 p<0.001 | r=-0.33 p<0.001 |
| Exploration rate | | 1 | r=-0.07 p=0.47 | r=0.29 p=0.002 | r=-0.16 p=0.09 | r=0.24 p=0.01 | r=-0.13 p=0.18 | r=0.20 p=0.03 |
| Maze activity | | | 1 | r=-0.52 p<0.001 | r=0.64 p<0.001 | r=-0.02 p=0.85 | r=0.64 p<0.001 | r=-0.24 p=0.01 |
| Maze rate | | | | 1 | r=-0.27 p=0.004 | r=0.13 p=0.16 | r=-0.27 p=0.003 | r=0.19 p=0.04 |
| Novel object activity | | | | | 1 | r=-0.10 p=0.30 | r=0.83 p<0.001 | r=-0.33 p<0.001 |
| Novel object rate | | | | | | 1 | r=-0.09 p=0.34 | r=-0.16 p=0.10 |
| Novel food activity | | | | | | | 1 | r=-0.35 p<0.001 |
| Novel food rate | | | | | | | | 1 |