

1 **Among-individual variation of risk-taking behaviour in group and solitary context is**  
2 **uncorrelated but independently repeatable in a juvenile Arctic charr (*Salvelinus alpinus*)**  
3 **aquaculture strain.**

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11 **Abstract**

12 Behavioural traits have been shown to have implications in fish welfare and growth  
13 performances in aquaculture. If several studies have demonstrated the existence of repeatable  
14 and heritable behavioural traits (i.e., animal personality), the methodology to assess personality  
15 in fishes is often carried out in solitary context, which appears to somewhat limit their use from  
16 a selective breeding perspective because these tests are too time consuming. To address this  
17 drawback, group-based tests have been developed. In Nordic country, Arctic charr (*Salvelinus*  
18 *alpinus*) is widely used in aquaculture, but no selection effort on behavioural traits has yet been  
19 carried out. Specifically, in this study we examined if risk-taking behaviour was repeatable and  
20 correlated in group and solitary context and if the early influences of physical environment  
21 affect the among-individual variation of behavioural trait across time in order to verify whether  
22 a group risk-taking test could be used as a selective breeding tool. Here, we found that in both  
23 contexts and treatments, the risk-taking behaviour was repeatable across a short period of 6  
24 days. However, no cross-context consistency was found between group and solitary, which  
25 indicates that Arctic charr express different behavioural trait in group and solitary.

26 **Keywords:** Animal personality, Repeatability, Cross-context consistency, Risk-taking,  
27 Individual variation, Welfare, Aquaculture.

28 **Introduction**

29 Behavioural traits have been shown to have implications in a wide range of biological fields  
30 and livestock productions including fish welfare and growth performances in aquaculture  
31 (Huntingford et al., 2006). Several studies have demonstrated the existence of repeatable and  
32 heritable behavioural traits in the behavioural ecology frameworks i.e., animal personality  
33 defined as consistent among-individual variation in average behaviour across repeated  
34 measures (Dingemanse et al., 2009; Dochtermann et al., 2019). Consistent behavioural traits  
35 have been shown in different fish species such as boldness and aggression in Zebrafish (*Danio*  
36 *renio*; (Ariyomo et al., 2013), boldness in Seabass (*Dicentrarchus labrax*; (Ferrari et al., 2016),  
37 boldness and aggression in Brown trout (*Salmo trutta*) (Kortet et al., 2014), suggesting that it  
38 may be possible to select individuals on the basis of behavioural traits.

39 One way to influence the behaviour in a farming context in order to increase welfare is to add  
40 complexity to the rearing condition (Huntingford, 2004; Näslund and Johnsson, 2016). The  
41 addition of a 3D physical enrichment (i.e., plastic plants and/or stones) can increase the  
42 environmental complexity and decrease maladaptive and aberrant traits compared to those  
43 observed in fish reared in a plain environment (Macaulay et al., 2021). It is also argued that  
44 physical complexity plays a major role in the development of such trait. According to Réale et  
45 al (2007) a behavioural trait can be biologically explained by the number of genes involved in the  
46 expression of this trait. It simply refers to the fact that the influence of the genetic background in a  
47 given environment will affect the expression of a given trait (i.e., Risk-taking). Indeed, the  
48 environmental influences at an early stage of development could affect the expression of a  
49 behavioural traits later in the lifespan (Stamps and Groothuis, 2010). Nevertheless, the effect of  
50 gene and environment could not be seen independently when the genotype of individuals is  
51 divergent (i.e., different populations in different environments) because both affect the expression  
52 of personality (i.e., among-individual consistency in behavioural trait) (Réale et al., 2007; Stamps

53 and Groothuis, 2010). Domesticated species tend to share the same genotype across selected  
54 generations but could however experience different environmental conditions and this is precisely  
55 where they are likely to express different behavioural traits (Cabrera et al., 2021; Castanheira et  
56 al., 2017; Ferrari et al., 2016; Johnsson et al., 2014; Stamps and Groothuis, 2010).

57 Several methodological approaches have been used to assess personality in fishes, including  
58 individual-based tests such as confinement in rainbow trout (*Oncorhynchus mykiss*; (Øverli et  
59 al., 2007, 2004), feeding recovery in a novel environment in African catfish (*Clarias*  
60 *gariepinus*; (Martins et al., 2006)) and the Nile tilapia (*Oreochromis niloticus*; (Martins et al.,  
61 2011)), exposure to a novel object in Nile tilapia (Martins et al., 2011), aggression tests in  
62 rainbow trout (*Onchorynchus mykiss*; (Øverli et al., 2007)) or boldness in Atlantic salmon  
63 (*Salmo salar*; (Benhaïm et al., 2020)). Most behavioural tests are therefore carried out in  
64 isolation conditions which appears to somewhat limit their use from a selective breeding  
65 perspective because these tests are too time consuming. To address this drawback, group-based  
66 tests have been developed. Most of these tests concern risk-taking in Seabass (*Dicentrarchus*  
67 *labrax*; (Ferrari et al., 2015)) or common carp (*Cyprinus carpio*; (Huntingford et al., 2010)).  
68 However, the link between individual- and group-based tests has not yet been clearly  
69 established. No link has for example been found in Seabass and Gilt head seabream  
70 (Castanheira et al., 2013; Ferrari et al., 2015; Millot et al., 2009).

71 It appears essential to characterize risk-taking behaviour in order to evaluate the potential  
72 ability of the targeted fish species to cope with potentially stressful conditions in their rearing  
73 conditions and to ensure good welfare conditions. Furthermore, selective breeding is widely  
74 practiced in fishes and selection has often been applied to growth as a major trait of interest.  
75 However, the distribution of behavioural traits within a group may play an important role in  
76 the welfare of reared fish (Adams and Huntingford, 2005). Developmental aspects such as  
77 raising conditions are of fundamental interest for behavioural traits and there are potential links

78 between risk-taking and growth performances. Indeed, risk-taking as well as other behavioural  
79 traits are known to influence growth parameters (Biro and Stamps, 2008). A link has been  
80 found between self – feeding behaviour and coping - styles (in Tilapia and Seabass (Benhaïm  
81 et al., 2017; Ferrari et al., 2014)), as well as a link between individual growth performance  
82 and various behavioural traits (Ferrari et al., 2016; Huntingford et al., 2010; Sundström et al.,  
83 2004). The link between individual performances and behavioural traits has been found to be  
84 context and/or species dependent. For example, boldness and swimming activity were  
85 positively correlated with growth rate in common Sole (*Solea solea*; (Mas-Muñoz et al., 2011)),  
86 whereas a negative correlation was found in Seabass, where shyer fish exhibited higher growth  
87 rate in a predictable environment in terms of food supplies. In studies on common carp, seabass  
88 and seabream, metabolic rate was found to be significantly higher in risk – taking fish (Herrera  
89 et al., 2014; Huntingford et al., 2010; Jenjan et al., 2013; Killen et al., 2011) whereas in species  
90 with a passive benthic lifestyle, such as the Senegalese sole (*Solea senegalensis*), bold  
91 individuals were shown to consume less oxygen (Martins et al., 2011). Therefore, there is  
92 clearly a need to develop tools that assess the behavioural among-individual variation in farmed  
93 species to improve their welfare and likely their farmed value.

94 In Nordic countries, Arctic charr (*Salvelinus alpinus*) is widely used in aquaculture for food  
95 production and represents a considerable economic value (Imsland et al., 2019). This  
96 production is the result of selective breeding programs run over the last 30 years with a focus  
97 on growth rate, feed conversion, survival rate, size, and age at maturation (Olk et al., 2019).  
98 However, no selection effort on behavioural traits has yet been carried out. In the present work,  
99 the effect of physical enrichment on the among-individual variation response in risk-taking  
100 behaviour was tested. Specifically, we compared this behavioural trait in an individual and a  
101 group-test over a short-term period in order to compare the among-individual variation in risk-  
102 taking consistency in both contexts and to verify whether there are correlated to each other. We

103 predicted (1) risk-taking behaviour to be repeatable in individual and group-based tests, (2) the  
104 existence of cross-context consistency in Arctic charr i.e., correlation between individual and  
105 group-based tests and, the influence of 3D physical environment on risk-taking behaviour  
106 repeatability in both contexts.

107 **Material & methods**

108 ***Biological model and housing***

109 An Icelandic aquaculture strain of Arctic charr from the Hólar University breeding program  
110 (Iceland) was used in this experiment. Eggs were incubated at 4°C in a flow through system.  
111 After hatching, the batch was split into six 20L-tanks with a biomass of 13.8 g per tank (i.e.,  
112 644 g.m<sup>3</sup>), which gave three replicates of each treatment. After first feeding (73 days post  
113 hatching; dph) three of the tanks were enriched in three dimensions for the environmental  
114 enrichment treatment: i.e., vertically with a green plastic plant, and horizontally with five black  
115 volcanic rocks. The temperature in the tanks was maintained at 5 ± 1 °C over the course of the  
116 experiment. The fish were fed three times a day (9:00, 13:00, 16:00) with commercial  
117 aquaculture pellets according to the Inicio guidelines (BioMar). The waterflow was 48 L.hour<sup>-1</sup>  
118 at hatching and increased gradually to 120 L.hour<sup>-1</sup> to keep the oxygen level at 100% of  
119 saturation. The batch was on a 12:12-hour light schedule.

120 ***Sampling and tagging***

121 A randomly selected sample of 32 individuals per tank was tagged. The tagging was done under  
122 anaesthesia (2-phenoxyethanol) at a concentration of 310 ppm at 259 dph. A small incision  
123 was made between the pectoral fins and a PIT-tag (Passive Integrated Transponder 1.4 x 8mm  
124 FDX-B PIT tags, Oregon RFID EU GmbH) was inserted into the peritoneal cavity. Behavioural

125 tests started 170 days after tagging, hence fish had totally recovered from the surgery at that  
126 time.

127 ***Experimental design***

128 Solitary and group risk-taking were each assessed twice, in an OFTS (i.e., Open Field Test  
129 with Shelter) and an GRT (i.e., Group Risk taking Test), respectively. The OFTS 1 (i.e., first  
130 trial repetition – R1) was assessed between 429 and 435 dph and the OFTS 2 (i.e., R2) between  
131 436 and 452 dph. The GRT 1 was assessed between 453 and 459 dph and GRT 2 between 453  
132 and 465 dph.

133 **Risk-taking**

134 ***Solitary risk-taking***

135 To assess the solitary risk-taking (SRT), an OFTS was used. The tests were carried out in a  
136 rectangular arena (29.5 cm x 39.7 cm) made of opaque white Plexiglas® with a shelter (6 cm  
137 x 14 cm) in its left corner (Figure 1). This non-forced test allowed individuals to stay hidden  
138 in the shelter. The decision to exit the shelter into the open area (i.e., exploration zone) was  
139 controlled by the individuals. The latency time to emerge from the shelter (s) was measured as  
140 a proxy of risk-taking. The OFTS arena was situated above a white LED backlight (110 x 110  
141 cm, Noldus, the Netherlands). A camera (Basler Ace acA1920-150 mm camera Germany, 30  
142 fps) was located 112 cm above the arenas and plugged into a computer. The videos were  
143 recorded using the Ethovision XT15 tracking software (Noldus, The Netherlands. The selected  
144 individuals were placed into the shelter through a roof door. After 5 minutes of acclimation the  
145 front door of the shelter was lifted, and the individuals were free to move around in the arena  
146 for 20 minutes. After 20 minutes the individuals were caught and anesthetized with 2-  
147 phenoxyethanol at a concentration of 310 ppm. The weight and the fork length were recorded,

148 and the individuals were returned to their home tank after full anaesthesia-recovery in clear  
149 freshwater.

150 ***Group risk-taking test***

151 To assess the among-individual risk taking in group, a Group Risk taking Test (GRT) adapted  
152 from Ferrari et al (2016) was used. The test was carried out in a 0.114 m<sup>3</sup> rectangular tank  
153 divided into three rooms (Figure 2): a dark shelter-room (0.0314 m<sup>3</sup>) covered by a black lid, a  
154 passing tunnel (0.0022 m<sup>3</sup>) and a risk-room (0.0314 m<sup>3</sup>). The device was in a flow through  
155 system (100 L.h<sup>-1</sup>). A white LED light was situated above the passing-tunnel and the risk-room.  
156 A PIT-tag reader circular antenna (diameter: 10 cm, Dorset) linked with an USB data logger  
157 (Dorset) was placed in the middle and around the tunnel. A group of 32 individuals were placed  
158 into the shelter-room by the roof door and acclimatized for 60 min. At the end of the  
159 acclimation time, the shelter-room front door was gently lifted, and the individuals were free  
160 to pass through the tunnel to access the risk-room for 24 hours (1440 min). The latency to first  
161 exit (s) was recorded. When the individual swam through the antenna, the PIT-tag number of  
162 the fish, the date and the time was recorded by the USB data logger. After the test, the  
163 individuals were caught and anesthetized with 2-phenoxyethanol at a concentration of 310  
164 ppm. The weight and the fork length were recorded, and the individuals returned to their home  
165 tank after full anaesthesia-recovery in clear freshwater.

166 **Statistical analysis**

167 All statistical analyses were performed using R v.1.4.1103 R Core Team, 2020. The  
168 assumptions for a linear mixed model and linear model (i.e., normality of residuals,  
169 homoscedasticity of the residuals and uncorrelated residuals) were examined and validated for  
170 each model.

171 ***Repeatability of risk-taking***

172 The repeatability was assessed using the package and function rptR (Nakagawa and Schielzeth,  
173 2010; Stoffel et al., 2017). This function allowed the use of a linear mixed model (LMM) and  
174 extract the variances of interest in order to calculate the repeatability estimates using Equation  
175 1. When the repeatability is calculated using the function, it is reasonable to follow a normal  
176 distribution for the response variable (Dochtermann and Dingemanse, 2013). A logarithm  
177 transformation of the latency in SRT and GRT was applied to fit a gaussian distribution. In the  
178 model, the logarithm of the latency to first exit of the shelter was the response variable, and the  
179 trial repetition was a fixed factor. The body mass was used as a covariate. The individual ID  
180 was used as a random factor. The parameters nboot and npermut allowed the formula to  
181 calculate the confidence intervals by random iterations and were set at 1000.

182 ***Among-individual correlation of risk-taking in solitary- and group-based test***

183 To assess the among-individual correlation of risk-taking behaviour between solitary- and  
184 group-based tests, generalized linear mixed model using Bayesian Markov Chain Monte Carlo  
185 (MCMC) methods were used with a non-informative parameter-expanded prior (Hadfield et  
186 al., 2010; Houslay and Wilson, n.d.). A bivariate model was used to associate SRT with GRT  
187 (i.e., joint response variables). The fixed effects were the trial repetition and the body mass.  
188 The individual ID was used as a random factor and defined as an unstructured covariance  
189 matrix in order to calculate the among-individual variance for the two response variables  
190 separately and for the covariance between them. Number of iterations were 420000; burn-  
191 in=20000; thin=100. To calculate the among-individual correlation (r) between the two risk  
192 taking tests, the posterior distribution of (co)variance between traits (i.e., cov(SRT, GRT))  
193 were divided by the product of the square root of their variances (Equation 2). The mean  
194 correlation estimate was extracted with the function mean and the confidence intervals with

195 the function HPDinterval. Here, as the correlation estimates can take on either positive or  
196 negative values, the credible intervals of correlation of the (co)variance (i.e., with standardized  
197 covariance to a scale of -1 to 1) were used to assess statistical significance (95% credible  
198 interval  $> 0$ ).

199 **Results**

200 ***Repeatability of risk-taking***

201 The repeatability estimates showed a significant consistency in both treatments and both risk-  
202 taking behaviours at short-time scale (Table 1; Enriched: SRT,  $R = 0.51 \pm 0.084$  [0.32, 0.68],  
203 GRT,  $R = 0.50 \pm 0.092$  [0.36, 0.63]. Plain: SRT,  $R = 0.50 \pm 0.095$  [0.43, 0.72], GRT,  $R = 0.45$   
204  $\pm 0.117$  [0.24, 0.59]).

205 ***Risk-taking correlation***

206 No association was found between SRT and GRT in either treatment. The correlation estimates  
207 were very low, and the confidence intervals spread between -1 and +1 (Enriched  $r = -0.22$  [-  
208 0.56, 0.17], Plain:  $r = 0.15$  [-0.29, 0.63]) (Figure 3, Table 2).

209 **Discussion**

210 The aim of this work was to assess the effect of two different contexts (i.e., solitary, and group)  
211 and treatments (i.e., enriched, and plain) on risk-taking behaviour. We examined if risk-taking  
212 behaviour was repeatable and correlated in different contexts across time in order to verify  
213 whether a GRT could be used as a selective breeding tool. In both contexts and treatments, the  
214 risk-taking behaviours were repeatable across a short period of 6 days. However, no correlation  
215 was found between the two contexts, suggesting that there are differences in risk-taking  
216 behaviours depending on the setting.

217 The results of this work are in accordance with those of previous studies that also showed  
218 consistency across a short-term period in individual context e.g., Seabass (Ferrari et al., 2014;  
219 Millot et al., 2009), Common carp (Huntingford et al., 2010) as well as in group-based context  
220 e.g, Seabass (Ferrari et al., 2015) and Gilthead seabream (Castanheira et al., 2013). It is  
221 therefore likely that risk-taking is repeatable across time in both contexts. Nevertheless, risk-  
222 taking was not cross-context consistent which indicates that different behavioural traits were  
223 expressed in each situation. An explanation for this difference is the influence of social  
224 interactions that are occurring when risk-taking behaviour is measured in a group context,  
225 which has been found in other studies. For example, no cross-context consistency has been  
226 found in Seabass despite independent repeatability in each context (Castanheira et al., 2013;  
227 Ferrari et al., 2015; Millot et al., 2009). The fact that cross-context correlations among  
228 behavioural traits is a fundamental aspect of animal personality theory, cross-context  
229 consistency in a behavioural trait is rarely found between individual and group-based contexts.  
230 In fact, cross-context consistency between individual and group-based tests has only been  
231 found in Gilthead seabream where group response to hypoxia was found to be correlated with  
232 individual feeding recovery (Castanheira et al., 2013).

233 Social interactions can be extremely complex in fish species and particularly in salmonids. It  
234 is likely that the relationships between individuals are dependent on the behavioural rank of  
235 each individual within a group. In other words, group organisation is mediated by among-  
236 individual variation in behaviour (Croft et al., n.d.); for example, bolder individuals become  
237 more dominant and shyer individuals become subordinates. Indeed, it is known that Arctic  
238 charr is a very territorial species with often one or two dominant individuals in one group  
239 (Adams et al., 1995). Therefore, one scenario that could explain the lack of cross-context  
240 consistency between individual and group contexts is the strong influence of social interactions

241 in Arctic charr and a need for subordinates to escape more dominant individuals in a group  
242 setting.

243 In this experimental setup, the group was at low density, and it is possible that an individual  
244 exiting the shelter-room does not express a risk-taking behaviour but rather escapes to the safe  
245 area to avoid dominant chase and aggression in the shelter-room i.e., the shy fish exit the safe  
246 area before the bold ones. Although these results do not explicitly support this hypothesis  
247 because no negative correlations between the individual and group were found, it seems likely  
248 that aggression could have been a factor influencing the exit behaviour (personal observation).  
249 Therefore, the time to exit the safe area could be somehow linked to the fish social rank, and it  
250 would be interesting to follow this idea further. This idea is also supported by studies on other  
251 salmonid species where the social rank could be correlated with risk-taking, i.e., risk-taking-  
252 aggressiveness syndrome as in Brown trout (Sundström et al., 2004) and Atlantic salmon  
253 (Adams and Huntingford, 2005).

254 Nevertheless, other scenarios where social learning and leadership could have driven exit  
255 behaviour could be put forward. These two theories are complementary to each other as social  
256 leaning refers to learning influenced by observation of other congeners, and this could lead to  
257 leadership where the initiation of a movement, made by one or some individuals is followed  
258 by the rest of the group (Galef and Giraldeau, 2001; Krause et al., 2000). Therefore, small  
259 groups of sociable (i.e., unrelated to boldness) individuals could have influenced the exit  
260 behaviour.

261 In conclusion, in the present study individual and group risk-taking behaviour were  
262 independently repeatable. However, no cross-context consistency was found, therefore, the  
263 group risk-taking test as designed in this experiment cannot be used to select for boldness in  
264 the Arctic charr. We also observed that the rearing condition did not have any effect on the

265 among-individual consistency or on the cross-context consistency. The theory of the  
266 development of among-individual consistency suggests that a series of continuous interactions  
267 between internal factors (i.e., genetic, and neural activity) and contextual factors (i.e.,  
268 environment) induces among – individual behavioural consistency (i.e., animal personality).  
269 Personality trait expression can be the result of epigenetic modifications (Stamps and  
270 Groothuis, 2010) based on a set of molecular processes altering genes activity and the  
271 maintenance of genetic activity variation mostly occurs through genotype by environment  
272 interaction (Réale et al., 2007; Stamps and Groothuis, 2010). Here, the fact that we did not find  
273 any difference in the among-individual structure of risk-taking between the two treatments  
274 suggest that genetic factors explained most of the behavioural phenotype and/or that the  
275 enrichment did not induce any developmental change over the period of this experiment.  
276 Further research is needed to better understand the link between individual and group  
277 behaviour. Indeed, it seems that social interaction strongly affects the risk-taking behaviour  
278 resulting in a biased behavioural measure (i.e., exit behaviour is not always a reliable risk-  
279 taking behaviour proxy). It is important to note that the measured behaviour is independently  
280 repeatable in both tests, which indicates that Arctic charr express different behavioural trait in  
281 group and solitary context. We therefore recommend further investigation into group and  
282 solitary risk-taking and social interaction (i.e., aggression, social learning, and leadership) in  
283 order to disentangle the real among-individual variation of risk-taking behaviour in the Arctic  
284 charr.

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292 **Credit authorship contribution statement**

293 **Joris Philip:** Investigation, GRT experimental device, Data curation, Statistical analysis,  
294 Writing original draft. **Marion Dellinger:** Data curation, Review-original draft. **David**  
295 **Benhaïm:** Funding acquisition, Supervision, Data curation, Review and editing.

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439 **Tables :**

Table 2: Repeatability estimates (R), standard error (SE) and confidence intervals (CI) in both risk-taking behaviours (i.e., solitary and group risk-taking, respectively SRT and GRT) and treatments (i.e., enriched, and plain).

<b>Trait</b>	<b>Treatment</b>	<b>R</b>	<b>SE</b>	<b>CI</b>
SRT	Enriched	0.51	0.084	[0.329, 0.683]
	Plain	0.50	0.095	[0.433, 0.723]
GRT	Enriched	0.50	0.092	[0.362, 0.639]
	Plain	0.45	0.117	[0.243, 0.592]

440

441

Table 1: Correlation estimates (r) and confidence intervals (CI) of group and risk-taking behaviours between treatments (i.e., enriched, and plain).

442

<b>Trait</b>	<b>Treatment</b>	<b>r</b>	<b>CI</b>
SGR, GRT	Enriched	-0.22	[-0.56, 0.17]
	Plain	0.15	[-0.29, 0.63]

447 **Equations:**

448 Equation 1 :

449  $\sigma^2(\text{Individual})$

450  $R = \frac{\sigma^2(\text{Individual})}{\sigma^2(\text{Individual}) + \sigma^2(\text{Residuals})}$

452

453 Equation 2:

454  $r(\text{Ind}_{\text{SRT}}, \text{Ind}_{\text{GRT}}) = \frac{\text{cov}(\text{ind}_{\text{SRT}}, \text{ind}_{\text{GRT}})}{\sqrt{\sigma^2 \text{ ind}_{\text{SRT}} \times \sigma^2 \text{ ind}_{\text{GRT}}}}$

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459 **Figures captions :**

460 Figure 1: Open Field Test with Shelter device. a. Front view of the overall device. b. Schematic  
461 (top view) of the arena.

462 Figure 1: Group risk-taking device. The water inlet (a) is situated in the shelter room and the  
463 outlet (b) in the passing room. To prevent from unbalanced oxygen concentration throughout  
464 the rooms, an oxygenation was constantly running in a back of the risk – room. The door was  
465 tied to a rope through two pulleys. When the acclimation time was over, the door was lifted  
466 through the rope.

467 Figure 3: Correlation estimates of trait association. The point is the mean estimate and the  
468 line the confidence interval.

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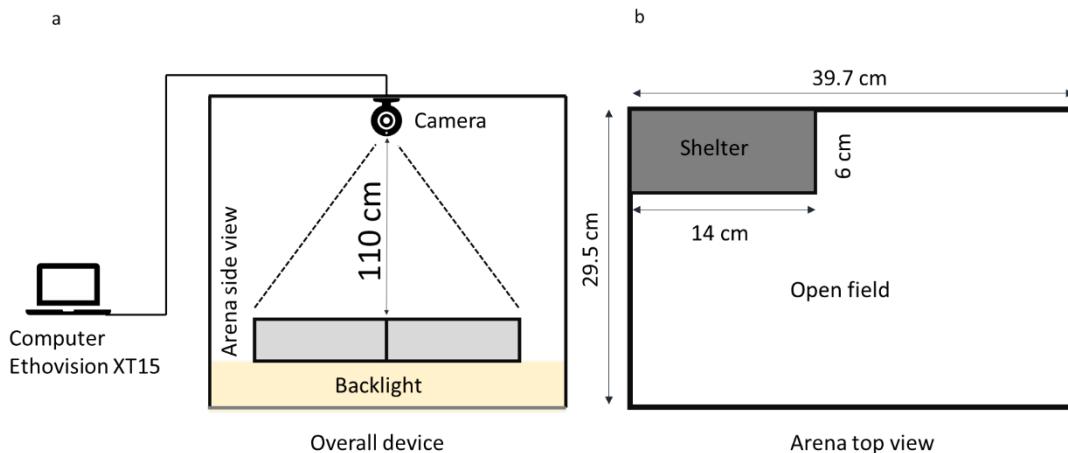


Figure 3: Open Field Test with Shelter device. a. Front view of the overall device. b. Schematic (top view) of the arena.

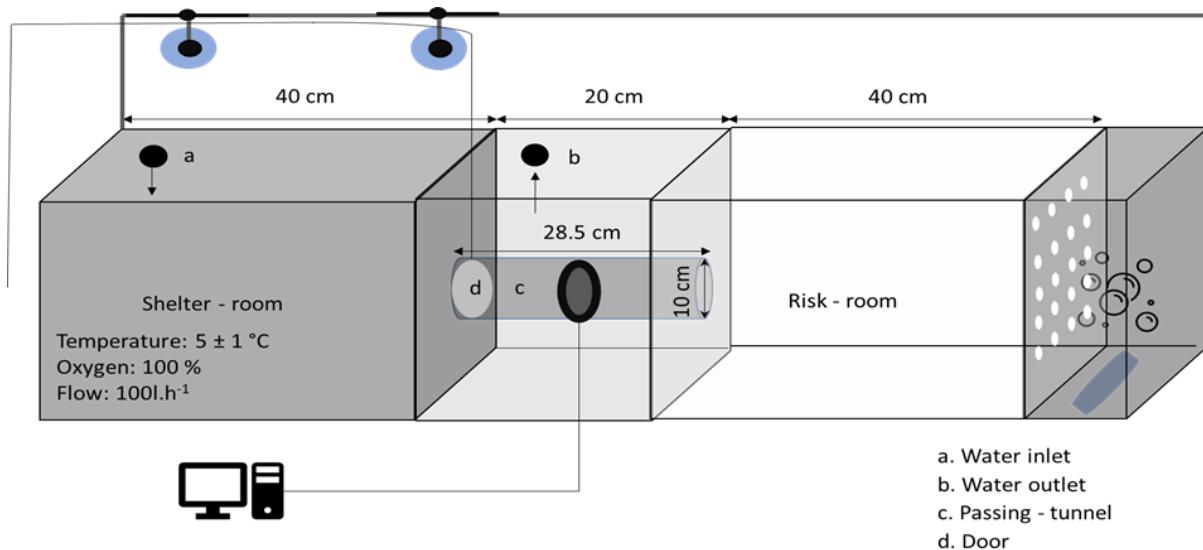


Figure 2: Group risk-taking device. The water inlet (a) is situated in the shelter room and the outlet (b) in the passing room. To prevent from unbalanced oxygen concentration throughout the rooms, an oxygenation was constantly running in a back of the risk – room. The door was tied to a rope through two pulleys. When the acclimation time was over, the door was lift through the rope.

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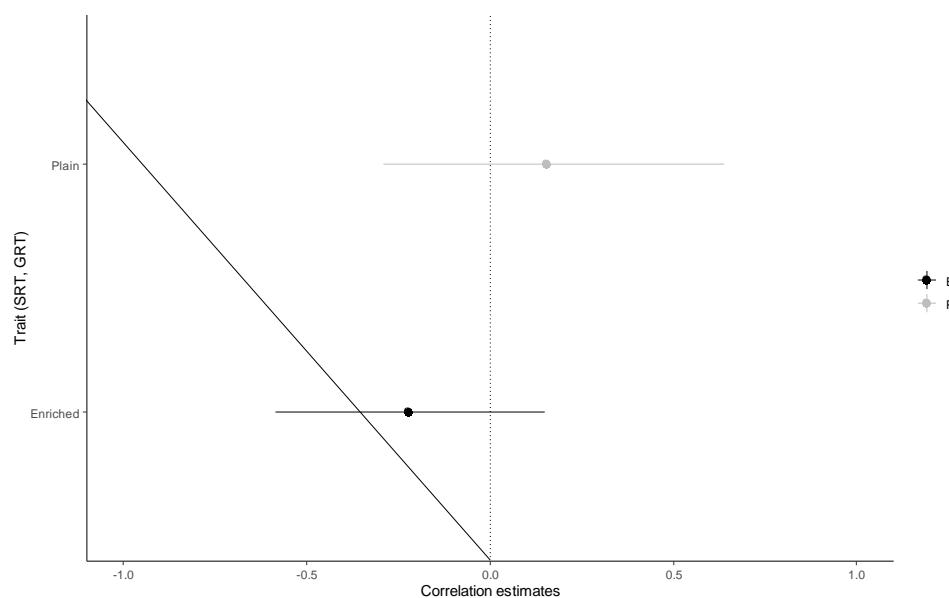


Figure 4: Correlation estimates of trait association. The point is the mean estimate and the line the confidence interval.