1   Plasticity and consistency of behavioural responses to predation risk in laboratory

2   environments

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ABSTRACT

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32   The individual animal is currently a major focus of behavioural research and an increasing

33   number of studies raise the question of how between-individual behavioural consistency and

34   behavioural plasticity interact. Applying the reaction norm concept on groups, our study

35   addresses both of these aspects in one framework and within an animal's natural social

36   environment. Risk-taking behaviour in one-year-old perch (*Perca fluviatilis*) was assayed in

37   aquarium experiments before and after the fish were subjected to the presence or absence of a

38   piscivorous predator for three weeks. To analyse the inter-individual behavioural variation

39   across the repeated measurements, we dissected the behavioural change across the predator

40   treatment into individual constant and plastic components using hierarchical mixed effects

41   models. During the predator treatment juvenile perch increased in boldness and decreased in

42   vigilance, the magnitude of these behavioural changes was influenced by group composition.

43   However, the behavioural changes were not influenced by the presence of a predator,

44   indicating the difficulties in generating realistic long-term predation pressure in the

45   laboratory. Individuals differed in the relative increase in boldness across the predator

46   treatment and, thus, varied in the shape of their reaction norms. In accordance, the best linear

47   unbiased predictors (BLUP), extracted from the random effects of separate linear mixed

48   effects models for the data before and after the predator treatment were only weakly

49   correlated. Hence, between-individual variation seems to change under laboratory conditions

50   and therewith not necessarily represents the initially present "natural" variation, giving

51   important implications for the conduction and interpretation of behavioural experiments.

INTRODUCTION

Behaviour is considered to be one of the most plastic phenotypic traits (Price et al. 2003) and many studies have documented the potential plasticity of behavioural traits in a variety of animals [mammals (Hayes & Jenkins 1997), cephalopods (Sinn et al. 2007), insects (Agrawal 2001), birds (Cresswell & Quinn 2005; Miller et al. 2006), fish (Coleman & Wilson 1998)]. Since a shift in focus to the individual, an increasing amount of studies have reported consistent behavioural differences within animal populations (reviewed in Sih et al. 2004; Bell 2007), but also between individual plasticity *per se* (Dingemanse et al. 2010). The observed consistent behavioural differences across time or situations have been ascribed to an animal's underlying distinct personality, also termed coping style, temperament or behavioural syndrome (Koolhaas et al. 1999; Sih et al. 2004; Dingemanse & Reale 2005). These, initially contradictory, findings raise the question of how inter-individual variability and intra-individual stability interact (Nussey et al. 2007; Dingemanse et al. 2010). Studies on fish have shown that behavioural stability along the shy-bold axis varies between species, but also within a species, when studied with regard to behavioural traits or situations. Wilson et al. (1993) found that pumpkinseed sunfish exhibited constant behavioural differences in the wild, and that these differences disappeared after the fish were held in the laboratory for some time. In sticklebacks, high predation risk altered the degree of aggression a stickleback displays towards conspecifics, and the observed overall decrease in boldness was due to selective predation, as the individual's degree of boldness did not change (Bell & Sih 2007).

Clearly, behavioural differences may have important fitness consequences (Dingemanse et al. 2004; Smith & Blumstein 2008). However, to assess the selective value of a trait, there is a need to understand how variable it is, both between and within individuals (Boake 1989; Hayes & Jenkins 1997; Dingemanse et al. 2010). One approach simultaneously addressing

81   variability and consistency is the reaction norm concept (Via et al. 1995; Nussey et a. 2007),

82   where an individual's behaviour is tested repeatedly along an environmental gradient. The

83   behavioural differences along the environmental gradient represent the plastic ability at the

84   population level. Deconstructed to the individual level, the presence of an interaction between

85   individual reaction and environment (I x E) suggests that individuals differ in their plastic

86   ability (Nussey et al. 2007; Briffa et al. 2008; Martin & Reale 2008; Dingemanse et al. 2010).

87   In juvenile Eurasian perch, *Perca fluviatilis* L., relative differences in boldness towards a

88   predator have been shown to be consistent between individuals across different social

89   contexts (Magnhagen & Bunnefeld 2009). Perch also display a high degree of behavioural

90   plasticity, changing their behaviour with status of nourishment (Borcherding & Magnhagen

91   2008), consumed prey (Heynen et al. 2010), social background (Magnhagen & Staffan 2005)

92   or the experienced intensity of predation pressure (Magnhagen & Borcherding 2008;

93   Hellström & Magnhagen 2011; Magnhagen et al. 2012).

94   The aim of the present study was to investigate whether the inter-individual behavioural

95   variation within a group of perch changes with the adaptation to a novel situation.

96   Furthermore, we wanted to test whether and how such changes, if any, are influenced by

97   predation risk. Boldness towards a predator was measured in groups of juvenile perch, before

98   and after participating in a three week tank treatment in absence or presence of an adult

99   piscivorous perch. To analyse the consistency of the inter-individual variation across the

100   repeated measurements, we compared the behavioural ranking within the same groups before

101   and after the predator treatment and the variation in the groups that experienced a predator

102   during the three weeks in the tank with those without predation risk. Using mixed effects

103   models to analyse our data, we were able to dissect the obtained behavioural variation across

104   the phenotypic response, at the group level, into individual constant and plastic components.

105

MATERIAL AND METHODS

In June 2009 one-year-old juvenile perch (body length, $X \pm SD$; 90.3 ± 6.4 mm, weight 7.4 ± 1.7 g, $N = 96$) were caught with a beach seine in Lake Ängersjön, close to the city of Umeå, Sweden (63° 47′N; 20°17′E). The fish were transported to Umeå Marine Research Centre (UMF, 45 km south of Umeå). In the 100-litre transport vessel, a pump run by a car battery was constantly recirculating and oxygenating the water. The fish were stocked to a circular tank (60 cm high, 0.471 m^2) with continuously running water (13L:11D, 14-15 °C) to acclimate to indoor conditions (5 or 10 days). They were fed daily with pre-frozen red chironomid larvae (6% of total body mass). The predators, older perch (body length, $X \pm SD$; 200.8 ± 13.5 mm, $N = 15$), were caught in a small stream near the laboratory and fed with earthworms daily. Fulton's condition factor was used as measure of the physical condition of the fish ($K=10^5 M*TL^{-3}$, where M=weight in g and TL=total length in mm; Bagenal & Tesch 1978). After the experiments the tested fish were killed with an overdose of MS222. The predator perch were released into their natural habitat.

Experimental design

Before being handled all fish were sedated with MS222. The juvenile perch were marked with individual colour codes, generated with 4 different colours and carefully applied with a needle and tattoo colours (Tattoo-Flame©) on the upper and/or lower caudal fin. Subsequently, fish were weighed, measured and randomly assigned to groups of four ($N = 24$ groups). Each group participated in two sets of behavioural experiments, the first one directly before and the second one directly after being exposed to a three week predator treatment in tanks (Table 1). After the first set of behavioural experiments were conducted, 4 groups were added to each of the 6 tanks used for the predator treatment ($N = 24$ groups). Those six tanks (60 cm high, 0.471 m^2, 50% cover with artificial vegetation) were circular and had continuously running

131   water. After three weeks all fish were collected from the tanks, sedated, weighed, measured

132   and the behaviour of the same groups was re-assayed (second set of behavioural experiments),

133   in the same way as during the first set of behavioural experiments. Due to the limited capacity

134   of experimental aquaria, the study was conducted in two successive experimental blocks,

135   starting five days apart. 12 groups (48 individuals) were tested in each block (see Table 1).

136

137   *Predator treatment*

138   In the experimental block 1 two tanks were stocked with a predator and one tank was predator

139   free, while the opposite was done for block 2, resulting in 3 predator and 3 non-predator tank

140   treatments. In each experimental block juvenile perch were allowed to acclimate to the tank

141   for one day before the predators were added. To generate a real impression of danger, but to

142   minimize the consumption of prey individuals the predator size ratio was chosen close to the

143   maximal border of ingestability (literature data: 0.45, Claessen et al. 2000; our data: $X \pm SD$;

144   0.39 ± 0.03 mm, range $0.34 - 0.45$) and the predator was only allowed to swim free in the

145   tank for 6 days out of the 21 days of the experiment. After 6 days the predator was transferred

146   into a transparent perforated plastic box (41 x 26 x 29 cm) within the tank, so that visual and

147   olfactory predator cues were still present. The tanks without predators were treated the same,

148   a net was swept through the tank and the box was opened and closed. During the tank

149   treatment juvenile fish were fed with pre-frozen chironomid larvae daily (6% of total body

150   weight) and the predators with earthworms every second day.

151

152   *Experimental aquaria*

153   The experimental aquaria were 170 l (95 x 41 x 44 cm) and had continuously running water

154   (17 °C; light regime 13L:11D). One-third of each aquarium was separated with a plastic net

155   (mesh size 5 mm) and used for the predator, the rest for the group of juvenile perch. To

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156 prevent the fish habituating to the predator during the behavioural assays an opaque plastic

157 screen was placed next to the net. The water inlet was placed in the section with the small

158 perch and the outlet in the predator section to minimize olfactory cues between observations.

159 The bottom of the aquaria was covered with gravel. Artificial vegetation was provided in the

160 predator space and in the half of the space for the perch group that was furthest away from the

161 predator.

162

163 *Behavioural experiments*

164 Both sets of behavioural experiments (before and after the predator tank treatment) consisted

165 each of three repeated observations. Prior to each set of three behavioural observations the

166 small perch were acclimatized to the aquarium for 3 days and fed daily with red chironomid

167 larvae in the open area. The fish were then observed three times, twice on the first day with a

168 break of three hours between experiments and once on the second day. Before each

169 observation the juvenile perch were enclosed by the opaque screen in the half of their section

170 that also contained the vegetation. Chironomid larvae (approx. 75 larvae, corresponding to 3%

171 of the total fish weight) were poured into the open space produced between the net and the

172 opaque screen and allowed to sink to the bottom. The observation started by lifting the opaque

173 screen, making the large perch visible to the juvenile perch though the net. Each aquarium

174 was observed for 10 min. The observer recorded (in real time) four different activities for

175 each individual fish: occurrence in the vegetation, occurrence in the open, feeding and

176 predator inspection. Thereby, feeding was defined as being oriented towards the bottom and

177 attacking the food and predator inspection as being within two fish lengths distance of the net

178 and being orientated exactly towards the predator. The activities were entered into a computer

179 program, which record one behavioural unit every second. The recorded behavioural data

180 were used to calculate 7 behavioural variables: (1) time spent in the open area, (2) total time

8

181 spent feeding, (3) time to start feeding, (4) duration of the first feeding bout, (5) activity

182 (number of changes between open area and vegetation), (6) time until first change of habitat,

183 and (7) time spent with predator inspection. After each observation the opaque screen was put

184 back next to the net. Each group was always tested in the same aquaria and in presence of the

185 same predator. The predators used during the behavioural experiments were different from

186 those used during the predator treatment in the tanks.

187

188 *Statistical analyses*

189 One group of four fish was excluded from the analyses, as two of its members were lost

190 during the tank treatment (non-predator tank treatment), leaving a total of 23 groups and 92

191 individuals that were used for the analyses.

192 All 7 calculated behavioural variables were entered into a principal component analyses

193 (PCA). By using a PCA we are able to use all data, and gain information about the

194 relationship of the different variables to each other. The resulting scores illustrate an

195 individual´s personality type rather than an isolated behaviour and retain the structure and

196 variation present in the recorded data. We retained all extracted principal components with

197 eigenvalues larger than 1 for further analyses.

198 To control for a possible ceiling effect due to the limit of the behavioural assays (10 min), we

199 conducted a second PCA including an additional imaginary individual, which was given

200 maximal values in each variable.

201 To analyse the effect of the predator tank treatment on the extracted principal components a

202 linear mixed effect model approach was set-up. To avoid pseudoreplication in the analysis a

203 nested design was created. Within individual repetition (behavioural observation 1-3) was

204 added as random effect at the innermost level. Between-individuals within group was added

205 as the next level, between-groups in one tank was added at the following level and between-

tanks was added as random effect at the outer level. Treatment (before and after the predator tank treatment), experimental block (block 1 and 2) and their interaction were included as fixed effects with two factor levels each. Hence, the models for PC1 and PC2 were fit with the predictors of predator tank treatment, experimental block and their interaction and the random intercepts of within-individual repetition, individual, group and tank ID.

The effect of predator presence during the predator tank treatment was analysed incorporating only the data obtained after the predator tank treatment. Keeping the previously described structure of the random effects (within individual (repetition)/between individuals/between groups/between tanks), we included predator (predator or no predator during the treatment), experimental block (block 1 and 2) and their interaction as fixed effects.

The equivalent mixed-effect model was run using the behavioural data from before the tank treatment, including only experimental block (block 1 and 2) as fixed effect. The most parsimonious models for the separate data from before and after the tank treatment were derived by testing the fixed effects using Wald statistics (Pinheiro & Bates 2000).

To obtain an individual score for the relative ranking of an individual within its group we extracted the best linear unbiased predictors (BLUPs) of the random effect of `between individuals` from the two most parsimonious models for PC1 for before and after the tank treatment (Magnhagen & Bunnefeld 2009). Using a linear model, BLUPs from before were correlated with the BLUPs from after, to analyse the relative individual behavioural consistency across the predator tank treatment (before and after). Additionally, we analysed the relative individual behavioural consistency across the predator tank treatment (before and after) using the average (observation 1-3) of the seven calculated behavioral variables and Kendall correlations, as the data was not normally distributed.

To analyse the magnitude of the behavioural change, the difference between the behaviour before and the behaviour after the predator tank treatment was calculated (PC1 after – PC1

231 before). The difference between the behaviour before and the behaviour after the predator

232 tank treatment was used as response variable to run a linear mixed effect model. In this model

233 we used the same nested hierarchy for the random effects as stated above (within individual

234 (repetition)/between individuals/between groups/between tanks). In addition to the categorical

235 fixed effects experimental block and predator, the mean change of the accompanying group

236 members (company change) and the change in condition factor during the predator tank

237 treatment (condition factor after – condition factor before) as continuous fixed effects.

238 The free software R for statistical computing (R Development Core Team 2009) was used for

239 all analyses. The PCA (*prcomp*) and the correlation (*lm*) were calculated with the standard

240 *stats* library. The library *nlme* v.3.1.-90 was used to run the mixed effect models.

241

242 *Ethical note*

243 No prey individual was consumed or harmed (no bite marks or injuries) during the

244 experiments. The experiments in this study comply with the guidelines of the Association for

245 the Study of Animal Behaviour, and were approved by the Local Ethics Committee of the

246 Swedish National Board for Laboratory Animals (CFN, license no A94-06).

247

248 **RESULTS**

249 The PCA on the 7 behavioural variables produced two principle components with eigenvalues

250 > 1 (PC1 and PC2), explaining together 72.5% of the variation (Figure 1). Positive scores on

251 PC1 indicated more time in the open, more time feeding, a longer duration of the first feeding

252 bout, a lower latency to leave the vegetation and lower latency to start feeding, which would

253 signify a fish with a high degree of boldness. Positive scores on PC2 indicated more time

254 spent with predator inspection and a lower duration of the first feeding bout, specifying

255 vigilance. Including an imaginary individual with maximal values in all variables in a second

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256   PCA showed that the boldest observed individual in our study showed 71.9% of the possible

257   maximum boldness, indicating that our results are not biased by any ceiling effect.

258

259   *The effect of the predator treatment*

260   The presence of a predator during the tank treatment did not have any effect on PC1

261   (boldness) and PC2 (vigilance) (Table 2), neither did experimental block, nor their interaction

262   show a significant effect. However, after the predator treatment, perch were significantly

263   bolder and less vigilant than before treatment (Table 3, Figure 2). For PC1 the predator

264   treatment additionally showed a significant interaction with the experimental block (Table 3).

265   Before the tank treatment PC1 scores were slightly lower for the first block than for the

266   second, while these relations were absent after the predator treatment.

267

268   *Magnitude of behavioural change*

269   For PC1, the most parsimonious models using the separate data from before and after the

270   predator treatment were the models without any fixed factors, which were used to extract the

271   BLUPs. The BLUPs for individual perch before the predator treatment were correlated with

272   the BLUPs from after the predator treatment (t_{90} = 2.3, P = 0.02, r^2 = 0.05), however, the data

273   points are scattered (Figure 3), and the low r^2-value indicates that the correlation is weak and

274   95% of the variation remains unexplained. Similarly, out of the seven calculated behavioral

275   variables, the behavior before and after the predator treatment was only significantly and

276   weakly correlated for two behavioral variables (Total time spend in the Open: p = 0.001;

277   Kendall's tau coefficient 0.235; Time until first change: p < 0.001; Kendall's tau coefficient

278   0.289).

279   During the predator treatment juvenile fish slightly decreased in condition factor ($t_{177.78}$ =

280   6.49, P = 0.001; condition factor, X ± SD.; before 0.99 ± 0.06, after 0.93 ± 0.08). This change

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281   in condition factor did not affect the magnitude of behavioural change (PC1 after the tank

282   treatment – PC1 before the predator tank treatment), nor did predator presence or the

283   experimental block (Table 4). An individual´s magnitude of change was significantly

284   influenced by the mean difference between the scores before and after predator treatment of

285   the accompanying group members (Table 4), in a way that the individual magnitude of change

286   increased with increasing company change (Figure 4).

287

288   **DISCUSSION**

289   We could show that the behavioural reaction towards a predator in groups of juvenile perch

290   can be expressed by two distinct behavioural axes. The behavioural measures that load on the

291   first (PC1) axis (e.g. time spent in the open or time to start feeding), comply with those used

292   in other studies on fish to investigate differences in boldness (Snickars et al. 2004;

293   Magnhagen & Borcherding 2008). Further, the variation in PC2 scores mainly reflects

294   whether the fish performed predator inspection or not, generally interpreted as vigilance

295   (Pitcher 1992).

296   Comparing the scores of the same groups of juvenile perch, before and after they participated

297   in the three week predator tank treatment, showed that juvenile perch increased in boldness

298   (PC1) and decrease in vigilance (PC2) across the repeated measurements. Similar results were

299   previously interpreted as habituation effects to a novel environment, represented by the

300   laboratory conditions (Millot et al. 2009), but were also observed in response to decreasing

301   predation risk (Goldenberg et al. 2014). Surprisingly, we found no behavioural difference

302   between the fish that experienced a predator during the treatment and those without predator

303   cues, although perch generally seem to adapt their behaviour to the experienced level of

304   predation pressure (Magnhagen & Borcherding 2008; Magnhagen et al. 2012; Goldenberg et

305   al. 2014). Laboratory studies have shown that juvenile fish rely on predator cues to optimize

the trade-off between foraging and anti-predator reaction, where juveniles responded strongest

to the connections of olfactory and visual cues (Mikheev et al. 2006; Martin et al. 2010).

When predator and prey belong to the same species the diet of the predator (Mirza & Chivers

2001), but also the relative size of prey and predator may be important factors influencing the

behavioural reaction (Lundvall et al. 1999). The predators in our study were fed earthworms,

but the prey/predator size ratio in the tanks was below the maximal ratio for ingestability

(Claessen et al. 2000) and juveniles responded to quick movements of the equally large

predators in the aquaria. However, fish are capable of learning (Braithwaite & Salvanes 2008)

and to habituate to initially threatening cues (Meliska & Meliska 1976), suggesting that, after

a habituation period the predator, confined to a box, might not have been considered a real

danger. Those results are indicative for a general problem and highlight the difficulty in

generating naturalistic, but harmless scenarios of predation risk, to study the effects of long-

term predation pressure in laboratory environments.

Analysing the behavioural consistency, we found a significant correlation of the BLUPs from

before and after the predator tank treatment, this correlation explained 5% of the variation (r^2

$= 0.05$). This indicates that the consistency of inter-individual behavioural differences within

a group of perch was rather low in this study. Individuals differed in the relative increase in

boldness across the predator tank treatment and, thus, varied in the shape of their reaction

norms. The analysis of the individual magnitude of behavioural change showed that the

individuals in our study were not influenced by changes in condition, which is a known factor

to alter boldness in juvenile fish (Vehanen 2003; Borcherding & Magnhagen 2008). Instead,

there was a relationship between the individual and the accompanying group members, as

individual magnitude of behavioural and the magnitude of behavioural change of the

accompanying group members were positively correlated. In many social species the

members of a group have been found to influence each other (Krause & Ruxton 2002). The

331 behavioural conformity in a group facilitated by these social mechanisms has been suggested

332 to further confuse an attacking predator (Zheng et al. 2005; Tosh et al. 2009). Thus, our result

333 suggests that the individuals within a group influenced each other in the magnitude of their

334 behavioural change, probably reflecting social constraints and increasing behavioural

335 conformity (Laubu et al. 2016).

336 Comparing the influence of holding conditions on the outcome and comparability of

337 behavioural experiments in birds, Miller et al. (2006) could show that the holding conditions

338 (e.g. presented food or structure within the cage) may substantially alter the obtained results

339 of behavioural experiments. Our results suggest that also the holding time might be a crucial

340 factor affecting behaviour, as the between-individual variation seems to change along the

341 temporal gradient and therewith not necessarily represents the initially present "natural"

342 behavioural variation. These results emphasize the practical implications of the reaction norm

343 concept and the benefits of measuring behavioural variation repeatedly across an influential

344 gradient.

345

346 In conclusion, we found juvenile perch to increase in boldness across the repeated

347 measurements, phenotypically adapting their behaviour to the predator tank treatment, but

348 individuals differed in the shape of their reaction norms. The magnitude of behavioural

349 change was influenced by group composition. However, there was no behavioural difference

350 between the fish that experienced a predator during the tank treatment and those without

351 predator cues, indicating the general difficulties in generating realistic long-term predatory

352 threat in laboratory environments. Furthermore, the between-individual variation seems to

353 change along the temporal gradient and therewith not necessarily represents the initially

354 present "natural" variation, emphasizing the importance of repeated behavioural

355   measurements and highlighting that initial holding/ laboratory acclimatisation time needs to

356   be chosen carefully.

357

358   *Acknowledgments*

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478　Tables

479　Table 1: Experimental design

480

	Block 1	Block 2
Day 1-5	acclimatization in tank	acclimatization in tank
Day 6-8	acclimatization to aquaria	acclimatization in tank
Day 9-10	behavioural experiments "before"	acclimatization in tank
Day 11-14	predator treatment	acclimatization to aquaria
Day 15-16	predator treatment	behavioural experiments "before"
Day 16-31	predator treatment	predator treatment
Day 32-34	acclimatization to aquaria	predator treatment
Day 35-36	behavioural experiments "after"	predator treatment
Day 38-40		acclimatization to aquaria
Day 41-42		behavioural experiments "after"

481

482   Table 2: Wald statistic for the fixed effects for PC1 and PC2 before and after the predator tank

483   treatment, tested separately with mixed effect models

484

	PC1 - boldness			PC2 - vigilance		
	F	df,df_{den}	P	F	df,df_{den}	P
Before						
Exp block	1.42	1,4	0.29	0.74	1,4	0.43
After						
Predator	1.18	1,2	0.39	0.24	1,2	0.67
Exp block	1.89	1,2	0.30	4.47	1,2	0.16
Predator x exp block	0.03	1,2	0.86	5.04	1,2	0.15

485

486

487 Table 3: Wald statistic for the fixed effects Treatment (before and after) experimental block

488 and their interaction for PC1 and PC2 tested with a mixed effect model

489

	PC1 - boldness			PC2 - vigilance		
	F	df,df$_{den}$	P	F	df,df$_{den}$	P
Treatment	*1160*	*1,270*	*0.001*	*8.87*	*1,270*	*0.003*
Exp block	0.37	1,4	0.57	4.85	1,4	0.09
Treatment x exp block	*21.69*	*1,270*	*0.001*	2.22	1,270	0.13

490

491

Table 4: Wald statistic for the fixed effects company change (mean magnitude of behavioural

change of the accompanying group members across the predator tank treatment), predator

(predator presence or absence during the treatment), condition factor change and experimental

block on the individual magnitude of change (before after difference in boldness score PC1

across the predator tank treatment)

497

	F	df,df$_{den}$	P
Company change	*43.28*	*1,179*	*0.001*
Predator	0.77	1,3	0.81
Condition factor change	0.14	1,68	0.52
Exp block	3.50	1,3	0.25

498

499

Figure legends

Figure 1: Biplot of the first two principal components, PC1 (Eigenvalue 4.02) and PC2 (Eigenvalue 1.06), extracted from a Principal Component Analysis (PCA) over the seven different measured behavioral variables [(1) time spent in the open area, (2) total time spent feeding, (3) time to start feeding, (4) duration of the first feeding bout, (5) activity (number of changes between open area and vegetation), (6) time to first change of habitat, and (7) time spent with predator inspection].

Figure 2: Mean boldness (PC1) and vigilance score (PC2) before and after the predator tank treatment, in absence or presence of a predator during the treatment
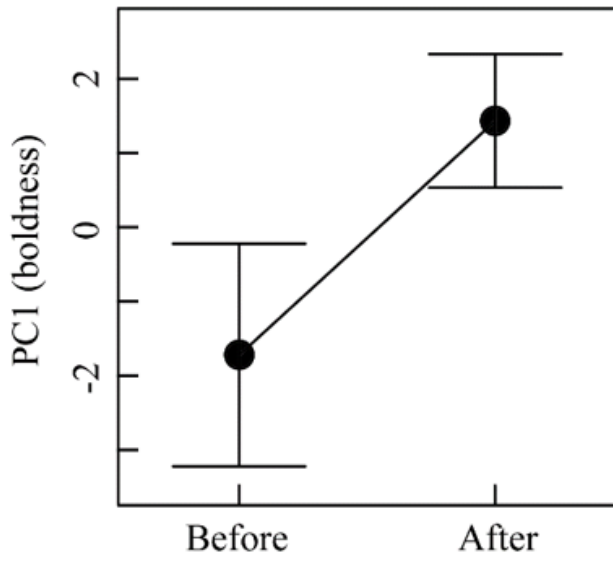
Figure 3: Correlation of the best linear unbiased predictors (BLUPs) from before the predator tank treatment with the BLUPs after the predator tank treatment, extracted on individual level from the most parsimonious mixed effect models for before and after the predator tank treatment, respectively

Figure 4: Mean individual increase in boldness (After – before difference PC1) plotted against the mean company difference (mean increase in boldness of the accompanying group members).