Invasive brook trout disrupts the diel activity and aggregation patterns of native brown trout

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1 **TITLE**

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26 ABSTRACT

27

28 In European streams, native brown trout (*Salmo trutta*) feed primarily on aquatic prey but consume a

29 higher proportion of terrestrial prey in sympatry with non-native brook trout *Salvelinus fontinalis*. This

30 is a rare example of diet convergence that may be associated with changes in diel activity or

31 aggregation pattern by brown trout in sympatry. We recorded the activity and positions of brown trout

32 from two origins and in two competition modes (allopatry versus sympatry, four combinations) placed

33 in replicated stream enclosures for 29 days to test these hypotheses. Brown trout originating from or

34 placed in sympatry were more diurnal and aggregated than those originating from or placed in

35 allopatry. Changes in the diel activity of brown trout placed in a novel competition mode occurred

36 progressively throughout the study. Thus, brown trout show strong behavioral flexibility in response to

37 the non-native competitor and can revert to allopatric behavior when brook trout is removed from the

38 system. These behavioral adjustments may have unsuspected effects on food webs and ecosystem

39 functioning, which deserves further attention.

40

41 **KEY WORDS:**

42

43 Allopatry, Biological invasions, Salmonidae, Sympatry

44 **INTRODUCTION**

45

46 Biological invasions have important ecological and evolutionary consequences on native biodiversity

47 (Strayer et al. 2006; Ehrenfeld 2010; Lowry et al. 2013). One of the most common and pervasive

48 effects of non-native species is competition for ecological resources (e.g. food and shelters) with native

49 species displaying overlapping habitat and/or trophic niches. This competition can have a number of

50 impacts on native species, such as reduced growth rate, increased mortality and displacement (Didham

51 et al. 2007). However, co-existence between native and non-native species can be facilitated by plastic

52 phenotypic changes such as behavioral adjustments allowing the partitioning in time and space of

53 resources used commonly by native and non-native species. Those include shifts in diel activity

54 patterns (Gerber et al. 2012), habitat use (Ayala et al. 2007), or prey selection (Strauss et al. 2006).

55

56   Because of competitive exclusion (Crowder and Snyder 2010), competition with non-native

57 species is generally expected to result in diverging resource selection (Day and Young 2004).

58 Depending on the relative competitive ability of non-native and native species, the former may change

59 their diet in response to the latter (Harrington et al. 2009), or vice-versa (Gerber et al. 2012).

60 Interestingly, co-existence between species using overlapping resources may also induce diet

61 convergence (Cucherousset et al. 2007; Fox and Vasseur 2008). Several hypotheses have been put

62 forward to explain this phenomenon. Convergence may occur when two species compete for several

63 nutritionally essential resources that are limited in abundance (Fox and Vasseur 2008). It may also be

64 caused by shifts in diel activity patterns (Gerber et al. 2012) or habitat use (Losos et al. 1993), whereby

65 native species feed on an alternative prey type that is more abundant during their new window of

66 activity or in their new habitat (Murdoch et al. 1975). Alternatively, diet selectivity of the native

67 species may change following the introduction of the non-native species, e.g. via inter-specific social

68   learning (Seppänen and Forsman 2007). Identifying the mechanisms behind such a seemingly counter-

69   intuitive phenomenon as diet convergence is crucial to understand how native and non-native species

70   interact. In particular, more empirical research is needed to evaluate to which extent the behavioral

71   plasticity of native species allows them to respond rapidly to competition with invaders (Strauss et al.

72   2006; Berthon 2015), and also how rapidly they may recover when measures are being taken to remove

73   non-native species.

74

75   Salmonids have been introduced worldwide (Stanković et al. 2015) and represent an ideal

76   model to study responses to invading competitors, as they demonstrate high behavioral plasticity (Dill

77   1983; Reebs 2002), and induce important ecological impacts on native salmonids (Buoro et al. 2016).

78   Brook trout (*Salvelinus fontinalis*) in particular has been continuously introduced since the late 1800s

79   in European streams, some of which were originally populated by native brown trout *Salmo trutta*

80   (Hutchings 2014). Using stable isotope analyses, previous studies have compared the diet of brown

81   trout in allopatry and sympatry with non-native brook trout (Cucherousset et al. 2007; Závorka et al.

82   2017) and demonstrated that, while brook trout consumed primarily terrestrial invertebrates, the

83   proportion of this food type in the diet of brown trout increased when they co-existed with brook trout

84   (Cucherousset et al. 2007). However, the mechanisms leading to this trophic niche convergence remain

85   unknown. Activity patterns may play an important role, because they mirror daily changes in food

86   availability in streams. Allopatric brown trout are primarily active during dusk and early night (Alanärä

87   et al. 2001; Závorka et al. 2016) and feed mostly on aquatic prey that drift at higher rate at night

88   (Young et al. 1997; Giroux et al. 2000). In contrast, brook trout are predominantly diurnal (Allan

89   1981), and feed on terrestrial insects (Allan 1981; Závorka et al. 2017) whose activity is higher during

90   daytime (Lewis and Taylor 1965). The diet of sympatric brown trout suggests that they may be more

91 diurnal than allopatric brown trout. Such shifts have been reported previously (Blanchet et al. 2008),

92 and may be due to behavioral plasticity, selection, or a combination of both.

93

94 This diet convergence may alternatively be explained by other behavioral mechanisms. A recent

95 laboratory experiment revealed that brown trout keep shorter distances to brook trout than to

96 conspecifics at the fry stage (Lovén Wallerius et al. 2017). If valid also for other life stages in the wild,

97 this could indicate that sympatric brown trout remain closer to hetero- than conspecifics. In turn, this

98 may induce diet convergence in at least two ways. Sympatric brown trout may be foraging in habitats

99 where terrestrial prey are relatively more abundant or may acquire a preference for terrestrial prey by

100 copying brook trout (Seppänen and Forsman 2007). Determining whether sympatric brown trout forage

101 closer to brook trout than to conspecifics would be an important first step towards measuring the spatial

102 overlap between the two species, and ultimately, understanding the proximate factors behind diet

103 convergence.

104

105 In the present study, we compared the behavior of juvenile brown trout (age 1+) originating

106 either from a sympatric or an allopatric site in presence or absence of non-native brook trout. For this

107 purpose, we performed a 29-day replicated mesocosm experiment using a 2×2 full-factorial design with

108 Origin (allopatry vs sympatry) × Competition mode (allopatry vs sympatry). Based on the reported diet

109 convergence (Cucherousset et al. 2007; Závorka et al. 2017), we predicted that brown trout will be

110 more day active in sympatry than in allopatry, and that brown trout of sympatric origin will be more

111 day active than those of allopatric origin. Based on previous laboratory studies on fry (Lovén Wallerius

112 et al. 2017), we predicted that brown trout from allopatric origin and in allopatric competition mode

113 should maintain longer distances to other individuals, and that in the sympatric competition mode,

114 brown trout should remain closer to brook trout than to conspecifics. Finally, we predicted that

115 behavioral responses would be plastic, i.e. brown trout will adjust their diel activity and aggregation

116 pattern rapidly (i.e. within a week) in response to the competition mode.

117

118 **MATERIAL AND METHODS**

119

120 STUDY SITE AND FISH SAMPLING

121

122 The study was conducted in stream Ringsbäcken, Sweden (57°39'44.1"N 12°58'58.6"E). Brown trout is

123 present throughout the stream and brook trout also occupies the upstream sections, separating the

124 stream into an allopatric part and a sympatric part (Závorka et al. 2017). On 29 May 2017, 90 brown

125 trout and 30 brook trout of age 1+ were captured in Ringsbäcken by electrofishing (Smith-Root LR-

126 20B, Vancouver, WA USA). More specifically, we captured 45 brown trout in the allopatric section, 45

127 brown trout and 30 brook trout in the sympatric section. Fish were maintained in stream containers

128 overnight and brown trout were separated from brook trout. On 30 May 2017, all individuals were

129 anesthetized with 2-phenoxyethanol (0.3 mL L^{-1}), measured for fork length to the closest mm

130 (measuring board) and body mass to the closest 0.01 g (Valor^{TM} 3000 Xtreme). On average (± standard

131 deviation), brown trout were 9.6 (± 1.8) cm and 9.61 (± 5.66) g. Brook trout were 9.0 (± 1.4) cm and

132 7.07 (± 3.51) g. Fish were then tagged with Visible Implant Elastomer (Northwest Marine Technology,

133 Shaw Island, WA USA). Four colors were used (red, green, orange, and yellow) and two tags were

134 injected in the dorsal fin to create unique individual combinations in each enclosures and facilitate

135 identification during overhead observations. Upon recovery, fish were released in one of the 12

136 enclosures to match experimental treatments.

137

138 EXPERIMENTAL SETUP

139

140   Between 25 and 28 May 2017, six pairs of enclosures made of nylon mesh (2.4 and 0.8 m along the

141   length and width of the stream, respectively, 75 cm high.) were set up in the stream at the downstream

142   limit of the distribution of brook trout. Enclosures were set up in pairs separated by 5–10 m and

143   enclosures within in a pair were separated by 20-80 cm (see supporting information). The mesh size

144   was 6 mm, which is small enough to contain fish, but large enough to allow the invertebrates that

145   salmonids feed on to drift through (Zimmerman and Vondracek 2006). The bottom of all enclosures

146   was filled with a mixture of rocks, pebbles and gravel from the study stream, to mimic its microhabitat

147   heterogeneity. This provided ample opportunity for fish to hide, e.g. in the interstitial zones between

148   the rocks. A grid made of bamboo sticks (80 cm long, 0.8 cm thick) was placed over the substrate to

149   serve as an x-y coordinate grid. Three sticks were placed along the length of the stream (y = 40), and

150   three were placed along the width (x = 40, x = 120, and x = 200). The sticks were taped every 10 cm so

151   the position of fish within enclosures could be determined to the closest 5 cm.

152

153   Brown trout were studied in two competition modes, i.e. allopatry (10 brown trout per

154   enclosure, 6 enclosures) or sympatry (5 brown trout and 5 brook trout per enclosure, 6 enclosures). We

155   also separated brown trout based on their origin, i.e. from the allopatric or sympatric section of the

156   stream. The four experimental treatments (allopatric origin – allopatric competition mode; allopatric

157   origin – sympatric competition mode; sympatric origin – allopatric competition mode; sympatric origin

158   – sympatric competition mode) were replicated three times. The question of the impact of brook trout

159   on native brown trout has yielded equivocal results, as some studies report negative impacts (Öhlund et

160   al. 2008; Závorka et al. 2017) while others suggest that brook trout use mostly places unoccupied by

161   brown trout (Korsu et al. 2009). In our study stream, total densities of fish were similar between

162   allopatry and sympatry sites. Therefore, a substitutive design was used: total density of fish was

163   constant and the proportion of each species changed according to the competition mode (Fausch 1988).

164

165   Only one of each pair of enclosures contained brook trout (i.e. sympatry), and its position was

166   alternated between the left and right side of the pair. The distribution of the origin among all enclosures

167   was selected randomly at the start of the study. There were significant differences in body size among

168   treatments, reflecting the natural distribution of brown trout body size between the allopatric and

169   sympatric sections of the stream. Specifically, enclosures with brown trout from sympatric origin had

170   larger individuals than those from allopatric origin (ANOVA, df = 1, P < 0.001 for length and mass).

171   This resulted in brown trout from sympatry, but not allopatry being larger than brook trout in sympatric

172   enclosures (ANOVA, df = 1, P = 0.012 and 0.868, respectively, for body mass). However, there were

173   no differences between brown trout in allopatry and sympatry (ANOVA, df = 1, P = 0.325 and 0.162

174   for length and mass, respectively).

175

176   After 17 days, a flooding event due to heavy rainfall led to the escape of 35 individuals from all

177   treatments (6 in the allopatric origin – allopatric competition, 12 in the allopatric origin – sympatric

178   competition, 13 in the sympatric origin – allopatric competition, and 4 in the sympatric origin –

179   sympatric competition). These individuals were replaced with new fish captured in the same locations

180   as the escaped individuals, and subjected to the same handling procedure, except one that was

181   recaptured in the sympatric origin – sympatric competition treatment. The experiment was terminated

182   on 27 June 2017 when all but eight individuals were recaptured and measured for body length and

183   mass. Stomach samples were also collected before fish were released in the stream. The eight missing

184   individuals were assumed to be dead.

185

186 HABITAT CHARACTERISTICS AND FOOD AVAILABILITY

187

188 Water depth and current velocity (OTT Compact Current Meter C20, Kempten, Germany) were

189 measured at 20 random locations in each enclosure at the start of the study. On average, water depth

190 was 17.02 (± 1.47) cm and current velocity was 17.62 (± 1.94) cm s^{-1}. Habitats were similar among

191 treatments (ANOVA, df = 3, P = 0.689 and 0.179 for depth and current velocity, respectively). The

192 flow varied during the study, but we ensured that it remained similar among enclosures. Water

193 temperature and light intensity were recorded automatically using three data loggers (UA-002-08

194 HOBO Pendant® Temp/Light, 8K) positioned in three different enclosures. On average, water

195 temperature was 13.41 ± 1.47 °C and light intensity was 1.69 ± 5.09 Klux.

196

197   To assess the diel patterns of food availability, we measured the relative abundance of terrestrial

198 and aquatic food at different times of the day. The amount of terrestrial input was estimated using 15

199 pantraps (30 × 40 cm) disposed randomly around the stream and containing 2 - 3 cm of water with a

200 drop of eco-friendly soap. Five traps were opened during the day (06:00 to 18:00), five during

201 crepuscular hours (03:00 to 06:00 and 18:00 to 21:00) and five at night (21:00 to 03:00). The

202 invertebrates captured in the traps were collected after two 24h cycles, and we repeated the process

203 once, yielding 30 samples in total. The abundance of aquatic invertebrates was determined using

204 driftnets (30 cm wide, 15 cm deep) positioned approximately 10 m downstream the enclosures to avoid

205 limiting food availability for experimental fish. Nets were set up in 22 – 26 cm water depth and 8 – 15

206 cm/s current velocity. The driftnet was maintained in the water for 40 min every three hours (starting at

207 00:00) for three 24h cycles distributed throughout the study, yielding a total of 24 samples. Too few

208 invertebrates were counted in the samples to determine food abundance, potentially because of the high

209 density of fish in the enclosures depleting the resource at a fast rate. Therefore, we decided to use the

210   number of exuviae in the sample instead, which has been reported to accurately estimate the abundance

211   of larvae (Ruse 1995). Daytime samples were collected at 09:00, 12:00 and 15:00, crepuscular samples

212   at 06:00 and 18:00 and night samples at 21:00, 00:00 and 03:00.

213

214   BEHAVIORAL OBSERVATIONS

215

216   Observations started on 1 July 2017 and finished on 24 July 2017. Pairs of enclosures were visited from

217   downstream to upstream or vice versa (alternatively) for 15 min by an observer that stood motionless

218   and recorded the activity status (active or inactive) of all individuals and the position of active

219   individuals. We recorded activity 8 times per day (i.e. every 3 hours) over six 24h cycles (i.e. every 3

220   days on average), yielding a total of 576 measurements of activity rates. The activity status of a fish

221   was determined by whether it was inside or outside a shelter. Such method, i.e. detectability of

222   individuals, has been used as a proxy for activity level in previous studies using telemetry (Roy et al.

223   2013; Závorka et al. 2017) and direct observations (appearance rates in Larranaga and Steingrímsson

224   2015). In the majority of observations, fish remained immobile, which facilitated the determination of

225   x-y coordinates. Because light intensity at night (00:00 and 03:00 observations) was too low to detect

226   fish, we used a flashlight with an adjustable beam size. The light was turned on only for a few seconds

227   every 2-3 min. The size was maximized so light intensity was low in order to minimize fish

228   disturbance. Most individuals could be correctly identified at that stage, but on few occasions, we

229   increased light by focusing the beam only to the point when a tag could be identified. Fish movement

230   was not more frequent under those conditions than during the day, which indicates that the use of a

231   flashlight had a negligible effect on fish (Larranaga and Steingrímsson 2015). The sides of the

232   enclosures were cleaned after each session of observations.

233

234   DATA ANALYSES

235

236   For each observation, and in each enclosure, we calculated the percentage of active brown trout,

237   hereafter referred to as "activity rates" (Larranaga and Steingrímsson 2015). Measurements obtained

238   within the same enclosure, as well as subsequent measurements (3 h difference) were not considered as

239   not being independent. Therefore, we analyzed all behavioral results with linear mixed models (LMM)

240   using *enclosure* and *day of observation* as random factors. Differences in activity rates among brown

241   trout of different *origin* (allopatry vs sympatry), *competition mode (*allopatry vs sympatry), and

242   between *times of day* (day vs night) were tested using a LMM. We included these three variables and

243   their interactions as fixed factors (model M1). Daytime observations corresponded to measurements

244   made between 06:00 and 18:00 and night observations from 21:00 and 03:00. In this model, the *day of*

245   *observation* was considered as a random factor nested within the variable t*ime of day* (i.e. day or night).

246   A separate model (LMM) was run to compare the activity rates between *species* (brown trout vs brook

247   trout), and *times of day* (day vs night) in the sympatric competition mode.

248

249   We separated our dataset into two subsets to distinguish immediate behavioral responses to

250   experimental conditions from slower responses. More specifically, we compared activity patterns

251   during the first 7 days of the study (period 1) with all observations performed later, i.e. from day 8 to

252   day 29 (period 2). Fish from six enclosures escaped after the second 24 h cycle of observations, and

253   were replaced with new individuals. We reset the time for those six enclosures after fish replacement.

254   To limit the number of variables in this analysis, we used a single variable *treatment* with four

255   categories (allopatric origin – allopatric competition mode, allopatric origin – sympatric competition

256   mode etc.) that encompasses information from the variables *origin* and *competition mode*. Activity

257   rates of brown trout were compared across *treatments*, *times of day* (day vs night) and *periods* (first vs

258   second) using a LMM (M2). In this model, the *day of observation* was a random factor nested within

259   the variable *period* (first or second).

260

261   For all observations after the first 24h cycle of measurements (five cycles in total), and when

262   two or more individuals were active, we calculated the distance between each fish and its nearest

263   neighbor. In the sympatric *competition mode*, we also measured the distance between a fish and the

264   nearest brown trout and brook trout. Hence, we were able to calculate three pair-types of distance:

265   brown trout – brown trout, brown trout – brook trout, and brook trout – brook trout. Based on these

266   data, we calculated an overall index of aggregation *sensu* Clark and Evans (1954), and modified by

267   Petrere (1985) to account for differences in number of active individuals among observations. High

268   values of this index indicate overdispersion, i.e. individuals are more dispersed than expected by

269   chance. We obtained 300 measurements of aggregation, that we analyzed using a LMM to measure the

270   effect of *competition mode*, *origin* of brown trout and their interaction (M3). A second analysis was

271   used to test if, in the sympatric *competition mode*, brown trout and brook trout maintain different

272   distances to hetero- and conspecifics (*pair type*, M4). In both models, *enclosure* and *day of observation*

273   were considered as random factors. When interaction terms were significant, Tukey post-hoc tests were

274   run to detect significant pairwise differences (see supporting information). Finally, differences in the

275   abundance of terrestrial and aquatic food were assessed with Wilcoxon sign-ranked tests. The lme4

276   package (Bates et al. 2015) was used to examine the effects of explanatory variables in all models

277   described above in R 3.4.3 (R Development Core Team 2015).

278

279   We calculated specific growth rate (SGR, sensu Ostrovsky 1995) for all individuals recaptured

280   at the end of the study. Most brown trout lost weight during the study (SGR = -0.38 ± 0.64 %/day in

281   allopatric origin – allopatric competition, -0.30 ± 0.74 %/day in the allopatric origin – sympatric

282   competition, -0.67 ± 0.85 %/day in the sympatric origin – allopatric competition, and -0.20 ± 0.65

283   %/day in the sympatric origin – sympatric competition). No difference was detected between brown

284   trout of different *origin* or in different *competition modes*, (ANOVA, P > 0.05 for both variables,

285   Dryad Digital Repository).

286

287   **RESULTS**

288

289   Overall (mean ± SD), 18.8 ± 11.6 % of brown trout were active during the observations. Brown

290   trout from sympatric origin placed in allopatry were less active (14.58 ± 13.32 %) than brown trout

291   from allopatric origin placed in allopatry (19.51 ± 22.66 %, post-hoc test, P = 0.009) or in sympatry

292   (19.72 ± 17.70 %, P = 0.006), and less active than brown trout from sympatric origin placed in

293   sympatry (21.81 ± 15.49 %, P < 0.001, Table 1A, Figure 1). Other pairwise comparisons were non-

294   significant (supplementary material). Brook trout were moderately, but significantly less active than

295   brown trout in sympatry, i.e. 18.1 (± 13.5) and 20.7 (± 16.6, P = 0.034)

296

297   Brown trout were more active during the night than during daytime (Table 1a, Figure 1).

298   Consistently with our predictions, brown trout were more diurnal in the sympatric than in the allopatric

299   *competition mode* (P < 0.001), and those from sympatric *origin* were more diurnal than those from

300   allopatric *origin* (P < 0.001). Brook trout distributed their activity more evenly throughout the day than

301   brown trout, with no difference in activity rates between *times of day* (post-hoc test, P = 0.921). Brown

302   trout in the allopatric *competition mode* became more nocturnal during the second period (P < 0.001).

303   In contrast, brown trout of allopatric *origin* placed in the sympatric *competition mode* became more

304   diurnal over time (P < 0.001, Table 1a, Figure 2). Brown trout of sympatric *origin* in the sympatric

305   *competition mode* distributed their activity similarly throughout the day during the first and second

306   period (see supplementary material for more detailed pairwise comparisons of activity rates between

307   *times of day*).

308

309   During the study, aggregation (modified Clark-Evans index) was on average 1.27 suggesting

310   that fish were more dispersed than expected by chance, with a standard deviation of 2.10 indicating

311   large variation. Fish in the sympatric *competition mode* (both species) were more aggregated (1.01 ±

312   2.26, average of brown trout and brook trout) than brown trout in the allopatric *competition mode* (1.74

313   ± 1.69, P < 0.001). In the allopatric *competition mode*, brown trout of sympatric *origin* (0.63 ± 1.88)

314   were more aggregated than those of allopatric *origin* (2.04 ± 2.08, P < 0.001, Table 1b, Figure 3A). An

315   analysis of the distance between individuals showed that in the sympatric *competition mode*, both

316   brown trout and brook trout maintained similar distance to hetero- and conspecifics (*Pair type*, P =

317   0.174, Table 1b). This was true regardless of the origin of brown trout (P > 0.05 in all post-hoc

318   pairwise comparisons). Brown trout from allopatric *origin* tended to keep longer distances to both

319   hetero- and conspecifics (P = 0.060, Table 1b) than those from sympatric *origin* (Figure 3B). Finally,

320   there was no significant difference in aggregation between the first and second period of the study (P >

321   0.05 in all four combinations of *origin* and *competition mode*).

322

323   On average, 4.44 (± 2.81) terrestrial invertebrates were captured in the pantraps per m^2 per h.

324   This abundance was higher during the day (7.14 ± 2.18 items m^{-2} $h^{-1)}$ than during crepuscular hours

325   (3.65 ± 2.25 items m^{-2} h^{-1}) and during the night (2.53 ± 1.71 items m^{-2} h^{-1}, Wilcoxon sign-ranked test, P

326   < 0.05 for all three pairwise comparisons). On average, 17.08 (± 8.03) exuviae drifted per m^2 per min

327   in the stream. This abundance was greater at night (24.93 ± 4.92 items m^2 min^{-1}) than during

328   crepuscular hours (17.60 ± 2.83 items m^2 min^{-1}) and daytime (8.89 ± 3.34 items m^2 min^{-1}) and the

329   differences were significant (Wilcoxon sign-ranked test, P < 0.05 for all three pairwise comparisons).

330

331   **DISCUSSION**

332

333   This study demonstrated that native brown trout become more diurnal when brook trout is present. This

334   effect was detected in less than one week and became stronger over the course of the study. When

335   placed in allopatry, brown trout from the sympatric site were more diurnal than those from the

336   allopatric site but gradually reverted to nocturnal activity. Sympatry also induces changes in

337   aggregation, as brown trout from sympatric origin or in sympatric conditions were more aggregated

338   than those from allopatric origin or in allopatric conditions.

339

340   CONTRASTING BEHAVIOR IN ALLOPATRY AND SYMPATRY

341

342   Consistently with previous studies, we found that allopatric brown trout were predominantly nocturnal

343   (Young 1999; Závorka et al. 2016), and that brook trout were more diurnal than brown trout in

344   sympatry (Allan 1981). Our results suggest that the longer brown trout are in sympatry with brook trout

345   (*origin* vs *competition mode*), the more diurnal they become. Inter-specific competition is generally

346   expected to promote divergent diel activity patterns, which has been observed previously in a variety of

347   organisms including mammals (Gerber et al. 2012), reptiles (Pianka 1969), and insects (Caveney et al.

348   1995). Here, we present evidence for the opposite, convergent diel activity pattern, which to our

349   knowledge has not been reported in the past. An earlier study suggested that native Atlantic salmon

350   *Salmo salar* became more diurnal in presence of non-native rainbow trout *Oncorhynchus mykiss*

351   (Blanchet et al. 2008), but did not report the activity patterns of the non-native species.

352

353   Several mechanisms may be responsible for these effects. One possibility is that they are

354   mediated by interspecific social interactions, especially as the non-native brook trout is closely related

355   to brown trout. During the day, stream-dwelling salmonids forage more efficiently (Rader et al. 2007),

356   but are exposed to increased predation risk compared with night conditions (Metcalfe et al. 1999).

357   Competition for food with brook trout may encourage brown trout to engage into a riskier, but more

358   rewarding activity pattern, e.g. to secure optimal foraging positions and maintain fast growth during

359   early life selective bottlenecks. Inversely, brown trout may have a preference for the more energetic

360   terrestrial prey, but adopt a risk-averse activity pattern with limited access to this prey type in allopatry.

361   The presence of day-active brook trout may render diurnal activity safer, through a dilution of

362   predation risk. This would also be supported by the higher aggregation in sympatric conditions. Brown

363   trout have been found to use visual cues of brook trout to adjust their behavior at the fry stage (Lovén

364   Wallerius et al. 2017). Similar adjustments may explain the present results, and may be further

365   strengthened if brown trout observe that brook trout activity patterns are rewarding and safe in our

366   stream enclosures where predation risk is virtually null. Size differences between brown trout

367   originating from sympatry and brook trout at the start of the study are unlikely to be a major driver of

368   the observed results for two reasons. First, salmonids generally become more nocturnal as they grow

369   (Imre and Boisclair 2004). In addition, activity timings became similar between brown trout originating

370   from sympatry and allopatry at the end of the study, which also suggests that competition mode was a

371   more important driver of behavior in this study.

372

373   Brown trout introduced to a novel *competition mode* compared with their *origin* showed

374   contrasting activity patterns compared with brown trout remaining in their original condition. These

375   changes occurred rapidly, i.e. within one week after introducing fish in our experimental mesocosms

376   indicating strong behavioral plasticity in brown trout. This is in line with previous studies that suggest

377   that salmonids adjust the timing of their activity rapidly in response to novel environmental conditions

378   like rare shelters or high density (Larranaga and Steingrímsson 2015; Fingerle et al. 2016). Brown trout

379   activity patterns in our study continued to change after the first week, which may be due in part to

380   seasonal changes, e.g. salmonids become progressively more nocturnal as light intensity and water

381   temperature decrease over the summer (Fraser et al. 1993). However, this alone cannot explain our

382   results, as brown trout from allopatric *origin* placed in the sympatric *competition mode* became more

383   diurnal, even during the second phase of the study. This suggests instead that long-term exposure to

384   non-native brook trout can influence the behavior of brown trout over several weeks.

385

386   Fish in sympatry were more aggregated, which was due in part to brown trout remaining closer

387   to brook trout. This is consistent with previous findings by Lovén Wallerius et al. (2017), and suggests

388   that positive association between brown trout and brook trout may remain past the fry stage.

389   Interestingly, brown trout from sympatric *origin* also reduced their distance to conspecifics, which may

390   indicate a generally relaxed competition for space when brook trout is present. Aggregation in the

391   sympatric *competition mode* may alternatively be a consequence of fish being more diurnal. Indeed,

392   schooling can be elicited as an anti-predatory response during the day when predation risk is higher

393   (Metcalfe et al. 1999), as was suggested by Larranaga and Steingrímsson (2015).

394

395   LINKING BEHAVIOR AND DIET CONVERGENCE

396

397   The present study suggests that activity patterns play an important role in the diet convergence

398   observed in brown trout. Terrestrial prey were comparatively more abundant during the day than at

399   night. All else being equal, if brown trout attack prey indiscriminately, terrestrial prey should constitute

400   a larger proportion of their diet, compared with allopatric trout. Importantly, the pattern we describe

401   may not be ubiquitous. For instance, co-existing related lizard species have been found to display

402   diverging activity patterns, but have similar diets (Rouag et al. 2007). On the opposite, competing

403   species of geckos displayed the least dietary overlap when their temporal activity overlap was high

404   (Cole and Harris 2011). The outcome may depend on a series of factors, e.g. food selectivity, the

405   relative competitive ability of native and non-native species, and whether one of the species

406   significantly decreases access to a specific food type for the other species (Cole and Harris 2011).

407

408   Other mechanisms not tested in the present study may also contribute to the diet shift observed

409   in sympatric brown trout. First, brook trout may usurp a significant fraction of the available aquatic

410   prey (Benjamin et al. 2013), forcing brown trout to feed more actively on the alternative prey, i.e.

411   terrestrial food. Brown trout placed in sympatry were also generally more exposed to brook trout than

412   expected by chance, by being active at similar periods and remaining closer to them. Thus, diet

413   preferences may be socially transmitted from brook trout to brown trout because of these frequent

414   interactions (Camacho-Cervantes et al. 2015). Another possibility is that foraging mode, and not diet

415   preference, is socially acquired. Brook trout attack prey at the surface more often (46 % in McLaughlin

416   and Grant 1994) than brown trout (5.8 % in Tunney and Steingrímsson 2012), where terrestrial insects

417   should be more abundant. These potential causes require that social information be transmitted to and

418   used by brown trout in sympatry. Determining the likeliness, and adaptive nature of such information

419   use is not easy, because exposure to brook trout represents an evolutionary novelty (i.e. less than 200

420   years), and selection may not have had enough time to select against it (Laland and Williams 1998). On

421   the other hand, changes in behavior based on the novel information provided by brook trout may be

422   neutral, or even adaptive for young stages of brown trout if they lead to higher food intake, e.g. to

423   survive early life selective bottlenecks (Elliott 1994). Higher aggregation in response to the presence of

424   brook trout may also have positive effects on survival (Wrona 1991).

425

426   PERSPECTIVES

427

428   The novel biotic interactions induced by the invasive species could cascade across levels of biological

429   organization (Buoro et al. 2016). For instance, the presence of brook trout may affect insect emergence

430   (Benjamin et al. 2013), which in turn may impact riparian communities and stream ecosystem

431   functioning (Baxter et al. 2004). Brook trout consume fewer aquatic prey items in our study stream

432   (Závorka et al. 2017), with potential consequences for primary productivity and insect emergence. The

433   shift in activity pattern and diet convergence of brown trout induced by co-existence with brook trout

434   should reinforce these effects. Co-existence between brown trout and brook trout may thus provide an

435   interesting and rare example of converging behavior and diet, with potentially important consequences

436   across levels of biological organization (Cucherousset and Olden 2011), which deserves further

437   attention.

438

439   ACKNOWLEDGEMENTS

440

450

451   DATA ACCESSIBILITY

452

453   Data on recaptured fish will be made available through the Dryad Digital Repository. This dataset

454   includes growth rates.

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TABLES

Table1: (a) Summary statistics (linear mixed model) of the effects of *origin* (brown trout originating either from allopatry or sympatry), *competition mode* (allopatry and sympatry with brook trout), *time of day* (day and night), and *period* (week 1 versus rest of the study) on activity rates of juvenile brown trout (M1 and M2). Summary statistics of the effect of brown trout *origin* and *competition mode* on aggregation (based on distance between individuals, M3). Summary statistics of the effect of brown trout origin and pair type (brown trout – brown trout; brown trout – brook trout; brook trout – brook trout) on the distance to the nearest neighbor, (M4). Bold characters indicate significant effects.

(a) Activity

Model	Variable	Df	Mean square	F value	P value
M1	Origin	1	1334.4	9.459	**0.014**
	Competition mode	1	80.1	0.582	0.471
	Time of day	1	11963.7	84.806	**< 0.001**
	Origin × Competition mode	1	627	4.445	0.068
	Origin × Time of day	1	30412.5	215.583	**< 0.001**
	Competition mode × Time of day	1	12931.1	91.66	**< 0.001**
M2	Treatment	3	860.3	6.736	**<0.001**
	Time of day	1	429.9	3.366	0.067
	Period	1	539	4.221	0.204
	Treatment × Time of day	3	4375.6	34.259	**< 0.001**
	Treatment × Period	3	410.6	3.215	0.236
	Daytime × Period	1	1637.8	12.824	**0.023**
	Treatment × Time of day × Period	3	2466.2	19.310	**< 0.001**

(b) Aggregation

Model	Variable	Df	Mean square	F value	P value
M3	Origin	1	94.16	25.116	**< 0.001**
	Competition mode	1	24.25	7.535	**0.021**
	Origin × Competition mode	1	0.01	0.002	0.968
M4	Origin	1	5617.7	24.208	0.060
	Pair type	2	281.38	1.922	0.174
	Origin × Pair type	2	279.26	2.171	0.141

457

458   **FIGURE CAPTIONS**

459

460   Figure 1: Activity rates (% of active individuals) of brown trout measured every 3 h over six 24 h

461   cycles in experimental enclosures in allopatry (left) or in sympatry with brook trout (right). In

462   sympatric conditions, the activity pattern of brown trout and brook trout are represented in black and

463   green, respectively. Brown trout originated either from an allopatric (top) or sympatric (bottom) section

464   of the study stream. Data are given as mean (solid line) ± 95% confidence interval of the mean (dashed

465   lines).

466

467   Figure 2: Change in the timing of activity of brown trout (% of active individuals every 3 h during six

468   24 h cycles) from allopatric origin and placed in sympatry (left), or from sympatric origin and placed in

469   allopatry (right), from the first period (week 1, black line) to the second period (rest of the study, grey

470   line). Data are given as mean (solid line) ± 95% confidence interval of the mean (dashed lines).

471

472   Figure 3: (A) Aggregation (modified Clark-Evans index) based on distance between individuals in

473   enclosures containing fish from allopatric or sympatric origin and competition mode. Positive and

474   negative values indicate situations when fish maintained longer and shorter distances than expected by

475   chance, respectively. (B) Distance between individuals and the nearest brown trout and brook trout in

476   enclosures   containing   both   species.

477