1   **Lay-summary:**

2   Should I stay or should I go: in Brown trout the migration strategy of the parents

3   interacts with the environmental conditions experienced by the offspring to potentially

4   influence its motivation to compete for feeding territories and hence its probability of

5   migration.

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7   # Prior resource availability and life history origin affect
8   # competitive behavior in territorial disputes

9
10 **Abstract**

11   Partial migration, in which some individuals of a population migrate and others

12 remain sedentary, is a phenomenon that occurs across a wide range of taxa, but the factors

13 that pre-dispose particular individuals to one or the other strategy are usually unknown.

14 Brown trout (*Salmo trutta*) initially compete for feeding territories in freshwater streams, but

15 while some individuals remain resident in fresh water throughout their lives, others undertake

16 an anadromous migration. Since one of the drivers for migration is the relative rates of

17 resource acquisition in different habitats, we compared the ability of juvenile offspring from

18 freshwater-resident and anadromous parents to compete for feeding territories; we also tested

19 how this depended on the quality of the environment previously experienced. Brown trout

20 derived from freshwater resident or anadromous parents were reared for ~7 months under

21 high, mid or low food regimes, and were then induced to compete for feeding territories in a

22 semi-natural stream channel. We found that the parental type had a significant effect on

23 dominance status in territorial interactions, with offspring of anadromous fish being dominant

24 over size-matched offspring of freshwater-residents, but only when both had been raised

25 under intermediate levels of food availability. The results suggest that the migration strategy

26 of the parents interacts with the environmental conditions experienced by the offspring to

27   potentially influence its motivation to compete for feeding territories and hence its probability

28   of migration.

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Introduction

Dominance hierarchies generally result in dominant individuals gaining preferential access to food, shelter or mates. Differences in dominance-related traits (e.g. aggression, food acquisition, competitive ability etc.) have been linked to variation in growth (Vøllestad and Quinn 2003; Adriaenssens and Johnsson 2011) and life history strategies (Biro and Stamps 2008; Chapman et al. 2011) but may be dependent upon condition. For example Van Leeuwen et al. (2011) demonstrated that dominant individuals experienced higher growth rates than subordinates when food was abundant but had lower growth rates than subordinates at low food as dominant individuals, being larger, became more constrained by the food availability in their habitat.

Maximizing energy intake (food consumption) without also increasing energy expenditure (through costs of foraging, defending territories and movement) is a problem faced by many organisms. If habitats differ predictably in their productivity, this net rate of energy intake is likely to have important implications as to whether it is more profitable for an individual to remain in a locality (resident approach) or leave (migratory approach; Gross et al. 1988). There will be individual variation in the net rates of energy intake in a given habitat, and as a result the trade-off between potential net energy intake as a resident or a migrant also differs between individuals. Partial migration, in which some individuals of a population migrate and others remain sedentary is a phenomenon that occurs across a wide range of taxa (see reviews in: Chapman et al. 2011; 2012; Dodson et al. 2013). The commonest form of this intraspecific variation in movement patterns is non-breeding partial migration (sensu Chapman et al. 2011), where migrants and residents breed sympatrically but forage in different habitats. There have been many hypothesized explanations for this category of migration, including intraspecific competition for limited food resources, predation risk trade-offs and intraspecific niche diversity (see Chapman et al. 2011).

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79   However, there is a lack of hard evidence of the factors that pre-dispose particular

80   individuals to one or the other strategy. Those that by chance have the advantage of greater

81   access to resources may be less liable to migrate (Sandell and Smith 1991). Similarly,

82   residency may be more likely in those encountering a low local density of competitors (as has

83   been demonstrated experimentally in red-spotted newts *Notophthalmus viridescens* by

84   Grayson and Wilbur (2009)), or those experiencing a higher food supply (as in salmonid fish:

85   Olsson and Greenberg 2004; Olsson et al. 2006; Wysujack et al. 2009). Body size may also

86   affect the selection pressures for/against migration, since larger individuals may generally

87   have less to gain from migration (Dodson et al. 2013, though see Brodersen et al, 2008 for an

88   exception) since they usually have the advantages of a higher competitive ability and/or

89   lower risk of starvation and predation (Chapman et al. 2011).

90   One area which has received a considerable amount of attention in explaining patterns

91   of partial migration, mainly in birds, has focused on the role of dominance-related traits and

92   body size (Gauthereaux 1982; Nilsson et al. 2008). More dominant individuals tend to

93   outcompete subordinates for limited food and breeding resources, which in turn forces

94   subordinates to migrate in search of more profitable environments (Gauthreaux 1982). While

95   this hypothesis has been supported in several studies (Lundberg 1985, Nilsson et al. 2008) it

96   has been rejected by others (Rogers et al. 1989; Boyle 2008), indicating that the role of

97   dominance status (and hence often body size) in explaining patterns of life history diversity

98   may be context dependent. In particular the environmental conditions that are experienced at

99   the time and whether or not an individual's migratory tendency is fixed (i.e. determined by its

100   parents through genetic or parental effects, so that offspring of migrants are themselves

101   migratory), as demonstrated by Berthold (1988) and Berthold and Pulido (1994) for

102   migratory tendency and migration distance in the Blackcap *Sylvia atricapilla*, or flexible

103   (condition-dependent; Brodersen et al. 2008).

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104   A well-documented example of partial migration is the brown trout *Salmo trutta*, a

105   polymorphic species that adopts a continuum of life history strategies, with the two most

106   common being freshwater-resident and anadromous migrant (i.e. born in freshwater but

107   growing at sea, before returning to fresh water to spawn). The two ecotypes can occur in

108   sympatry, possibly derived from a single gene pool, with anadromous and freshwater-resident

109   adults having the ability to interbreed and both being able to produce offspring apparently

110   capable of adopting either life history, depending on food availability (Olsson et al. 2006;

111   Wysujack et al. 2009; O'Neal and Stanford 2011), although the probability of adopting either

112   life history may vary depending on parentage (as demonstrated for a closely related species

113   the rainbow trout (*Oncorhynchus mykiss*; Nichols et al. 2008).

114   While it is likely that genetics interacts with growth history, current body size and

115   physiological condition to determine whether or not the animal migrates, there may also be a

116   role for inherent differences in dominance-related traits independent of body size. Soon after

117   emergence from the nest, brown trout fry rapidly establish dominance hierarchies that are

118   temporally stable (Johnsson and Forser 2002; Jonsson and Jonsson 2010) and engage in intra-

119   and inter-specific competition for preferred feeding territories (Lahti et al. 2002; Klemetsen

120   et al. 2003). It is generally accepted that dominance is advantageous since it gives preferential

121   access to food (Alanärä and Brännas 1996) and so facilitates increased growth (Klemetsen et

122   al. 2003), including in the wild (Höjesjö et al. 2002). The degree to which an individual

123   competes for a territory may also depend on its previous experience. In brown trout fry it has

124   been shown that both previous rearing density (Sundström et al. 2003) and habitat

125   preferences (Johnsson et al. 2000) influence territorial competitiveness, which may also be

126   influenced by the fish's nutritional state (Johnsson et al. 1996)

127   Therefore given that one of the drivers for migration is the relative rates of resource

128   acquisition in different habitats that is likely dependent on traits associated with dominance

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129   of the individual we test 1) whether size-matched juvenile offspring of freshwater resident

130   and anadromous brown trout differ in dominance related traits (food acquisition, spatial

131   position, color and aggression) in dyadic contests when competing for feeding territories in a

132   semi-natural stream channel and 2) whether differences in these dominance related traits

133   depends on the level of food availability that individuals have experienced earlier in life.

134   Differences in relative dominance traits of offspring from alternative life histories would

135   provide evidence for parental effects (genetic and/or non-genetic) as a potential mechanism

136   perpetuating the maintenance of alternative life histories in partially migrating populations,

137   whereas an effect of prior food availability would indicate that dominance related traits could

138   be influenced by non-genetic differences in the quality of their early environment.

139   **Methods**

140   BROODSTOCK COLLECTION

141   Twenty-four mature freshwater-resident (12 male and 12 female) and 14 anadromous

142   (7 male and 7 female) brown trout were captured using electrofishing on 11 and 23 October

143   2013 from two neighbouring sub-tributaries of the River Tweed, Scotland. Freshwater-

144   resident trout were collected from above an impassable dam on the Whiteadder River (55°

145   88'N, 2°57'W) while the anadromous trout were collected from the College Burn (55° 77'N,

146   2°18'W). Fish were classified as freshwater-resident or anadromous based on **existing**

147   **knowledge of the composition of the populations present from previous scale readings,**

148   size and coloration (Eek and Bohlin 1997): freshwater-resident fish were smaller and dark

149   brown in color with red spots, while anadromous fish were larger and silvery-grey in color

150   with black spots. Both ecotypes were transported to the Belhaven Trout Company, Scotland,

151   where they were held separately in two round 1530 L aluminum tanks supplied with 8.1 ± 0.4

152   °C (mean$\pm$SD) well water under ambient photoperiod and assessed every three days for

153   ripeness.

154   Ripe fish were anaesthetized, blotted dry, and their eggs or sperm extruded by

155 abdominal massage. Eggs were fertilized with sperm from a haphazardly-chosen male of the

156 same life history origin to create 12 full sibling freshwater-resident families and 7 full sibling

157 anadromous families. Freshwater-resident and anadromous fish were artificially spawned

158 from 3 November - 29 November and 17 November - 4 December 2013 respectively.

159 EGG REARING, HATCHING AND FISH HUSBANDRY

160 Each family of eggs was housed separately in a plastic mesh egg basket, placed in one of two

161 (1m X 3m X 0.4m) rearing troughs supplied with well water and covered with dark plastic

162 sheeting to ensure eggs were in complete darkness. Water temperature during incubation was

163 8.1 ± 0.4 °C and was recorded daily along with any dead eggs which were carefully removed.

164   Eggs were checked daily for hatching; those from freshwater-resident and

165 anadromous fish hatched from 19 December 2013 - 17 January 2014 and 30 December 2013

166 - 24 January 2014 respectively. Once eggs began to hatch, the newly emerged offspring

167 (alevins) were separated from the remaining eggs and gently placed into a small mesh basket

168 (one per family) located in the same two troughs as the egg baskets.

169   On 31 January 2014 alevins (i.e. hatched embryos still dependent on the yolk sac for

170 nutrition) were transported to the Scottish Centre for Ecology and the Natural Environment,

171 Scotland. Families were housed separately in 15 L (50cm X 30cm X 15cm) clear plastic

172 aquaria on a partial recirculation system at a constant temperature of 9.2 ± 0.2 °C (mean$\pm$SD)

173 and simulated ambient photoperiod. The aquaria each contained a single air stone and were

174 supplied with water pumped directly from Loch Lomond, which was first treated with an

175 ozone generator (Sander S1000, Germany) before being discharged into a large sump. Water

176 from the sump was pumped through an in-line 110W UV sterilizer (Tropical Marine Center

177 (TMC), Manchester, UK) before entering the aquaria. Return water was gravity fed into a

178 large free standing filter before being discharged back into the main sump. Fish were

179   monitored daily and any mortalities removed. On 3 March 2014, once all fish had used up

180   their yolk sac and began feeding on exogenous food consistently, equal numbers of offspring

181   from each family were haphazardly assigned into twelve round 121 l **(r=40cm, h=24cm)**

182   tanks (keeping parental type discrete), with six tanks per parental type and 200 fish per tank.

183   Tanks were supplied with water pumped directly from Loch Lomond and held under

184   simulated ambient photoperiod and temperature **(12.3 $\pm$ 1.7 °C (mean$\pm$SD))**. Tanks were

185   assigned to one of three food treatments (giving 2 replicate tanks per food treatment per

186   offspring ecotype) and fed twice daily on a standard commercial salmon pellet (Biomar,

187   Aarhus, Denmark) for the remainder of the experiment. The three food treatments were high

188   food (approximately 4.3 % body wt. day^{-1}), mid food (approximately 2% body wt. day^{-1}) and

189   low food (0.7% body wt. day^{-1}). High food treatments were based on feed amounts for a

190   given size of fish and temperature recommended by Biomar (Aarhus, Denmark) for

191   maximum growth in trout, with low food and mid food treatments selected to achieve growth

192   rates slightly above maintenance and intermediary between maximal and minimal growth

193   rates respectively, similar to Wysujack et al. (2009).

194   METHODOLOGY FOR TESTING RELATIVE DOMINANCE

195   The fish were tested for dominance between 25 Sept. 2014 and 15 Nov. 2014, when

196   they were approximately ~7 months old. All trials were conducted in an oval shaped artificial

197   stream channel located at the Scottish Centre for Ecology and the Natural Environment,

198   Scotland (Fig.1). Water to the stream channel was pumped at approximately 15 l min^{-1}

199   directly from Loch Lomond, and so was at the same temperature as in the fish's rearing tanks.

200   Straight sections of the stream channel contained a clear glass window which ran the entire

201   length of the channel to allow observations to be carried out. A canopy of dark sheeting

202   between the straight sections of the stream channel allowed for observations of fish to be

203   carried out from a concealed location and increased the contrast of light to further prevent

204   detection of observer by fish. Both arms were fitted with plastic meshed transverse dividers

205   mounted on wooden frames to give a total of 15 smaller compartments (60cm X 60 cm X 60

206   cm; Fig.1). The substratum was homogenously landscaped with gravel. A 10cm X 5cm rock

207   was placed in the middle of each compartment to produce a single preferred position (so

208   increasing the likelihood of competition between the two fish; Metcalfe et al. 2003). An

209   electric pump ensured relatively uniform velocity (~0.15 ms^{-1}) throughout the artificial

210   stream channel.

211   All trials used a single pair (one freshwater-resident and one anadromous parental

212   type) of fish from the same food treatment in each compartment. Fish were haphazardly

213   selected from the holding tanks, anaesthetized and sized-matched within pairs for fork length

214   ($\pm$0.6 mm; Fig. 2A) and mass ($\pm$ 0.13 g; Fig. 2B). Once sized-matched, one of the two

215   parental types in a pair (type alternated between compartments to prevent any bias due to

216   tagging) was given an alcian blue dyemark on the dorsal fin prior to the experimental trial.

217   The two fish were then released into a compartment of the stream channel and allowed to

218   acclimate for two days prior to a two day period of behavioral observations. Because the

219   artificial stream channel was divided into 15 compartments we were able to run 15 trials

220   simultaneously. All 15 trials in any one run of the experiment were conducted with pairs of

221   fish from the same food treatment. Fish were fed periodically during the two day acclimation

222   period by flushing a single food pellet through a plastic pipe so that it dropped into the centre

223   of the stream at the upstream end of each compartment. **All procedures were carried out**

224   **under the approval of the UK Home O̲office under project no. 60/4292**

225   DATA COLLECTION

226   Four observation sessions were conducted daily (09:00, 11:00, 13:00, 15:00 h) over

227   the course of two days for each pair of fish. Each observation session consisted of first visual

228   recordings of aggression, color, and spatial position for each pair during a 3 min period. After

229 the 3 min period a single food pellet was introduced (as above) into the upstream part of the

230 compartment and a record made of the fish that obtained it. Then a second recording was

231 made of color and spatial position, followed by a second recording of any aggression over a 3

232 min period.

233   Aggression was scored as the total number of aggressive behavioral acts (categorized

234 as fin nips, chases, bites, charges and dorsal displays) exhibited by each individual (Adams et

235 al. 1995) during the 3 min observational periods.

236   Body coloration is a reliable indicator of social stress in juvenile salmonids, with

237 more subordinate individuals being darker (O'Connor et al. 1999; Kaspersson et al. 2010).

238 Coloration was assessed visually in each fish on a three point integer scale, with brighter fish

239 receiving a score of +1 and darker ones a score of -1. Because coloration was scored twice

240 per trial (before and after feeding) and summed across all 8 observation sessions, a fish's total

241 score for body coloration could range from -16 to +16.

242   Spatial position was assessed using a protocol developed from earlier research on

243 juvenile salmonids (Metcalfe et al. 2003; Burton et al. 2011). Spatial positions were

244 quantified in three dimensions by marking each axis of a compartment into three equal

245 lengths, using equally distributed marbles on the substrate and marks on the inside viewing

246 window. These marks defined 27 (i.e. 3 x 3 x 3) equal-sized cuboid zones. Since previous

247 research has shown that dominant salmonids occupy central-rear positions, often just above

248 the substrate and behind an object (Metcalfe et al. 2003; Burton et al. 2011), we gave fish that

249 occupied zones in the lower two thirds of the water column at the centre and back of the

250 compartment a score of +1, while those in zones in the corners of the compartment were

251 given a score of -1 and those in all other positions a score of 0 (Burton et al. 2011).

252 Furthermore fish that were observed to be resting against the downstream meshed divider

253 were given an additional score of -1, as were those resting on the substrate. Because spatial

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254 position was scored twice per trial (before and after feeding) and summed across all 8

255 observation sessions, a fish's total score for spatial position could range from -48 (if it was

256 always resting on the gravel and against the mesh divider in a corner position) to +16 (if it

257 was consistently in a middle position and not touching the mesh or substrate).

258   The ability to acquire food under competition was scored with reference to the fate of

259 the single food pellets introduced in each observation session. Individuals that made no

260 attempt at acquiring the pellet were given a score of 0, those that attempted but failed to

261 acquire it were given a score of +1 and the fish that succeeded in getting the pellet was given

262 a score of +2. Total scores for competitive ability were summed across all 8 observational

263 periods and ranged from 0 (if an individual made no attempts at feeding) to +16 (if an

264 individual was successful in acquiring the food pellet during every observational period).

265   Once observations were complete, the fish were anaesthetized, adipose fin clipped (to

266 ensure they weren't used again) and returned to their holding tank **(to be used as part of an**

267 **on-going experiment examining the potential factors driving ~~sea~~ anadromous migration**

268 **in brown trout)** and new fish selected; each fish was therefore only used once. A total of 30

269 pairs from each food treatment were tested during the course of the experiment.

270 CALCULATIONS AND DATA ANALYSIS

271   Offspring condition was calculated to illustrate **differences between food**

272 **treatments.** Relative condition factor, K_{rel}, was calculated according to Froese (2006) using

273 the following equation:

274 $K_{rel} = W/aL^b$

275   where W is the mass of the individual offspring in grams, L is the fork length in

276 millimetres and a and b are the exponential form of the intercept and slope derived from the

277 regression of weight vs. length plotted on double logarithmic axes for all the offspring

278 combined. These values in addition to the mass and length measurements were used

279 separately as the response variable in a linear model (LM) with parental type and food

280 treatment as explanatory variables. **Furthermore condition, mass and length were**

281 **analysed using ~~a~~ paired t-test~~s~~ to ~~ensure~~ check that the pairs in dyadic contests did not**

282 **differ systematically between parental types in condition, mass or length. ~~Results of the~~**

283 ~~**t-test revealed that our pair matching was successful as they did not differ.**~~

> **Comment [NBM1]:** This is a result (and is presented in the Results section) so inappropriate to mention it here.

284   Individual scores for position, food acquisition, color and aggression were normalized

285 prior to analysis (by subtracting the mean score of all 180 fish from each individual's score

286 and dividing this value by the standard deviation for all fish; Burton et al. 2011). These

287 normalized scores were then used as the response variable in a **generalized** linear **mixed**

288 **effects** model (LME) with parental type and food treatment as explanatory variables and .pair

289 ID as a random factor **to control for the non-independence of measures.** Associations

290 between normalized scores of the four measures (aggression, color, spatial location and food

291 acquisition) were described using Pearson correlations and then summarized with a principal

292 components analysis (PCA) summarizing all four behaviors as a general index of fish

293 dominance. Principal Component 1 (PC1) was found to be highly associated with each of

294 these four separate measurements, with more positive scores indicating more dominant

295 individuals. PC1 scores were therefore analyzed using a LM**E** with parental type and food

296 treatment as explanatory variables **and pair ID as a random factor**. All LME models

297 initially included all two way interactions. **Variance inflation factors (VIF's) for all**

298 **explanatory variables were calculated prior to analysis; all VIF's were less than 3,**

299 **indicating that collinearity among explanatory variables was unlikely to have affected**

300 **our analyses (Zuur et al. 2009). All statistical models were validated by visual inspection**

301 **of residual plots which did not reveal any obvious deviations from homoscedasticity or**

302 **normality. Likelihood ratio tests comparing models with and without a given term were**

303 **used to sequentially compare model fit; models were progressively simplified provided**

304 **that any increase in the log-likelihood ratio statistic was not significant (p > 0.05) and**

305 **checked using AIC criterion to validate the model of best fit.** Initial analyses combined

306 both parental types and all three treatments. If a significant food by parental type interaction

307 was found, data for each food treatment was analyzed separately using the above procedure

308 and parental type as a fixed effect. Analyses were conducted using the R version 3.0.1

309 statistical software (R Core Team, 2013) **and the lme4 function (Bates, Maechler &**

310 **Bolker, 2012).**

311 **Results**

312 GROWTH AND CONDITION OF FISH

313 There was a significant effect of prior rearing environment on offspring length and

314 mass ($F_{(2,176)} = 42.60$, $p < 0.001$; $F_{(2,176)} = 38.72$, $p < 0.001$; Fig. 2A and B), with pairs drawn

315 from the low food treatments being shorter and lighter compared to those from high (Tukey,

316 p<0.001) and mid food treatments (Tukey, p<0.001). There was no significant difference in

317 length or mass between mid and high food treatments (Tukey, length: p=0.55; mass: p=0.94).

318 A significant effect of prior rearing environment on relative condition factor ($F_{(2,176)} = 22.78$,

319 $p < 0.001$) was primarily driven by a lower condition in fish drawn from the low food

320 treatments and mid food treatments compared to those from high (Tukey, p<0.001), since

321 there was no significant difference in condition between mid and low food treatments (Tukey,

322 p=0.19). The size-matching of fish within each food treatment was successful, since there

323 were no differences between parental types **in length, mass or condition (t_{89}=-0.09, p=0.93;**

324 **t_{89}=0.83, p=0.41; t_{89}=1.33, p=0.19; Fig. 2).**

325 AGGRESSION

326 There was no significant interaction between parental type and prior rearing

327 environment (χ^2**=3.67, df= 2, p=0.16**) on aggression score. There was however, a significant

328 effect of prior rearing environment on aggression score (χ^2**=17.25, df= 2, p<0.001; Fig. 3A**),

329 with pairs drawn from the low food treatments having a lower aggression score compared to

330 those from high (**Tukey, p<0.001**) or mid food treatments (**Tukey, p<0.01**). There was also

331 an effect of parental type (χ^2**=12.43, df= 2, p<0.001**), with anadromous offspring having a

332 significantly higher aggression score compared to freshwater-resident offspring. Analysis of

333 the food treatments separately revealed that this overall effect was driven primarily by the

334 significant difference in aggression between the two parental types in mid food pairs

335 (χ^2**=4.16, df= 1, p=0.041**), as there was no difference in aggression between parental types

336 from the low (χ^2**=0.16, df= 1, p=0.069)** or high food treatments (χ^2**=2.37, df= 1, p=0.12).**

337 COLOR

338 There was a significant interaction between parental type and prior rearing

339 environment (χ^2**=10.96, df= 2, p=0.004**), indicating that the color of the freshwater-resident

340 and anadromous offspring differed depending on their prior rearing environment. Analysis of

341 the food treatments separately revealed a significant difference in coloration between the two

342 parental types in pairs of mid food treatment fish (χ^2**=9.08, df= 1, p=0.003; Fig. 3B**), with

343 freshwater-resident offspring having a more subordinate coloration, whereas there were no

344 differences in color between parental types in pairs from the high (χ^2**=2.38, df= 1, p=0.012**)

345 or low food treatments (χ^2**=0.063, df= 1, p=0.080**).

> **Comment [NBM2]:** But this difference IS significant!

346 POSITION

347 There was a significant interaction between parental type and prior rearing

348 environment χ^2**=7.32, df= 2, p=0.026** indicating that the position occupied by freshwater-

349 resident and anadromous offspring differed depending on their prior rearing environment.

350 Analysis of the food treatments separately again revealed a significant difference between the

351 two parental types in the mid food treatment (χ^2**=6.88, df= 1, p=0.009; Fig. 3C**)), with

352 anadromous offspring in that treatment occupying higher scoring positions compared to

353 freshwater-resident offspring; there were no differences in spatial position between parental

354 types in either the high (χ^2**=0.46, df= 1, p=0.50**) or low food pairs (χ^2**=0.20, df= 1, p=0.65**).

355 FOOD ACQUISITION

356   There was no significant interaction between parental type and prior rearing

357   environment (χ^2=0.812, df= 1, p=0.67) or an effect of parental type or prior rearing

358   environment on food acquisition score (χ^2=5.58, df= 1, p=0.061; χ^2=1.48, df= 1, p=0.22; Fig.

359   3D).

360   DOMINANCE

361   Pearson correlations indicated that the four traits recorded in the behavioral

362   observations were significantly correlated (Table 1). Principal component analysis indicated

363   that they could successfully be combined into a single PC that summarized 64% of the

364   variation (Table 1), with high PC1 scores indicating individuals with high aggression, pale

365   coloration, favourable spatial positions and high scores for food acquisition; PC1 was

366   therefore defined as a composite measure of dominance. There was a significant interaction

367   between parental type and prior rearing environment (χ^2=6.23, df= 2, p=0.04), indicating that

368   the relative dominance score of freshwater-resident and anadromous offspring depended on

369   their prior rearing environment. Analysis of the food treatments separately revealed a

370   significant difference in dominance between parental types in pairs of mid food treatment fish

371   (χ^2=6.91, df= 1, p=0.009; Fig. 3E), with offspring of anadromous fish having a higher

372   dominance score than those of freshwater-residents, but there were no differences in

373   dominance score between parental types in pairs from either the high (χ^2=0.147, df= 1,

374   p=0.70) or low food treatments (χ^2=0.29, df= 1, p=0.59).

375   **Discussion**

376   By rearing offspring from parents with contrasting life histories under different food

377   regimes we have demonstrated that both the effect of migration history of the parents and

378   offspring rearing environment influenced dominance status in competition for feeding

379   territories. Interestingly, we found that anadromous offspring scored consistently higher in

380   position, aggression, color and overall dominance than offspring of freshwater residents when

381   fish had previously experienced an intermediate level of food availability, but the two

382   offspring types behaved similarly when reared on low or high food rations. When reared on

383   low food rations both parental types occupied relatively poorer spatial positions and showed

384   very low (= more subordinate) scores for color, aggression and overall dominance. In

385   contrast, if they had previously experienced high food availability they were observed to

386   occupy more favorable spatial positions, were more aggressive and had more dominant

387   coloration.

388   The positive relationship observed between correlates of dominance and rearing

389   environment suggests that the foraging and territorial strategy adopted is dependent on the

390   individual's previous experience of the profitability of the environment. It has previously

391   been argued that the strength of territorial defence should depend on resource availability,

392   with greatest resource defence at intermediate levels (Myers et al. 1979; Toobaie and Grant

393   2013). Individuals from the low food treatment, which were in poorer average body

394   condition, may have been less able to engage in costly aggressive interactions (Johnsson et al.

395   1996). As a result they were likely adopting an "energy minimizing" or "sit and wait"

396   strategy, whereby individuals sacrificed the option of obtaining a territory in a good feeding

397   position to avoid the energetic costs of both swimming against the water flow and potential

398   battles over territories (as seen by the low aggression scores in this treatment group). Since

399   investment in territorial aggression can be costly for growth (Vøllestad and Quinn 2003),

400   minimization of costs may have been the best strategy for these fish (Metcalfe 1986). While

401   these fish showed less inclination to establish a feeding territory, they nonetheless tended to

402   acquire more food than pairs from the higher food treatments, suggesting that short-term gain

403   was more important than the long-term benefits of a territory. In contrast, individuals from

404   the high food treatment, which were in better body condition, tended to adopt a more active

405 and aggressive strategy (i.e. competing for the best foraging position in the centre of the

406 water column) that may be geared toward longer-term access to food.

407   The differences in foraging and competitive strategies based on an individual's prior

408 experience of access to food that were observed in our study have parallels in the study by

409 Sundström et al. (2003), which showed that brown trout reared in a hatchery were more

410 aggressive in territorial defence than wild-reared conspecifics. These findings may help to

411 explain inconsistences in the relationship between dominance status and growth found in

412 other experimental studies. For example, juvenile Atlantic salmon with higher social status

413 have been shown to have higher grow rates than subordinates when fed ad libitum from a

414 point source in the laboratory (Metcalfe et al. 1989) but have similar or lower growth rates

415 relative to subordinates when food predictability decreases (Huntingford and Leaniz 1997;

416 Höjesjö et al. 2002; Reid et al. 2012).

417   Although traits related to dominance did not differ between offspring from

418 freshwater-resident and anadromous parents if they had been reared on high or low food

419 rations, there was a significant difference in dominance if they had been reared at an

420 intermediate food level (with offspring from anadromous parents behaving in a more

421 dominant and competitive manner). This asymmetry suggests that the two parental types

422 differ in the environmental threshold at which they adopt a more competitive and aggressive

423 foraging strategy, with offspring from anadromous parents switching to territorial behavior at

424 a lower food level. One possibility for the observed difference between parental types is

425 inherent differences in foraging motivation driven by asymmetries in physiology or projected

426 life history. Differences in motivational state linked to hunger have been shown to increase

427 aggression and strengthen social interactions in birds (Andersson and Ahlund 1991) and

428 fishes (Dill et al. 1981; Johnsson et al. 1996), and it may be that the offspring of anadromous

429   parents have either a different food requirement or threshold for territoriality, leading to the

430   observed differences in aggressiveness between parental types on mid food rations.

431   Another possibility for the parental type by food level interactions could be the timing

432   of the experiment with respect to whether or not individuals were destined to migrate. Given

433   their size at the time of the experiment, the earliest that any of the experimental fish would

434   migrate to sea would be in the following spring. Morinville and Rasmussen (2003)

435   demonstrated that individual migrant brook trout (*Salvelinus fontinalis*) had higher food

436   consumption rates and lower growth efficiencies in the year leading up to migration

437   compared to sympatric resident brook trout, suggesting that the migrant brook trout had

438   higher metabolic costs. Furthermore, Thorpe et al. (1998) proposed that the decision to

439   migrate in the closely-related Atlantic salmon occurs soon after mid-summer (around the time

440   of this study): fish that fall below their individual threshold for growth rate at this time

441   subsequently decline in appetite, cease growth and defer migration, while those individuals

442   who are above the growth threshold maintain their appetite throughout late summer and

443   autumn and undergo migration the following spring. If this pattern of migration holds for

444   brown trout, then all fish in the low food treatment may have already failed to reach the

445   threshold triggering migration. However, if the tendency to migrate is partially genetically

446   determined (Berthold 1988; Berthold and Pulido 1994), then under the mid food treatment

447   offspring of migrants might have had a lower growth threshold triggering migration, so

448   would have a greater motivation to acquire feeding territories so as to be able to maintain

449   their growth rate. Meanwhile all fish reared on the high food treatment may have passed their

450   respective thresholds, leading to aggressive and dominant behavior being expressed by both

451   parental types in preparation for migration the following spring.

452   One potential caveat to our study is that we were unable to determine whether the

453   differences between offspring behavior were primarily due to genetic or maternal effects, but

454 this would be difficult to establish given that the resident-anadromous dichotomy by its very

455 nature prevents the use of the standard approach of rearing the parents in a common garden to

456 rule out maternal effects.

457   In conclusion, the results of this study demonstrate that both the life history strategy

458 of the parents and the rearing environment of the offspring may have a significant effect on a

459 range of dominance related traits. Therefore we suggest that inherent differences in

460 dominance-related traits, when coupled with spatial variation in environmental productivity,

461 may play a significant role in the perpetuation of non-breeding partial migration within

462 populations.

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639

640 **Table and Figure Captions.**

641

642 Table 1. Pairwise Pearson's correlation coefficients and PC1 coefficients from PCA analysis,

643 for all four behavioral traits observed. All four traits were significantly correlated with one

644 another (df=178, p<0.001), with the first Principal Component summarizing 64% of the

645 variation.

646

647 Fig.1. Schematic diagram of the experimental stream channel used in this experiment with

648 the straight sections of stream channel divided into 15 equally sized test arenas (Ta); arrows

649 indicate water direction (Wd), with the pump (P) and water inflow (Wi).

650

651 Fig.2. The mean (±SE) length (A), mass (B) and relative condition (C) of offspring of

652 freshwater-resident (closed circles) and anadromous (open circles) parents used in the

653 dominance trials. Data shown separately for fish from low, mid and high food treatments.

654 Note that fish were selected to be size-matched within food treatments, but differences

655 between food treatments reflect effects of treatment on growth and condition.

656

657 Fig.3. The mean (±SE) scores for aggression (A), color (B), position (C), food acquisition (D)

658 and dominance (E) of offspring of freshwater-resident (closed circles) and anadromous (open

659 circles) parents, plotted separately for pairs from low, mid and high food treatments. Data are

660 plotted as z-scores except for (E) which shows scores for the first principal component in a

661 PCA of the other four variables (A-D). See text for statistical analysis.

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663