

1 **Is there genetic variation in the response to competition intensity in juvenile**
2 **brown trout, *Salmo trutta*?**

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Running title: Genetic variation in response to competition

ABSTRACT

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25 Effects of intraspecific competition intensities on the relative performance (growth and
26 movement) of juvenile brown trout *Salmo trutta* originating from nine different families were
27 tested in tank experiments and in semi-natural streams. Both growth and movement differed
28 consistently among families, indicating genetic variation in these traits. However, there were
29 no significant interaction effects between the intensity of competition and family on
30 performance in either of the two experimental systems. Thus, genetic variation in responses to
31 competition intensity appeared to be limited in the population from which the juveniles used
32 in this experiment originate.

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47 Key words: density dependence; dispersal; environmental heterogeneity; genotypic selection;

48 intraspecific competition; salmonids.

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INTRODUCTION

50 Despite being heritable, under continuous selection and highly connected to fitness, genetic
51 variation for life history traits is maintained within populations. This apparent paradox has
52 received considerable interest in evolutionary ecology (Roff, 1992, 2002; Stearns, 1992) and
53 several explanations have been proposed. These include the potential for temporal variation in
54 selection pressures, balance between mutation rate and selection, selective advantage of
55 heterosis, antagonistic pleiotropy, and frequency-dependent selection (reviewed in Roff,
56 1992). Finally, the environment can be spatially heterogenous with regard to selection
57 pressures (Levene, 1953; Roff, 1992). Since no single genotype can be superior under all
58 environmental conditions, different genotypes will be selected for in different spatial locations
59 within populations and this may contribute to maintenance of variation (Roff, 1992).

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61 Several environmental variables typically vary over large spatial scales, and can thus be
62 responsible for differences in selection pressures among distinct populations or sub-
63 populations. Indeed, empirical studies have often investigated the effect of abiotic factors
64 (such as latitudinal gradients, temperature and climate) on life-history trait variation (e.g.
65 Williams & Moore, 1989; Weber & Schmid, 1998; Bronikowski, 2000; Allan & Pannell,
66 2009; Wagner & Simons, 2009). Uncovering environmental variation over smaller spatial
67 scales (i.e. within populations) that could lead to differential local selection pressures, and
68 thus contribute to the maintenance of within-population genetic variation, may be less straight
69 forward (but see e.g. Kittelson & Maron, 2001). One biotic variable which may frequently
70 vary substantially over small spatial scales is the local population density. By influencing the
71 intensity of intraspecific competition it can affect local selective regimes. If competition is
72 asymmetric the relative performance of individuals would likely rely on their competitive
73 ability, with competitive individuals having an advantage at high density. However, having

74 traits connected to high competitive ability could be costly and may not pay off in the absence
75 of competition. For example, under high levels of competition a fast growing individual could
76 profit from high competitive ability as it will gain a cumulative size advantage (Arendt, 1997).
77 In the absence of competition these benefits could be offset by costs, such as increased
78 exposure to predators (Sundström *et al.*, 2004; Brodin & Johansson, 2004) and reduced
79 tolerance to low oxygen conditions (Sundt-Hansen *et al.*, 2007). Traits associated with
80 competitive ability can be heritable, and thus different genotypes may be optimal at different
81 densities (Sinervo *et al.*, 2000; Joshi *et al.*, 2001).

82

83 Rather than being homogeneously distributed within the spatial range inhabited by a
84 population, individuals from a variety of organisms are often aggregated at some spatial scale
85 (e.g. Taylor *et al.*, 1978; Perry, 1995). Spatial heterogeneity in population density has often
86 been observed in both plants and other sessile organisms (e.g. Rees *et al.*, 1996; Law *et al.*,
87 1997), as well as in mobile animals (Hassell *et al.*, 1987; Brown *et al.*, 1995; Ray & Hastings,
88 1996; Wilkin *et al.*, 2006). Certain aspects of their biology may cause such local scale
89 variation in density to be more pronounced in some organisms than in others. In particular,
90 having a patchy propagule (offspring, seeds, eggs) distribution and high fecundity may
91 potentially lead to high local densities in the juvenile stage even if overall population density
92 is low. In such organisms spatial heterogeneity in population density, and hence intensity of
93 intraspecific competition, is likely to be pronounced.

94

95 One group of organisms that has received considerable attention with regard to spatial
96 variation in local density are the stream-spawning salmonid fishes. The eggs of such species
97 (e.g. brown trout, *Salmo trutta* L. and Atlantic salmon, *Salmo salar* L.) are deposited in
98 distinct nests in the streambed gravel. After hatching juveniles emerge from the gravel and

99 establish feeding territories (Titus, 1990; Elliott, 1994; Milner *et al.*, 2003). The high
100 fecundity of salmonids, together with this patchy distribution of eggs and the restricted
101 movement of the juveniles leads to spatial heterogeneity in the local density, and hence levels
102 of competition experienced by the juveniles varies over space (Einum & Nislow, 2005; Einum
103 *et al.*, 2006, 2008; Foldvik *et al.*, 2010). Selection on traits providing competitive advantages
104 may therefore be hypothesised to vary accordingly, thereby contributing to the maintenance
105 of within-population genetic variation. In the present study this hypothesis is tested by
106 comparing the relative performance (growth and movement) of individuals from different
107 full-sib *S. trutta* families under different competitive intensities in both semi-natural streams
108 (by manipulating fish density) and in tanks (by manipulating feeding regime).

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METHODS

111 Eighteen adult *S. trutta* (nine males and nine females) from a 1st generation hatchery reared
112 strain (i.e. offspring of wild parents) from the Tunhovd population (60°22'59N, 08°51'57E)
113 were used to produce nine full-sib family groups in the fall of 2006 at the Norwegian Institute
114 for Nature Research (NINA) Research Station, Ims, south-western Norway. All experiments
115 were also conducted at this location. During May 21-25 2007, approximately 2 months after
116 onset of exogenous feeding, a random sample of the resulting juveniles (mean fork length, L_F
117 $\pm S.D.$: 41.2 ± 2.6 mm) were anaesthetized (benzoat), photographed for later measurements of
118 L_F (using ImageJ v. 1.41), assigned to different treatments (see below) and marked
119 accordingly with visible implant elastomer tags (VIE).

120

FAMILY-SPECIFIC GROWTH RATES UNDER CONTRASTING FEEDING REGIMES

122 To estimate family specific growth rates under two contrasting feeding regimes, five
123 individually VIE marked juveniles from each family were put into each of ten tanks (450 mm

124 x 450 mm, 600 mm deep with a water level of 300 mm) and 1) fed *ad libitum* with EWOS
125 (Bergen, Norway, www.ewos.com) commercial pelleted food (five tanks), or 2) given a
126 reduced ration of a natural prey (chironomid larvae) allowing a mean energy intake half way
127 between maintenance and maximum (five tanks). For this second treatment rations were
128 calculated according to Elliott (1976) and Elliott *et al.* (1995), taking into consideration fish
129 body size and expected water temperatures (ration range: 80 – 135 mg individual⁻¹ day⁻¹). To
130 increase the potential for competitive interactions and dominance in the reduced diet
131 treatment, the fish were fed twice each day by placing an ice cube containing half of the daily
132 ration of chironomid larvae in a tube which was placed vertically in the tank such that its
133 lower opening protruded 100 mm below the water surface. Thus, as the ice thawed larvae
134 were gradually made accessible for the fish at a certain location within the tank. The
135 experiment was started on May 25 and ended after thirty-one days, when the fish were killed
136 by an overdose of anaesthetics and subsequently identified and L_F measured.

137

138 FAMILY-SPECIFIC RESPONSE TO HIGH AND LOW DENSITY

139 On May 25, juveniles which were VIE marked according to family-group were released
140 simultaneously at either high or low density close to the inlets of the two parallel artificial
141 streams (107 x 1.5 m). The high and low density streams received 20 and 100 individuals
142 from each of the nine families, respectively. The streams contained gravel suitable for
143 juvenile salmon rearing and had fish traps at the outlets. Water to the streams was drawn from
144 a nearby lake and both streams had a water discharge of ~16 l s⁻¹. Only natural food items
145 entering through the inlet water or present in the substrate were available for the fish. During
146 the course of the experiment the fish were allowed to move into the fish traps. The traps were
147 checked every day and movers were killed and frozen for subsequent processing. Thirty-one

148 days after the fish were released, three pass electro-fishing was conducted and all fish were
149 identified and L_F measured.

150

151 STATISTICS

152 All statistical analyses were conducted in R, v. 2.10.0. (R Development Core Team 2009).

153 Linear mixed models (using the *lme* function in the *nlme* package; Pinheiro *et al.*, 2009) were
154 used to model variation in individual growth rate in the tank experiment.

155 A model including family-group, treatment and the interaction between these was made to

156 check for effects on final L_F . Initial individual L_F was included as a covariate and tank as a

157 random factor (random intercept). To enable estimation of family-specific intercepts between

158 initial L_F and final L_F (i.e. a proxy for family-specific growth rate) the interaction between

159 initial L_F and family was not allowed for in the full model. The variance of the residuals from

160 this model differed among families. To account for this the *varIdent* function was applied,

161 which led to a decrease in AIC ($\Delta AIC = 22.3$, calculated using REML). Evaluation of fixed

162 effects was done according to the protocol recommended in Zuur *et al.* (2009), and thus based

163 on sequential removal of fixed effects with subsequent ANOVA comparisons until log-

164 likelihoods (based on ML) decreased significantly ($P < 0.05$).

165

166 Differences among families in relative movement rates from the two streams throughout

167 the experimental period were also tested for. For each focal family and stream, the expected

168 number of movers (i.e. expected if relative movement from the two streams was not different

169 from that of the rest of the families) were calculated based on 1) the total number of movers

170 from the focal family and 2) the proportion of the total observed movement (sum from both

171 streams) that occurred at high and low density, respectively, after the family in question was

172 excluded. The observed number of movers at high and low density for the focal family was
173 then compared to these expected numbers of movers using a Chi-squared test.

174

175 Variation in final L_F of the fish left in the streams until the end of the experiment was
176 modelled using the generalised least squares (*gls*) function (in the *nlme* package; Pinheiro et
177 *al.*, 2009). Stream (high or low density treatment), family-group and mean initial family L_F
178 were included as main effects in the initial model. Interactions between stream and family-
179 group as well as between stream and initial L_F were also included. To account for
180 heterogeneity of residual variance among families the *varIdent* function was applied. This led
181 to a decrease in AIC ($\Delta AIC = 7.8$, calculated using REML). Significance of the explanatory
182 variables in this model was assessed using the backwards model selection procedure as
183 described for the *lme* models. Family 2 was excluded from this analysis since no individuals
184 from this family were left in the low-density stream at the end of the experiment.

185

186 Next, model selection of *gls* models was used to test whether family-specific probabilities
187 for movement depended on stream, the relative family growth rates estimated in the tank
188 experiment, mean initial L_F , or two-way-interactions among these. Family proportions of the
189 individuals moving at different points in time or staying until electro-fished were arcsine-
190 square root transformed prior to statistical analyses.

191 To analyze whether the effect of relative family growth rates estimated from the tank
192 experiment, stream or the interaction between these had an effect on L_F of the fish remaining
193 in the streams at the end of the experiment, linear mixed effects models (*lme*) were used. To
194 control for family specific traits other than the estimated specific growth rate that could
195 influence final L_F , family was included as a random variable (random intercept). The model
196 including the random term was significantly better the model that did not (ANOVA

197 comparisons of log-likelihoods calculated using REML, $P < 0.05$). Again, to evaluate the
198 significance of the fixed effects, the backwards model selection procedure was used.

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200

RESULTS

201 FAMILY-SPECIFIC GROWTH RATE UNDER CONTRASTING FEEDING REGIMES

202 In the tank experiment all families grew better when given food in excess than when
203 subject to a restricted monopolizable feeding regime (Fig. 1). Further, the mean coefficient of
204 variation in growth (final L_F – initial L_F) was significantly lower in the tanks with food in
205 abundance (CV = 30%) than in the tanks with a restricted feeding regime (CV = 99%, t-test, P
206 < 0.001). The higher growth variation in the latter treatment indicates greater levels of
207 competition when the food was monopolizable and restricted than when food was given in
208 excess. The linear mixed model with tank as a random factor that included the main effects of
209 all the explanatory variables (family, treatment and initial L_F) performed best in explaining
210 variation in final L_F (Table I, decrease in AIC > 2 between consecutive models, increase in
211 AIC > 22.4 for removal of further terms). The lack of an interaction between family-group
212 and treatment in this model implies that the relative growth of the different families did not
213 depend on treatment. The estimates of relative family growth rates given by this model were
214 used as parameters in a movement model.

215

216 FAMILY-SPECIFIC MOVEMENT AND GROWTH AT HIGH AND LOW DENSITY

217 In the artificial streams a large fraction of the fish moved into the fish-traps during the first
218 four days of the experiment (Fig. 2). During this period a significantly higher proportion
219 (56%) moved at high density compared to at low (38%) (2-sample test for equality of
220 proportions, $P < 0.01$). Between day 12 and 18 a second movement wave occurred, during
221 which 31% and 42% of the fish that had not moved during the first 11 days moved from high

222 and low density, respectively (Fig. 2). The difference between these proportions was not
223 significant ($P > 0.05$). When the streams were electro-fished at the end of the experiment,
224 22% of the initial number of fish were left at high density and 24% at low ($P > 0.05$).

225

226 Family-specific proportions of the number of fish released that moved at high and low
227 density were positively correlated during the first movement wave (day 1-4) (Fig. 3a, $r_s =$
228 0.85, $P < 0.01$). What seems to be a similar pattern, although non-significant, was observed
229 during the second movement wave (day 12-18, Fig. 3b, $r_s = 0.62$, $P > 0.05$). Finally, family-
230 specific proportions of the total number released that were recaptured during electro-fishing
231 were significantly positively correlated (Fig. 3c, $r_s = 0.75$, $P < 0.05$).

232

233 Observed numbers of movers at high and low density did not differ significantly from the
234 expectations for any of the families (Table II). Thus, there was no pattern suggesting family
235 differences in response to density in terms of movement rates.

236

237 A model including the main effects of family and stream performed best in explaining
238 variation in final L_F of the fish remaining in the streams at the end of the experiment (Table
239 III, sequential ANOVA comparisons of log-likelihoods of preceding models, $P > 0.05$;
240 removal of further terms, $P < 0.01$). The lack of an interaction between family-group and
241 stream in this model implies that the relative growth of the different families did not depend
242 on stream (high or low density treatment).

243

244 EFFECT OF FAMILY-SPECIFIC GROWTH RATE ON MOVEMENT AND GROWTH AT
245 HIGH AND LOW DENSITY

246 None of the main effects (relative family growth rate, family mean initial L_F or density) or
247 interaction terms remained in the *gls* models best explaining variation in movement rates
248 during the two waves or proportions staying in the streams until electro-fished (ANOVA
249 comparisons of log-likelihoods, Bonferroni corrected for multiple comparisons, all $P > 0.05$).
250 Family-specific movement probabilities were therefore not related to the relative family
251 growth rates as estimated in the tank experiment.

252

253 Overall, final L_F of stayers in the low-density stream were larger than of those in the high-
254 density stream (mean $\pm S.D.$, low density: 55.2 ± 3.5 mm; high density: 50.4 ± 4.7 mm). The
255 mixed effects model that best described L_F of individual stayers included the main effect of
256 density treatment, but not the relative family growth rate estimates or the interaction between
257 these ($S.D.$ for the random intercept = 1.01 and $S.D.$ of residual variation = 4.37; low density
258 = 55.28 ± 0.75 ($S.E.$), $t = 73.29$, $P < 0.001$; high density relative to low density = -4.88 ± 0.73
259 ($S.E.$), $t = -6.65$, $P < 0.001$; n is 244 individuals from 9 groups).

260

261

DISCUSSION

262 By manipulating the level of intraspecific competition both in tank experiments and semi-
263 natural streams family-specific effects on the relative performance (growth and movement)
264 were tested for. Overall, both growth and movement were found to vary considerably among
265 families, indicating genetic variation in these traits. This is consistent with previous studies
266 (growth: Bailey & Loudenslager, 1986; Gjerde, 1986; Vøllestad & Lillehammer, 2000;
267 Vøllestad & Quinn, 2003; movement: Webb *et al.*, 2001). Yet, no significant interaction
268 effects between competition regime and family origin on performance were detected in either
269 of the two experimental systems. Thus, in contrast to previous studies performed on
270 organisms such as plants and shrimps (e.g. Shaw, 1986; Coman *et al.*, 2004), the relative

271 performance of individuals from different families was not conditioned by the strength of
272 competition. This result does not lend support to the hypothesis that spatial heterogeneity in
273 population density can be responsible for maintaining within-population genetic variation for
274 traits influencing competitive ability.

275 Two potential explanations for the lack of family-by-competition interactions in the present
276 study are suggested. First, the treatments could have failed in generating sufficient differences
277 in levels of competition. In the stream experiment, high density-dependent movement during
278 the initial period (day 1-4) caused a substantial reduction in the density contrast, which may
279 have reduced the power to detect such an interaction. Yet, although there was no evidence for
280 density-dependent movement following this initial period, the differences in density were
281 sufficient to produce effects on final body size, and hence growth rates. Furthermore, the
282 treatments in tanks (i.e. given non-monopolizable food in excess or restricted rations of
283 monopolizable food) had pronounced effects on both mean growth and variation in growth.
284 Thus, the different treatments were clearly successful in creating contrasting strengths of
285 competition in both experimental systems.

286

287 A second, and perhaps more likely, explanation for a lack of a family-by-competition
288 interaction could be that stabilising selection for the optimal competitive ability during the
289 juvenile life stage can be intense and spatiotemporally consistent in wild populations. If so,
290 this would lead to low genetic variation in traits influencing competitive abilities, and
291 manipulations of traits as well as intensity of competition would be required to detect the
292 effects of potential trade-offs. Due to the high fecundity and patchy egg distribution of
293 salmonids, high density of juvenile *S. trutta* after emergence from the gravel may be
294 ubiquitous in some populations. The *S. trutta* juveniles used in the current study originate
295 from the population in Lake Tunhovd, which is a relatively large lake (approximately 25 km²)

296 within which most of the feeding (including piscivory) and growth of sub-adults and adults
297 occur. Lake Tunhovd provides favourable growing conditions, resulting in relatively large
298 and highly fecund adults (many between 2-6 kg), whereas access to spawning areas in its
299 tributaries is limited (Åge Brabrand, Freshwater Ecology and Inland Fisheries Laboratory,
300 Natural History Museum, University of Oslo, pers. comm.). Accordingly, early-life
301 competition among juveniles after emergence from nests can be expected to be consistently
302 high in this population. Thus, experienced levels of competition may rarely be sufficiently
303 low to select for trait values that are beneficial under low competition during this early
304 juvenile stage in this population.

305

306 The authors are not aware of previous vertebrate studies experimentally testing for within-
307 population genetic variation in competitive ability. This is true even for juvenile salmonids, in
308 which genetic variation has been the subject of much attention (reviewed in Garcia de Leaniz
309 *et al.*, 2007). Other studies have shown relative performance of juvenile salmonids to depend
310 on phenotypic traits under different levels of competition, but these have focused on the
311 maternal effect of egg size rather than the genetic characteristics of the offspring (Hutchings,
312 1991; Einum & Fleming, 1999). Such effects include both maternal age- and size-dependent
313 traits (e.g. egg size increase with female size in salmonids, reviewed in Fleming, 1996; Heath
314 & Blouw, 1998) as well as environmental influences on mothers that have accumulated
315 throughout their lives (Fleming, 1996; Mosseau & Fox, 1998; Bonduriansky & Day, 2009).
316 Therefore, variation in such traits may be pronounced even under strong stabilising selection.
317 Since maternal effects generally are believed to be limited to the first period after hatching in
318 fish (Heath & Blouw, 1998; Perry *et al.*, 2004), and the juveniles used in this study had been
319 feeding exogenously for more than a month before the experiment was initiated, such effects
320 were not expected to be pronounced. Thus, even if the families may well have had different

321 competitive abilities associated with them due to maternal effects at an earlier stage, this
322 would not be expressed in the present study where the focus was on genetic effects.
323 The consistent among-family variation in growth rates across competitive regimes revealed in
324 the tank experiment allowed for a test of whether this trait had an effect on performance
325 (movement or final body length) in the semi-natural streams. Contrary to our expectations no
326 effect of the relative family growth rate estimates was revealed. This result adds to studies
327 that have failed in finding a correlation between individual performance in lab experiments
328 and under more natural conditions (Niva & Jokela, 2000, Martin-Smith & Armstrong, 2002;
329 Harwood *et al.*, 2003). These results do imply that relative performance among families, such
330 as growth, may depend highly on environmental conditions, and that traits beneficial in one
331 environment can be less beneficial, or even incur costs in another. Yet, there is currently no
332 support for the hypothesis that the relative performance of different genotypes of juvenile
333 salmonids depends on population density or competition intensity within a single type of
334 environment.

335

336 The present results indicated a lack of genetic within-population variation in response to
337 competitive intensity. It seems possible that the spatial heterogeneity in local juvenile
338 densities may not have been sufficient for differential genetic selection among patches to
339 occur for our population. If so, this would prevent spatial variation in level of competition to
340 contribute to maintaining genetic variation. Yet, previous studies of maternal effects in
341 salmonid fishes have shown strong effects of the intensity of competition on the relative
342 performance of different phenotypes (e.g. Hutchings, 1991; Einum & Fleming, 1999). It
343 would therefore be surprising if offspring genetics in general plays no role in determining
344 their response to competition intensity. Thus, it may prove fruitful to test for genetically based

345 variation in response to competition intensities for populations or species that have evolved
346 under different ecological settings from those of the population used in the present study.

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ACKNOWLEDGEMENTS

349 We thank the staff at the NINA Research Station at Ims, A. Foldvik and M. Teichert for
350 assistance with the experiment. This study was funded by the Norwegian Research Council
351 and the Norwegian University of Science and Technology. This study was conducted
352 according to national regulation for treatment and welfare of experimental animals under
353 licence number 051 granted by the Norwegian Animal Research Authority to the NINA
354 Research Station, Ims.

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489

FIGURE CAPTIONS

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Fig. 1. Mean ($\pm S.E.$) of the mean family growth (final L_F – initial L_F , mm) in different tanks under the restricted ($n = 5$ tanks) and the maximum ($n = 5$ tanks) feeding regime. Numbers denote families.

Fig. 2. Number of juvenile brown trout moving each day and the number left at the end of the experiment (day 31) in the (a) high and (b) low density stream.

Fig. 3. Relationship between family proportions of brown trout juveniles at low and high density that (a) moved within the first four days ($r_s = 0.85$, $P < 0.01$), (b) stayed in the streams until day 11 and moved during day 12-18 ($r_s = 0.62$, $P > 0.05$) and (c) stayed in the streams until the end of the experiment ($r_s = 0.75$, $P < 0.05$). Numbers denote families.

514 **Table I.** Summary of the best linear mixed effects model explaining variation in final body
515 length (L_F , mm) of juvenile brown trout, *Salmo trutta* in the tank experiment. Tank is included
516 as a random factor (random intercept). The fixed effects parameters are given as treatment
517 contrasts with Family 1 and the maximum feeding regime as intercept. Estimated parameters
518 for Random is *S.D.* of the random intercept in the model, with *S.D.* of residual variation given
519 in brackets. n is 390 individuals from 10 groups.

	Parameter \pm <i>S.E.</i>	<i>T</i>	<i>P</i>
Random	0.65 (2.87)		
Intercept	46.72 \pm 0.61	76.06	< 0.001
Initial L_F (mm)	0.03 \pm 0.001	20.07	<0.001
Family 2	2.11 \pm 0.66	3.21	< 0.01
Family 3	2.50 \pm 0.71	3.51	< 0.01
Family 4	1.92 \pm 0.75	2.56	< 0.05
Family 5	0.27 \pm 0.58	0.47	> 0.05
Family 6	0.48 \pm 0.52	0.91	> 0.05
Family 7	-0.57 \pm 0.54	-1.05	> 0.05
Family 8	0.38 \pm 0.68	0.56	> 0.05
Family 9	0.88 \pm 0.54	1.64	> 0.05
Treatment (Restricted diet)	-7.93 \pm 0.50	-15.9	< 0.001

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525 **Table II.** Numbers of individual brown trout, *Salmo trutta* juveniles from each family moving
 526 at low (LD) and high density (HD), together with the proportion of total movers of the
 527 remaining families moving at LD (LD Prop) and HD (HD Prop), respectively (expected
 528 movement rates). Chi-square tests compare observed numbers of individuals from each family
 529 moving at high and low density with expected numbers.

Family	LD	HD	LD Prop	HD Prop	χ^2	<i>P</i>
1	14	91	0.16	0.84	0.55	> 0.05
2	18	92	0.16	0.84	0.06	> 0.05
3	13	75	0.16	0.84	0.06	> 0.05
4	15	75	0.15	0.85	0.09	> 0.05
5	16	77	0.15	0.85	0.23	> 0.05
6	11	62	0.16	0.84	0.02	> 0.05
7	9	58	0.16	0.84	0.29	> 0.05
8	16	64	0.15	0.85	1.47	> 0.05
9	11	70	0.16	0.84	0.32	> 0.05

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532 **Table III.**

533 Summary of the generalised least square model that best explains variation in final lengths (L_F ,
 534 mm) of juvenile brown trout, *Salmo trutta* staying in the streams until electrofished.

535 Parameters are given as treatment contrasts with Family 1 and the low density stream as
 536 intercept. $n = 237$ individuals; Family 2 was excluded from this analysis since no individuals
 537 from this family were left in the low density stream when the experiment was finished.

	Parameter \pm S.E.	t	P
Intercept	55.47 \pm 1.6	34.57	< 0.001
Family 3	-2.35 \pm 1.89	-1.25	> 0.05
Family 4	1.16 \pm 1.85	0.62	> 0.05
Family 5	1.45 \pm 1.77	0.81	> 0.05
Family 6	-1.24 \pm 1.72	-0.72	> 0.05
Family 7	0.74 \pm 1.6	0.46	> 0.05
Family 8	-1.50 \pm 1.66	0.9	> 0.05
Family 9	-0.82 \pm 1.66	-0.49	> 0.05
Stream (High density)	-4.86 \pm 1.66	-7.27	< 0.001

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