Who will become dominant? Investigating the roles of individual behaviour, body size, and environmental predictability in brown trout fry hierarchies

[1]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden
*Corresponding author, E-mail: joacim.naslund@gmail.com

[2]Department of Ecosystem Biology, Faculty of Science, University of South Bohemia in České Budějovice, České Budějovice, Czech Republic

[3]Present address: Department of Zoology, Stockholm University, Stockholm, Sweden

Joacim Näslund[1,2,3]*, David Berger[1], Jörgen I. Johnsson[1]

ABSTRACT

This paper presents a study investigating performance of brown trout fry, with different behavioural characteristics, in environments differing in food predictability. Based on previous experimental findings, we hypothesised that more active individuals would be favoured by a predictable environment, as compared to an unpredictable environment, as a consequence of being more aggressive and likely to dominate the best feeding stations. This hypothesis was not supported, as more active individuals instead tended to perform better, in terms of growth and survival, in unpredictable environments. However, this effect may stem from initial size differences, as more active fish also tended to be larger. In predictable environments, no trends between activity (or size) and performance were detected. Dominant individuals could be identified based on lighter body colouration in 9 out of 10 rearing tanks, but dominance appeared not to be related to activity score. The results highlight a potential advantage of more active and/or larger fry in unpredictable environments, while performance in predictable environments is likely depending on other phenotypic characteristics. Our general experimental approach can be useful for further developments in the investigation of performance of different ethotypes of brown trout fry.

KEYWORDS

Behavioural variation; Salmonids; Dominance hierarchies; Growth; Colouration

INTRODUCTION

Standardized activity scores, in particular from an open-field context where animals are forced into a barren arena for trial (Walsh & Cummins 1976), is relatively consistent within individuals over days, weeks, and months (Adriaenssens & Johnsson 2013; Kortet et al. 2014; Näslund & Johnsson 2016; Wengström et al. 2016; Näslund et al. 2017a), indicative of different behavioural types which may reflect different life-strategies (e.g. Héland 1999). Standardized laboratory activity tests can predict stream performance in brown trout during the initial critical period of their life, with more active individuals generally having a higher survival chance (as indicated by higher recapture rate: Adriaenssens & Johnsson 2013; Näslund et al. 2017a). Activity also covary with aggression towards a mirror image, forming an activity-aggression syndrome (Kortet et al. 2014; Näslund & Johnsson 2016).

Following the classical production-mortality trade-off, individuals with higher productive rate (i.e. growth for juveniles, or reproductive output for adults) are predicted to require higher activity rates, leading to increased exposure to predators and aggressive competitors (Werner & Anholt 1993; Réale et al. 2010). However, the young brown trout do not follow this predicted trade-off, as survival is positively related to activity. This may be a consequence of the highly aggressive and territorial behaviour of brown trout fry, which could be positively linked to competitiveness and growth potential (Kalleberg 1958; Titus 1990). Being territorially competitive may influence performance positively in several ways, e.g. through the securing of food resources to avoid starvation and outgrow both vulnerable stages and competitors, and through securing of shelter resources to avoid predation (Johnsson et al. 2004).

Several studies support the hypothesis that more active fry are more likely to become territorially dominant. For

instance, activity (as measured in a group of individuals) was positively linked with territory quality in hatchery-origin brown trout kept in experimental aquaria (Hoogenboom et al. 2013). In addition, brown trout fry becoming dominant have a higher aggression level toward their mirror images than those becoming subordinate (Höjesjö et al. 2004). However, dominant individuals are negatively influenced by habitat complexity, suggesting that environmental variability may reduce the benefit of being territorial (Höjesjö et al. 2004, 2011). Thus, being non-territorial could be an alternative adaptive life-strategy for stream living salmonids (Héland 1999; Roy et al. 2013).

In this pilot laboratory experiment, we addressed the hypothesis that more active individuals of brown trout fry are benefitted when an environment favours resource defence. Generally, resource defence should be based on whether its benefits exceed the costs (Grant 1997). A predictable environment, in which a fixed number of individuals are situated, should typically favour defence of the best foraging site(s), leading to an ideal distribution where rank in competitive strength of the individuals matches the rank in habitat quality (e.g. food abundance) of the area in which they reside (Reid et al. 2011; Sloat & Reeves 2014). In an unpredictable environment resource defence may be less favoured, leading to lower growth advantage of dominant individuals (Grant 1997). Thus, we predicted that more active individuals, presumably belonging to a more territorial phenotype, will become dominant to a higher extent and grow faster in a predictable environment than in an unpredictable environment. Less active individuals may be more flexible in their space utilization and benefit from an unpredictable environment.

1. MATERIALS AND METHODS

Small groups of trout fry with mixed activity scores were subjected to two different competition scenarios in standardized arenas. The two scenarios consisted of (1) predictable, and (2) unpredictable food delivery over 12 days.

1.1. Experimental animals – capture and acclimation
On June 15, 2015, 119 trout fry were caught using electrofishing (LUGAB L-600, Lug AB, Sweden 300V) at a brown trout spawning site in Norumsån (58°2.5930N, 11°50.7580E), a small stream on the Swedish west coast, and brought to the zoological laboratory at the Department of Biological and Environmental Sciences, University of Gothenburg. The fish were initially kept in one 60-l holding aquarium furnished with gravel and plastic plants, rocks, and plastic plates for shelter.

On June 19, 90 fish were randomly selected and divided into three separate 60-l aquaria (A, B, and C; each containing 30 individuals and furnished like the initial holding tank) to facilitate finding specific individuals when splitting fish into treatments. The same day, these fish were subcutaneously tagged with elastomers (North West Marine Technology Inc., USA), which were injected, using a fine needle, into one position next to the dorsal fin and one position next to the anal fin. Six elastomer colours (red, blue, yellow, orange, black and white) were used. During the tagging procedure, the fish were anesthetized with 2-phenoxyethanol (0.5 ml · l⁻¹). Fish from group A were tagged on the right side (both positions), group B on the left side (both positions) and C on right and left side (dorsal and anal fin respectively). Combining colours and positions allowed for each fish to receive a unique tag pattern. After tagging the fish were returned to their holding tanks for another two days.

During the period preceding the competition trial, all fish were provided with chironomid larvae until satiation, twice a day, morning and afternoon. The water temperature was kept between 10.4°C and 10.8°C in the acclimation aquaria, using a circulatory flow-through system which supplied a constant flow of fresh water.

1.2. Activity scoring and initial size measurement
The methodology used for scoring individual activity in the trial was adapted from previous studies (Näslund & Johnsson 2016; Näslund et al. 2017a). On June 23, all tagged fish were placed individually in plastic containers (L × W × H: 280 × 190 × 250 mm, with approximately 5 cm of water) and recorded using digital HD cameras (Toshiba Camileo S20, Toshiba Corp., Japan). Three cameras were used and each camera recorded four containers simultaneously through twenty-minute trials. The fish were left undisturbed for 10 minutes before swimming activity was scored, to eliminate the effect of individuals "freezing" when being transferred to the novel, barren environment. The water in the trial arena was changed between every session. After the trial, each fish was anesthetized, weighed, and photographed along with a millimetre-scale for length measurements (Canon EOS 40D; lens: EF 100/2,8 USM Macro 1:1; Canon Inc., Japan).

Grids of twelve equally sized rectangles (4 × 3; each rectangle being 70 × 63.3 mm), drawn on plastic film, were placed on a computer screen, matching the area of the water surface in the containers. The number of times a fish crossed any of the lines in the grid during ta ten-minute period was counted using the software VLC media player (VideoLan, France). A line-crossing was recorded only when the entire body of a fish had crossed a line. One of the films (4 fish) was too dark to be scored and therefore discarded. Based on cluster analysis (Two-step cluster analysis, SPSS 22, IBM Corp., USA) of the activity scores, the fry were divided into two groups; active and passive.

1.3. Competition trials
During the competition trial (Jun 28 – Jul 10), fish were kept in ten plastic containers (700 x 420 x 180 mm; bottom area ≈ 0.29 m²). We opted for an open arena design, where the different food provision areas were visually separated by walls (Fig. 1). In every section, a rock was placed to provide a shelter structure for the fish. Three fish from the active cluster and three fish from the passive cluster were put in each container; the group size was determined based on field observations of maximal

group sizes of brown trout fry (Elliott 1990). Within each container, the fish were size-matched to reduce size effects on social hierarchies. Size matching was carried out by splitting each activity-cluster into five size classes (for clustering assignment, see Fig. 2). From these classes, fish were randomly assigned to a container so that each treatment consisted of five groups of six fish (size differences within groups are visualized in Fig. 3). The containers were covered with plastic lids to prevent fish from escape by jumping. The approximate water depth was 10 cm and the substrate consisted of approximately 1 cm of coarse sand.

One active fish (in the predictable treatment, replicate P5) had escaped at the onset of the experiment, and had to be replaced by a passive fish from the left-overs from the group assignment, as no more fish classified as active were available. The replacement fish was selected based on activity (as one of the more active out of the remaining passive fish) and body size.

The water temperature was kept between 13.6°C and 14.4°C degrees during the competition trial.
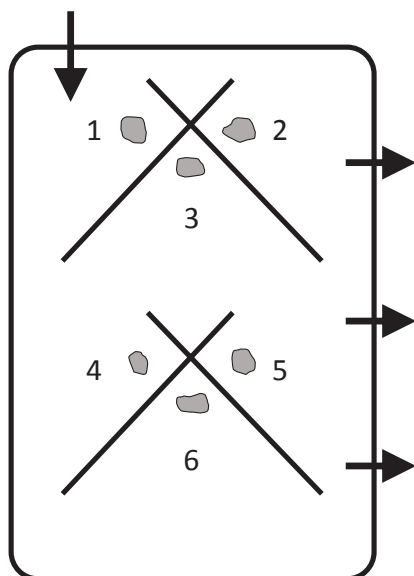

Figure 1. Arena design, as seen from above. Black lines inside arena: vertical opaque gray walls, blocking the whole water column; gray shapes: stones, for shelter and landmarks. Arrows show the inlet and outlets for water flowing through the arena. Numbers show the different feeding locations used.
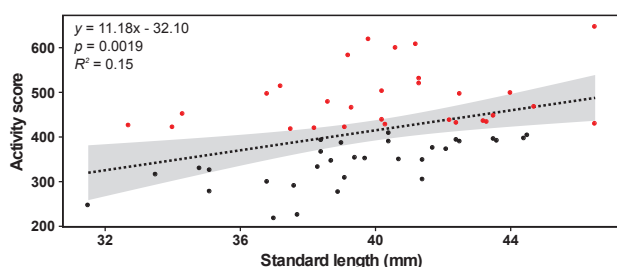

Figure 2. Relationship between body size and activity in the open-field test. Formula for the regression (dotted line, with 95% confidence band shaded in grey) is presented, along with p-value and R2-value, in the top left corner of the figure. Red dots mark the individuals in the higher-activity cluster; black dots mark individuals in the lower-activity cluster.

1.4. Feeding treatments

Five containers were provided with chironomids in a predictable manner and five in an unpredictable manner. In the predictable treatment, the same rations were provided at the same feeding location twice every day (morning and afternoon), while in the unpredictable treatment the rations shifted among different feeding locations (Fig. 1). Food rations, in terms of number of average sized chironomids larvae, were based on the average mass of the fry within each pair (active and passive) of containers. For complete food ration tables, see Appendix 1.

When a fry in the predictable environment died, the smallest ration of that particular container was removed, assuming that the dead individual had occupied the least good foraging position with respect to ration size. When a fry in the unpredictable environment died, the smallest ration of its size-matched stabile container was subtracted from the total number of larvae given during subsequent feedings.

1.5. Final measurements

After twelve days of treatment the fish were identified, weighed, and photographed once again. Since bright body coloration is an indicator of dominance and dark body colour indicates a subordinate individual (Kalleberg 1958; Keenleyside & Yamamoto 1962; Watt et al. 2017), bright and dark individuals were noted.

1.6. Data handling and statistical analyses

Standard length (distance between the tip of the nose and the end of the caudal peduncle, not including the tail fin) was measured from photographs using Image J (Schneider et al. 2012) (precision 0.1 mm). Dependence of activity on body size (SL) was analysed using a linear regression. Spearman rank correlations based on activity and growth, and initial size and growth, were calculated for each group of fish. The rank correlation coefficients (ρ) were used to analyse the overall pattern of correlation within and between treatments, using one-sample and two-sample t-tests, respectively. Mortality patterns were analysed using χ^2-tests, with data from all compartments pooled.

Ethical note

The experimental procedures in this study were approved by the Ethical Committee for Animal Research in Gothenburg (ethical license number 8–2011).

2. RESULTS

2.1. Size-dependence of open-field activity

Activity in the open-field test showed a significant positive size-dependence (Fig. 1). Notably, there was a relatively large variation around the predicted line, as the regression only explained 15% of the variance.

2.2. Body coloration and dominance rank

In 9 out of 10 rearing containers, a lightest-coloured individual could be visually determined. In all cases, subsequent weighing revealed that these lightest-coloured individuals were the ones with the highest increase in mass (Fig. 4). Only 4 clearly darker individuals could be recognized (Fig. 3).

2.3. Dominance rank in relation to relative activity and size in the lab

Rank correlation coefficients (Spearman's ρ) between activity and growth suggested that there was a stronger pattern for

positive association in unpredictable environment (mean ρ: 0.32), than in predictable environment (mean ρ: 0.07) (Table 1; Fig. 5). However, the comparison between the two environmental treatments rendered no significant differences ($p = 0.31$; Table 1), likely a consequence of low statistical power ($n = 5$). Using initial size (mass or length) as a predictor of dominance rendered similar results as using activity, with patterns being stronger in the unpredictable treatment [mean ρ: 0.39 (mass), 0.42 (length)] than in the predictable [mean ρ: -0.01 (mass), -0.08 (length)]; but, again, without significant differences between the treatments ($p = 0.19$; Table 1).

2.4. Mortality patterns

Overall mortality was 25% (see distribution of mortalities in Fig. 3). Overall, fish from the low-activity cluster tended to show a higher mortality rate than fish from the high-activity cluster ($\chi 2 = 2.82$, $p = 0.093$). Within the unpredictable treatment the mortality was higher among passive fish ($\chi 2 = 6.42$, $p = 0.011$).
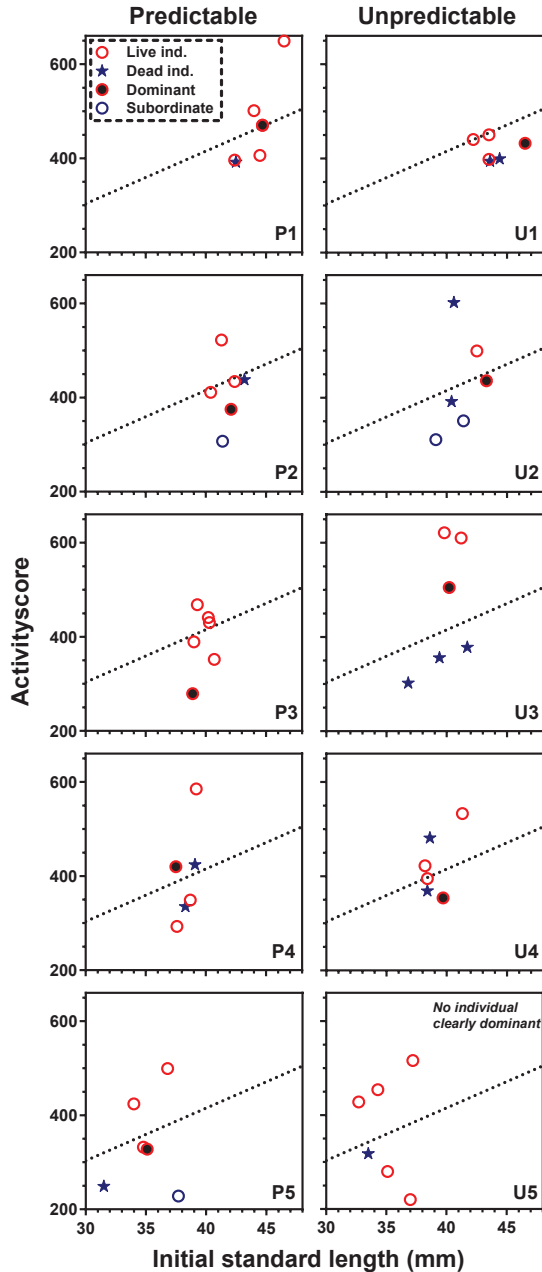
Figure 3. Illustration of dominance and mortality patterns in relation to initial body size and open-field activity for all replicates: P1-P5 denote the replicates from the predictable treatment; U1-U5 denote replicates from the unpredictable treatment. Dotted line show predicted activity levels based on initial body size (Fig. 2).
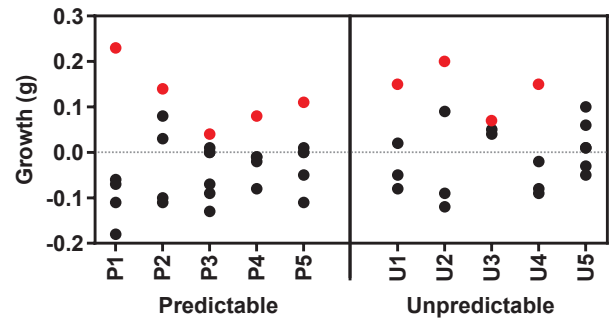
Figure 4. Performance in terms of absolute growth and dominance of surviving individuals. Red dots mark the individuals scored as dominant based on having the lightest body coloration, prior to weighing. P1-P5 denote the replicates from the predictable treatment; U1-U5 denote replicates from the unpredictable treatment.
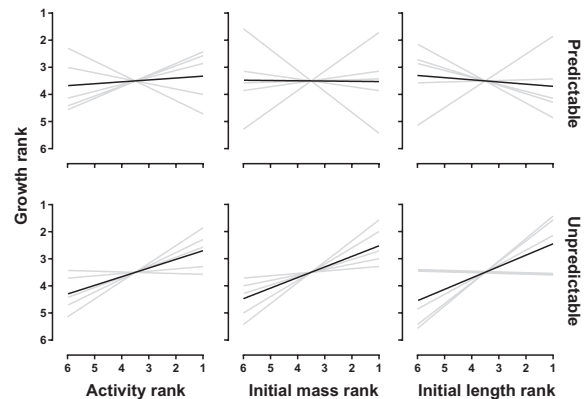
Figure 5. Rank correlations between growth and activity, initial mass, and initial total length. Black lines show average rank correlation patterns, grey lines show correlation patterns for individual replicates. Summary statistics are found in Table 1.

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Table 1: Summary of statistics for Spearman rank correlations between growth and activity, initial mass, and initial length (with t-statistics for deviance from 0), and for the t-tests of differences in rank correlation factor (Spearman's ρ) between treatments.

	Rank correlations			Difference between treatments
	Predictable env. Mean ρ (SD) $\lvert t \rvert$; p	Unpredictable env. Mean ρ (SD) $\lvert t \rvert$; p		Predictable − Unpredictable $\lvert t \rvert$; p
Activity - Growth	0.07 (0.40) 0.41; 0.70	0.32 (0.28) 2.49; 0.07		1.10*; 0.31
Initial mass - Growth	-0.01 (0.53) 0.03; 0.98	0.39 (0.28) 3.11; 0.04		1.48*; 0.19
Initial length - Growth	-0.08 (0.46) 0.41; 0.71	0.42 (0.42) 2.21; 0.09		1.79; 0.11

* Walsh t-test for unequal variances

3. DISCUSSION

### 3.1. Dominance rank in relation to relative activity and size in the lab

Overall, no strong patterns emerged to signal that activity played any major role in obtaining a dominant position in the social hierarchy. The dominant fish, identified as the individual with the highest absolute growth rate, was typically not the most active fish in either predictable or unpredictable environments (Fig. 3). Despite inconclusive results, the experiment renders no support to our *a priori* prediction of high activity being favoured in a predictable environment. Instead, active individuals seem to be favoured in unpredictable environments, but this hypothesis should be followed up in new experiments with higher replication of groups. It seems possible that dominance can be achieved by a fish regardless of its activity profile. A previous laboratory experiment on similar sized groups of trout fry, indicated that there could be two types of dominant individuals, one being proactive in a novel environment (quickly moving away to new areas) and one being reactive (waiting to move until the other individuals in the group has moved away) (Závorka et al. 2015b).

3.2. Weak but significant effect of size on open-field activity

Size-dependency of open-field activity appears to be robust when comparing with a previous study on trout fry from the same population (Näslund & Johnsson 2016). Larger fry are generally more active also in other types of standardized behavioural trials such as mirror aggression tests (Näslund & Johnsson 2016), and start-box emergence tests (Näslund et al. 2015, 2017b).

3.3. Body coloration is suitable to identify dominant individuals

Using visual assessment of body coloration to score the dominant individual in small groups appears to be a suitable method for the type of experimental trials conducted in the present study. The assessment should be done immediately when collecting the individuals from the experimental container, as colour can change rapidly due to stress; coloration was not clearly visible from pictures taken on the anaesthetised fish a few minutes after being netted. Lighter colouration of dominants is consistent with other studies on several species of salmonids (Kalleberg 1958; Keenleyside & Yamamoto 1962; Abbott & Dill 1985; Gibson 2015; Watt et al. 2017). Several previous studies have used body colouration to specifically assign subordinance to the darkest individual among competing fish, typically in dyads (Abbott & Dill 1989; Berejikian et al. 1999; Höjesjö et al. 2004), but assigning the most subordinate fish in the present study proved to be more difficult. We only found four notably dark fish in total; two in the same container. Thus, assigning dominance, rather than subordinance, may be more useful in groups of fish, since typically one fish is dominant while several can be strongly subordinate. However, as exemplified here, not all groups will have a clearly dominant individual.

3.4. Mortality patterns

Fish from the low-activity cluster had higher mortality than fish from the high-activity cluster in the unpredictable environment, which suggests that lower activity ethotypes may be more vulnerable in a scramble competition situation. In the stable environment, no such pattern was found. However, since the analysis did not include tank-effects, an intentional omission stemming from low statistical power, we treat these results as suggestive, rather than conclusive. Nevertheless, the results indicate that mortality patterns in different environments may be a fruitful area of future research investigating performance of different ethotypes of brown trout.

3.5. Results in relation to previous laboratory and field observations

At least two previous studies have shown that activity is positively related to the chance of survival in the first year of life in brown trout (Adriaenssens & Johnsson 2013; Näslund et al. 2017a). This has been hypothesised to be a consequence of being territorial, since high activity is also associated with high aggression (Näslund & Johnsson 2016). However, with the present results in mind, we suggest an alternative explanation for the higher survival of the more active fry. The natural environment is likely variable in nature, and an explorative aggressive style may be advantageous for overtaking temporary territories. If the main cause of mortality is starvation due to competition,

rather than predation, this may explain the higher survival of more active and aggressive fish, since quality of shelter would play a minor role for survival. With a pressure to grow quickly, being able to claim new foraging stations could be favoured during early life. In older trout juveniles being relocated, more active individuals only did well in terms of growth when having a small home-range, which may signal that they have been able to claim a good foraging territory (Závorka et al. 2015a). Less active individuals, on the other hand, performed roughly at the average level regardless of their new home-range (Závorka et al. 2015a). However, at the fry stage, when overall mortality is high, performance at the average level may not be enough for survival in the long term. What we may see in the wild fry, is the best performing active fry having a survival advantage, while all other fish (i.e. underperforming active ones, and the bulk of the passive ones) are disadvantaged. This would result in a pattern where activity is positively related to the chance of survival over the fry stage.

Success of a territorial strategy can be reduced by environmental factors, such as environmental complexity or population density, both in intra- and inter-specific competition (Höjesjö et al. 2004; Warnock & Rasmussen 2013). Höjesjö et al. (2004) manipulated environmental complexity in a laboratory experiment on brown trout fry competition, and found that higher complexity disfavoured dominant (and more aggressive) individuals. Warnock and Rasmussen (2013) found that more a territorial and aggressive species of charr (brook charr *Salvelinus fontinalis*), was outcompeted by a less territorial and aggressive species (bull trout *Salvelinus confluentus*), when the environment was simple. Grand and Grant (1994) found that aggression and monopolization increased with predictability of food supply in convict cichlids *Amatitlania nigrofasciata*. In the present study, we cannot determine aggression or monopolisation directly, but the mortality suggests that the conflict level may be higher in the unpredictable environment. This could be explained by the fact that the fish must maintain a high and costly aggression level in an unpredictable environment to secure the food each day. Supporting this hypothesis are studies showing that Atlantic salmon *Salmo salar* fry in stream tanks show higher aggression when they occupy central positions, where food is supposedly more likely to be encountered (Kalleberg 1958).

Field observations of juvenile coho salmon *Oncorhynchus kisutch* have identified three different ethotypes: territorial-, non-territorial-, and floater individuals. In coho salmon, floaters actively move around and are the most aggressive individuals (Puckett & Dill 1985); similar ethotypes are also found in Atlantic salmon (Roy et al. 2013). Floaters are more active in the river, and it is possible that the most active individuals in previous brown trout studies were floater-ethotypes and not territorial individuals (Näslund & Johnsson 2016). However, given that only two activity clusters are commonly found among brown trout fry based on the open-field test, there may be need for additional tests to separate three different ethotypes. Floating

may be a conditional strategy among the active and aggressive individuals, which could be adopted in unpredictable environments by the strongest individuals, who then could temporarily take over currently good territories. Speaking against this hypothesis, is the fact that floater coho were small sized and mainly seemed to lose fights, thus rather resembling an alternative strategy for non-territorial fish (Puckett & Dill 1985). Puckett and Dill (1985) also observed that less aggressive non-territorial fish were mainly found in pools, which would likely be the most stable and predictable environments when e.g. water levels change – an observation which makes sense if the less aggressive fish have a higher chance of being dominant in these environments. Similar observations have also been made on wild brook charr (McLaughlin et al. 1999). The latter study also found that the most aggressive individuals were either very active or inactive, with non-aggressive individuals having intermediate activity levels in the field (McLaughlin et al. 1999).

The activity-aggression syndrome is present in brown trout, but it is nevertheless relatively moderate with substantial variation among individuals (correlation factors between 0.3-0.4; Adriaenssens & Johnsson 2010; Näslund & Johnsson 2016). More specific comparative studies investigating the main behavioural characteristic that facilitate dominance, if any, remains to be conducted.

3.6. Caveats

The experiment was conducted in standardized laboratory environments, which deviates from the natural environment in several aspects. Firstly, the holding containers had a bottom area of approximately 0.29 m^2. Brown trout fry defend territory areas of approximately 0.06 and 0.1 m^2 (Elliott 1990), so the area available may have been too small to fit full sized territories for all fish in the holding containers. However, dividing walls were inserted to reduce the territory size needed. Nevertheless, some individuals died, which may have been due to territorial aggression (see e.g. Závorka et al. 2015b). Secondly, the holding containers restrict movements of the fish, which means that mortalities that would not occur in nature may occur in the lab. In nature, a subordinated individual is unlikely to stay within the territory of the winner of the conflict. Thus, the mortalities in this experiment may not reflect a natural mortality pattern. Problems of movement restrictions are difficult to solve in laboratory environments, due to restricted space. Nevertheless, using larger containers to house the fish may improve the performance of subordinate fish. Finally, we delivered the food by hand, and because of restrictions in our time-schedules, the food was temporally clumped. Fish would have time to move beyond their primary foraging location to search for more food during the day. This may have led to aggressive interactions outside of their territories and may have increased variation in the results. If possible, future studies could utilize programmable feeding automats to provide a continuous flow of food in predictable and unpredictable manner.

4. CONCLUSIONS

The study resulted in inconclusive results regarding the association between activity and dominance, but the overall pattern suggests that our main hypothesis, that high activity being favoured in predictable environments, is not supported in this experiment. We also verify that light body coloration is a suitable indicator of dominance in small groups of brown trout fry.

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APPENDIX 1.

Food rations (number of chironomids) for the first six days of the trials. Rations and the order in which they were provided were identical for the last six days of treatment. Bold numbers represent the total amount of chironomids given during the first six days.

Table A1. Food rations for predictable container P1.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	16	12	10	8	6	4	56
Day 2	16	12	10	8	6	4	56
Day 3	16	12	10	8	6	4	56
Day 4	16	12	10	8	6	4	56
Day 5	16	12	10	8	6	4	56
Day 6	16	12	10	8	6	4	56
Total	96	72	60	48	36	24	336

Table A2. Food rations for predictable container P2.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Day 2	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Day 3	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Day 4	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Day 5	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Day 6	13.6	10.2	8.5	6.8	5.1	3.4	47.6
Total	81.6	61.2	51	40.8	30.6	20.4	285.6

Table A3. Food rations for predictable container P3.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	12	9	7.5	6	4.5	3	42
Day 2	12	9	7.5	6	4.5	3	42
Day 3	12	9	7.5	6	4.5	3	42
Day 4	12	9	7.5	6	4.5	3	42
Day 5	12	9	7.5	6	4.5	3	42
Day 6	12	9	7.5	6	4.5	3	42
Total	72	54	45	36	27	18	252

Table A4. Food rations for predictable container P4.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Day 2	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Day 3	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Day 4	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Day 5	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Day 6	10.4	7.8	6.5	5.2	3.9	2.6	36.4
Total	62.4	46.8	39	31.2	23.4	15.6	218.4

Table A5. Food rations for predictable container P5.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	8	6	5	4	3	2	28
Day 2	8	6	5	4	3	2	28
Day 3	8	6	5	4	3	2	28
Day 4	8	6	5	4	3	2	28
Day 5	8	6	5	4	3	2	28
Day 6	8	6	5	4	3	2	28
Total	48	36	30	24	18	12	168

Table A6. Food rations for unpredictable container U1.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	18	10	0	18	10	0	56
Day 2	10	0	18	10	0	18	56
Day 3	18	10	0	18	10	0	56
Day 4	0	18	10	0	18	10	56
Day 5	10	0	18	10	0	18	56
Day 6	0	18	10	0	18	10	56
Total	56	56	56	56	56	56	336

Table A7. Food rations for unpredictable container U2.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	8.5	0	15.3	8.5	0	15.3	47.6
Day 2	0	15.3	8.5	0	15.3	8.5	47.6
Day 3	0	15.3	8.5	0	15.3	8.5	47.6
Day 4	15.3	8.5	0	15.3	8.5	0	47.6
Day 5	8.5	0	15.3	8.5	0	15.3	47.6
Day 6	15.3	8.5	0	15.3	8.5	0	47.6
Total	47.6	47.6	47.6	47.6	47.6	47.6	285.6

Table A8. Food rations for unpredictable container U3.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	0	13.5	7.5	0	13.5	7.5	42
Day 2	13.5	7.5	0	13.5	7.5	0	42
Day 3	0	13.5	7.5	0	13.5	7.5	42
Day 4	13.5	7.5	0	13.5	7.5	0	42
Day 5	7.5	0	13.5	7.5	0	13.5	42
Day 6	7.5	0	13.5	7.5	7.5	13.5	42
Total	42	42	42	42	42	42	252

Table A9. Food rations for unpredictable container U4.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	6.5	0	11.7	6.5	0	11.7	36.4
Day 2	11.7	6.5	0	11.7	6.5	0	36.4
Day 3	0	11.7	6.5	0	11.7	6.5	36.4
Day 4	0	11.7	6.5	0	11.7	6.5	36.4
Day 5	6.5	0	11.7	6.5	0	11.7	36.4
Day 6	11.7	6.5	0	11.7	6.5	0	36.4
Total	36.4	36.4	36.4	36.4	36.4	36.4	218.4

Table A10. Food rations for unpredictable container U5.

	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Total
Day 1	5	0	9	5	0	9	28
Day 2	0	9	5	0	9	5	28
Day 3	9	5	0	9	5	0	28
Day 4	0	9	5	0	9	0	28
Day 5	5	0	9	5	0	5	28
Day 6	9	5	0	9	5	9	28
Total	28	28	28	28	28	28	168