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Interspecific association of brown trout (*Salmo trutta*) with non-native
brook trout (*Salvelinus fontinalis*) at the fry stage

Magnus Lovén Wallerius¹ (Corresponding author), Joacim Näslund², Barbara Koeck³,
Jörgen I. Johnsson¹.

¹Department of Biological and Environmental Sciences, University of Gothenburg, Box 463,
SE-405 30 Gothenburg, Sweden

²Department of Ecosystem Biology, University of Southern Bohemia in České Budějovice,
České Budějovice, Czech Republic

³Institute of Biodiversity, Animal Health, and Comparative medicine, Graham Kerr Building,
University of Glasgow, Glasgow G12 8QQ, UK

Corresponding author: magnus.loven.wallerius@bioenv.gu.se

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Abstract

The introduction of non-native brook trout (*Salvelinus fontinalis*) in Europe has led to displacement and decreasing populations of native brown trout (*Salmo trutta*). Some studies have found that brown trout shift to a diet niche similar to brook trout when the two species live in sympatry, which conflicts with the competitive exclusion principle. A change in feeding niche may be a sign of early interspecific association and social learning, leading to behavioral changes. As a first step to address this possibility, it is essential to assess the interspecific association between the species during the early ontogenetic life-stages. In the present study, we therefore assess whether juvenile brown trout associate with non-native juvenile brook trout to the same extent as with conspecifics by setting up two experiments: (1) a binomial choice test allowing visual and chemical cues to estimate the species-specificity of group preference; and (2) an association test without physical barriers to estimate the degree of association of a focal brown trout with a group of either conspecifics or heterospecifics. In experiment (1), we found that focal juvenile brown trout preferred to associate with the stimuli groups and did not discriminate either against conspecific or heterospecific groups. Furthermore, more active individuals showed stronger preference for the stimuli group than less active ones, regardless of species. In experiment (2), we found that brook trout groups had a tighter group structure than brown trout groups, and that focal brown trout showed stronger association with brook trout than with brown trout. These results indicate that brown trout may associate with brook trout at an early life-stage, which would allow for interspecific social learning to occur. Future studies should look closer into causes and consequences of interspecific association and social learning, including potential effects on the phenotype selection in brown trout populations.

Introduction

One of the main threats to ecosystems today is the introduction of new species (Mack et al., 2000; Freyhof & Brooks, 2011). Such introductions can have substantial impact on native populations and biodiversity (Mack et al., 2000), with effects that range from the lowest level of biological organization (i.e. genetic) up to the highest (i.e. ecosystem) (Cucherousset & Olden, 2011). When an introduced species has negative effects on the ecosystems and its native species, it is classified as an invasive alien species (Pejchar & Mooney, 2009).

In western Eurasia, brown trout (*Salmo trutta*) is a native species that inhabit streams and lakes across the continent (Jonsson & Jonsson, 2011). Since the late 1800s, continuous introduction of non-native brook trout (*Salvelinus fontinalis*), has led to naturalized populations of this species in many parts of Europe (MacCrimmon & Campbell, 1969; Hutchings, 2014), including in systems where brown trout naturally occurs. Previous studies have shown that non-native brook trout can have negative effects on brown trout survival (Korsu, Huusko & Moutka, 2007; Spens, Alanärä & Eriksson, 2007) and growth (Závorka et al., 2017; Öhlund, Nordwall, Degerman & Eriksson, 2008), although these effects are not universal (Blanchet, Grenouillet & Brosse, 2007; Korsu, Huusko & Moutka, 2009).

These variable outcomes of competition between brown trout and brook trout may depend on several interacting factors (Spens et al., 2007). Overlap in spawning period and redd-site preferences of the two species (Gunn, 1986; Witzel & MacCrimmon, 1983) can sometimes lead to hybridization, and generate sterile offspring called tiger trout (Chevassus, 1979). Hybridization will impair the reproductive success of individuals in both species, potentially leading to long-term negative effects on their populations (Cucherousset, Aymes, Poulet, Santoul & Céréghino, 2008; Grant, Vondracek & Sorensen, 2002). Moreover, brown trout living in sympatry with brook trout differ in several phenotypic and ecological niche traits

74 compared to allopatric populations, suggesting a break-down of an adaptive trait integration
75 which could be caused by interspecific interactions (Závorka et al., 2017).

76 When two competing species co-exist and share the same ecological niche, the
77 competitive exclusion principle states that one of them will eventually become extinct, or will
78 experience an evolutionary shift in ecological niche, thus reducing competition (Hardin, 1960).
79 Contrary to this principle, several diet studies have shown that brown trout shift to a diet niche
80 more similar to brook trout when they live in sympatry, compared to more divergent feeding
81 niches in allopatry (Cucherousset, Aymes, Poulet & Céréghino, 2007; Závorka et al., 2017).
82 While many studies have found negative effects on brown trout following interspecific
83 interactions between the two species (Korsu et al., 2007; Spens et al., 2007; Závorka et al.,
84 2017; Öhlund et al., 2008, but see Blanchet et al., 2007; Korsu et al., 2009), the underlying
85 mechanisms behind the feeding shift have not yet been explained. There is evidence that
86 interspecific social interactions during early ontogenetic stages can shape the social behavior
87 (Ancillotto, Allegrini, Serangeli, Jones & Russo, 2015; Arnold & Taborsky, 2010), and mate
88 choice of individuals (Verzijden & ten Cate, 2007). Species discrimination in fish may be based
89 on visual (Warburton & Lees, 1996), behavioral and chemical cues (Burnard, Gozlan &
90 Griffiths, 2008). However, brown trout and brook trout are morphologically similar at the
91 fry stage (Fig 1.), and have a short evolutionary history of coexistence (Hutchings, 2014). This
92 raises the possibility that brown trout do not yet perceive brook trout as a competitor, which
93 could facilitate interspecific association between the species at an early life-stage, eventually
94 leading to social learning that change the feeding preference of brown trout in sympatry with
95 brook trout?

96 We address this question in two successive behavioral experiments: (1) a binomial
97 choice test allowing visual and chemical cues to estimate the species-specificity of group
98 preference in brown trout fry, and (2) an association test without physical barriers to estimate

the degree of association of a focal brown trout towards a group of either conspecifics or heterospecifics. Based on the morphological similarity hypothesis discussed above, we make the following alternative predictions for the binomial choice test: (H_0) brown trout associate to the same extent with conspecifics and heterospecifics; (H_1) brown trout preferentially associate with conspecifics. For this result to be ecologically relevant we also expect the pattern found in the binomial choice test to be reflected in the association test. By studying these early association patterns, we aim to shed light on the interspecific interactions at an early life-stage where major selection occurs (Elliot, 1989b), a stage that is often neglected in studies investigating interactions between native and non-native salmonids.

Methods

Sampling and holding

The study was conducted in two parts during late spring and early summer of 2016. To avoid size biased association of the fry (Duffy, Pike & Laland, 2009), due to differences in emergence time, fish were sampled at two different sites in Sweden; Ringsbäcken (WGS84 decimal (lat, long): 57.670827°N, 12.988458°E) with both native brown trout and non-native brook trout, and Norumsån (WGS84 decimal (lat, long): 58.04318°N, 11.84589°E) with native brown trout. Fish were sampled using electro-fishing (LUGAB L-600, Lug AB, Luleå, Sweden; DC, 200 – 300 V).

Brook trout fry were collected in Ringsbäcken on May 23 (N=8) and May 27 (N=77), and brown trout fry were collected in Norumsån on June 1 (N=178) for Experiment 1, and June 27 (N=80) for Experiment 2. After collection, fish were brought to University of Gothenburg.

The two species were kept separately in large groups in five aquaria ($65 \times 35 \times 35$ cm), two aquaria for brook trout and three aquaria for brown trout. Each aquarium was supplied with water (stable temperature: $\sim 12.3 \pm 1^\circ\text{C}$) from the in-house flow through system and supplemented with a constant air supply through air-stones. Environmental enrichment was provided in the form of gravel substrate, plastic aquarium plants, cobble and PVC plates and pipes. The daytime light intensity was 60 lux at the water surface, at 12:12 h light:dark photoperiod with a 30 minute dimming period. Fish were fed to satiation five days a week with frozen chironomid larvae. After the experiments, all fish were euthanized with an overdose of benzocaine followed by decapitation.

Experiment 1 – Binomial choice test

To assess if brown trout fry individuals preferred to associate with brown trout groups or brook trout groups, three different preference tests with 24 replicates each were conducted. The preference tests were conducted in three aquaria ($65 \times 35 \times 35$ cm) filled with 15 cm water, constant water flow (1 L min^{-1}) and bottom covered with light brown gravel (width 2-3 mm). To avoid physical contact between the fish, each aquarium was divided lengthwise in three different compartments, two side compartments (9×35 cm) and one mid compartment (15×35 cm), using perforated transparent acrylic glass (3 mm holes with 5 cm distance between each hole; glass width 3 mm) (Fig 2.). The number of fish ($n=7$) in each side compartment is within the range of previously observed group sizes of brown trout in the wild (Elliott, 1990). The following three preference tests were carried out (BT = Brown trout, BK = Brook trout and EM = Empty side):

1. Brown trout vs Brook trout (BT vs BK): One focal fish (brown trout) in the mid-section and a group of brook trout (n=7) in one compartment and a group of brown trout (n=7) in the other compartment.

2. Brown trout vs Empty side (BT vs EM): One focal fish (brown trout) in the mid-section and a group of brown trout (n=7) in one of the two side compartments. One compartment left empty.

3. Brook trout vs Empty side (BK vs EM): One focal fish (brown trout) in the mid-section and a group of brook trout (n=7) in one of the two side compartments. One compartment left empty.

Before each trial, two grey PVC-plates were lowered next to the acrylic glass to avoid visual contact before the focal fish was introduced into the mid-section. Before introducing the focal fish, they were individually anaesthetized with benzocaine (0.3 ml L^{-1}) for mass and length measurements, and released in a 1 L holding tank for recovery. A total of 72 brown trout were used as focal fish (mean \pm SD: mass = 0.49 ± 0.24 g; fork length 35.5 ± 4.87 mm). After recovery, the focal fish was gently netted into the mid-section of the trial aquaria and recorded with a video camera (Canon IXUS 175, Canon Inc., Tokyo, Japan). Each replicate lasted for 30 minutes divided into three 10 minute parts. The first 10 minutes were dedicated to acclimation to the new environment, the second part was used as a scoring of individual activity. Activity was scored by watching each video, dividing the mid-section in a grid net (5×5 cm squares) and count each time the focal fish crossed a line. After the activity measurement period, the PVC-plates were gently lifted to allow visual contact between the focal fish and the group(s). The 10-minute preference period was video-scored by dividing the mid-compartment lengthwise in three different sections (5×35 cm) (Fig. 2). To facilitate unambiguous interpretation of group preference, the mid-section was considered as a neutral zone and the sections on the side as preference zones. By scoring which section a focal fish was located every 10th second, a total of 60 location points was assigned to each individual. The cumulative

number of points were divided by 60 to get the proportion of time spent in each section. After a trial was completed, the PVC-plates were lowered and the focal fish was removed and replaced by a new focal fish, following the same procedure as described above. Before feeding in the afternoon, we removed the group(s) in each aquarium and replaced them with a new group (for the next day trials) of the same species in the opposite side compartment to minimize bias effects of side preference. Group individuals were anaesthetized with benzocaine (0.3 ml L⁻¹) for mass and length measurements and allowed to recover before they were introduced to the side compartment. A total of 112 group individuals were used in the experiment, 56 brown trout (mean \pm SD: mass = 0.42 \pm 0.17 g; fork length = 34.1 \pm 4.35 mm) and 56 brook trout (mean \pm SD: mass = 0.52 \pm 0.17 g; fork length = 38.08 \pm 3.6 mm). Experiment 1 was conducted between 9 June and 12 June 2016, and after completion, the brook trout fry were kept for 17 days in large groups in two holding aquaria until they were reused in experiment 2.

Experiment 2 – Association test

To estimate the association among the two species of fry under more natural conditions, focal brown trout fry were allowed to associate freely (without physical barriers) with a stimuli group consisting of either brook- or brown trout (17 replicates each). Experiment 2 was conducted between 30 June and 1 July 2016. Four white plastic arenas (65 \times 45 cm with rounded corners), filled with 5 cm water were used. A focal fish (brown trout), was placed in a covered cylinder (10.5 cm diameter) in the middle of each arena, and a group of either five brown trout (BT group) or five brook trout (BK group) placed outside of the cylinder (group size was within the range described in Elliott (1990)). The day before each round of sampling, focal fish and fish in the stimuli group were gently netted from separate holding tanks and anaesthetized in benzocaine (0.3 ml L⁻¹) before mass measurements. Thereafter, each focal fish was separately

put in a 1 L container and the stimuli fish were put in groups of five in 3 L containers overnight. On the day of the sampling, one focal fish was placed inside the cylinder of each arena, whereupon one stimuli group (n=5) was netted and put in each arena outside of the cylinder. After an initial 15-minute acclimation period, each cylinder was removed to allow visual and physical contact between the focal fish and the group for the remaining 15 minutes. Thus, each replicate was recorded (Canon IXUS 175, Canon Inc., Tokyo, Japan) during 30 minutes. Association measurements included the minimum convex polygon (cm²) of the stimuli group (excluding the focal fish), and the nearest neighbor distance (cm) of the focal individual to the closest individual in the stimuli group. After one round of recording, the focal fish and the group were removed and put in separate holding tanks. Before releasing new fish in each arena (following the same procedure as described above), the water in each arena was replaced and the cylinder was put back in the middle again. A total of 34 focal brown trout (mean \pm SD: mass = 0.59 ± 0.14 g) and 170 group individuals, 85 brown trout (mean \pm SD: mass = 0.55 ± 0.24 g) and 85 brook trout (mean \pm SD: mass = 0.59 ± 0.24 g) were used in the experiment. Association measurements were analysed on the last 10 minutes of each video by taking a screenshot every 10th second, giving a total number of 60 screenshots. Each screenshot was then handled in TpsDig2 v2.26 (Rohlf, 2006) to digitize 60 XY-coordinates to each individual.

Statistical analysis

Data characteristics and distribution were assessed to employ suitable models. For experiment 1, we used two generalised linear models (GLM) (“glm” function in the stats package for R (version 3.3.2), R Core Team 2016) with binomial distribution (trials = 60), one was constructed to test treatment (BT vs BK) against treatment (BT vs EM) (Model 1), and the other to test treatment (BT vs BK) against treatment (BK vs EM) (Model 2). In model 1, the proportion of

time spent with brown trout was used as response variable and relative length (eq. 1.1) and activity as explanatory variables. In model 2, the proportion of time spent with brook trout was used as response variable and relative length (eq. 1.1) and activity as explanatory variables. A pairwise t-test was used for treatment (BT vs BK) to compare the relative preference when brown trout could choose between both conspecifics and heterospecifics.

Relative length of the focal individual vs stimuli group (L_r) was calculated as:

$$L_r = \frac{L_f - \bar{L}_S}{L_f} \quad (1.1)$$

Where L_f = length of focal individual, \bar{L}_S = mean length of fish in the stimuli group. Since the group area measurements and nearest neighbour distance in Experiment 2 were strictly positive with positive skew, we constructed two log-link gamma regression models (glm function, stats package for R 3.3.2); (Model 1): the median group area as response variable and stimuli group (BT or BK) and the geometric mean mass of the group as single explanatory variables and as an interaction term. The geometric mean was used rather than the arithmetic mean to reduce the effects of large size differences within the stimuli groups. (Model 2): The median nearest neighbour distance was used as response variable and stimuli group (BT or BK) and relative mass (using the same equation (1.1) as for relative length) as single explanatory variables and as an interaction term.

Results

Experiment 1 – Binomial choice test

In the binomial choice test with two stimuli groups (BT vs BK). Focal brown trout showed no species-specific preference towards any of the stimuli groups ($t = -0.940$, $p = 0.36$; Fig. 3). Furthermore, focal brown trout showed a stronger preference for the stimuli group when they

only had one group to associate with (mean proportion of time \pm SD: BT vs EM = 0.518 ± 0.263 ; BK vs EM = 0.484 ± 0.201 ; Fig. 3), compared to when they could choose between conspecifics and heterospecifics (mean proportion of time \pm SD: BT vs BK; BT side = 0.351 ± 0.209 ; BK side = 0.432 ± 0.232 ; Fig. 3) (Table 1a, Table 1b). The latter analyses confirmed that the lack of species-specific preference in the BT vs BK-treatment was not due to a general avoidance of the stimuli groups by the focal fish. Additionally, the proportion of time spent by focal fish with both the brown trout stimuli group (GLM: $z = 4.945$, $P < 0.001$; Table 1a) and the brook trout stimuli group (GLM: $z = 4.020$, $P < 0.001$; Table 1b) was positively related to their individual activity, as scored before exposure to the groups. The relative length of the focal fish did not significantly affect the preference in any of the two models (Table 1a, Table 1b).

Experiment 2 – Association test

We found that focal brown trout resided significantly closer (Nearest neighbour distance, NND) to the brook trout group than they did to the conspecific group (GLM: $t = 38.873$, $P < 0.001$; Table 2a; Fig. 4). Moreover, a significant interaction (NND \times relative body mass) indicated that relatively larger focal brown trout tended to be closer to the brook trout group than smaller individuals, whereas no such effect was seen in the conspecific treatment with only brown trout (GLM: $t = -2.572$, $P = 0.015$; Table 2a; Fig. 4). Brown trout groups were also significantly more dispersed (i.e. had larger median group area) than brook trout groups (GLM: $t = 3.988$, $P = 0.015$; Table 2b; Fig. 5). Moreover, brook trout groups with larger mean body size tended to be more dispersed, whereas no such trend was found in brown trout groups (Interaction effect: GLM: $t = 1.996$, $P = 0.055$; Table 2b; Fig. 5). Thus, the general association test supports the results from the binomial choice test showing that juvenile brown trout show no species-specific discrimination against associating with juvenile brook trout.

Discussion

Heterospecific group composition has been found in several studies and in different animal groups, including mammals (reviewed in Stensland, Angerbjorn & Berggren, 2003), birds (e.g. Hino, 2000), and fish (e.g. Krause & Godin, 1996; Hoare, Ruxton, Godin & Krause, 2000). In fish, native heterospecific group composition at the juvenile stage is a common phenomenon and is considered as a behavioral response to reduce predation risk (Pavlov & Kasumyan 2000). However, previous studies on interspecific association and group composition between native and non-native fishes at the juvenile stage are scarce (see Beyer, Gozlan & Copp, 2010; and Camacho-Cervantes, Ojanguren, Deacon, Ramnarine & Magurran, 2014 for adult interactions between native and non-native *Poecilia* spp.). In this study, we present evidence for heterospecific association between native brown trout and non-native brook trout at an early life stage. In the binomial choice test we found that brown trout do not discriminate against heterospecific brook trout, either when presented alone, or when the focal brown trout had the option to associate with both conspecifics and heterospecifics at the same time. Additionally, we found that active individuals had a higher preference score with both conspecifics and heterospecifics groups. In the follow-up experiment when the species were allowed physical contact, brook trout formed tighter groups than brown trout, and focal brown trout associated more closely with heterospecific brook trout than with conspecifics. Thus, by assessing the association between the species in two separate experiments, we found complementary information about group behavior and individual association patterns that would not have been found if only one of the experiments had been conducted alone.

Previous studies have found non-native heterospecific associations and interactions between different guppy species (*Poecilia* spp.) (Camacho-Cervantes et al., 2014), as well as

network associations between non-native sunbleak (*Leucaspius delinatus*) and native species (Beyer et al., 2010). However, both guppies and sunbleak are more social species with a high shoaling tendency (Croft et al., 2006; Andörfer, 1980) compared with brown trout which is generally more aggressive with strong hierarchies and defend territories as both juveniles and adults (Kalleberg, 1958). Even though brown trout may have a grouping tendency as fry (Elliott, 1990), the close association with brook trout is surprising. Whether the lack of species-specific preference seen in this study reflects cognitive limitations of juveniles that will prevent discrimination between the morphologically similar brown trout and brook trout (Fig. 1), or whether brown trout recognized the behavior of brook trout as non-aggressive which induced a grouping response to increase vigilance (Griffiths, Brockmark, Höjesjö & Johnsson, 2004) and reduce individual predation risk at the vulnerable juvenile stage (Godin, 1986; Pavlov & Kasumyan, 2000), cannot be concluded. Nonetheless, the non-discriminatory association is a sign that brown trout can co-exist with brook trout at an early life-stage and supports our hypothesis; that brown trout does not discriminate between conspecifics and brook trout early in life.

Since early social association between heterospecifics can influence individual behavior (Verzijden & ten Cate, 2007), the higher propensity to group with heterospecifics may provide opportunities for social learning (Laland & Williams, 1997; Camacho-Cervantes, Ojanguren & Magurran, 2015) which may alter the feeding niche of brown trout when living in sympatry with brook trout (Cucherousset et al., 2007; Závorka et al., 2017; but see: Horká et al., 2017). Even though brook trout emerge from the incubation in the spawning gravel earlier than brown trout in Ringsbäcken (M. Lovén Wallerius, Pers. Observation), the general size difference between the species at the time of brown trout emergence does not have to inhibit social learning, rather it may enhance the social information transfer. This can be explained by the *copy-successful-individuals* strategy (Laland, 2004), where observers can be more prone to

copy larger individuals (Duffy et al., 2009) and/or if social information transfer is faster between experienced and unexperienced individuals (Brown & Laland, 2002). In our study, however, there was no size-effect on preference strength in the binomial choice test, and in the following association study, relatively larger brown trout actually tended to be closer to the brook trout group (Fig 4.) which is the opposite pattern to the one predicted from the *copy-successful-individuals* strategy.

Since brook trout had a tighter group structure than brown trout and focal brown trout associated closer to brook trout, the higher heterospecific grouping tendency of brown trout may induce a competitive disadvantage. If the feeding niche is socially transmitted, competition for food with aggregated heterospecifics may decrease the feeding rate (Ward, Axford & Krause, 2002), possibly leading to reduced growth rate and increased mortality. Additionally, these effects may alter the relative fitness of consistent individual behavioral phenotypes, i.e., if there are inter-individual differences in social learning as indicated in some previous studies on three-spined stickleback and great tits (Nomakuchi, Park & Bell, 2009; Marchetti & Drent, 2000, but see, Harcourt, Biau, Johnstone & Manica, 2010), individuals more prone to use interspecific social information may be at a selective disadvantage. The higher preference score for active individuals seen in the binomial choice test may give an indication of this pattern. Since repeatable individual differences in activity have been shown in juvenile brown trout (Adriaenssens & Johnsson, 2013; Näslund & Johnsson, 2016), the higher interspecific association tendency might give active individuals a feeding disadvantage due to increased competition with aggregated brook trout, compared to less active individuals showing less interspecific association.

Since the evolutionary history of sympatry between native brown trout and non-native brook trout is relatively short (Hutchings, 2014), the heterospecific association patterns of sympatric brown trout, with its possible effects on the feeding niche may be a maladaptive

behavior that has not yet been selected against (Strauss, Lau & Carroll, 2006). Future studies should address if the early association of brown trout with non-native brook trout give rise to consistent inter-individual differences in social information use and, ultimately, how such effects translate into phenotypic selection and related effects on the native population.

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561 **Figures**

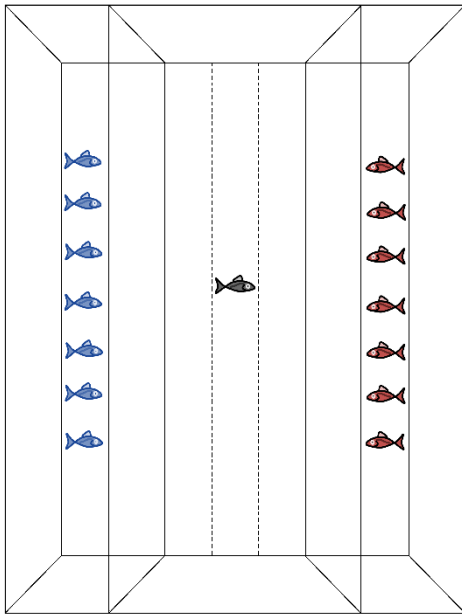
562 **Fig 1.** Photograph of brook trout (*Salvelinus fontinalis*) fry from Ringsbäcken (above) and
563 brown trout (*Salmo trutta*) fry from Norumsån (below).



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566 **Fig 2.** Aquarium setup of experiment 1, as seen from above. Side compartments (9×35 cm)
567 and mid-section (15×35 cm). Dashed lines in the mid-compartment represent the manual lines
568 during the association scoring, where the mid-section was used as neutral zone. Focal brown
569 trout (mid) and stimuli groups of brown trout (right) and brook trout (left) are shown in
570 accordance with treatment 1 (BT vs BK).



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Fig 3. Box-plot showing the proportion of time spent by focal brown trout with either the brown trout (red) or brook trout (blue) stimuli group, or the empty side (black). The box plots show the median, 50% interquartile range and the error bars represent the 95% confidence interval.

BT = brown trout, BK = brook trout and EM = empty side

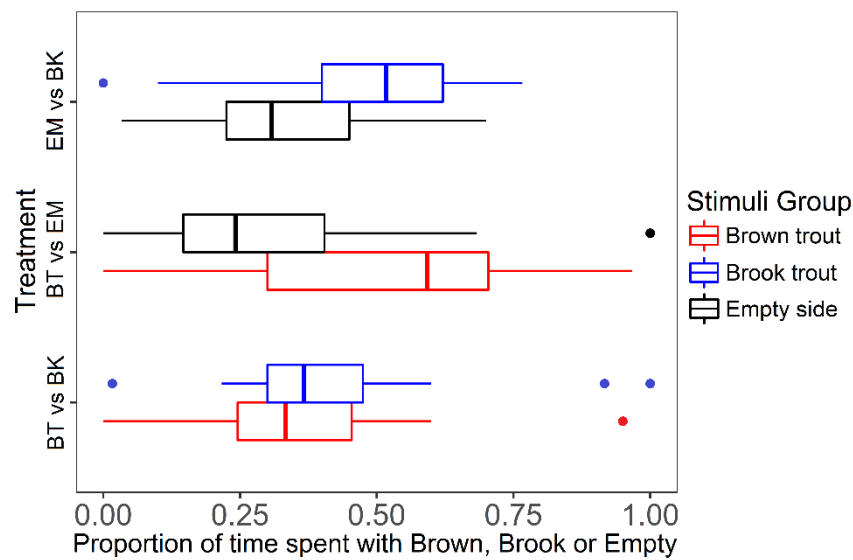


Fig 4. Relative body mass (g) of focal fish in relation to focal fish median distance (cm) to the nearest neighbor of the brown trout group (red) or the brook trout group (blue). Grey area represents 95% confidence interval from model prediction. BT = brown trout and BK = brook trout.

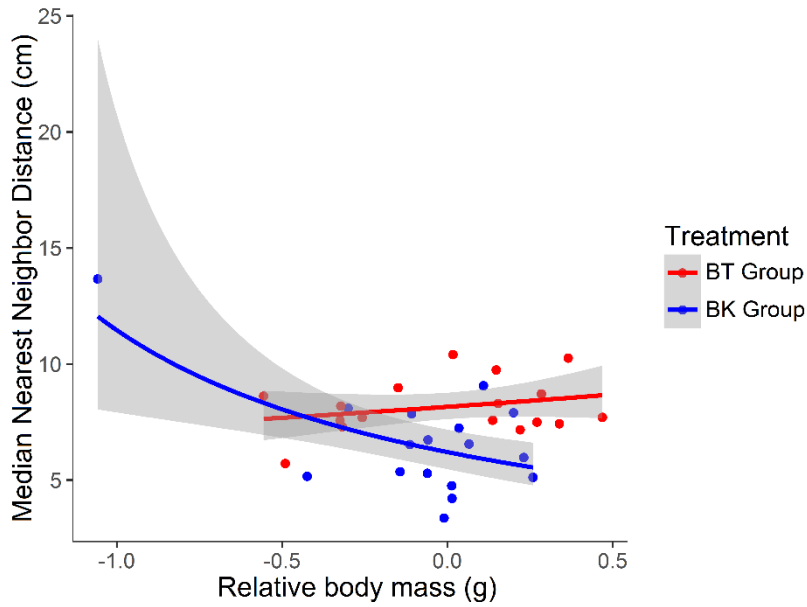
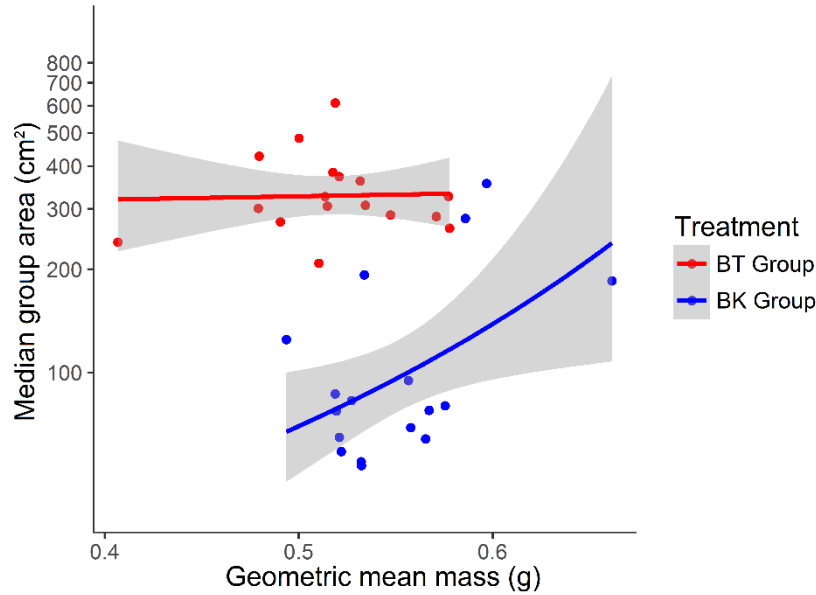


Fig 5. Median group area (fitted on log10 scale) in relation to geometric mean mass (g) of the group body mass of the two treatments, brown trout group (red) and brook trout group(blue). Grey area represents 95% confidence interval from model prediction. BT = brown trout and BK = brook trout.



Tables

Deviance residuals:				
<i>Min</i>	<i>1Q</i>	<i>Median</i>	<i>3Q</i>	<i>Max</i>
-8.5960	-2.3667	-0.3537	2.4774	10.9988
Coefficients:				
<i>Intercept</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>z-value</i>	<i>p-value</i>
<i>Intercept</i>	-0.9138	0.0813	-11.23	< 0.001 ***
<i>Treatment (BT vs EM)</i>	0.7401	0.0777	9.519	< 0.001 ***
<i>Relative length</i>	0.0515	0.3253	0.159	0.87
<i>Activity</i>	0.0013	0.0002	4.945	< 0.001 ***

Table 1a. Generalized Linear Model analyzing the effect of treatment (BT vs BK) and (BT vs EM). A binomial proportion distribution of the brown trout proportion of time spent was used as response variable. Treatment (BT vs BK) was used as base line level of the corresponding variables. BT = brown trout, BK = brook trout and EM = empty side.

Deviance residuals:				
<i>Min</i>	<i>1Q</i>	<i>Median</i>	<i>3Q</i>	<i>Max</i>
-8.3051	-1.8712	-0.2363	1.7609	9.4447
Coefficients:				
<i>Intercept</i>	<i>Estimate</i>	<i>Std.Error</i>	<i>z-value</i>	<i>p-value</i>
<i>Intercept</i>	-0.4988	0.0826	-6.033	< 0.001 ***
<i>Treatment (BK vs EM)</i>	0.2267	0.0755	3.003	0.002 **
<i>Relative length</i>	-0.0686	0.2378	-0.289	0.772
<i>Activity</i>	0.0009	0.0002	4.020	< 0.001 ***

Table 1b. Generalized Linear Model analyzing the effect of treatment (BT vs BK) and treatment (BK vs EM). A binomial proportion distribution of the brook trout proportion of time spent was used as response variable. Treatment (BT vs BK) was used as base line level of the corresponding variables. BT = brown trout, BK = brook trout and EM = empty side.

Deviance				
<i>Min</i>	<i>1Q</i>	<i>Median</i>	<i>3Q</i>	<i>Max</i>
-0.568	-0.130	-0.010	0.123	0.455
Coefficients:				
	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>p-value</i>
<i>Intercept</i>	2.099	0.054	38.873	< 0.001 ***
<i>BK group</i>	-0.262	0.077	-3.379	0.002 **
<i>Relative mass</i>	0.125	0.171	0.734	0.468
<i>Group*Rel. mass</i>	-0.641	0.249	-2.572	0.015 *

Table 2a. Generalized Linear Model over model 2 in experiment 2, using Gamma distribution (log = link) of median nearest neighbor distance (cm) as response variable. BT group was use as base line level of the corresponding variables. BT = brown trout and BK = brook trout.

Deviance residuals:				
<i>Min</i>	<i>1Q</i>	<i>Median</i>	<i>3Q</i>	<i>Max</i>
-0.604	-0.358	-0.112	0.088	0.905
Coefficients:				
	<i>Estimate</i>	<i>Std.Error</i>	<i>t-value</i>	<i>p-value</i>
<i>Intercept</i>	5.826	1.461	3.988	< 0.001 ***
<i>BK group</i>	-5.596	2.187	-2.558	0.015 *
<i>Geometric mean mass</i>	-0.001	2.816	0.000	0.999
<i>Group*Geo. mean</i>	8.138	4.077	1.996	0.055

Table 2b. Generalized Liner Model over model 1 in experiment 2, using Gamma distribution (log = link) of median group area (cm²) as response variable. BT group was use as base line level of the corresponding variables. BT = brown trout and BK = brook trout.