Original Article

Competition level determines compensatory growth abilities

Francisca H. I. D. Segers[a] and Barbara Taborsky[a,b]
[a]Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland and [b]Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria

In many animal taxa, size-selective predation favors fast growth early in life. However, same-aged juveniles can diverge in size due to differences in genotype, environmental conditions, and parental effects and thus may vary in competitive ability. Under food scarcity, competitively inferior juveniles may suffer suppressed growth, whereas under benign conditions, small juveniles may exhibit growth compensation and perform as well as large ones. However, studies testing this while controlling for parental effects are lacking. Here, we hand-raised cichlids, *Simochromis pleurospilus*, from a wide range of egg sizes and manipulated their size by differential feeding. Afterward, high- and low-ration siblings were kept in groups assigned to either a high- or low-competition environment. We investigated how the degree of competition affected aggressiveness and growth of juveniles with different feeding histories. As predicted, when competition was high, high-ration offspring grew fastest. Interestingly, when competition was weak, low-ration juveniles grew at a similar rate as high-ration ones and many were able to catch up in size. High-ration fish were more aggressive than low-ration ones, and this effect was strongest under high competition. Additionally, in the high-competition environment, received aggression was negatively related to growth, and inflicted aggression correlated positively with the growth of the aggressor. These relationships were absent under low competition. Our findings suggest that the abilities to compensate for early growth depression depend on the prevalent level of competition. Aggression is likely used to monopolize food by juvenile *S. pleurospilus*; however, when competition is strong, aggression cannot compensate for a size disadvantage. *Key words:* cichlids, compensatory growth, early environment, egg size, food competition. [*Behav Ecol* 23:665–671 (2012)]

INTRODUCTION

From the moment of fertilization, individual phenotypes vary in their developmental trajectories through differences in genetic and nongenetic parental contributions and properties of the physical environment (e.g., Pepin et al. 1997; Crespi and Lessig 2004; Rideout et al. 2004; Bergenius et al. 2005; Hegyi et al. 2006; Paitz et al. 2007; Segers and Taborsky 2011). In aquatic systems, survival of juveniles is thought to depend strongly on body size because of negative size-selective predation (Sogard 1997). Large juveniles are assumed to suffer lower rates of mortality because of a gape-size limitation of their predators. Individuals that are born small or experienced a period of growth depression shortly after birth should therefore benefit from processes allowing a recovery of body size, such as compensatory growth (Ali et al. 2003). Consequently, growth potential has been highlighted as an important determinant of juvenile survival (e.g., Meekan and Fortier 1996; Vigliola and Meekan 2002; Gagliano and McCormick 2007). Furthermore, the inability to reach a certain growth trajectory can negatively affect fitness later in life, for example, it can delay maturation (Wiegmann et al. 1997) or result in a smaller reproductive size and lower fecundity (Semlitsch et al. 1988).

Growth compensation is often realized through enhanced food consumption (Ali et al. 2003). However, the possibilities for compensatory growth in natural systems can be constrained, as food availability is often limited and the access to this resource might be contested. Dissimilarities between offspring can result in some individuals being competitively superior over others, which consequently will impair the growth of small conspecifics (Persson 1985). Once established, even the smallest initial size differences can be reinforced, as slightly larger individuals may claim a proportionally larger share of resources, resulting in faster growth (Brown 1946). Information about how juveniles of various sizes cope under different competitive regimes helps to understand the population dynamics (e.g., Eitam et al. 2005; Kaspersson and Höjesjö 2009), spatial distribution (e.g., Grand 2002; Davey et al. 2005), and reproductive strategies (e.g., Taborsky 2006a; Kindsvater et al. 2010) of animals.

Offspring that are larger due to a greater per propagule investment have been shown to impair the growth of smaller conspecifics, particularly in highly competitive environments (Booth 1995; Marshall et al. 2006; Bashey 2008; but see: Huss et al. 2007). However, it is usually unknown whether larger offspring are competitively superior in harsh environments due to size per se or because of other effects confounded with egg or offspring size, as for example, steroid hormones or carotenoids (McCormick 1998; Groothuis and Schwabl 2002; Svensson et al. 2006). A larger deposit of steroid hormones in an egg, for example, can influence an offspring's competitive ability regardless of its size (e.g., Eising and Groothuis 2003). Next to a larger per propagule investment, various environmental factors can cause size differences among juveniles (e.g.,

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food availability, Booth and Hixon 1999; weather conditions, Bergenius et al. 2005; brood care, Reardon and Chapman 2010). For example, the sizes at which offspring of the maternally mouthbrooding cichlid, *Simochromis pleurospilus*, become independent of brood care vary from 12.8 to 21.0 mm, mainly due to differences in brood care between mothers (Segers et al. 2011). It is unknown, however, whether environmentally induced effects on size lead to the same competitive dissimilarities between juveniles as do differences in per propagule investment (Booth 1995; Marshall et al. 2006; Bashey 2008).

Highly competitive environments can be created experimentally by varying competitor densities or food levels, and both are known to vary in nature (e.g., Triplet et al. 1999). Although most studies manipulated resource availability through varying competitor density (Booth 1995; Svensson and Sinervo 2000; Marshall et al. 2006; Huss et al. 2007; Bashey 2008), as far as we know, no study has directly manipulated food availability. The latter is important because manipulating competitor density does not only affect food availability but also space and the frequency of social interactions. Thus, testing for direct effects of food availability on competitive abilities of different-sized young is expected to provide new insights.

We investigated the potential for compensatory growth of growth-depressed offspring of *S. pleurospilus* in environments that varied in the degree of competition. We directly manipulated the phenotypic trait of interest (juvenile size) by varying food regimes shortly after the egg stage. This allowed us to use a split-brood design, yielding siblings that only differed in size but not in age, yolk composition, or genetic background. We tested whether smaller siblings differ in their ability to catch up in size with larger ones in high- and low-competitive environments, respectively.

Studies on size-dependent competitive interactions among conspecifics are abundant (see for review on fishes: Ward et al. 2006). However, unless size is manipulated, cause and effect cannot be disentangled in the relationship between size and dominance. Furthermore, actually observing the competitive interactions over a resource can give information about which behavioral mechanism underlies the competitive advantage of certain phenotypes in food-limited environments. This behavioral component is often ignored (e.g., Svensson and Sinervo 2000; Huss et al. 2007; Bashey 2008). Therefore, next to growth, we also monitored the aggressive behavior of size-manipulated siblings in environments which varied in degree of competition. For example, certain phenotypes may be better at depleting a resource (exploitative competition) or at monopolizing a food source (contest competition) (Persson 1985; Ward et al. 2006). Here, we explored how an experimentally controlled phenotypic difference in size results in differences in aggressive behavior and how these behavioral differences are linked to differences in growth.

MATERIALS AND METHODS

Study species and animal husbandry

Simochromis pleurospilus is a maternally mouthbrooding cichlid that lives along the rocky shores of Lake Tanganyika (Taborsky 2006a), where both adults and young feed on turf algae and debris (Taborsky 2006b). Our laboratory stock originates from a population inhabiting the southern tip of the lake near Nkumbula Island, Zambia. Our experimental subjects were second and third generation descendants from wild-caught individuals. To obtain clutches, we established a total of 10 breeding groups, consisting of 4–10 females together with a single male in large tanks (dimensions: 122 × 33 × 51 and 122 × 61 × 61 cm). The light regime was set to a 13:11 h

light:dark cycle, and water temperatures were kept between 26.0 and 28.0 °C. The spawning population was fed twice daily with Tetramin flakes and once a week with a mixture of small crustaceans. All tanks were equipped with biological filters, and flowerpot halves as shelters.

Directly after egg laying, females brood their young for about 2 weeks in their mouth while the eggs hatch and the emerged larvae consume most of their yolk sac. Gill movement by the female provides her brood with aerated water. This phase is followed by a 2-week period during which the mother releases the young regularly for foraging (Taborsky 2006b).

Clutch collection and hand raising of young

As soon as possible after spawning (1 h–2 days), we removed the eggs from a female's buccal cavity by slightly pressing her cheeks. All clutches were from different mothers, and 2 shared the same father because their mothers inhabited the same breeding tank. We placed the eggs on a slightly moistened cotton pad to remove excess water from the egg surface before weighing them. The eggs were weighed with an electronic balance to the nearest 0.1 mg. We selected the experimental clutches so they covered the range of egg sizes observed for *S. pleurospilus* in the laboratory (7.0–27.3 mg, based on 63 clutches; Segers FHID, Taborsky B, unpublished data) as fully as possible. In total, 11 clutches were used for this experiment, with mean clutch weights ranging from 12.6 to 22.3 mg. Egg weight variance is larger between females than within females in *S. pleurospilus* (Segers FHID, Taborsky B, unpublished data). To test for effects of egg size on growth, we used the mean egg weight of the clutch from which the fish originated.

After measuring, we placed the eggs in 250 ml Erlenmeyer flasks. The flasks were diagonally fixed in a 100-l tank while submerged in a water bath of 28 ± 1.0 °C. Plastic tubes (2 mm in diameter) connected to air pumps blew air into the flasks, resulting in continuous tumbling movements of the eggs to simulate gill movement by the mother. The setup was covered with a cloth to protect the eggs and larvae from potential light stress. Five days post-hatching, all yolk sac larvae from a clutch were transferred to net cages (dimensions 16.5 × 12 × 13.5 cm) placed near the water surface of small tanks (dimensions 40 × 25 × 25 cm) to finish development.

Manipulation of food ration

Nineteen days after spawning, when the juveniles had nearly used up all their yolk, we randomly selected 8 individuals from the surviving juveniles of a clutch. These fish were individually raised in net cages for 2 weeks. We randomly created 2 groups of 4. Each group was assigned either to a low or to a high daily food regime of Tetramin junior flakes (2.5 and 7.5 mg, respectively) to create 2 size classes of fish within each clutch. At the end of this period, the standard lengths (SLs) were measured to the nearest 0.1 mm, and wet weights (to the nearest 0.1 mg) were obtained following the same procedure as when weighing eggs. At the end of the food treatment, the high-ration fish had an average SL of 15.3 mm ± 0.12 standard error (SE) and the low-ration fish of 13.8 mm ± 0.09 SE.

Creation of experimental groups

Subsequently, we distributed the 8 fish of a clutch over 2 small tanks (dimensions 40 × 25 × 25 cm), such that in each tank, 2 fish from the low-ration group and 2 fish from the high-ration group were housed together. The 2 tanks were assigned to either a high- or a low-food regime (see below) to create different competitive environments. Thus, we created 4 treatment groups: high- and low-ration juveniles exposed to a low-competition

treatment, and high- and low-ration juveniles exposed to a high-competition treatment. Our 2 weeks of food manipulation had allowed us to create 2 distinct size groups, however, we could not predetermine the exact initial size of a fish at the onset of the competition treatment. Therefore, size differences between the large and small siblings sometimes varied slightly between the 2 competitive environments when we installed the group tanks. To control for this, we ensured that the larger initial difference in SL between the high- and low-ration groups was equally distributed across the low-competition and the high-competition environment. Average initial differences across tanks between the high- and the low-ration group did not differ between treatments (high-competition: 1.6 mm ± 0.13 SE, low-competition: 1.5 mm ± 0.14 SE, paired *t*-test, t = −0.43, degrees of freedom [df] = 10, P = 0.68). Also, we minimized the difference in SL between the 2 members of the same ration within each tank as far as possible. At the onset of group housing, members of the same ration differed on average by 0.3 mm SL ± 0.05 SE. The difference between the members of the ration groups did not differ significantly among the 4 treatments (Kruskal–Wallis rank sum test, χ^2 = 3.77, df = 3, P = 0.29).

Growth experiment

The juveniles remained in the experimental setup for 6 weeks. Six days a week, the juveniles were fed Tetramin Junior flake food corresponding to 12% (low-competition) and 4% (high-competition) of the mean age-specific weight of *S. pleurospilus* (see Taborsky 2006a, 2006b). The lower of the food levels did not harm the development of the fish; all individuals used in this study remained lively and without injuries throughout the experiment, and in a previous study, *S. pleurospilus* raised at this food level readily matured and reproduced (Taborsky 2006a, 2006b). The food levels were recalculated every 2 weeks to account for the increasing body mass of the fish. When feeding the fish, we administered the entire daily food ration at a single spot on the bottom of the tank with the help of a plastic tube. This prevented the food from dispersing throughout the tank and thus forced the fish to feed on the bottom of the tank and in close proximity of each other. After the food was dispensed, most of the flakes remained located in a patch of about 5 cm in radius, whereas some of the food would disperse over the bottom of the tank due to the movements of the fish.

As we were only interested in comparing the behavior and mean growth of the 2 ration groups in the respective competitive environments, we did not identify the individuals of the same ration group in a tank individually. We only distinguished between the ration groups, which was done based on the size differences between the groups. To obtain the times it took the low-ration fish to catch up in size with the high-ration fish, we checked every 3 days whether we were still able to see a size difference between the ration groups within a tank. Two observers had no problem distinguishing high-ration from low-ration fish because the size differences between the 2 groups are, relative to body size, quite noticeable. Furthermore, with increasing length, juveniles also become more bulky, which makes detecting size differences easier. When we were not able to distinguish clearly 2 large from 2 small individuals in a tank, the behavioral observations were terminated, and the date was noted as the time of catch-up growth in this tank. Subsequent measurements on all fish confirmed that in the tanks that we classified as "low-ration caught up with high-ration," the size differences among the siblings were smaller than in the tanks where size differences between the ration groups were still visible. The size differences between the second largest individual and the second smallest individual in the

tanks classified as low-ration caught up with high-ration were considerably smaller (mean: 0.4 mm ± 0.13 SE) than in tanks with 2 distinguishable size classes (mean: 1.5 mm ± 0.18 SE). For the statistical analysis of the day of successful catch-up growth, those tanks in which the low-ration group did not catch up were given the highest possible value of 43 days (1 day after the last experimental day).

Every 2 weeks, we measured the SLs of all fish. Subsequently, we took the mean length of the 2 fish in the same ration group and calculated the specific growth rate (SGR) for each ration group over the previous 2 weeks as:

$$\text{SGR} \left(\% \times d^{-1} \right) = \left(\ln\text{SL}_2 - \ln\text{SL}_1 \right) / \left(\text{age}_2 - \text{age}_1 \right) \times 100,$$

where SL_1, SL_2, age_1, and age_2 are initial and final SLs and ages of 2 successive measurements. When the low-ration group had caught up with the high-ration group at the end of a measurement period, we used the mean SL of all 4 fish in the tank as the SL_2 for both the low-ration as the high-ration group, to be able to calculate the SGR for the previous 2-week period. Afterward, the tank was no longer used to calculate mean growth rates for the ration groups, as they were no longer distinguishable.

For statistical analysis, we compared the differences of SGR between the size groups housed in the same tank (ΔSGR = SGR low-ration group − SGR high-ration group). We calculated the ΔSGR for days 14–28 after first feeding only, as this was the period for which we could calculate a growth rate for all tanks.

Aggressive interactions

Every 2–4 days, we observed for 3 min the aggressive interactions between the ration groups during feeding. This time period was long enough to record most of the food-related aggression because most of the daily food ration was consumed during this time, however, it was short enough for none of the tanks to run out of food during the observations. The ration group of the initiator and recipient of the following aggressive acts was noted: 1) attacks, where one fish pecks at the other and 2) pursuits, where one fish was chasing another. Individual recognition was not possible but was also not necessary for the purpose of our study. We only recorded aggressive interactions during the first 4 weeks of group housing (14–42 days after first feeding) because in many tanks, the ration groups could not be distinguished anymore after these 4 weeks. We observed each of the 22 tanks for a maximum of 7 times. In 5 tanks, the ration groups became impossible to distinguish before the end of the 4-week period, and thus, these tanks were observed less than 7 times (1 tank was observed once, 1 tank thrice, and 3 tanks 6 times). In total, we obtained 141 observations, 65 of the tanks in the low-competition environment and 76 of the tanks in the high-competition environment.

Data analysis

All analyses were done in R 2.9.2 (R Development Core Team 2009). All tests were two-tailed. We predominantly used general and generalized linear mixed-effects models (LME and GLMM), depending on the distribution of the response variable. We added clutch as the random effect term to the models or, when appropriate, experimental tank nested within clutch. We did not test for significance of the random effect terms as we chose to always keep them in the model to control for repeated measures, and they were not important for our question (Bolker et al. 2009).

We used an LME to model ΔSGR as a function of 3 variables: 1) competitive environment, 2) the initial difference in SL between the ration groups at the onset of group housing, and 3)

mean egg weight of the clutch. We included the mean egg weight of a clutch because a recent study showed that egg weight negatively correlates with growth rate several weeks after hatching (Segers et al. 2012). To test whether received aggression can suppress growth, we composed LMEs with the SGR of the recipient ration group as dependent variable and number of received aggressive acts and mean egg weight of the clutch as the 2 explanatory variables. For LME model selection, we used a step-down protocol (Zuur et al. 2008). The nonsignificant terms were backward eliminated, using maximum likelihood (ML) to check for significance, with a significance level set to $\alpha = 0.05$. The optimal model was in the end fitted with restricted maximum likelihood (REML). The final models contain all significant main effects. We give the ML ratios (L) and P values of the nonsignificant factors that were removed from the model. We did not test for the significance of interactions in the LMEs, as we had not enough df.

To compare aggression levels between and within ration groups depending on competitive environment, we used a GLMM with Poisson error structure because the data were not normally distributed. The number of aggressive acts observed during the 3-min period was modeled as a function of ration group, competitive environment, and the ration group of the fish to which the aggression was directed. For the GLMM, we used Wald tests to test the significance of the fixed effects, and we fitted the models with the glmmPQL function from the MASS package. The final GLMM contains all significant main effects and interactions, as well as nonsignificant main effects involved in significant interactions.

RESULTS

Catching up

In 7 of the 11 tanks from the low-competition environment, the low-ration group reached the same SL as their high-ration siblings within the time frame of the group housing (6 weeks). In contrast, only in one tank of the high-competition treatment, the low-ration group caught up with the high-ration group. Remarkably, their low-ration siblings kept in the low-competition treatment also caught up particularly fast (6 days). Overall, low-ration groups in the low-competition environment had a significantly higher likelihood to catch up with their high-ration siblings (McNemar's χ^2 test, $\chi^2 = 4.17$, df = 1, $P = 0.04$), and they did so faster than their counterparts in the high-competition treatment (Wilcoxon signed-rank test, $V = 0$, $P = 0.02$; Figure 1).

In the low-competition treatment, the low-ration fish took longer to catch up when the initial size differences between the ration groups were larger (linear model, $F_{1,9} = 5.68$, $R^2 = 0.39$, $t = 2.38$, $P = 0.04$). The initial size difference (1.6 mm) between the ration groups of the only tank in the high-competition treatment where catch-up occurred did not particularly deviate from the mean difference in starting size between the ration groups of the other tanks (1.6 mm ± 0.14 SE).

Growth

Competitive environment had a highly significant effect on the difference in SGR between the ration groups (ΔSGR) (LME, $N = 22$, $t = -7.50$, $P < 0.001$; see also size trajectories; Figure 2) during days 14–28 after first feeding. The difference in SL between the ration groups at the onset of group housing was added to the initial model, but it was removed as it had no effect ($L = 0.76$, $P = 0.38$), as was the mean egg weight of the clutch ($L = 0.06$, $P = 0.80$). During days 14–28 after first feeding, the low-ration group in the high-competition environment grew slower than the high-ration group (Figure 3;
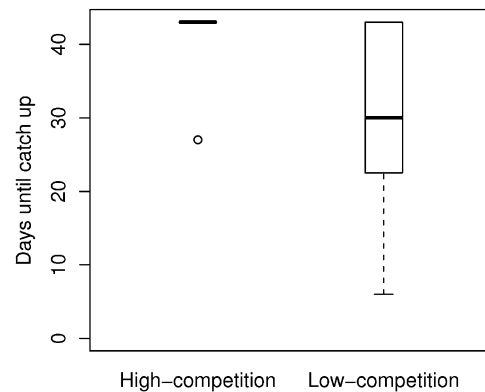

Figure 1
The experimental days until the low-ration group caught up in SL with the high-ration group for the 2 different competitive environments. The boxplots show medians, quartiles, and 5th and 95th percentiles. At 42 days, the experiment was terminated and tanks in which no catch-up had taken place were given the value of 43 days.

paired t-test, $t = -7.35$, df = 10, $P < 0.001$), whereas in the low-competition situation, the low-ration group grew at a similar rate as the high-ration group (Figure 3; paired t-test, $t = 0.83$, df = 10, $P = 0.43$).

Aggression

The high-ration group was much more aggressive than the low-ration group (Table 1; Figure 4). Competitive environment and ration group interactively affected the frequency of aggressive behavior: the high-ration group was less aggressive in the low-competition than in the high-competition environment, whereas the opposite was true for the low-ration group (Table 1; Figure 4). The high-ration group was more aggressive toward the low-ration group than members of the high-ration group were among themselves (Table 1; Figure 4).

To test if receiving aggression might suppress growth rate, we calculated the SGR of a ration group over the first 4 weeks of group housing (days 14–42 after first feeding). Over the same time period, we averaged all behavioral observations for each
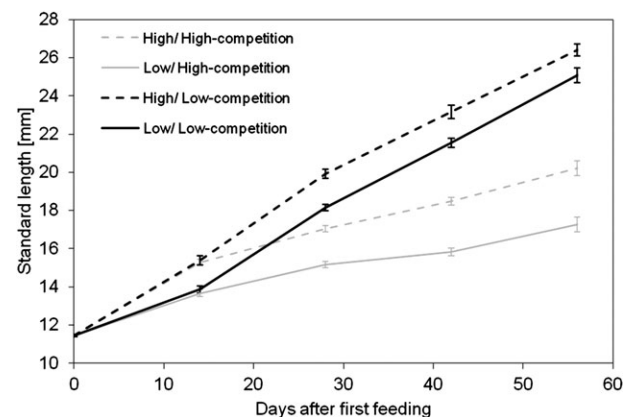

Figure 2
The size trajectories of SL of the 2 ration groups for both competitive environments. The error bars represent the standard errors of the mean. The figure is based on data from all tanks. The high- and low-ration groups that were no longer distinguishable were given the same values for SL.
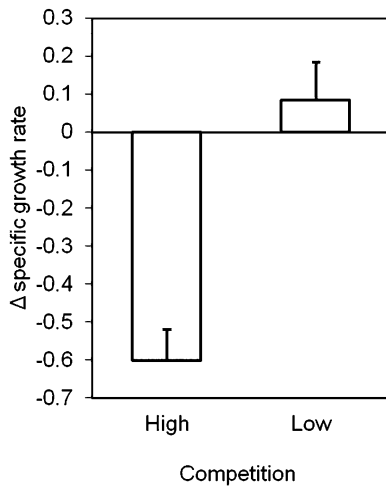
Figure 3
The difference of SGR between the ration groups (Δ = low-ration − high-ration) for the 2 different competitive environments during days 14–28 after first feeding. Error bars as in Figure 2.

Figure 4
The rate of aggressive acts per minute inflicted between and within ration groups (H = high-ration, L = low-ration). The x-axis indicates from which ration group the aggression came from and to which ration group the aggressive act was directed. Black boxes: low-competition environment; white boxes: high-competition environment. Boxplots as in Figure 1.

ration group in each tank. We did not add ration as a factor to the model as we wanted to test if aggression is a potential mechanism behind the differences in SGR between the ration groups. As competitive environment and aggression by the high-ration group toward the low-ration group were not independent (see above), we tested for a relationship between aggression and SGR of a ration group within both competitive environments separately, instead of adding competitive environment as an explanatory variable to our model. Within the high-competition treatment, the frequency of received aggression was negatively related to the SGR (LME, $N = 22$, $t = -2.27$, $P = 0.05$). Additionally, the mean egg weight of the clutch from which the ration group originated had a negative effect on its SGR ($t = -2.30$, $P = 0.05$). Within the low-competition treatment, received aggression was not related to SGR (LME, $N = 20$, $L = 0.40$, $P = 0.53$). Again the mean egg weight of the clutch from which the ration group originated negatively influenced its SGR ($t = -3.65$, $P = 0.008$).

To examine if showing aggression toward a conspecific could be positively related to the growth rate of the aggressor, we performed a correlation analysis, as it is not clear which is cause and which is effect. After controlling for the effect of egg weight on SGR, within the high-competition treatment, the frequency of aggressive behavior by a ration group was positively correlated with its SGR (partial correlation, $N = 22$, $r = 0.46$, $P =$
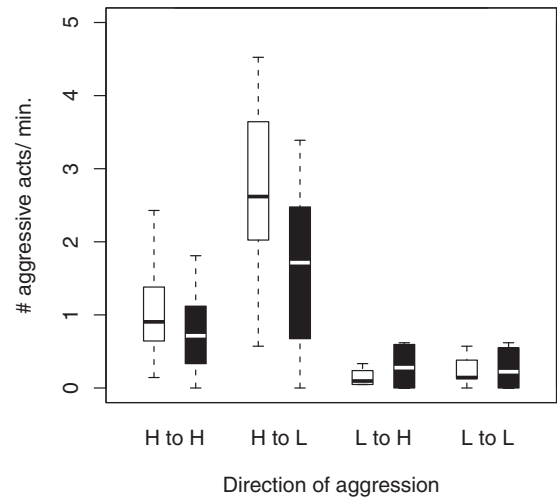
0.02). Within the low-competition treatment, this correlation was not significant (partial correlation, $N = 20$, $r = -0.15$, $P = 0.55$).

DISCUSSION

In a highly competitive situation, *S. pleurospilus* juveniles that had previously received a high ration and thus had a larger body size were clearly superior competitors over smaller fish previously exposed to a low ration. They were able to grow much faster and thus expanded their size advantage over time. Additionally, the larger individuals responded to a stronger food competition by increasing their aggressive behavior, suggesting that by these means, they claimed a larger share of the common food resource than their smaller siblings. Thus, when competition is fierce, competitive inferiority may increase the time it takes a relatively small juvenile to outgrow a mortality window (Sogard 1997), thereby considerably increasing its likelihood of being eaten. In contrast, when competition was low, the small juveniles grew faster than their larger siblings and in most cases caught up in size. The fast growth rates expressed by the small offspring that caught up in size with large young in the low-competitive environment are characteristic of compensatory growth (Ali et al. 2003). Our results hence suggest that the potential for compensatory growth of growth-depressed offspring depends strongly on the subsequent intensity of competition.

Compensatory growth may result in costs later in life (reviewed in Metcalfe and Monaghan 2001). Thus, the fast growth of the low-ration individuals can be expected to have negative long-term fitness consequences. Therefore, compensatory growth should be advantageous only under certain conditions, such as when smaller individuals experience higher predation pressures (Ali et al. 2003).

In contrast to previous work, our experimental approach controls for age and genetic background. Furthermore, by using clutches over a wide egg size range and by hand-raising young from known egg sizes, we excluded maternal effects potentially confounding offspring or egg size, which can influence growth through, for example, androgen content (e.g., Groothuis and Schwabl 2002) or nutrient composition of eggs

Table 1
Results from the GLMM for aggressive behavior ($N = 564$)

Model terms	Aggressive acts	
	Z	P
Competition treatment	2.64	**0.008**
Ration	20.54	**<0.001**
Opponent	1.56	0.12
Competition × ration	−7.85	**<0.001**
Competition × opponent	1.64	0.10
Ration × opponent	−7.72	**<0.001**
Competition × ration × opponent	−1.35	0.18

Nonsignificant interactions were removed from the model. The significant P values are marked in bold.

(e.g., Brown and Taylor 1992). In our experiment, it was indeed important to control for egg size, as this was negatively related to growth at the ages of 2–6 weeks after first feeding. This delayed effect of egg size on growth in *S. pleurospilus* is linked to higher growth hormone receptor expression levels in yolk sac larvae from small eggs (Segers et al. 2012).

In both environments, the high-ration fish were overall more aggressive than the low-ration fish during feeding, which can be due to their larger size per se as observed in other fish (e.g., Post et al. 1999). Additionally, the level of aggression of large toward small juveniles was higher in the high- than in the low-competition environment. This suggests that the behavioral response of fish to competitive situations is dependent on their size relative to their opponents. This size-dependent behavioral response implies that a stronger competition for food does not necessarily raise the general levels of aggression as suggested by previous studies (e.g., Sakakura and Tsukamoto 1998; Grant et al. 2002). Observing the fish outside the feeding period might have revealed different patterns, however, this was beyond the scope of our study.

Importantly, growth was affected differentially by aggression in the 2 environments: under high-competition, fish that were attacked more often grew slower and fish showing more aggression grew faster, whereas these relationships were absent in the less competitive situation. The causal relationship between aggression and growth is not straightforward, as higher levels of aggressive behavior may be a response to increased hunger associated with high metabolic demands (Metcalfe et al. 1995). Therefore, the relationship between growth and aggressive behavior performed in the high-competition environment might be due to higher metabolic demands or to a more successful defense of food resources. However, as the frequency of received aggression impaired the growth of fish, our findings rather suggest that aggression helps to monopolize food when it is limited. Similarly, food intake of rainbow trout was highly correlated with dominance, but this relationship became weaker when food was provided in larger quantities (McCarthy et al. 1992). In Atlantic salmon, a larger size of dominant individuals was a consequence rather than a cause of dominance, as some individuals were innately more aggressive than others (Huntingford et al. 1990). However, as we manipulated the initial size of the fish through different food rations, innate aggression differences cannot explain the differences in dominance between large and small juveniles that we detected in the high-competition treatment.

Growth rate often strongly depends on food intake (e.g., Jobling and Baardvik 1994; Amundsen et al. 2007), and this also holds for *S. pleurospilus* (Taborsky 2006b). Individuals can affect each other's resource acquisition by reducing the resource availability (exploitative competition) or by actively preventing each other from exploiting a resource by aggressive interactions (contest competition; Ward et al. 2006). Both mechanisms might have reduced the food intake of the smaller low-ration fish in the high-competition environment and thereby decreased their growth directly. In particular, as received aggression was associated with slower growth when food was scarce, *S. pleurospilus* juveniles seem to actively prevent other conspecifics from feeding. In addition to competitive interactions, other mechanisms may have caused the slow growth of the smaller fish in the high-competition environment. Commonly, subordinate fish have chronically elevated resting metabolic rates associated with high cortisol levels as a response to stress (Pottinger and Pickering 1992; Sloman et al. 2001; Millidine et al. 2009), and resultantly, growth rates may be reduced (Lee et al. 2011). Moreover, we often witnessed small individuals fleeing from large ones during our observations, which is likely to involve direct energy costs (Post et al. 1999). We do not know if high-ration fish were also more aggressive toward low-ration individuals outside the feeding period, which might have increased the social stress of the low-ration fish even more.

Similar growth patterns as those found in this study were observed when competitor density was manipulated in guppies (*Poecilia reticulata*): in a high-competition environment, offspring growth depended on initial body size, whereas this pattern was absent in a low-competition environment (Bashey 2008). In the low-competition treatment, size differences between small and large juveniles remained constant throughout the experimental period (Bashey 2008), whereas initially smaller *S. pleurospilus* offspring fully caught up in size with their larger siblings in more than half of the low-competition replicates. It is possible that guppy offspring are less flexible in adjusting their growth, as species may differ in their capacity for compensatory growth (Ali et al. 2003). Furthermore, maternally induced size differences between offspring might last longer than environmentally induced differences. Additionally, we tracked growth for a longer time period, which naturally increases the opportunity for small juveniles to catch up with their larger siblings.

CONCLUSION

Our results support the hypothesis that the compensatory growth potential of young depends on the severity of intraspecific food competition. In contrast to previous works, our study examines the consequences of environmentally induced body size differences on juvenile competitive abilities while controlling for age, genetic background, and maternal effects. Furthermore, our results suggest that larger *S. pleurospilus* juveniles increase their aggressive behavior toward smaller individuals particularly when competition is strong, and thus, they might actively prevent them from feeding in this situation.

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