Behavioural type affects dominance and growth in staged encounters of cooperatively breeding cichlids

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In animals, behavioural properties such as aggressive propensity are often consistent over a life span, and they may form part of a behavioural syndrome. We studied how aggressive propensity influences dominance, contest behaviour and growth in the cooperatively breeding cichlid fish *Neolamprologus pulcher*. We tested whether intrinsic aggressive propensity (1) influences dominance in paired contests, (2) causes different aggression levels in contests with partners matched for aggressive propensity compared to unmatched partners, and how it (3) affects growth rate in groups that were either matched or unmatched for aggressive propensity. Intrinsic aggressive propensity was first scored with a mirror test and classified as high, medium or low. Thereafter we tested fish with either high or low aggressive propensity with partners matched for size and either matched or unmatched for aggressive type in a paired contest for a shelter. We scored dominance, aggression and submission. As predicted, (1) dominance was more clearly established in unmatched than in matched contests and (2) individuals with high aggressive propensity launched more attacks overall than fish with low intrinsic aggressiveness, suggesting a higher propensity to escalate independently of winning or losing the paired contest. However, contrary to expectation, (3) individuals with low aggressiveness grew faster than aggressive ones in unmatched groups, whereas the opposite occurred in matched groups. This suggests that individuals with low aggressive propensity may benefit from conflict evasion, which might allow them to gain dominance in the future owing to larger body size.

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Individuals in natural populations often show consistent differences in how their behaviour responds to environmental and social challenges. These consistent differences have been termed behavioural syndromes, animal personalities, coping styles or temperaments (reviewed in Gosling & John 1999; Sih et al. 2004a; Bergmüller & Taborsky 2010). Typically, different behavioural axes are correlated with each other, for instance aggressiveness, novelty seeking and exploratory propensity. The strength of these behavioural correlations and the frequency of occurrence of different behavioural types may differ between populations (Coleman & Wilson 1998; Dingemanse et al. 2009). Behavioural correlations may exist between different situations within a certain behavioural context, for instance in foraging across a range of different habitats, or between different contexts, for instance among behavioural traits related to predator evasion, mating or resource competition (Sih et al. 2004a, b). Although research on animal personality has proceeded rapidly, the social consequences of the coexistence of different behavioural types in group-living species have been underexplored (Armitage & Johns 1982; Armitage 1986a, b; McGuire et al. 1994; Capitanio 1999; Gosling & John 1999; Bergmüller et al. 2007; Schürch & Heg 2010a, b). For instance, it has not been tested whether individuals with a high aggressive propensity gain dominance in social groups, and whether individuals with a low aggressive propensity accept a subordinate position instead. Moreover, more tests are needed that relate high and low levels of aggressiveness to social behaviour in general, for example energy expenditure, expulsion risk or costly conflicts within groups (i.e. escalated fights resulting in injuries), and subdominant - dominant interactions (Schürch & Heg 2010b).

So far most studies of behavioural syndromes have focused either on risk-taking behaviour or exploration (van Oers et al. 2005; Brown et al. 2007). However, in group-living animals, especially when novel groups are formed and dominance relationships are established, other behaviours might be more important, such as aggressiveness, which can affect dominance and access to food, shelter and mates. Recent work provides evidence that behavioural traits such as aggressive propensity are positively correlated with life history traits such as food intake and growth rates (Stamps 2007; Biro & Stamps 2008). In group-living species

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aggressiveness may affect the body size of group members through access to food and size-dependent expulsion of subordinates. Physical traits such as body size or mass can substantially influence the formation of dominance relationships (Otronen 1988; Rosenberg & Enquist 1991; Olsson 1992; Faber & Baylis 1993; Huntingford & deLeaniz 1997), and it might be expected that behavioural traits should covary with such determinants of dominance (i.e. resource-holding potential or resource value; Hurd 2006). Our aim was to study the effects of aggressive propensity on conflict behaviour, dominance and growth rates in a cooperatively breeding fish, while controlling for the effects of body size by size matching fish.

Neolamprologus pulcher is a cichlid fish endemic to Lake Tanganyika (Duftner et al. 2007), which defends territories and raises broods cooperatively (Taborsky & Limberger 1981; Taborsky 1984; Balshine et al. 2001). Groups of *N. pulcher* consist of related and unrelated individuals (Dierkes et al. 2005) and are structured in a linear dominance hierarchy based on body size (Hamilton et al. 2005). The breeding pair (the largest male and female in the group) are dominant over all other group members and largely monopolize reproduction (Taborsky & Limberger 1981; Taborsky 1984, 1985; Dierkes et al. 1999, 2008; Heg et al. 2006, 2008a, b; Heg & Hamilton 2008; Mitchell et al. 2009a, b). They are assisted by several subordinate helpers of both sexes and of a wide size range, which participate in territory maintenance, defence and brood care (Taborsky & Limberger 1981; Taborsky 1984; Bruintjes & Taborsky 2008; Heg & Hamilton 2008). Evidence suggests that helpers pay 'rent' to remain tolerated in the dominants' territory (i.e. they 'pay-to-stay'; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Bergmüller et al. 2005; Bergmüller & Taborsky 2005; Bruintjes & Taborsky 2008). In this species aggressive and submissive behaviours are energetically costly, raising metabolic expenditure by about four times in comparison to inactive periods (Grantner & Taborsky 1998; Taborsky & Grantner 1998).

Individuals of *N. pulcher* vary systematically in behaviour along a bold–shy continuum (Bergmüller & Taborsky 2007; Schürch & Heg 2010a, b). Individuals with a high aggressive propensity might be prospective competitors for the dominant position in the same or a different group. However, aggressive helpers might also bear higher costs, for instance because of an increased likelihood of engaging in escalated conflicts, with the possible consequence of being expelled from the group (Taborsky 1985; Balshine-Earn et al. 1998; Schürch & Heg 2010a, b). Therefore, helpers of different aggressive propensities may opt for different strategies on the trade-off curve between current and future reproductions (Schürch & Heg 2010a, b; Witsenburg et al., in press). Helpers with a high aggressive propensity might be inclined to challenge the dominants and go for current reproduction (subject to an increased risk of expulsion), whereas helpers with a low aggressive propensity might be inclined to assist the dominants instead and opt for future reproduction (e.g. inheritance of the dominant position after the same-sex dominant dies). Dominance relationships are sex specific within groups of *N. pulcher* (Mitchell et al. 2009a, b), which reflects intrasexual competition for reproduction (Balshine-Earn et al. 1998; Dierkes et al. 1999; Heg et al. 2004; Hamilton et al. 2005). The aggressive propensity of dominants in *N. pulcher* affects their reproduction, dominant–subordinate interactions and expulsion of subordinates (Schürch & Heg 2010a), but not the growth rates of individuals kept singly (Schürch & Heg 2010b). However, it remains unclear how aggressive propensity influences the likelihood of becoming dominant, and whether and how it affects the growth rates of individuals living in groups. These two aspects are the main focus of this study.

We aimed to test for three potential social consequences of differences in aggressive propensity among individuals of similar body size. First, we tested whether a high aggression propensity allows individuals (called type H) to attain a dominant position in pairwise contests with less aggressive individuals (type L; treatment HL), when body sizes are matched. As controls, we staged pairwise contests between high–high (HH) and low–low aggressive fish (LL). We expected behavioural consistency and therefore predicted that H individuals would dominate L individuals, and that dominance outcomes would be less clear in HH and LL contests than in nonmatched interactions. Second, we evaluated whether escalation depends on the aggressive propensity of individuals, and whether the risk of escalated fights is reduced by increased frequencies of submissive behaviour shown by the subdominant. Owing to the expected behavioural consistency, we predicted more aggression would be shown by H individuals than L individuals in all treatments, independently of whether they had won or lost the contest.

Third, we tested whether individuals with high and low aggressive propensities would grow differently in a social context, for instance because of different abilities to obtain food or different metabolic costs. For this purpose, we compared the growth rates of H and L individuals living in matched groups (HH or LL) or mixed groups (HL). If H individuals dominate L individuals in the above paired contests, we accordingly expected that in mixed groups (HL) growth rates should be higher in H individuals than in L individuals to maintain the dominant position over a longer period. We further expected that growth rates should be generally lower in matched groups (HH and LL) than in mixed groups (HL) owing to a higher escalation potential in social conflicts. If costly escalation increases in matched groups depending on the behavioural types of the individuals involved, growth rates should accordingly decrease from HH to MM to LL groups (where M are fish of medium aggressive propensity only measured in matched groups). Finally, we tested whether H, L and M differed in their body condition at the end of the experiment. This is important, because an increase in growth rate may come at the expense of disposing of less body reserves.

METHODS

Study Animals and Laboratory Conditions

Focal individuals used in this study were laboratory-reared offspring of wild-caught *N. pulcher* from the southern end of Lake Tanganyika (near Mpulungu, Zambia). They were kept in four 400-litre mixed-sex storage tanks without breeding shelters at a water temperature of 27 ± 1 SD °C. The storage tanks contained groups of 50 individuals of only small (less than 45 mm standard length) or only large fish (more than 45 mm standard length). Plastic bottles at the water surface were provided as refuges for expelled individuals to reduce aggressive interactions. Chemical attributes of the water closely matched the values of Lake Tanganyika (Taborsky 1984) and the light regime was 13:11 h light:dark. All fish were fed four times a week with commercial dry food (Tetramin) and twice a week with frozen fresh food (consisting of daphnia, *Artemia salina* and chironomid larvae) ad libitum.

The 63 focal animals used in this study were caught from the four storage tanks with hand-nets. To reduce potential effects of familiarity in the paired contests, similar numbers of fish were caught from each storage tank, and care was taken to pair fish from different storage tanks as much as possible. Body size was measured to the nearest 0.1 mm using a binocular microscope (measurements at start of experiment: standard length SL, mean $\pm$ SD $= 42.9 \pm 4.8$ mm, range 34.0–54.4 mm), body mass was determined in mg (mean $\pm$ SD $= 2168.8 \pm 745.5$ mg, range 1040–4115 mg) and the sex was determined by inspection of the

genital papilla (31 males and 32 females). Owing to the short handling time, to minimize stress animals were not anaesthetized. The focal fish were kept in two 1000-litre aquaria, visually isolated from each other, in individually labelled isolation nets (20×11 cm and 11 cm high) for an experimental period of 8 days (test phases 1 and 2). Between days 9 and 14 they were kept in group compartments (test phase 3) as described in detail below. All fish were checked daily for aberrant behaviour or illness and they were fed at the end of each day (after testing) with commercial dry food. After 14 days, all test fish were released again into their respective holding tanks. The experiment consisted of three phases (Fig. 1): (1) testing for aggressive propensity using a mirror (Fig. 1a), (2) paired contests (Fig. 1b), and (3) determination of growth rates in groups (Fig. 1c). The three phases are described in more detail below.

Aggressive Propensity Tests

First, we tested each fish for its intrinsic aggressive propensity by exposing it to a mirror. For this purpose, every focal fish was transferred with a small container from its isolation net to an experimental tank (30×50 cm and 30 cm high) that was covered on the left and right sides with black cardboard for visual isolation from neighbouring tanks. The experimental tank contained a clay pot half serving as shelter, and a mirror was placed at the back wall of the tank (Fig. 1a). After the first agonistic behaviour was shown against the mirror, all agonistic behaviours towards the mirror image were counted for the following 5 min (restrained: raising fins, lifting gill lids, fast approaching without contact, head-down display and s-shaped bending; and overt aggression: mouth contact with mirror; see Hamilton et al. 2005; Bergmüller & Taborsky 2007 for a similar set-up). Schürch & Heg (2010a) showed that behavioural characteristics of *N. pulcher* remain constant over long periods of time; therefore a single measure of aggressiveness provides a reliable estimate of an individual's intrinsic aggressive propensity. After this test, we ranked the 63 individuals according to their aggression frequencies. Based on this rank order the population of test fish was divided into three groups: high aggressive (H fish; $N = 24$ individuals, range 12–45 aggressive acts/5 min), medium aggressive (M fish; $N = 15$ individuals, range 7–11 aggressive acts/5 min) and low aggressive (L fish; $N = 24$ individuals, range 0–6 aggressive acts/5 min). The M fish were not used in the following paired contest experiment but served as an intermediate treatment in the growth experiment (comparing their growth to H and L fish in unmixed groups). H, M and L individuals
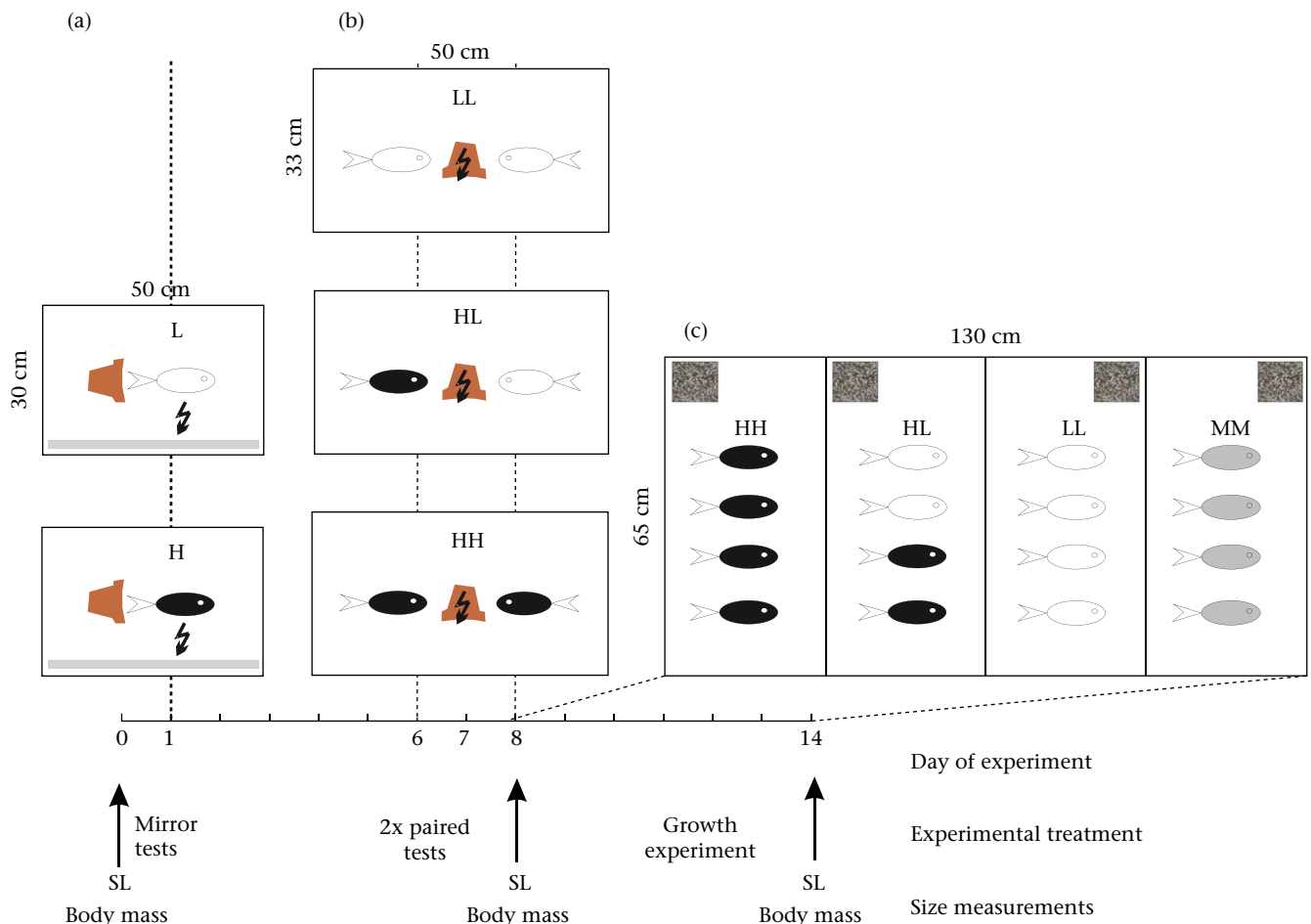
Figure 1. Set-up of the three experiments. Body measurements (standard length, SL, in 0.1 mm and mass in mg) were taken on days 0, 8 and 14. (a) The behavioural type of each focal fish was determined on day 1 in a mirror test; fish with high aggressive propensity (black H, $N = 24$) and low aggressive propensity (white L, $N = 24$) fish entered. (b) The paired contests, where they were tested once against an opponent of the same type and on the next day against an opponent of a different type, in randomized sequence (HH, HL and LL paired contests). (c) On the evening of day 8, new groups were formed of four focal fish each, using four compartments in four 400-litre tanks (grey squares are filters; note that no shelters were provided). Three groups contained four and one group three H fish each (HH), four groups contained four L fish each (LL), and four groups were mixed with two H and two L fish (HL). We also established four groups with four fish of intermediate aggressiveness in the mirror test (grey, MM, $N = 14$, two groups contained only three fish). Growth in this social situation was measured as $SL_{day\ 14} - SL_{day\ 8}$ and body mass$_{day\ 14}$ − body mass$_{day\ 8}$.

did not differ in body length (SL) and body mass on day 0 ($N = 63$; ANOVAs: $F_{2,60} = 0.5$ and 0.9, $P = 0.61$ and 0.42, respectively), and we had similar numbers of males and females in the treatment groups (12 and 12 H, 7 and 8 M, 12 and 12 L; $\chi^2_2 = 0.05$, $P = 0.98$).

Paired Contest Trials

Second, we tested whether intrinsic aggressive propensity determines the dominance outcome of staged encounters with partners of the same or different aggressive propensity. All 24 H and 24 L focal fish were tested twice: once with an H and once with an L opponent, in randomized order. Hence, there were three different treatments: two matched paired contests HH ($N = 12$ pairs) and LL ($N = 12$ pairs) and one mixed paired contest: HL ($N = 24$ pairs; see Fig. 1b). The experimental pairs were matched for body size (mean difference in SL $\pm$ SD: HH: 1.67 ± 2.38 mm, $N = 12$, range 0.0–8.0 mm; LL: 1.35 ± 0.86 mm, $N = 12$, range 0.30–2.70 mm; HL: 1.75 ± 1.51 mm, $N = 24$, range 0.0–6.3 mm; there was no size difference between the treatments: ANOVA: $F_{2,45} = 0.23$, $P = 0.79$), which resulted also in similar body mass of individuals in test pairs (mean difference in mass $\pm$ SD: HH: 365.6 ± 367.9 mg, $N = 12$, range 65–1128 mg; LL: 239.1 ± 172.3 mg, $N = 12$, range 21–537 mg; HL: 287.1 ± 255.8 mg, $N = 24$, range 14–1258 mg; there was no difference in mass between the treatment groups: ANOVA: $F_{2,45} = 0.67$, $P = 0.52$). Size matching was used to prevent possible dominance effects based on body size differences (Barlow et al. 1986; Hamilton et al. 2005). The pairs were also matched for sex as much as possible, and we tested whether sex might have influenced dominance outcomes (sexes tested: HH: $N = 5$ male–male, 5 female–female, 2 male–female; LL: $N = 4$ male–male, 5 female–female, 3 male–female; HL: $N = 9$ male–male, 9 female–female, 6 male–female). To distinguish the individuals during the contest, one of the fish drawn at random was marked with a small fin clip at the back of the dorsal fin. The experimental tank (33×50 cm and 30 cm high) had a clear front screen to allow observation and black cardboard was attached to the other three sides; the tank contained a clay flowerpot half in the middle (Fig. 1b). Both fish were transferred from their isolation net to the experimental tank in a container and released at exactly the same time at opposite sides of the experimental tank.

Behavioural recording of the test fish started when the first contact between them occurred and lasted for 10 min. We recorded for each fish the number of restrained (raising fins, lifting gill lids, fast approaching without contact, head-down display and s-shaped bending) and overt aggressive behaviours (ramming, fin slapping, biting and mouth fighting; Taborsky 1984) and the frequency of submissive behaviours (tail quivering and zigzag swimming; Hamilton et al. 2005). We scored individuals as attaining dominance over the other ('won') if they prevented the opponent from approaching close to the shelter and chased it when it came near. The other fish was scored as subdominant ('lost') if it was constantly avoiding the other fish or displaying submissive behaviour. If we could not determine a clear winner and loser within the observation period, the contest was filed as a 'draw'. Afterwards the fish were transferred back to their isolation nets. The second test of each focal fish was performed on a different day but within 2 days after the first test.

Growth Rate

Third, to test whether intrinsic aggressive propensity influences growth in a social situation with different group compositions, we measured body size and mass of all 63 focal fish again 8 days after the initial measurements (Fig. 1b). To assess the growth rates of test fish in different group compositions, we established four treatment

groups: HH, LL, MM and HL. Each treatment was repeated four times, with three or four fish in each replicate (Fig. 1c). Experimental group compositions in the HH treatment consisted of three replicates with four H individuals each (two groups with two males/two females, one group with three males/one female) and one replicate with three H individuals (two females/one male; this was due to one male dying shortly after release). The LL treatment consisted of four replicates with four L individuals each (three groups with two males/two females, one group with one male/three females). In the mixed treatment HL, there were four replicates with two H individuals mixed with two L individuals (males/females: HH/LL, H/HLL, HHL/L, LL/HH). In the MM treatment: there were two replicates with four M individuals (both two males/two females) and two replicates with three M individuals (three males, one male/two females; the latter group contained only three fish owing to one female dying shortly after release).

The group members were size matched as much as possible, based on their body size estimates on day 8: mean maximum difference in SL $\pm$ SD $= 3.39 \pm 2.06$ mm, $N = 16$ groups, range 0.9–7.9 mm (no difference between the treatments: ANOVA: $F_{3,12} = 1.4$, $P = 0.28$) and mean maximum difference in body mass $\pm$ SD $= 515.1 \pm 347.3$ mg, $N = 16$ groups, range 96–1468 mg (no difference between the treatments: ANOVA: $F_{3,12} = 0.9$, $P = 0.48$). The groups were randomly assigned to four 400-litre tanks (130×65 cm and 50 cm high), divided into four compartments each (33×65 cm and 50 cm high) by opaque PVC sheets (Fig. 1c). Every 400-litre tank contained all four treatments (HH, LL, HL and MM), but the order was randomized over the four tanks. To keep water quality constant, each compartment contained an air-driven biological filter. In each tank, all groups were released at the same time. After 6 days, we again measured the body size (SL) and body mass of the 61 focal fish, blindly for behavioural type and treatment (third measurement on day 14; see Fig. 1c). To provide each group with the same amount of food, a teaspoon was used to measure the ration. Each group received one teaspoon of food daily that was distributed over the whole water surface of the tank. The food sank and floated in the water column, so that all fish had good access to it. As *N. pulcher* is mainly a zooplankton feeder (Gashagaza & Nagoshi 1986; Gashagaza 1988), food is not defended. Growth rates were calculated from the difference in SL and body mass between days 14 and 8.

Statistical Analyses

We used mainly generalized estimating equations (GEE; Norusis 2008) for analysis, which are particularly suitable for (1) correcting the estimates of the main effects for repeated testing of the same objects (in our case, individuals in the paired contest or groups in the growth experiment), without claiming to be able to estimate the random effects accurately (which in our case would be based on only two tests, i.e. individuals in the paired contests, or four growth measurements, i.e. the four individuals within each group); and (2) count data (frequencies of behaviour in the paired tests). The scaling parameter was adjusted using the deviance method in each model (Norusis 2008). The aggressive and submissive behaviours in the paired contests were analysed with GEE with a log-link, with individual identifiers as subjects to account for repeated measures of the same individuals (two contests per individual). We added to the mixed model the fixed effects of behavioural type (H or L), treatment (matched contest HH or LL versus mixed contest HL), dominance (lost, draw or won: see Results) and their interactions. We removed nonsignificant terms stepwise. Only the final models are presented. In the paired tests one individual was often more aggressive than the other and the receiver typically responded by submission, so these data are strictly speaking not independent.

Methods for analysing nonindependent data in a contest situation have been given by Briffa & Elwood (2010). However, the methods they suggested were not applicable to our data as we were using pairs matched as much as possible in sex and body sizes. Our response variable should only be influenced by intrinsic escalation potential and not by extrinsic factors such as body size or mass; therefore independent and dependent variables are not expected to be the 'wrong way round' as Briffa & Elwood (2010) discussed. Nevertheless, we accounted for the fact that the experimental unit is the pair, as they experience the same situation, by (1) assessing the robustness of the GEE models with bootstrap analyses. This was done by using 50 randomly drawn cases from the whole sample for 100 runs to validate *P* values of the GEE for aggressive and submissive behaviour. (2) To explore this further, we tested whether aggression shown by the more aggressive fish in the dyads (or less submissive fish in the case of ties) predicted the submission shown by the less aggressive fish, depending on the treatment (generalized linear models with a log-link and Poisson distribution). We added to these models the fixed effects of the focal fish's aggression, treatment (matched or mixed pair) and the interaction between aggression and treatment to predict submission by the less aggressive partner, and repeated this removing two extremes (see Results).

The growth rates in SL, body mass and body condition at the end of the experiment (day 14: [body mass/SL^3] $\times$ 100) were analysed with GEE (normal distribution), with group identifiers as subjects to account for three to four individuals measured per group. Again, the scaling parameter was adjusted using the deviance method. In the first three models (see Results) we added the fixed effects of behavioural type (H or L), treatment (matched group containing either four H fish or four L fish versus mixed group containing two H fish and two L fish), and their interaction. In the last three models (see Results) we tested for differences in growth and condition between H, M and L individuals in their matched groups (treatments HH, MM and LL, respectively). We also tested for effects of focal sex, body size on day 8 and the size rank within the group on day 8 (rank 1 for the largest to rank 4 for the smallest fish in their group) in all six models, but since these effects were all nonsignificant they are not presented. Note that one H individual in an HH group and one M individual in an MM group died between days 10 and 14 (Fig. 1c), so these had to be excluded from the growth analyses, resulting in three groups containing only three fish instead of four (one HH and two MM groups). However, when corrected for treatment effects (HH, LL or MM), group size did not influence growth in SL ($P = 0.11$) or in mass ($P = 0.93$), so our results were not significantly affected by these small differences in group size. All statistical analyses were performed with SPSS 17.0 (Norusis 2008).

Ethical Note

None of the fights between the focal individuals in the paired contests escalated and no injuries were detected. In cases with a clear dominant and subordinate, the latter appeased the former by submissive behaviour and consequently no fights occurred. The fin clips caused no aberrant behaviour or long-lasting effects (i.e. reduction of growth or increased probability of sickness or death). Fin clipping has been successfully used in several previous studies of this species as a short-term marking procedure or to collect tissue for DNA analysis (e.g. Mitchell et al. 2009a, b). Two to three fin rays were removed using small scissors, without anaesthetics. We opted not to use anaesthetics to minimize stress, as we know from previous studies that recovery of these fish from anaesthesia takes at least 1 h, whereas they usually recover from handling within a few minutes. In addition,

the recovery time from anaesthesia might differ between behavioural types, which would interfere with the experimental protocol. The fish were monitored after the treatment until they displayed normal behaviour, which usually took a few minutes. The growth experiments were done in large compartments with ample space for all four individuals and with plastic bottles provided for shelter near the water surface. The cause of death of two experimental fish as mentioned could not be determined, but it was probably not the experimental treatment because levels of aggression observed within the experimental groups were minimal owing to the absence of breeding shelters, which prevented territoriality. Additionally, natural fish densities are often higher and all groups behaved peacefully as they do in small aggregations in nature (Taborsky & Limberger 1981; Taborsky 1984; Heg et al. 2008a). All experiments were approved and licensed by the LANAT of the Canton Bern.

RESULTS

Dominance in Paired Contests

There was no effect of sex on winning a contest (females: 10 of 19; males: 10 of 21 contests won; $\chi^2_1 = 0.10$, $P = 0.75$), and winners and losers did not differ in their body size (mean SL $\pm$ SD: winner: 42.6 ± 4.4 mm; loser: 42.8 ± 5.1 mm; both $N = 20$; paired *t* test: $t_{19} = -0.51$, $P = 0.62$).

In both matched pairings HH and LL, the majority of the contests ended in a draw (58% and 83%, respectively), which means that neither individual succeeded in dominating the other in the contest after the 10 min observation. In contrast, in the HL pairs more contests had a clear outcome (Table 1), where one individual dominated the other and had exclusive access to the shelter. H individuals won contests significantly more often than L individuals in mixed pairs (binomial test: $N = 13$ contests with a winner and loser in HL pairs, $P = 0.022$; Table 1). Furthermore, H individuals won significantly more often in mixed (HL) than in matched (HH) pairs (Kendall's $\tau_b = 2.1$, $P = 0.036$), whereas L individuals lost more often in mixed (HL) than in matched (LL) pairs (Kendall's $\tau_b = 2.6$, $P = 0.010$). Since dominance is likely to affect the behaviour of the individuals irrespective of their behavioural type (H or L), further analyses on behavioural interactions in paired contests were additionally corrected for dominance effects. So, for the analyses of aggressive and submissive behaviours we included in the models whether a focal individual had lost or won a contest, or whether the contest resulted in a draw.
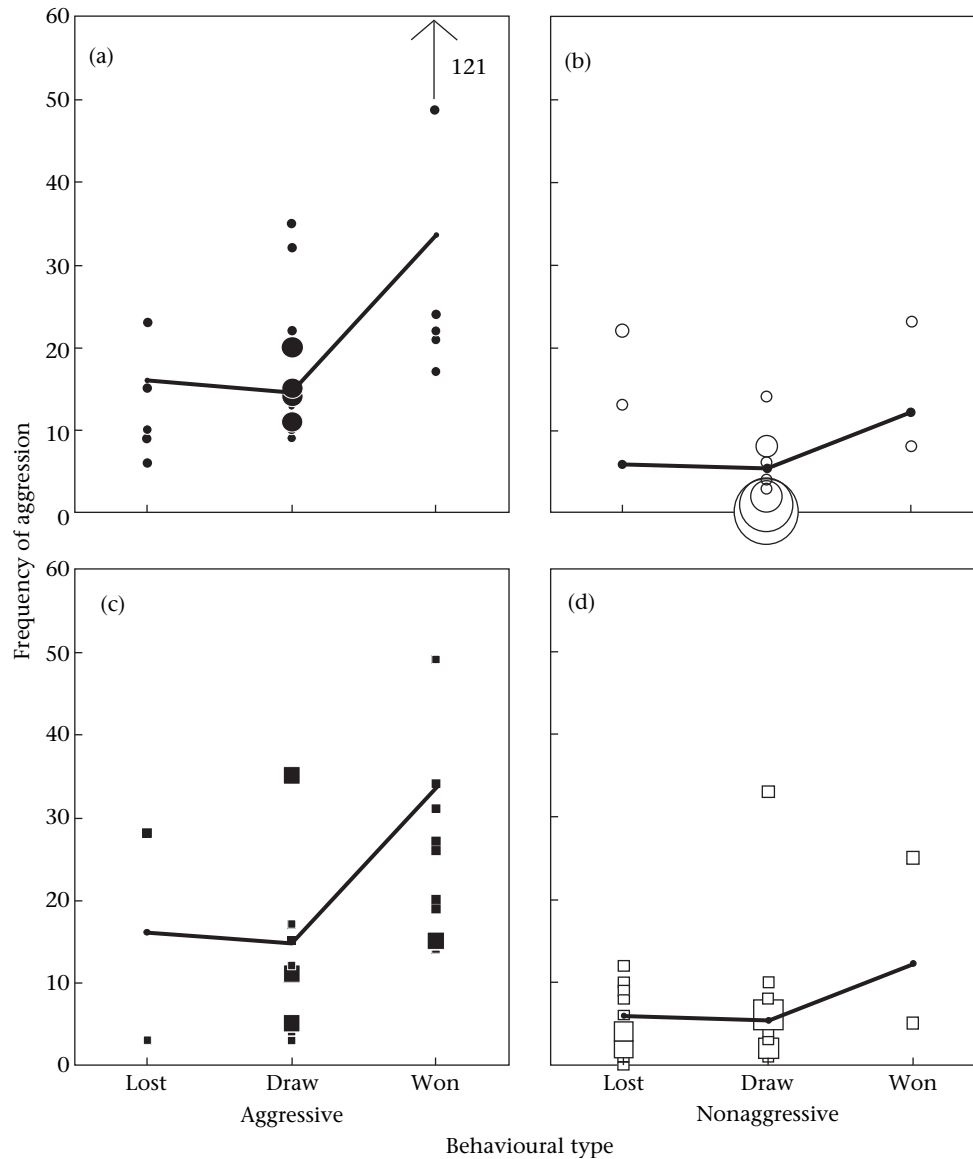
Behaviour in Paired Contests

Corrected for additional effects of winning, losing or being even, H individuals were significantly more aggressive towards their opponent in the paired contests than L individuals (Fig. 2, Table 2), and this effect was independent of the treatment (compare Fig. 2a

Table 1
Frequencies of paired contest outcomes (lost, drawn or won the contest) depending on behavioural type (H: aggressive; L: nonaggressive) and treatment (matched groups HH or LL, versus mixed groups HL)

Behavioural type	Treatment	Dominance			N
		Won	Draw	Lost	
H	Matched	5	14	5	24
	Mixed	11	11	2	24
L	Matched	2	20	2	24
	Mixed	2	11	11	24

Figure 2. The frequency of aggressive behaviour in paired contests for the individuals of the two behavioural types: H individuals in the (a) HH treatment and (c) HL treatment; L individuals in the (b) LL treatment and (d) HL treatment. Model fits are given by the lines; symbol sizes reflect the number of cases. See Table 1 for sample sizes and Table 2 for statistical test results.

versus Fig. 2c and Fig. 2b versus Fig. 2d). In contrast, submissiveness showed a significant interaction effect between behavioural type and treatment (again corrected for dominance, Table 2): both H and L individuals were more submissive to H opponents than L opponents (compare Fig. 3a versus Fig. 3c and Fig. 3d versus Fig. 3b). To account for nonindependence of the data, we analysed the frequencies of aggression and submission by using a bootstrap approach (see Methods for details). We found that the frequency of aggressive behaviour was still dependent on behavioural type and dominance, but for submissive behaviour the interaction between aggressive type and treatment was significant in only 10% of the cases, indicating that this interaction is strongly dependent on some extreme values (Table 2, Fig. 4). Hence, the frequency of submissive behaviour seems to be primarily affected by the outcome of the interaction regarding dominance, with subdominant individuals showing higher frequencies of submission than dominant individuals. We further tested whether the frequency of aggression of the focal fish that showed the highest level of

aggression in a paired test or, in the case of ties, the lowest level of submission, predicted the frequency of submission shown by the partner, depending on the treatments (matched pairs HH/LL or mixed pairs HL). Indeed, we found that the frequency of submission shown by the partner could be predicted by the amount of aggression performed by the focal individual (Table 3). Additionally, the interaction between aggression and treatment was significant (Table 3), indicating that in mixed groups (HL) frequencies of aggression shown by the partner, and therefore also frequencies of submission, are even higher than in matched groups (HH/LL; Fig. 4: thin lines). However, the interaction effect was highly dependent on the two extreme values (submission larger than 30) in Fig. 4. When these two extreme values were removed, only the amount of aggressive behaviour of the focal individual remained significant, whereas treatment and the interaction were no longer significant (model 2, Table 3, Fig. 4: bold line). This is in line with the results of the bootstrapping that pointed out the impact of some extreme values.

Table 2
Results of two generalized estimating equation models (GEE) for the frequency of aggressive and submissive behaviours (Poisson distributed, log-link), respectively, in the paired contests depending on the behavioural type of the focal fish (H: aggressive; L: nonaggressive), the dominance (lost, drawn or won the contest) and treatment (matched groups HH or LL, versus mixed groups HL)

Parameter	Wald χ^2	df	P	Coefficients±SE	%Bootstrap P
Frequency of aggression					
Intercept	499.3	1	**<0.001**	2.50±0.27	100
Behavioural type	23.5	1	**<0.001**	1.01±0.21	100
Dominance	11.8	2	**0.003**	Lost: −0.74±0.27	100
				Draw: −0.83±0.24	
Frequency of submission					
Intercept	1.7	1	0.20	−0.36±0.62	0
Behavioural type	0.03	1	0.86	−0.83±0.57	4
Dominance	24.0	2	**<0.001**	Lost: 2.45±0.55	96
				Draw: −0.83±0.24	
Treatment	0.001	1	0.98	−0.91±0.58	3
Type×treatment	5.6	1	**<0.02**	1.80±0.76	10

Sample sizes are 48 individuals × 2 paired contests = 96. The scaling parameter was adjusted using the deviance method. Individual identifiers were subjects. Behavioural type L, treatment HL, and dominance Won are the reference categories with their coefficients set to zero. Nonsignificant effects and interactions were removed, in particular for the frequency of aggression: treatment $P = 0.84$ and type × treatment $P = 0.16$. The %bootstrap P is the percentage of bootstrap models (100 runs) where this factor was significant at $\alpha = 0.05$. Significant P values are shown in bold.

Growth Rates Within Groups

We compared the growth of H and L individuals living in groups of three or four fish in matched groups (HH or LL) or mixed groups (HL). L individuals gained body length faster than H individuals in the HL treatment, whereas L individuals grew slower than H individuals in the matched treatment (Fig. 5a; this is indicated by the significant interaction between type and treatment in model 3, Table 4). No such effects were detected in the change in body mass (Fig. 5b; model 4, Table 4), although there were indications that L individuals accumulated less mass than H individuals overall ($P = 0.11$; Table 4). In contrast, H individuals showed higher body condition than L individuals in mixed groups (Fig. 5c; model 5, Table 4). We also compared the growth of H, M and L individuals in the matched groups (treatments HH versus MM versus LL, see Fig. 1c). The effect of treatment was significant for change in both size (Fig. 5a; model 6, Table 4) and body mass (Fig. 5b; model 7, Table 4), but no differences in body condition were detected (Fig. 5c; model 8, Table 4). Pairwise comparisons indicated no difference in body size and mass between H versus L individuals (GEE: $P = 0.17$ and 0.36 for SL and mass, respectively), and H versus M individuals (GEE: $P = 0.62$ and 0.15), but highly significant differences between L and M individuals (GEE: $P<0.001$ and 0.004).

DISCUSSION

We aimed to test whether consistent behavioural differences between individuals can play a major role in social interactions (i.e. competition for resources such as breeding opportunities or shelter; or in the establishment of dominance) in animal groups. Schürch & Heg (2010a) showed that intrinsic aggressive propensity is a key component in defining distinct behavioural types in *N. pulcher*, with social and reproductive consequences. Here, we demonstrated that individual differences in intrinsic aggression propensity can explain the establishment of dominance in the hypothesized direction, but with surprising effects on growth in a social context.

Behavioural Types and Dominance

As predicted, individuals with a higher aggression propensity than their opponents obtained the dominant position more

frequently than less aggressive individuals, and contests between individuals with different aggression propensities were settled quicker and more clearly than interactions among individuals with similar aggression propensities. This confirms predictions of game theory: contests between individuals that are similar in their resource-holding potential (RHP; Parker 1974) and/or motivation to escalate should take longer than asymmetric contests (Maynard Smith & Parker 1976; Hammerstein 1981; Enquist & Leimar 1987) and eventually lead to a 'war of attrition' (Hammerstein & Parker 1982). If intrinsic aggressive propensity of an individual is correlated with its propensity to escalate in a contest, aggressive propensity could be used as a reliable cue to assess the opponent's propensity to escalate (Laidre 2007). Indeed, we found that individuals with a high intrinsic aggression propensity attacked their opponents more often, irrespective of their dominance, which suggests a higher escalation tendency than individuals with lower intrinsic aggression propensity. These individuals displayed more submissive behaviour when they lost the contest. In other species, for instance in mammals, contestants often try to avoid escalating encounters through ritualized displays or vocalizations (Bartos et al. 2007). In *N. pulcher*, subordinates avoid aggression by appeasing the dominant individuals through increased rates of submissive and helping behaviour (Bergmüller et al. 2005; Bergmüller & Taborsky 2005). Our results also reflect such appeasement: with increased likelihood of being dominated by another individual (i.e. when facing an individual with a high aggressive propensity), the frequencies of submissive behaviour also increased. Additionally, both individuals with a high aggressive propensity and those with a low aggressive propensity tended to show higher frequencies of submissive behaviour towards a highly aggressive opponent than towards a much less aggressive one, even though this interaction was influenced by some extreme values of submissive behaviour (see Table 2, Fig. 4). Individuals seemed to assess the conflict motivation of the opponent based on the frequency of aggression received and adjusted their rate of appeasement behaviour accordingly to reduce the risk of escalation (cf. Bergmüller & Taborsky 2005), but the adjustment of the appeasement behaviour seemed to be independent of the opponent' aggressive type.

For the establishment of dominance in a contest, differences in RHP (e.g. through different body size) or motivation (e.g. expressed by aggressiveness), or a combination of both, may be important (Hamilton et al. 2005; Hurd 2006; Vervaecke et al. 2007). As social groups of *N. pulcher* are structured in a linear hierarchy and teleost fish grow continuously, size difference between group members is a crucial factor determining dominance (Hamilton et al. 2005). Our results suggest that dominance relationships in *N. pulcher* are mediated not only through life history traits, such as size, but also through intrinsic differences in motivation as expressed by aggressive propensity.

Often, individual aggressive propensity and the way individual's value resources are treated as two independent traits, but it has been argued that they are tightly correlated, reflecting the same underlying characteristic (Hurd 2006). Recent theoretical studies (Wolf et al. 2007, 2008) shed light on the potential mechanisms explaining why individual resource value estimation and aggressive propensity might show a tight correlation. For instance, individuals that generally value highly resources that they currently encounter might do better by showing a high aggressive propensity to obtain them, because they pursue a 'fast' life history strategy converting resources into immediate fitness benefits (i.e. survival or reproduction). In contrast, individuals that place little value on resources currently encountered (or are more responsive to the actual quality of the encountered resources) might do better by showing a low aggressive propensity to minimize conflict costs,
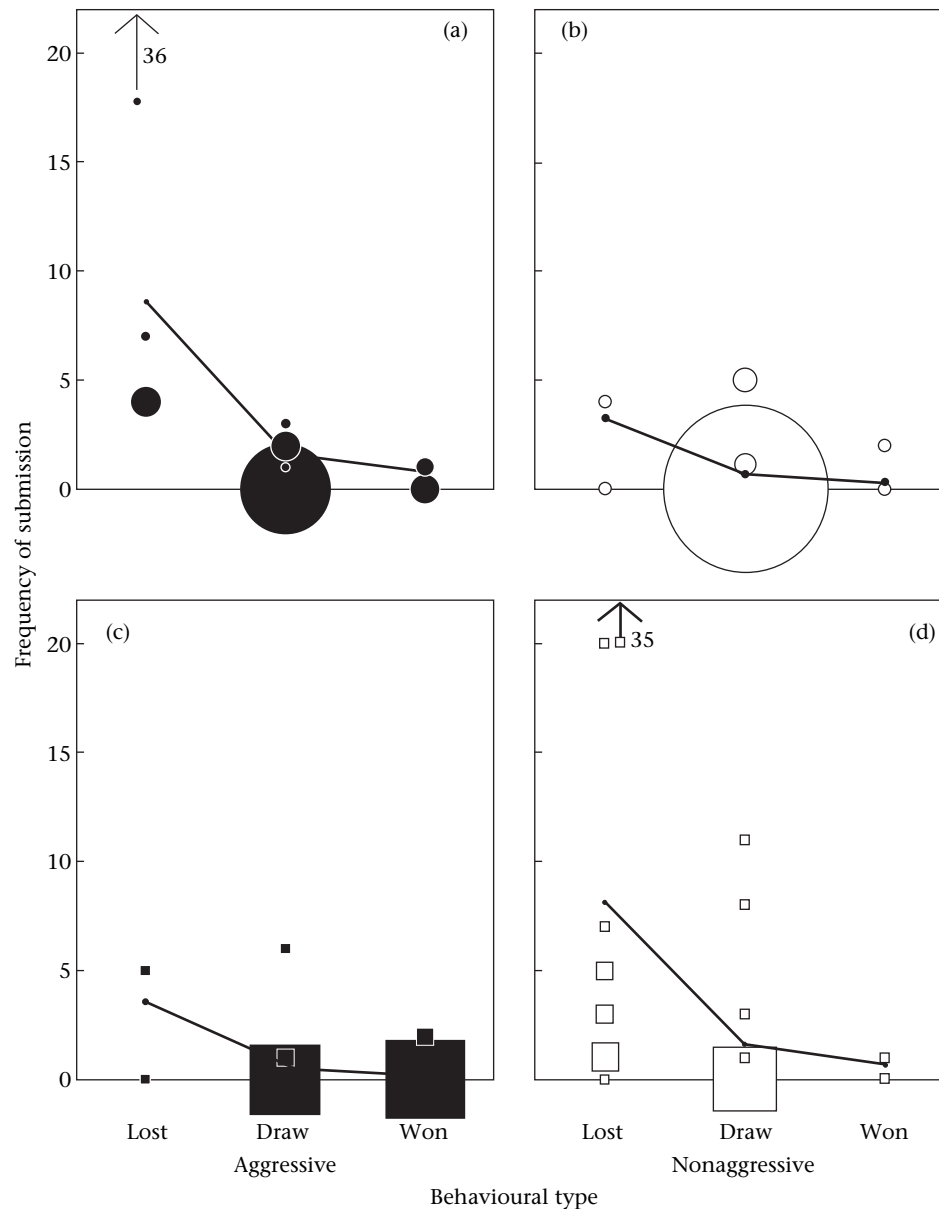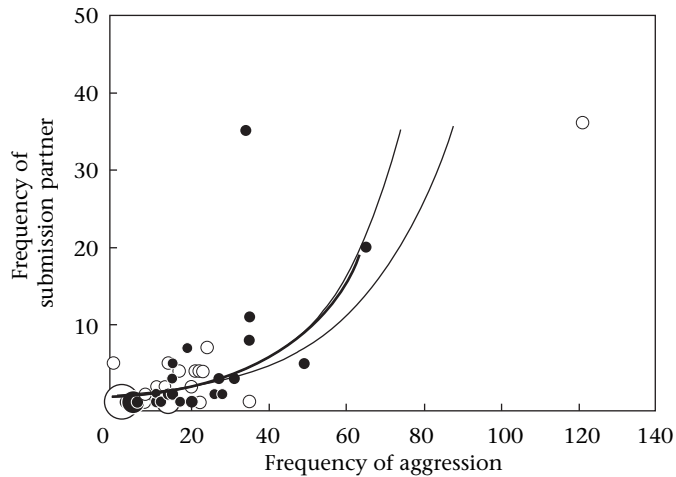
Figure 3. The frequency of submissive behaviour in paired contests for the individuals of the two behavioural types: H individuals in the (a) HH treatment and (c) HL treatment; L individuals in the (b) LL treatment and (d) HL treatment. Model fits are given by the lines; symbol sizes reflect the number of cases. See Table 1 for sample sizes and Table 2 for statistical test results.

because they adopt a 'slow' life history strategy, evaluating resources against alternatives that might be encountered in the future (Wolf et al. 2008, in press). In other words, highly aggressive individuals would focus on immediate fitness benefits, whereas individuals with little aggressive propensity would value future fitness benefits higher than current ones, with both strategies expecting similar lifetime fitness payoffs. Since it is likely that frequency dependence is involved, alternative behavioural types may coexist in a population (Barlow et al. 1986; Wolf et al. 2007). Using this theoretical framework, authors have argued that in *N. pulcher* stable differences in behavioural types might coexist, that is, L individuals opting for prolonged group membership, low dispersal rates and delayed reproduction, and H individuals opting for dispersal, independent breeding and early reproduction (Bergmüller & Taborsky 2007; Schürch & Heg 2010a, b; see also Bergmüller & Taborsky 2010).

Behavioural Types and Growth Rates in Groups

A proximate mechanism explaining a divergence between 'fast' and 'slow' life histories might be inherent differences in metabolic costs and growth rates. Previous studies of *N. pulcher* have shown that dominant group members grow faster than subordinates in general (Taborsky 1984; Heg et al. 2004; Bergmüller et al. 2005). However, aggressive propensity did not relate to the growth rate of individuals housed singly over a 6-month period (Schürch & Heg 2010b). Accordingly, as H individuals dominated L individuals in our paired contests, we expected that in mixed groups growth rates of H individuals would exceed those of L animals, as the former were dominant over the latter. Surprisingly, we found the opposite effect: in groups with mixed behavioural types, individuals with low aggressive propensity grew quicker than their social partners with a high aggressive propensity. In addition, aggressive fish grew

Figure 4. Frequency of submissive behaviour shown by the opponent compared to the frequency of aggression shown by the focal individual in the paired contest. Open circles represent matched partners (HH/LL, $N = 24$, model 1, Table 3: lower thin line), filled circles denote mixed partners (HL, $N = 24$, model 1, Table 3: upper thin line). Symbol sizes reflect the number of cases (up to three overlapping cases). The bold line shows the model 2 fit (Table 3) removing the two extremes (submission $>30/10$ min).

more quickly in length when among each other than when paired with nonaggressive fish, whereas the opposite occurred in nonaggressive fish. The results presented in Fig. 5 suggest that resource allocation to growth (i.e. length) and body reserves (i.e. weight) depends on behavioural and contest type (see Table 4). When aggressive fish were paired with nonaggressive partners they seemed to allocate energy to storage (weight increase) rather than growth, probably because their dominance was not challenged anyway. Similar results have been found by Taborsky (1984) where fish from aggregations showed increased growth rates but accumulated less body reserves. Territorial fish, however, showed increased accumulation of body reserves, rather than structural growth, which helps to prevent challenges by other group members and reduces the risk of expulsion (Taborsky 1984; Hamilton et al. 2005). So it seems that, in less challenging social environments, aggressive fish might be able to afford to accumulate energy in storage, as they are able to maintain dominance because of their behavioural type, rather than by their size, and probably will not be challenged by group members with a low propensity for aggression. When paired with aggressive fish, however, they allocate energy to growth (structural size) rather than storage,

Table 3
Results of two generalized linear models for the frequency of submissive behaviour of the partner (Poisson distributed, log-link), in the paired contests depending on the frequency of aggression of the focal fish, treatment and their interaction (matched groups HH or LL, versus mixed groups HL)

Parameter	Wald χ^2	df	P	Coefficients±SE
Model 1: all pairings ($N=48$ pairs): HH/LL versus HL				
Intercept	0.109	1	0.74	0.05±0.46
Aggression	93.69	1	**<0.001**	0.05±0.007
Treatment	0.03	1	0.86	0.10±0.51
Aggression×treatment	9.26	1	**0.002**	−0.02±0.007
Model 2: removed two extremes ($N=46$ pairs): HH/LL versus HL				
Intercept	2.69	1	0.101	−0.48±0.29
Aggression	83.39	1	**<0.001**	0.028±0.003

The scaling parameter was adjusted using the deviance method. Treatment mixed group (HL) was the reference category with coefficients set to zero. Model 2: the two extremes removed had a submission frequency larger than 30, and in this model treatment ($P = 0.56$) and the interaction ($P = 0.69$) were both nonsignificant and were removed from the model. Significant P values are shown in bold.
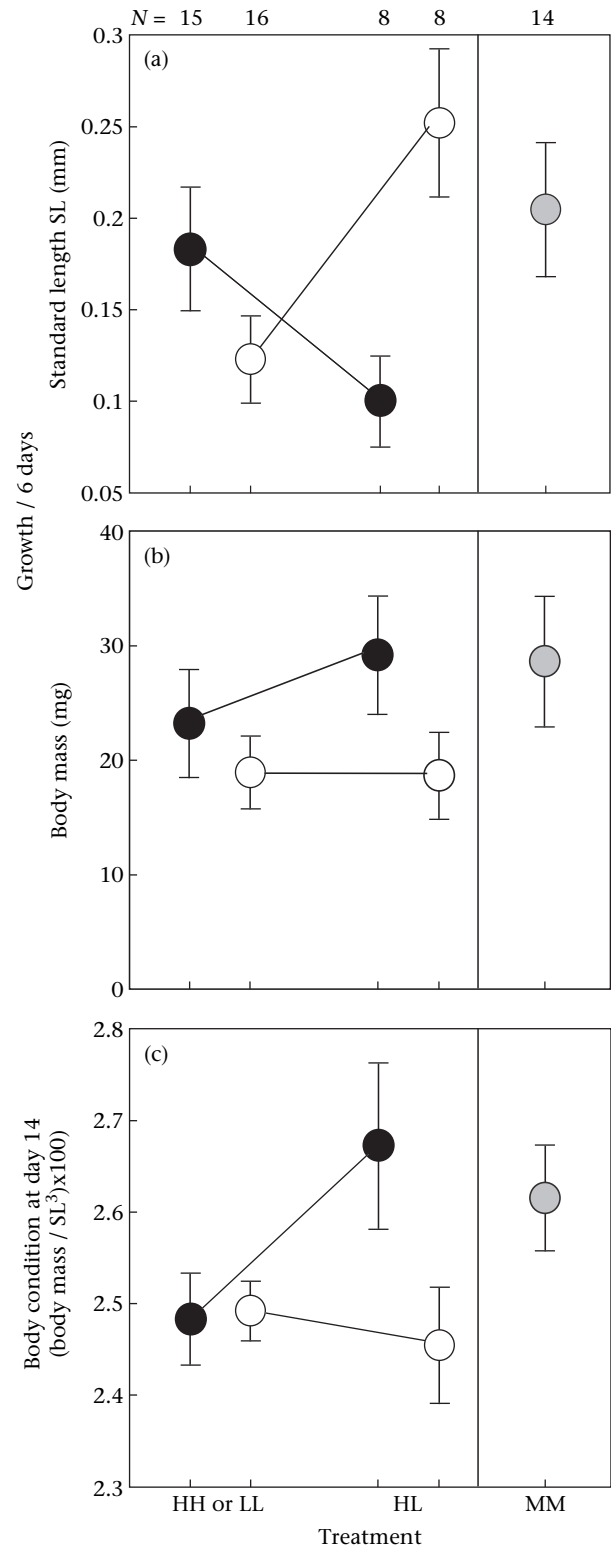
Figure 5. Growth in (a) standard length and (b) body mass; and (c) body condition at the end of the experiment for individuals of the different behavioural types (black: H; white: L; grey: M) in the four treatments. Means ± SEM are depicted (sample sizes on top of a). See Table 4 for statistical test results.

probably because dominance is challenged and large size could be advantageous. Fish with low aggression propensity, in contrast, allocate energy primarily to growth when paired with aggressive partners, perhaps to increase the chance of obtaining dominance in

Table 4
Results of four general estimating equation models for growth rates in standard length and body mass depending on the behavioural type of the focal fish (H: aggressive, M: intermediate aggressive; L: nonaggressive) and treatment (matched groups HH or MM or LL, and mixed groups HL)

Parameter	Wald χ^2	df	P	Coefficients±SE
Model 3: growth rate SL ($N=47$ individuals): HH/LL versus HL				
Intercept	106.2	1	**<0.001**	0.25±0.03
Behavioural type[†]	3.2	1	0.075	−0.15±0.028
Treatment	0.5	1	0.47	−0.13±0.03
Type×treatment	17.0	1	**<0.001**	0.21±0.05
Model 4: growth rate body mass ($N=47$ individuals): HH/LL versus HL				
Intercept	2.0	1	**<0.001**	18.65±1.60
Behavioural type	3.2	1	0.074	10.52±6.83
Treatment	0.8	1	0.38	0.30±3.50
Type×treatment	0.6	1	0.45	−6.22±8.28
Model 5: body condition at day 14 ($N=47$ individuals): HH/LL versus HL				
Intercept	6471.3	1	**<0.001**	2.45±0.06
Behavioural type[†]	8.7	1	**0.003**	0.22±0.02
Treatment	1.4	1	0.24	0.04±0.07
Type×treatment	10.5	1	**0.001**	−0.23±0.07
Model 6: growth rate SL ($N=45$ individuals): HH versus MM versus LL				
Intercept	127.4	1	**<0.001**	0.12±0.01
Treatment	21.9	2	**<0.001**	HH: 0.06±0.04
				MM: 0.08±0.02
Model 7: growth rate body mass ($N=45$ individuals): HH versus MM versus LL				
Intercept	210.0	1	**<0.001**	18.9±3.11
Treatment	9.1	2	**0.01**	HH: 4.30±4.69
				MM: 9.67±3.40
Model 8: body condition at day 14 ($N=45$ individuals): HH versus MM versus LL				
Intercept	8787.2	1	**<0.001**	2.49±0.04
Treatment	5.1	2	0.077	HH: −0.01±0.07
				MM: 0.12±0.06

The scaling parameter was adjusted using the deviance method. Group identifiers were subjects (four groups per treatment). Behavioural type L and treatment HL (first two models) or LL (last two models) were the reference categories with their coefficients set to zero. Nonsignificant effects and interactions were removed: sex, size rank within the group on day 8 (1–4) and body size SL on day 8. Significant P values are shown in bold.

[†] Behavioural type remained nonsignificant when added to a model with the intercept only: $P = 0.11$.

the future. When paired with other nonaggressive fish, they seem to balance energy allocation more evenly between growth and storage, probably because a size advantage is not of primary importance when the current social environment is not such a great challenge. Storage of energy might be advantageous as it could be transformed instantly into direct fitness benefits if a possibility to breed emerges, for instance.

Although both aggressive and submissive behaviours incur metabolic costs that should affect important life history traits such as growth rate, survival probability and reproductive potential (Taborsky 1984; Taborsky & Grantner 1998), our results suggest that the particular social situation should be taken into account when relating differences in behavioural type to differences in growth rates. For example, in juvenile coho salmon, Oncorhynchus kisutch, the level of aggression was negatively correlated with growth rate, indicating an energetic cost (Vollestad & Quinn 2003). In salmonids, social status and aggression levels are positively correlated with each other, which then affect growth. Highly aggressive individuals, that is, the dominant fish in the local population, showed higher growth rates than subordinates owing to their disproportionate access to food (Cutts et al. 1998; Tiira et al. 2009). However, as N. pulcher mainly feeds on zooplankton (Gashagaza & Nagoshi 1986; Gashagaza 1988), food is not monopolized, so disproportionate access to food does not explain differential growth rates, as in many other species.

In contrast to most previous studies in which growth of N. pulcher was measured, our test fish were not able to settle and defend a territory. This corresponds to the aggregation phase where individuals remain in a waiting position before being able to settle in a territory as dominant breeder or helper (Taborsky & Limberger 1981; Taborsky 1984; Heg et al. 2008a). It seems that depending on the social environment, that is, the composition of behavioural types in an aggregation, important life history traits such as growth can show divergent responses in this species. Assuming L individuals were also subdominant to H individuals in our groups (as in the paired contests), it appears that in mixed aggregations dominant individuals accumulate more body reserves at the expense of being outgrown by subdominants in structural growth (when dominants are less likely to be challenged), whereas in less mixed groups, especially with many H individuals, individuals invest more resources in structural growth (when dominants are more likely to be challenged).

In general, our results elaborate on the previous studies showing growth adjustments of N. pulcher depending on the social context (Taborsky 1984; Heg et al. 2004). In contrast to other experimental studies, our unexpected results on growth rates cannot be explained by disproportionate access to food (e.g. Noel et al. 2005; Chiba et al. 2007), or competitive exclusion from food (Maclean & Metcalfe 2001; Whiteman & Cote 2004), since (1) H individuals dominated L individuals in the paired contests, but the former grew slower than the latter in the mixed groups, and (2) the fish were fed ad libitum during the experiment.

Conclusions

In conclusion, our results show that individual behavioural idiosyncrasies affect contest behaviour, establishment of dominance hierarchies and energy allocation decisions. In addition, the social context seems to be important for the allocation of energy to storage or growth. The fitness effects of such divergent allocation decisions of aggressive and nonaggressive individuals, depending on social context, should be addressed in future studies.

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