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Behavioural type, status and social context affect behaviour and resource allocation in cooperatively breeding cichlids

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Individuals often show consistent differences in behavioural traits that may belong to a behavioural syndrome. Aggressive propensity is usually an important component of consistent behavioural types, potentially generating benefits in resource competition with conspecifics that may be traded off against costs in other contexts (e.g. acquisition of mates or coexistence with group members). Such trade-offs have not yet been studied in highly social species. We investigated how aggressive propensity influences competition for dominance, shelters and mates in the cooperatively breeding cichlid *Neolamprologus pulcher*. Following an established protocol we compared growth trajectories of groups of four fish either matched or unmatched for aggressive type. Furthermore, we analysed social interactions, the acquisition of shelter and possible mating partners (by proximity to shelters and prospective mates) according to aggressive type, showing either high or low aggression levels. Contrary to prediction we found that differences in behavioural idiosyncrasies affected the likelihood of obtaining the dominant position and high-quality territories only marginally. Social interactions, growth rates and body reserve accumulation were affected by behavioural differences. However, the patterns observed in this experiment differed from previous studies and suggest a modulating effect of the social environment on the link between behavioural types and life history decisions. Hence, we suggest that in future studies this relationship should be thoroughly investigated under varying social contexts, especially in highly social species.

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Suites of correlated behavioural traits that remain consistent within individuals but differ between individuals (Sih et al. 2004a, b) have been referred to as coping styles, personality, temperament or behavioural types and have been described in various animal species (Budaev 1997; Réale et al. 2000; Øverli et al. 2004; Dingemanse et al. 2007; see also for a review: Gosling & John 1999). Individual behavioural types are known to affect for instance dominance (e.g. Riebli et al. 2011), risk taking (e.g. van Oers et al. 2005), feeding rate (e.g. Bergvall et al. 2011), mate choice (e.g. Schuett et al. 2010), reproduction (e.g. Both et al. 2005) and helping behaviour (Bergmüller & Taborsky 2007). However, the impact of different personalities on dominance status and on social behaviour in general has not received as much attention (Armitage 1986a, b; McGuire et al. 1994; Bergmüller et al. 2007; Magnhagen 2007; Schürch & Heg 2010a, b). In contrast, other potential correlates of animal personalities (i.e. life history consequences) have been

studied in a wide variety of animal species ranging from wild to captive and domestic to laboratory species (reviewed in Smith & Blumstein 2008). Especially within social groups, differences in intrinsic aggressive propensity might predict effects on both social repulsion (e.g. aggression directed towards group members, escalated fighting for dominance with group members, eviction of group members) and affiliation (e.g. tolerance and support of mates, subordinates and offspring inside the group). Physical attributes such as body size or mass have been repeatedly shown to influence substantially the outcome of competition for dominance (Otronen 1988; Huntingford et al. 1990; Olsson 1992; Faber & Baylis 1993), but the influence of behavioural idiosyncrasies on such competition is much less clear. It has been suggested that life history traits such as body weight or size, which can be summarized as resource-holding potential, might be correlated with consistent behavioural properties (Hurd 2006). Indeed, it has been demonstrated that differences in intrinsic levels of aggression may significantly influence life history traits and Darwinian fitness such as growth rates, food intake and the outcome of competition for dominance (Stamps 2007; Biro & Stamps 2008; Adriaenssens & Johnsson 2011; Riebli et al. 2011). Thus, an important aim of this study was to test for potential effects of intrinsic behavioural

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properties, especially aggressive propensity, in a highly social vertebrate on traits that are important for life history optimization, such as the ability to compete for mates or breeding opportunities, to grow and to accumulate reserves.

Our model species is *Neolamprologus pulcher*, a cooperatively breeding cichlid endemic to Lake Tanganyika, East Africa (Taborsky & Limberger 1981; Taborsky 1984; Duftner et al. 2007; Wong & Balshine 2011). Typical groups of *N. pulcher* consist of one dominant breeding pair and several smaller, related and unrelated subordinates (Dierkes et al. 2005; Heg et al. 2005; Brintjes & Taborsky 2008; Heg & Hamilton 2008). Groups are organized in linear size hierarchies, where the large dominant pair largely monopolizes reproduction (Taborsky & Limberger 1981; Taborsky 1984, 1985; Dierkes et al. 1999, 2008; Heg et al. 2006, 2009; Heg 2008; Heg & Hamilton 2008; Mitchell et al. 2009a, b). In order to be tolerated by the dominants, subordinates 'pay rent' by engaging in energetically costly and risky behaviours such as alloparental brood care, territory defence and maintenance ('pay-to-stay'; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Taborsky & Grantner 1998; Bergmüller & Taborsky 2005).

Previously it has been shown that individuals of *N. pulcher* differ consistently from each other in their levels of aggression (tested towards a mirror; abbreviated 'aggressive propensity' throughout), novelty appeal (tested with a novel object) and exploration of a novel environment (Bergmüller & Taborsky 2007; Schürch & Heg 2010a). These three behavioural traits are closely correlated with each other (Schürch et al. 2010), and the personalities in *N. pulcher* have been shown to be repeatable over life, and heritable (Chervet et al. 2011). It has also been shown that aggressive propensity may influence dominant–subordinate interactions (Schürch & Heg 2010b), but has negligible effects on the dominance acquired and on group formation (i.e. group size; Schürch et al. 2010). However, dominant males mainly accepted subordinates of similar behavioural type; and there were type effects on social behaviour (i.e. individuals of low aggressive propensity showed higher levels of affiliative social network connections; Schürch et al. 2010). Finally, Riebli et al. (2011) showed that individuals of high aggressive propensity dominated individuals of low aggressive propensity in staged pairwise encounters, as they showed higher levels of aggression in these contests. However, the effect of aggressive propensity on the likelihood of gaining dominance, mates and shelters in a social group still remains to be tested in a standardized setting (cf. Schürch et al. 2010, where the setting was not standardized with respect to the behavioural types of the individuals involved).

In this study we aimed to test for potential social consequences of consistent differences in individual aggressive propensity, in particular, the acquisition of dominance status and the abilities to obtain shelters and mates. Additionally, we tested whether the availability of breeding substrate would affect growth decisions of fish depending on their aggressive propensity. Riebli et al. (2011) found that in groups composed of fish with high and low aggressive propensity, highly aggressive fish grew more slowly than their less aggressive social partners, whereas this difference was opposite in unmixed groups. This was interpreted as a possible conflict evasion tactic of less aggressive fish in mixed groups, possibly in order to gain dominance by having a larger body size in resource competition later on.

In the current study we used the experimental design of Riebli et al. (2011), where in the first phase individuals were tested for their aggressive propensity using a mirror test (dividing the individuals into low, L, medium, M, and high, H, aggressive propensity), and in the last phase four equally sized fish were released in a tank to test for behaviour and growth patterns in groups consisting of individuals of the same or different

aggressive propensity. In contrast to the preceding study these four fish were now two males and two females, where the two individuals of the same sex were either matched or unmatched for their aggressive propensity. These fish competed for a low- and a high-quality breeding site. We tested four treatments (types of the two males/types of the two females: treatment LL: LL/LL; treatment HL: HL/HL; treatment HH: HH/HH; treatment MM: MM/MM). We predicted that H individuals would attain dominance with a higher probability than L individuals in the HL treatment, that is, H individuals should be more likely to dominate access to the shelters and to gain breeder status, thus becoming the dominant individuals in the group; in contrast, L individuals should be more likely to become subordinate individuals. We predicted that dominance outcomes would be less clear in matched (HH, LL and MM) than in unmatched groups. Furthermore, we tested whether the probability of acquiring a high-quality shelter depends on intrinsic aggression levels. We predicted that H individuals would be more likely to obtain the high-quality shelter and L individuals the low-quality shelter in the HL treatment, leading to assortative pairing by type. Note that Schürch et al. (2010) did not detect pairing by type, but in their design individuals were released sequentially, which renders a test of this hypothesis equivocal. In our experiment, the other treatments (LL, MM and HH) served as controls. In these groups of fish matched for aggressive propensity we predicted the likelihood of two pairs forming would decrease from LL to MM to HH, as aggressive propensity should influence the likelihood of accepting a neighbouring pair in close vicinity. We tested also whether H and L individuals differed in their social interactions depending on the mixture of aggressive types within the groups (matched or unmatched groups). We predicted H individuals would show higher levels of aggression compared to L individuals and a reverse relationship for submission, particularly in the HL treatment (cf. Riebli et al. 2011). Finally, we tested how growth and reserve accumulation differed in accordance with aggressive type, social context, size and rank.

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 storage tanks without breeding shelters at a water temperature of 27 ± 1 °C. The chemical attributes of the water closely matched the values of Lake Tanganyika (Taborsky 1984). Each tank contained mixed-sex groups of about 50 individuals of only small (less than 45 mm standard length) or of only large fish (more than 45 mm standard length). To reduce aggressive interactions, plastic bottles were provided at the water surface serving as refuges for expelled individuals. 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).

After catching the focal animals from their storage tanks with hand-nets, we measured their body length to the nearest 0.1 mm using a binocular microscope (mean \pm SD: 48.2 ± 5.6 mm, range 34.9–62.4 mm) and body mass in mg (mean \pm SD: 2929.5 ± 968.4 mg, range 1088–5682 mg) and determined the sex (45 males and 45 females; assessment based on inspection of the genital papilla; measures given are the first measurement on day 0; Fig. 1a). Ninety individuals were used in total. The focal fish were kept in two 1000-litre aquaria, visually

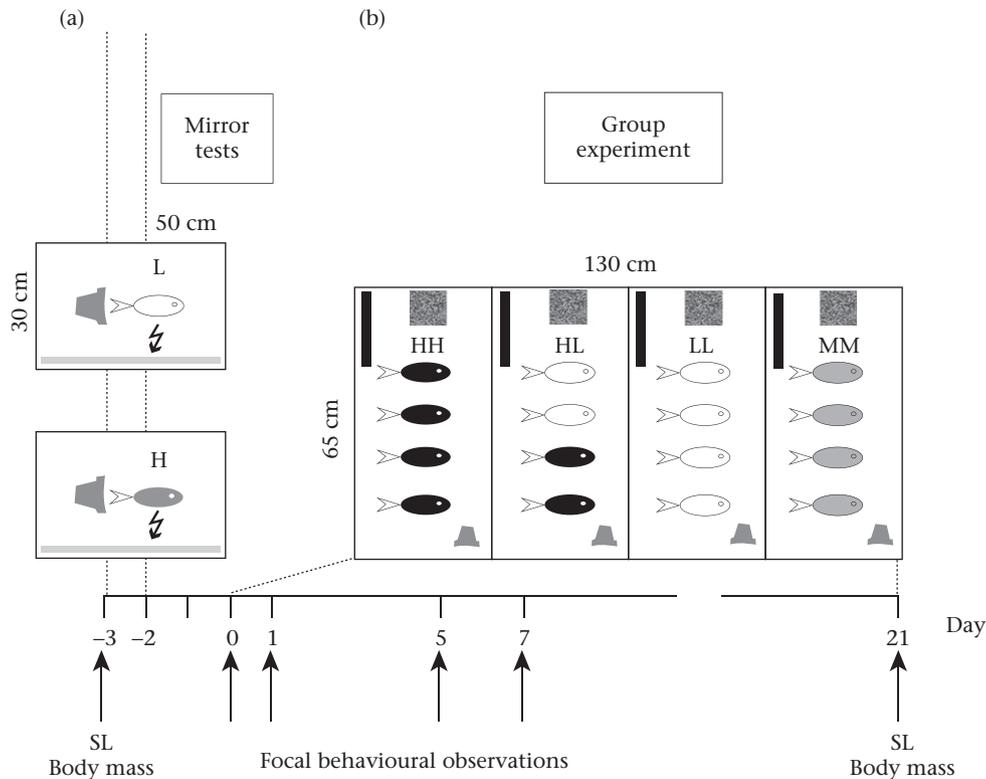


Figure 1. Set-up of the experiments. (a) On day -3 or -2 all focal individuals were tested for their aggressive propensity using a mirror test. Focal individuals were divided into those with low aggressive propensity (L), medium aggressive propensity (M) or high aggressive propensity (H), based on this score. (b) On day 0 four focal fish of about equal body size entered one of four compartments inside a 400-litre tank, according to their treatment (matched: LL, MM and HH; unmatched: HL). The order of the groups was randomized between the different tanks. A high-quality breeding site was provided at the back (stone slab: black bar) close to the filter (grey square), and a low-quality breeding site was provided at the front (small clay pot half) on the opposite side (in this example: right) of the tank. Whether the stone slab was placed left (pot right) or right (pot left) was randomized between tanks.

isolated from each other, in individually labelled isolation nets (20 × 11 cm and 11 cm high). They were checked daily for aberrant behaviour or illness and were fed with commercial dry food each day after experimental tests had been performed. After the experiments all individuals were returned to their respective holding tanks. The experiment consisted of two phases (Fig. 1): (1) tests for aggressive propensity using a mirror (Fig. 1a) and (2) group contest tests (Fig. 1b). The phases are described in more detail below.

Aggressive Propensity Tests

Three or two days before the start of the experiment focal fish were transferred from their isolation nets into a small experimental tank (30 × 50 cm and 30 cm high) to test them for their aggression levels. The experimental tank had a clear screen in front to allow observations and was covered on the left and right sides with black cardboard for visual isolation from neighbouring tanks. It contained a clay pot half serving as shelter (Fig. 1a). A mirror (25 × 15 cm) was placed at one side wall of the tank. To determine intrinsic aggressive propensity, the mirror was presented to each focal fish for 5 min, and agonistic behaviours towards the mirror were counted (restrained and overt aggression; see Hamilton et al. 2005; for a similar set-up see Bergmüller & Taborsky 2007). The 5 min observation periods started after the focal fish showed the first agonistic behaviour towards the mirror. After all 90 individuals had been tested they were ranked according to their aggression frequencies and divided into three groups, corresponding to the tertiles of the frequency distribution

of aggressive behaviours: high aggressive propensity (behavioural type abbreviated as H; $N = 35$ individuals, range 43–272 aggressive acts/5 min), medium aggressive propensity (M; $N = 23$ individuals, range 20–42 aggressive acts/5 min) and low aggressive propensity (L; $N = 32$ individuals, range 0–19 aggressive acts/5 min). Aggression frequencies measured in this study represent the typical range of aggression rates observed in this species. In previous work with *N. pulcher* high repeatabilities for test–retest relationships in aggression, boldness and exploration have been demonstrated (Bergmüller & Taborsky 2010; Schürch & Heg 2010a, b; Schürch et al. 2010; Witsenburg et al. 2010; Chervet et al. 2011; Le Vin et al. 2011; Riebli et al. 2011). In one of the most comprehensive studies done so far in a vertebrate model system (more than 1000 individuals of different life stages tested and over 4000 tests), Chervet et al. (2011) demonstrated a repeatability of behavioural type of 0.83 for repeated tests conducted within a test period of 24 h. Moreover, they showed that repeatability of aggression towards a mirror image, as we used in this study, was 0.85. As Chervet et al.'s study was done alongside the current one, we decided to use aggression towards a mirror as a representative axis for the behavioural type of *N. pulcher* without reassessing the individuals. H, M and L individuals did not differ in body length and body mass on day 0 ($F_{2,90} = 1.7$ and 1.8, $P = 0.18$ and 0.17, respectively). Of these 90 tested individuals we used 80 fish for our experimental groups, excluding the 10 individuals least fitting the requirements of (balanced) size and sex per experimental group. By design, we used equal numbers of similar-sized males and females in these groups (in total 15 and 15 H, 10 and 10 M, 15 and 15 L).

Group Contest Trials and Growth Rates

To assess competition for breeding and mates according to group composition we established four treatment groups: HH, LL, HL and MM. Each treatment was repeated five times with four fish each (Fig. 1b). Experimental group compositions were as follows: HH treatment: five replicates with four H individuals each (two males/two females); LL treatment: five replicates with four L individuals each (two males/two females); HL treatment: five replicates with two H and two L individuals each (males/females: HL/HL); MM treatment: five replicates with four M individuals each (two males/two females). We attempted to size-match the members of experimental groups based on their body length estimates on day 0 (mean maximum difference between smallest and largest group members in body length \pm SD: 4.3 ± 5.4 mm, $N = 20$ groups, range 0.3–22.8 mm). Body length of test fish differed slightly between treatments (ANOVA: $F_{3,16} = 3.615$, $P = 0.036$), but body mass did not (867.1 ± 890.7 mg, $N = 20$ groups, range 174.0–4074.0 mg; ANOVA: $F_{3,16} = 1.093$, $P = 0.381$). Note that potential effects of body length on social dominance and behaviour of group members were statistically accounted for throughout (see *Statistical Analyses* methods, below). The groups were randomly assigned to five 400-litre tanks (130×65 cm and 60 cm high), divided into four compartments each (33×65 cm and 50 cm high) by opaque PVC sheets. To keep water quality constant, each compartment contained an air-driven biological filter. To create a high- and a low-quality breeding site we divided the group compartments in half and equipped them with different types of breeding substrate. The breeding substrate in the back part was of high quality (a stone slab leaning against a side wall), whereas the breeding substrate in the front half was of low quality (one clay pot half positioned at the opposite side of the tank from the stone slab, Fig. 1b). Stone slabs are preferred over pot halves by females of all sizes as spawning substrate (D. Heg, unpublished data) and cichlids prefer to use the back part of any tank in general (T. Riebli, M. Taborsky & D. Heg, personal observations). Every 400-litre tank contained all four treatments (HH, LL, HL, MM), but the order was randomized over the five tanks. To distinguish the different individuals of a group, the fish were marked with small fin clips at a particular position of their dorsal or anal fins.

Each group was provided with the same amount of food, that is, one teaspoon of dry food (mean \pm SD: 1.250 ± 0.210 g) every day 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), areas with food are not monopolized and we never observed individuals chasing other individuals while feeding.

To assess the growth rates of the fish in the different experimental treatments, the fish were measured at the start and end of the experiment (body length to the nearest 0.1 mm using a binocular microscope; body mass to the nearest 0.001 mg). The fish were measured three times, 3 days before the groups were composed, at day 7 and day 21. Growth rates for body length and body mass were calculated from the difference between the first measurement that was taken 3 days before the grouping and the last at day 21, as the fish had not accumulated enough size or mass on day 7 to warrant analyses. Body condition was calculated at the end of the experiment using Fulton's body condition index ($[\text{mass on day 21}/\text{size}^3 \text{ on day 21}] \times 100$; Bolger & Connolly 1989).

Group Contest Behavioural Observations

We carried out 5 min focal observations of each individual on days 0, 1, 5 and 7 after release in their compartments (Fig. 1b). The

order of individuals observed was randomly chosen and observations were done blindly with respect to the treatments. For each individual we determined the frequency of aggression (overt and restrained), submission (tail quivering and zigzag swimming), territory maintenance (digging; i.e. taking up sand and carrying it away), shelter visits (separately for the high- and low-quality shelters) and changes between the tank halves containing the high- and low-quality shelters, respectively (back versus front half). Additionally to the behavioural observations, another experienced observer (T.R. or D.H.) determined the social dominance of each individual inside its compartment on a daily basis (again blindly to the treatments and also to the behaviour these individuals had shown during the 5 min observations): dominant (access to breeding substrate; aggressive behaviour) or subordinate (no access to shelter; submissive behaviour). In addition, we determined for dominants whether they occupied the high-quality shelter, low-quality shelter or both shelters. Subdominants were scored as being either accepted or rejected by the dominant individuals; however, owing to small sample sizes obtained for certain classes of individuals, we pooled these two categories for the statistical analyses. Social dominance and shelters occupied did not change after day 6, so only the dominance and shelter(s) acquired by day 7 were entered in the analyses.

Statistical Analyses

Likelihood ratio tests were used to check whether, depending on treatment, individuals with different aggressive propensities differed in their likelihood of becoming dominant. We used 'dominant' and 'subdominant' (pooled variable from accepted and evicted subdominants) as individual dominance categories (dominance achieved at day 6) throughout the analyses. Ordinal regression analyses on the dominance acquired (dominant or subordinate) were run with the independent variables treatment, behavioural type, sex, size rank and their interactions. To test whether individuals with different aggressive propensities were equally likely to become dominant a likelihood ratio test and an ordinal regression analysis were performed. To evaluate whether the quality of shelters acquired by dominant and subordinate individuals differed, ordinal regression analyses were performed testing for the effects of experimental treatment, behavioural type, sex and size rank. Differences in mate acquisition rates were analysed with likelihood ratio tests. Analyses of the behavioural interactions (aggression, submission, territory maintenance and visits to the shelter) were performed using Poisson generalized linear mixed models (Crawley 2007). These analyses were done to compare H and L fish in matched and unmatched groups (Appendix Table A1) and to compare all matched groups among each other (Appendix Table A2). Growth rates in body length, body mass and body condition at the end of the experiment (day 21) were analysed with generalized estimating equations, GEE (normal distribution), with group identifiers as subjects to account for four individuals measured per group. The scaling parameter was adjusted using the deviance method. Generalized estimating equations were used as they are particularly suitable for correcting the estimates of the main effects for repeated testing of the same individuals without claiming to be able to estimate the random effects precisely. In the first three models (see Table 2 in the 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 unmatched group containing two H fish and two L fish), dominance at day 6 (dominant or subordinate), sex and size rank (one largest to four smallest fish in their group) and their interactions. In the last three models (see Table 2 in the Results) we tested for differences in growth and condition between H, M and L individuals in their

Table 1

Settlement status on day 7 of the experiments for groups of four fish in the unmatched (two H and two L fish) and matched treatments (four H, four L, or four M fish)

Treatment aggressive type			Total		
			Dominant	Subdominant	Total
Unmatched	Type	H	8	2	10
		L	4	6	10
Matched	Type	H	12	8	20
		L	11	9	20
		M	11	9	20
	Total	46	34	80	

matched groups (treatments HH, MM and LL, respectively). In all models, nonsignificant (α level > 0.05) interaction terms were removed, except type * treatment where appropriate, as this tests our main hypothesis. Note that our general modelling approach reflects our knowledge of main factors affecting dominance, behaviour and growth in this species. Consequently, (1) the main effects type, sex, treatment and size rank were retained in all models regardless of their significance (see Tables 2 and 3 in the Results); and dominance was added as main effect for all models concerning behaviour and growth. (2) Behavioural type was deleted for those models where it is redundant with treatment (i.e. comparisons between matched treatments). (3) A priori, there was only one two-way interaction testing our primary hypothesis in unmatched groups, type * treatment, and therefore this is always reported. Tests of other two-way interactions (significant or not) should be regarded as exploratory and do not relate to our main hypothesis. Statistical analyses were performed with SPSS 17.0 (Norusis 2008); generalized linear mixed-effects models were performed using the package lme4 (Bates & Maechler 2010) from the open source statistical software R (R Development Core Team 2010).

Ethical Note

The experiments were done in large compartments with ample space for all four individuals and with tubes provided for shelter near the water surface for fish that were not allowed access to the shelters on the ground by dominant individuals. After dominance relationships were settled after the first few hours, groups behaved peacefully as in nature (Taborsky & Limberger 1981). Test fish were

Table 2

Settlement status on day 7 depending on the effects of the focal individual's aggressive type (H or L), sex (female or male), size rank (1, 2, 3 or 4; covariate) and treatments

Parameter	Ordinal regression statistics		
	Wald χ^2	df	P
Treatments compared: matched (HH or LL) versus unmatched (HL)			
Aggressive type	0.269	1	0.604
Sex	2.041	1	0.153
Treatment	0.893	1	0.345
Size rank	8.488	1	0.004
Sex*Treatment	4.052	1	0.044
Treatments compared: matched HH versus MM versus LL			
Treatment	0.164	2	0.921
Sex	4.676	1	0.031
Size rank	8.80	1	0.003

L: low aggressive propensity; M: medium aggressive propensity; H: high aggressive propensity. The table shows the results of two ordinal regressions with a cumulative Cauchit-link (Norusis 2008). All two-way interactions were tested ($P > 0.05$) and only sex * treatment was significant in the first model. Significant relations are marked in bold.

Table 3

Results of six general estimating equation models (GEEs) for growth rates in standard length, body mass and body condition depending on the aggressive type of the focal fish (H, M or L), dominance (dominant or subdominant), treatment (matched groups HH, MM or LL, and unmatched groups HL), sex and size rank

Parameter	Wald χ^2	df	P	Coefficients \pm SE	
Model 1: Growth rate SL (mm; N=60 individuals): HH/LL versus HL					
Intercept	1.493	1	0.222	0.091	0.068
Aggressive type	2.274	1	0.132	-0.239	0.141
Treatment	0.380	1	0.537	-0.081	0.060
Sex	1.685	1	0.194	-0.120	0.065
Size rank	2.148	1	0.143	0.033	0.022
Dominance	0.469	1	0.493	-0.027	0.039
Type*Treatment	1.982	1	0.159	0.191	0.136
Type*Sex	3.695	1	0.046	0.082	0.041
Model 2: Change in body mass (mg; N=60 individuals): HH/LL versus HL					
Intercept	2.412	1	0.120	10.812	16.972
Aggressive type	1.567	1	0.211	-44.639	26.600
Treatment	0.261	1	0.609	-15.598	12.326
Sex	1.532	1	0.216	-26.129	10.844
Size rank	3.068	1	0.080	7.597	4.337
Dominance	0.019	1	0.892	1.117	8.196
Type*Treatment	1.511	1	0.219	33.259	27.054
Type*Sex	4.167	1	0.041	22.286	10.918
Model 3: Body condition on day 21 (N=60 individuals): HH/LL versus HL					
Intercept	1101.666	1	<0.001	2.460	0.092
Aggressive type	0.051	1	0.822	0.011	0.090
Treatment	0.708	1	0.400	-0.069	0.096
Sex	0.215	1	0.643	-0.033	0.072
Size rank	1.614	1	0.204	0.040	0.032
Dominance	0.742	1	0.389	0.060	0.069
Type*Treatment	0.001	1	0.986	0.002	0.104
Model 4: Growth rate SL (mm; N=60 individuals): HH versus MM versus LL					
Intercept	0.134	1	0.714	0.043	0.036
Treatment	0.150	2	0.928	HH: -0.054	0.017
Sex	5.553	1	0.018	-0.057	0.017
Size rank	1.021	1	0.312	0.011	0.011
Dominance	4.268	1	0.038	-0.047	0.023
Treatment*Sex	45.277	2	<0.001	HH: 0.094	0.025
				MM: 0.191	0.031
Model 5: Change in body mass (N=60 individuals): HH versus MM versus LL					
Intercept	3.065	1	0.080	-6.443	5.161
Treatment	0.044	2	0.978	HH: -9.382	5.658
Sex	2.970	1	0.085	-13.780	2.938
Size rank	4.972	1	0.026	4.259	1.910
Dominance	0.674	1	0.412	8.075	3.932
Treatment*Sex	19.698	2	<0.001	HH: 31.497	11.421
				MM: 37.530	10.183
Treatment*Dominance	10.393	2	0.006	HH: -11.586	6.099
				MM: -23.417	7.617
Model 6: Body condition on day 21 (N=60 individuals): HH versus MM versus LL					
Intercept	2494.329	1	<0.001	2.483	0.083
Treatment	0.097	2	0.953	HH: -0.094	0.098
				MM: -0.058	0.088
Sex	0.473	1	0.492	0.040	0.059
Size rank	0.509	1	0.476	0.011	0.016
Dominance	2.265	2	0.132	-0.044	0.054
Treatment*Dominance	7.041	2	0.030	HH: 0.187	0.109
				MM: 0.148	0.061

L: low aggressive propensity; M: medium aggressive propensity; H: high aggressive propensity. The scaling parameter was adjusted using the deviance method. GEEs with group identifier as subjects (five groups per treatment). Aggressive type (L), treatment (HL: Models 1–3; LL: Models 4–6), sex (female) and dominance (dominant) were the reference categories with their coefficients set to zero. Size rank was treated as a covariate in all six models. Nonsignificant interactions were removed, but note that the interaction type * treatment was always retained in Models 1–3, as it tests several of our main hypotheses. Significant relations are marked in bold.

individually marked by small fin clips which have been successfully used as a short-term marking procedure or to collect DNA samples (see Mitchell et al. 2009a, b). By using a small scissor, two to three fin rays of the dorsal or anal fin were removed without anaesthetizing the fish. To minimize stress levels and potential interference with the experimental protocol we opted not to use anaesthetics. From previous work we know that recovery time from anaesthetics takes at least 1 h for these fish, whereas they usually recover from handling within a few minutes. The fish were monitored until they displayed normal behaviour after this treatment. Individuals not integrated into the groups were not harmed by the other individuals, as enough shelters were provided. All experimental fish were checked daily for injuries from fights. Again, no escalated physical fights between the focal individuals and no injuries were detected in this experiment. All experiments were approved and licensed by the LANAT of the canton Bern (no. 16/09).

RESULTS

Dominance Achieved on Day 7

H fish tended to be more likely to become dominant in the unmatched treatment than the L fish (Table 1; LR: $\chi^2_1 = 3.45$, $P = 0.06$, comparing dominant versus subordinate); however, the likelihood of becoming dominant did not differ between treatments (matched and unmatched) and behavioural types (H and L fish; Table 1; LR: $\chi^2_2 = 1.76$, $P = 0.42$). An ordinal regression analysis showed no significant effects of treatment and behavioural type on the dominance the focal individuals achieved (evicted, subordinate or dominant), but a positive effect of the size rank and a significant interaction between sex and treatment (Table 2, first model). Also in the three matched treatments among H, L and M fish sex and size rank had significant effects on the acquisition of dominance (Table 2, second model).

Shelter and Mate Acquisition

Dominant and subordinate individuals acquired only the low-quality shelter (flower pot half, $N = 7$), only the high-quality shelter (stone slab, $N = 11$) or both shelters ($N = 36$). The quality of the shelters acquired was analysed with ordinal regressions (N shows number of focal fish that acquired only the low-quality, only the high-quality or both shelters, respectively). However, contrary to prediction, H fish were not more likely to acquire better shelters (unmatched: $N = 0, 3, 5$; acquiring only low-quality, only high-quality or both shelters) compared to the L fish (unmatched: $N = 2, 1, 4$, respectively). An ordinal regression showed no effects of treatment ($P = 0.92$), aggressive type ($P = 0.18$), focal sex ($P = 0.17$), size rank ($P = 0.30$) and their two-way interactions (all $P > 0.18$). Running a second ordinal regression on the matched treatments only (with M fish: $N = 1, 1, 10$ respectively) also showed no effects of treatment ($P = 0.13$), focal sex ($P = 0.35$), size rank ($P = 0.32$) and their two-way interactions (all $P > 0.53$).

Behaviour within Groups

Five-minute focal behavioural observations were conducted on days 0, 1, 5 and 7 after release into the respective groups ($N = 80$ individuals \times 4 days = 320 observations in total). Although the focal individuals showed considerable differences in their reaction to the mirror in the pregrouping phase, these differences were only subtly reflected in how these focal individuals behaved within their groups depending on their aggressive type and the treatment (unmatched versus matched groups, see Appendix Table A1 for Poisson generalized linear mixed models for four types of focal

individuals' behaviour: aggression, submission, territory maintenance and visits to the pot or stone slab). Aggression of focal animals depended on the interactions aggressive type \times size rank, aggressive type \times day, treatment \times day and treatment \times dominance (Fig. 2a, b; Model 1, Appendix Table A1). Overall, both H and L fish showed lower levels of aggression in matched groups compared to unmatched groups, but this difference resulted from the high aggression levels in unmatched groups at the start of the experiment, which dropped to very low levels 1 day thereafter (Fig. 2a). In contrast, in matched groups aggression levels did not change much throughout the experiment (Fig. 2b), while the course of submission differed between fish with high and low aggressive type: submission rates declined throughout the experiment for H fish and increased for L fish; M fish showed intermediate levels of submission (Fig. 2e, f; Model 6, Appendix Table A2: significant aggressive type \times day interaction). Moreover, there was an effect of group composition found on digging effort, with dominant individuals showing more territory maintenance behaviour in unmatched groups than in matched groups (significant treatment \times dominance interaction in Model 2, Appendix Table A1).

A comparison of the matched groups only (HH versus MM versus LL, Appendix Table A2) revealed significant effects of dominance status of focal fish on their shelter visits (Model 8: significant effect of dominance, Appendix Table A2). Dominant fish made more visits, particularly towards the end of the observation period, suggesting that they were able to occupy the breeding substrate provided (Model 8: significant dominance \times observation day interaction).

Growth Rates in Matched versus Unmatched Treatments

In contrast to expectation we found only minor effects of the main variables affecting growth rates between H and L fish in body size as well as in body mass (Fig. 3). The only significant effect found was a sex effect influencing growth rates of H and L fish: less aggressive males grew quickest in body size and mass (Table 3, Model 1 and Model 2). This difference in growth rates vanished when we checked for the accumulation of body reserves: there were no main effects of the aggressive types and the treatments on the accumulation of body reserves (body condition on day 21, Table 3, Model 3).

Growth Rates within Matched Groups

When comparing growth rates within matched treatment groups (HH, LL and MM) we found behavioural differences had a significant effect. MM groups generally showed the highest variance in growth compared to HH and LL groups, which was additionally influenced by dominance and sex effects. Sex strongly influenced body size growth in matched groups: while females grew larger in H and M groups, they gained less body size in L groups (interaction treatment \times sex; Table 3, Model 4).

A similar effect of sex was also found for body mass growth: females of H and M groups grew heavier than males, whereas this was the opposite in L groups (interaction treatment \times sex; Table 3, Model 5). In addition to this sex effect, there was also an effect of status: whereas in H and L groups there were no differences in body mass change between dominant and subdominant fish, dominant individuals of M groups gained overall the least body mass, but also significantly less than subdominant M group members (interaction treatment \times dominance; Table 3, Model 5).

An effect of dominance was also found when we checked for body reserve accumulation between the different treatments. In contrast to individuals in L groups, individuals in H and M groups

accumulated more body reserves at day 21 if they were dominant (interaction treatment * dominance; Table 3, Model 6).

DISCUSSION

Here we tested whether aggressive type affects the acquisition of social dominance and of mates, the type and intensity of social interactions, and individual growth rates. Furthermore, we tested whether such influence differs if the fish compete with individuals of similar (matched) or dissimilar behaviour type (unmatched treatments). Contrary to several predictions partly derived from previous work on this species (Riebli et al. 2011), aggressive type, the treatments and their interaction had only minor effects on our dependent variables. However, aggressive type and treatment had strong interaction effects on traits such as change in body size, and these effects were additionally modulated by sex and social dominance.

Dominance Achieved on Day 7

We predicted that in groups with mixed behavioural types, fish with high intrinsic aggressive propensity should be more likely to

achieve the dominant position than individuals with low intrinsic aggressive potential (Riebli et al. 2011). In contrast, we found no significant difference in the likelihood of becoming dominant between fish with different aggressive types. However, H fish tended to achieve the dominant position more often in unmatched groups (HL) than L fish. This is in line with results of a previous study, where in a two-player situation highly aggressive individuals were more likely to dominate same-sized less aggressive opponents, but when competing with opponents of similar aggression levels, dominance establishment was more difficult and resulted in fewer conflicts where a clear dominance hierarchy between the contestants was established (Riebli et al. 2011). This suggested that behavioural asymmetries might be a cue enabling individuals to determine fighting ability of an opponent quickly, thus leading to fast resolution of dominance interactions, which might be important especially if there are no other asymmetries influencing the outcome of an interaction (i.e. size differences). In contrast to behavioural asymmetries, advantages in fighting ability caused by asymmetries in morphology are well known in both invertebrates (Otronen 1988; Tibbetts et al. 2010) and vertebrates (Young 2003; Bartos et al. 2007; Sacchi et al. 2009). However, as we created a four-player situation with either two (H and L) or four (H, L or M)

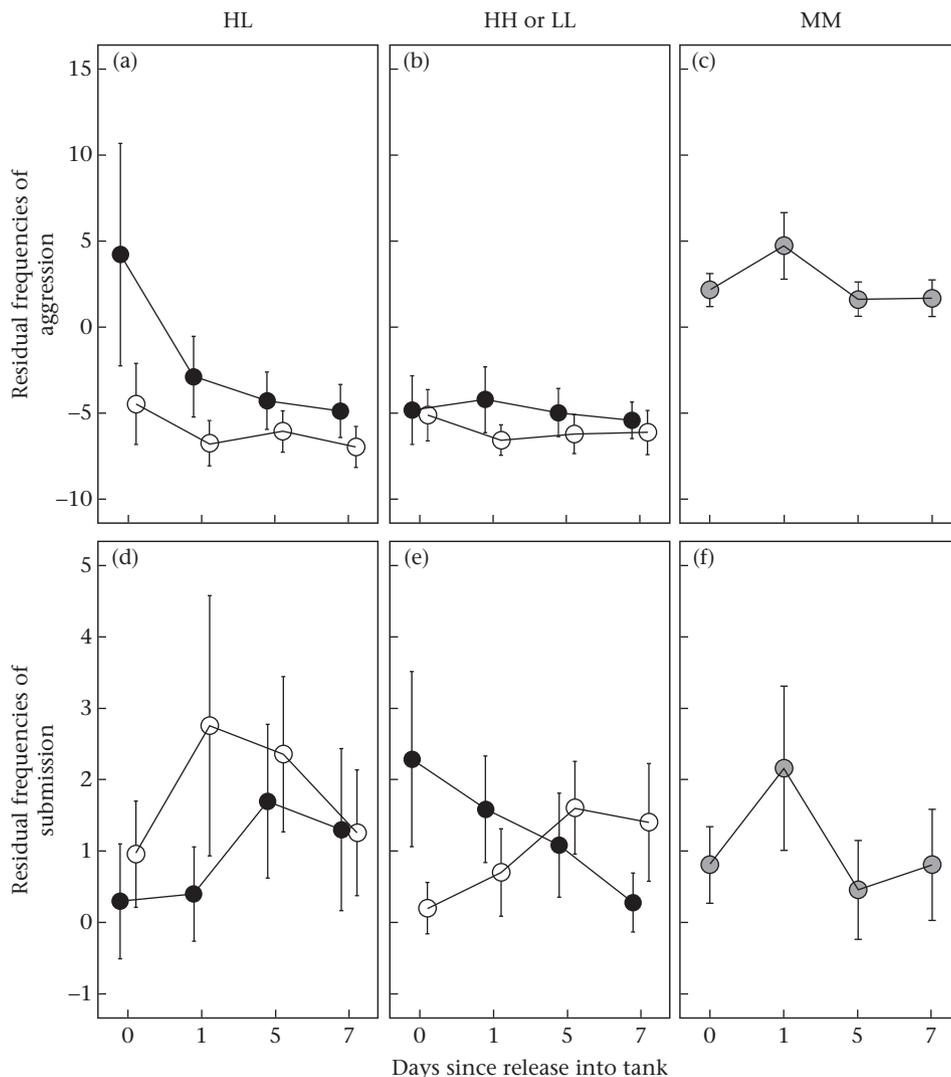


Figure 2. Residual frequencies of aggression (a–c) and submission (d–f) per day depending on the aggressive type and treatment of the focal fish (means \pm SEM). H fish: black circles; L fish: white circles (residuals from Model 1 (a, b); Model 2 (d, e), Appendix Table A1); M fish: grey circles (residuals from Model 5 (c); Model 6 (f), Appendix Table A2). Residuals were calculated from the Poisson generalized linear mixed models, corrected for all other effects except aggressive type, treatment and their interactions with day.

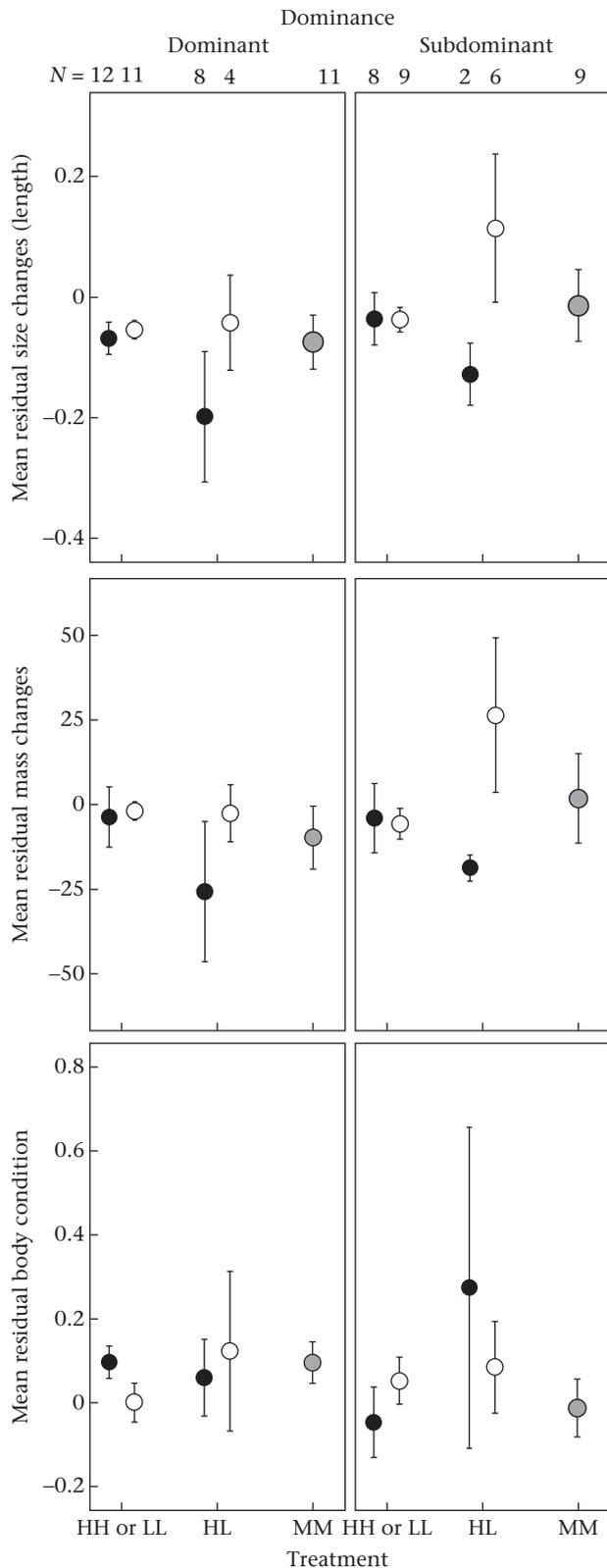


Figure 3. Residuals of growth rates (mean \pm SEM) for body size, mass and condition of the focal fish depending on their aggressive type, the treatment and social dominance (breeder; helper; evicted). H fish: black circles; L fish: white circles (residuals from Models 1–3, Table 3); M fish: grey circles (residuals from Models 4–6, Table 3). Residuals were calculated from the general estimated equations models, corrected for all other effects except aggressive type, treatment, dominance and their interactions. For statistical results see Table 3.

individuals of similar size, this resulted in at least one symmetric situation with regard to aggressive type in each group. We expected that if conflict resolution is based on aggressive type in such encounters, this should lead to extended periods of conflict (Riebli et al. 2011). Hence, small differences in traits other than behaviour (e.g. body size) might be used to reduce the risk of extended conflicts possibly leading to a 'war of attrition' (Hammerstein & Parker 1982). Dominance relationships in *N. pulcher* are strongly dependent on body size (Hamilton et al. 2005). Indeed, body size differences, even if experimentally minimized, apparently affected the establishment of dominance hierarchies more strongly in our study than differences in aggressive type. This is in line with a recent study of convict cichlids, *Amatitlania nigrofasciata*, which demonstrated that even small morphological asymmetries can modulate fighting ability, for instance enabling slightly larger individuals to compete for longer periods of time (Copeland et al. 2011).

Shelter and Mate Acquisition

In *N. pulcher*, differences in behavioural type may affect the composition of social groups and the establishment of territories. Schürch et al. (2010) showed that dominant males accepted different behavioural types of females and subordinates in their groups depending on their own behavioural type. Here we tested whether aggressive type affects territory establishment in a balanced situation where in principle each individual had the same likelihood of establishing a territory. Two different shelter qualities were presented to each group at the same time. As *N. pulcher* prefers wedge-shaped over open crevices as shelters and the back part of a tank over the front (personal observations) we predicted that dominants would be more likely to settle in the stone slab in the back half of the tank than in the clay pot half in the front. However, in about half of the groups the dominant individuals monopolized both shelters. Shelter preference of dominant fish was unaffected by either aggressive type or group composition.

Behaviour within Groups

Against prediction, in matched groups fish with high and low aggressive propensity both performed fewer aggressive acts overall than in unmatched groups. However, aggression levels in unmatched groups were initially much higher than in matched groups, in which aggression levels increased continuously over the course of the experiment (Fig. 2a, b). This pattern is consistent with previous results showing that in matched groups it takes longer to establish a dominance hierarchy than in unmatched groups (Riebli et al. 2011). The delayed establishment of hierarchies in matched than unmatched groups in our experiment is also reflected by the submission frequencies shown. As individuals use ritualized displays to avoid escalated conflicts (McElligott et al. 1998; Bergmüller & Taborsky 2005; Bartos et al. 2007) it seems reasonable to assume that the establishment of hierarchies relates to the levels of submission exhibited by the members of a group. In our matched groups, submission rates decreased in highly aggressive fish whereas they increased in fish with low aggression levels throughout the experimental period (Fig. 2e).

Individuals of different aggressive type also diverged in behaviours other than social interactions. Fish with low aggressive propensity generally visited shelters more often than highly aggressive fish, especially if they were the largest fish in the group. Males with low aggressive propensity showed more territory maintenance, confirming previous evidence about personality-dependent task specialization in *N. pulcher* (Bergmüller & Taborsky 2007; Schürch & Heg 2010a). Task specialization and

division of labour are well known from eusocial hymenoptera (Wilson 1971; Johnson 2008, 2010; Woyciechowski & Moron 2009; Waddington & Hughes 2010) and have been demonstrated also in cooperative vertebrates (Clutton-Brock et al. 2004; Bruintjes & Taborsky 2011), in which assuming certain tasks may be context dependent (Heg & Taborsky 2010). Little is known, however, about task specialization depending on different behavioural types (Bergmüller & Taborsky 2007). In rooks, *Corvus frugilegus*, for instance, bolder individuals are more likely to participate in a cooperative task, whereas shy individuals are more influenced in their decision by the partner's behaviour (Scheid & Noe 2010). The territory maintenance varying with aggressive type in *N. pulcher* is a cooperative behaviour, because the group members use dug-out holes and crevices to hide from predators and as breeding shelters (Taborsky & Limberger 1981; Taborsky 1984). Therefore, removing sand from shelters is a crucial behaviour yielding potential direct (survival: Taborsky 1984; Heg et al. 2004) and indirect fitness benefits to all group members (Brouwer et al. 2005). Sand may imperil survival of small offspring (Taborsky & Limberger 1981) that may be close kin of helpers (Dierkes et al. 2005).

Growth Rates

Theory suggests that resource value estimation and behavioural types can be tightly correlated with each other, which might explain differential resource allocation by individual animals (Hurd 2006; Wolf et al. 2008, 2011). For instance, individual *N. pulcher* allocate resources differentially to growth or reproduction depending on the mixture of aggressive types in a social group (Riebli et al. 2011). These results suggested that individuals with a high aggressive propensity might pursue a 'fast' life history strategy by converting resources into immediate fitness benefits (i.e. reproduction), thereby being less responsive to the quality of the resource. On the other hand, individuals with a low aggressive propensity allocated more resources to growth than highly aggressive fish when living in groups mixed for aggressive type, suggesting a 'slow' life history strategy evaluating current resources against future alternatives (Riebli et al. 2011; cf. Wolf et al. 2011).

Here we tested the predictions derived from our earlier study by providing the animals with breeding resources. As predicted (cf. Brown et al. 2007; Biro & Stamps 2008; Wolf et al. 2011), we detected differential resource allocation decisions reflecting behavioural idiosyncrasies. Divergence in allocation decisions depending on behavioural types was linked to sex. Males with low aggressive propensity generally grew more quickly in size and mass than highly aggressive males. This suggests that individuals of different aggressive types might opt for different life history strategies. However, especially in groups in which all individuals were of the same aggressive type, no general pattern could be observed, suggesting that growth rates between different aggressive types seemed to be strongly dependent on the current dominance status of individuals, independently of whether the groups were matched or unmatched for aggressive type. This strong context dependence (see Table 4) might explain why the pattern of growth rate differences looks rather complex. We should like to stress also that we obtained rather large sample sizes for dominant and subdominant individuals, particularly in matched groups, whereas the sample size of some categories in the unmatched treatment was lower, which may have affected statistical power.

In comparison with other studies of *N. pulcher*, diverging results suggest that life history decisions (e.g. resource allocation) are strongly context dependent (see Table 4). It has been

Table 4

A summary of results from experimental studies testing for effects of aggressive type (L, H or M) on growth rates (size or mass) in *Neolamprologus pulcher* in different social contexts

Social context	No. of fish in tank	Result	Trait	Generality of the effect	Source
Single	1	L=H	Size	Both in males and females	Schürch & Heg 2010a
Aggregation	4	L>H	Size	Within unmatched groups: 2H and 2L fish	Riebli et al. 2011
		L<H	Size	Between matched groups: 4H vs 4L vs 4M fish	
Breeding group	4	L>H	Size	Males in unmatched groups: 2H and 2L fish	This study
		L>H	Mass	Males in unmatched groups: 2H and 2L fish	
Breeding group	6	L=H	Size	Only tested in subordinates	T. Riebli & M. Taborsky, unpublished data
		L>H	Mass	Only tested in subordinates	
		L<H	Size	Only in females living in aggregations	
Multiple breeding groups	72	L<H	Mass	Only in females living in aggregations	Heg et al. 2011
		L<H	Size	Only in females living in aggregations	
		L<H	Mass	Only in females living in aggregations	

L: low aggressive propensity; M: medium aggressive propensity; H: high aggressive propensity.

proposed that the social environment (i.e. the social interactions and the position within a social network) might be the driving force shaping the evolution and maintenance of personalities in animal populations (van Oers et al. 2005; Krause et al. 2010). The social environment is thought to provide 'social niches' (analogous to ecological niches) promoting the generation and evolution of behavioural idiosyncrasies (Bergmüller & Taborsky 2010). Owing to social conflicts, individuals might specialize in different behavioural and life history strategies fitting best their behavioural prerequisites and the respective social context. If individuals cannot obtain their preferred social niche and therefore assume an alternative social role, such character displacement might cause differential resource allocation decisions according to behavioural differences and social contexts. For instance, while there may be selection for a positive correlation between aggressive type and growth in one social context, there might be a negative correlation in another context (e.g. living in groups mixed or uniform regarding aggressive type; with or without breeding context). Depending on the social context, individuals might therefore shift their decision to allocate resources differentially (e.g. growing in size rather than mass) if their preferred social niche is already occupied by another group member (Cote et al. 2008; Smith & Blumstein 2008; Dyer et al. 2009; Bergmüller & Taborsky 2010). To study fitness effects of such context-dependent allocation and life history decisions sophisticated experimental approaches are needed.

Behavioural Types and Repeatability

Even though a link between differences in behavioural properties and life history traits has been proposed theoretically (Hurd 2006; Stamps 2007; Biro & Stamps 2008) and also tested empirically (reviewed in Smith & Blumstein 2008; Riebli et al. 2011), repeatability measures of study animals over prolonged periods of time are still lacking. If one considers the fact that behavioural types may change over time, as shown by the decline in repeatability scores of Chervet et al. (2011), current models are insufficient to predict how such differences will affect the future of individuals concerning, for instance, growth and dominance.

We do not believe in the simple one-to-one relationship between behavioural type and life history decisions. In the current study we assessed behavioural differences just before the dominance and growth experiments, and behavioural differences could not explain the outcome. Therefore, if low levels of repeatability (i.e. change of behavioural types) come into play, it is even less likely that behavioural types can explain such differences in life history decisions; but they might be explained by current differences in social context. Generally, there is information missing on factors that change behavioural types over time, even a feedback between life history traits, such as growth, and behavioural types cannot yet be ruled out (e.g. faster growing individuals might become more aggressive). Building upon a series of papers that critically examined the relationship between behavioural types and life history decisions in a cichlid fish (see Table 4), we cannot support the recent literature's notion that there is a 'clear' relationship between behavioural types and life history decisions. Even relationships expected to be simple, such as aggression and dominance, appeared not to be as simple as predicted and showed other modulating effects. Thus, we strongly encourage researchers to address context dependency more frequently in studies dealing with the issue of relating life history decisions to behavioural idiosyncrasies.

General Conclusions

Contrasting with our predictions, we found only few main effects of aggressive type on the establishment of territories and mate acquisition and on social interactions in general. However, aggressive type did affect social interactions (aggression and submission) as well as task specialization. Theory suggests that life history decisions and behavioural traits are linked (Stamps 2007; Biro & Stamps 2008) and that both traits need to be considered when studying either behavioural or life history traits. The connection between consistent behavioural properties and resource allocation decisions has recently attracted considerable scientific attention (Moore et al. 1997; Stamps 2007; Biro & Stamps 2008; Adriaenssens & Johnsson 2011; Riebli et al. 2011; Wolf et al. 2011); nevertheless, effects of the social context on this correlation are still underexplored. Our results suggest that the relationship between behavioural traits and life history decisions might be more flexible than presumed, allowing individuals to choose among various options depending on their current social situation. Apparently the social environment, not only behavioural differences, may feed back on resource allocation decisions, profoundly affecting life history traits such as growth rates. Hence, we suggest that differences in social context should be taken into consideration when dealing with the relationship between personalities and life history decisions, especially in social species such as *N. pulcher*. Fitness consequences of personalities have been tested in several species (Cote et al. 2008; Dyer et al. 2009; reviewed in Smith & Blumstein 2008), but not repeatedly under different social settings. Our results imply that effects of the detailed social context on the relationship between personality, life history decisions and fitness consequences might be of general importance in social species. We therefore encourage repeated testing under different social conditions in order to check for context dependence in the relationship between animal personalities, life history decisions and fitness in future studies of this subject.

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Appendix

Table A1

Results of four generalized linear mixed models (GzLMs) for the frequencies of behaviours observed, comparing the matched treatments (HH and LL) with the unmatched treatment (HL)

Parameter	z	P	Coefficients±SE	
Model 1: Aggression (N=240 observations): HH/LL versus HL				
Intercept	6.735	<0.001	2.378	0.353
Aggressive type	-2.793	0.005	-1.163	0.416
Treatment	-0.685	0.494	-0.165	0.241
Observation day	-2.327	0.020	-0.050	0.021
Dominance	0.788	0.431	0.260	0.330

(continued on next page)

Table A1 (continued)

Parameter	z	P	Coefficients±SE	
Sex	1.796	0.073	0.752	0.419
Size rank	-1.191	0.234	-0.168	0.141
Aggressive type*Size rank	2.073	0.038	0.322	0.155
Aggressive type*Observation day	3.058	0.002	0.070	0.023
Treatment*Dominance	-3.211	0.001	-1.207	0.376
Treatment*Observation day	2.166	0.030	0.050	0.023
Sex*Size rank	-2.124	0.034	-0.341	0.161
Sex*Observation day	-2.436	0.015	-0.054	0.036
Observation day*Dominance	-7.376	<0.001	-0.262	0.036
Model 2: Submission (N=240 observations): HH/LL versus HL				
Intercept	-0.928	0.353	-0.543	0.585
Aggressive type	-1.121	0.262	-0.394	0.351
Treatment	-0.137	0.891	-0.055	0.400
Observation day	1.775	0.076	0.084	0.047
Dominance	1.450	0.147	0.542	0.374
Sex	0.209	0.834	0.069	0.329
Size rank	1.603	0.109	0.212	0.176
Aggressive type*Observation day	3.852	<0.001	0.123	0.032
Sex*Observation day	1.999	0.046	0.062	0.031
Size rank*Observation day	-4.278	<0.001	-0.068	0.016
Model 3: Territory maintenance (N=240 observations): HH/LL versus HL				
Intercept	2.420	0.016	0.713	0.295
Aggressive type	-0.2074	0.038	-0.868	0.419
Treatment	-0.664	0.507	-0.269	0.362
Observation day	5.775	<0.001	0.136	0.024
Dominance	0.412	0.681	0.202	0.492
Sex	-3.506	<0.001	-1.269	0.351
Size rank	-1.920	0.055	-0.269	0.140
Treatment*Dominance	-2.304	0.021	-2.050	0.890
Sex*Dominance	-2.877	0.040	-2.247	0.781
Model 4: Stone slab or pot visiting frequency: (N=240 observations): HH/LL versus HL				
Intercept	1.101	0.271	0.572	0.520
Aggressive type	2.213	0.027	0.791	0.358
Treatment	-0.684	0.494	-0.284	0.415
Observation day	-0.383	0.702	-0.015	0.038
Dominance	-1.959	0.050	-0.922	0.471
Sex	-3.785	<0.001	1.357	0.359
Size rank	-1.392	0.164	-0.217	0.156
Aggressive type*Observation day	-2.458	0.014	-0.130	0.053
Sex*Observation day	5.991	<0.001	0.320	0.053
Observation day*Dominance	-2.691	0.007	-0.724	0.269

L: low aggressive propensity; M: medium aggressive propensity; H: high aggressive propensity. Aggressive type (H or L), experimental treatment, observation day, dominance (dominant or subdominant), sex and initial size rank were treated as fixed effects. Individuals ($N = 60$) nested within groups ($N = 15$) and groups nested within treatments were fitted as random effects. All models were fitted by the Laplace approximation. Aggressive type (H), experimental treatment (matched), dominance (dominant) and sex (female) were the reference categories with their coefficients set to zero. Observation day and size rank were treated as covariates. Nonsignificant effects and interactions were removed. Significant relations are marked in bold.

Table A2

Results of four generalized linear mixed models (GzLMs) for the frequencies of behaviours observed, comparing all matched treatments (HH, LL and MM)

Parameter	z	P	Coefficients±SE	
Model 5: Aggression (N=240 observations): HH versus LL versus MM				
Intercept	6.059	<0.001	1.965	0.324
Treatment	-0.104	0.917	MM: -0.024	0.229
			LL: -0.118	0.230
Observation day	-0.513	0.608	0.001	0.012
Dominance	0.070	0.944	-0.984	0.235
Sex	-4.187	<0.001	-0.010	0.213
Size rank	-0.047	0.962	-0.076	0.104
Observation day*Dominance	-0.730	0.465	-0.357	0.047
	-7.489	<0.001		
Model 6: Submission (N=240 observations): HH versus LL versus MM				
Intercept	0.518	0.604	0.277	0.534
Treatment	0.109	0.914	MM: 0.048	0.440
			LL: -0.628	0.450
Observation day	-1.397	0.162	-0.063	0.047
Dominance	-1.344	0.179	0.429	0.323
Sex	1.328	0.184	-0.197	0.299
Size rank	-0.646	0.518	0.093	0.155
Treatment*Observation day	0.598	0.550	MM: 0.044	0.038
	1.165	0.244	LL: 0.182	0.040
	4.596	<0.001		
Observation day*Dominance	3.018	0.003	0.104	0.035
Observation day*Size rank	-2.216	0.027	-0.035	0.016
Model 7: Territory maintenance (N=240 observations): HH versus LL versus MM				
Intercept	1.301	0.191	1.063	0.813
Treatment	0.258	0.797	MM: 0.161	0.624
			LL: 0.282	0.606
Observation day	0.614	0.539	0.045	0.074
Dominance	-3.909	<0.001	-2.701	0.692
Sex	-3.391	<0.001	-1.825	0.538
Size rank	-1.975	0.048	-0.561	0.284
Treatment*Observation day	-2.293	0.022	MM: -0.153	0.067
	-0.857	0.391	LL: -0.052	0.061
Size rank*Observation day	2.340	0.019	0.063	0.027
Model 8: Stone slab or pot visiting frequency: (N=240 observations): HH versus LL versus MM				
Intercept	0.628	0.530	0.368	0.587
Treatment	-0.311	0.756	MM: -0.133	0.427
			LL: 0.131	0.420
Observation day	0.311	0.756	0.072	0.027
Dominance	2.737	0.006	-0.934	0.496
Sex	-1.884	0.060	-0.734	0.391
Size rank	-1.879	0.060	-0.229	0.191
Observation day*Dominance	-1.194	0.232	-0.388	0.134
	-2.893	0.004		

L: low aggressive propensity; M: medium aggressive propensity; H: high aggressive propensity. Aggressive type (H, M or L), observation day, dominance (dominant or subdominant), sex and initial size rank were treated as fixed effects. Individuals ($N = 60$) nested within groups ($N = 15$) and groups nested within types (as all groups are matched) were fitted as random effects. All models were fitted by the Laplace approximation. Treatment (HH), dominance (dominant) and sex (female) were the reference categories with their coefficients set to zero. Observation day and size rank were treated as covariates. Nonsignificant effects and interactions were removed. Significant relations are marked in bold.