

Original Article

Behavioral type and growth rate in a cichlid fish

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Behavioral syndromes or animal personalities may emerge due to covariation with different life-history strategies individual animals pursue, like risk-associated feeding rates translating in different growth trajectories. However, less clear is how this might affect individuals in cooperatively breeding species, where subordinates assist dominants in raising offspring, and growth has profound life-history and social consequences. Here, we examined the effects of behavioral type on growth rates and feeding in the cooperatively breeding cichlid fish *Neolamprologus pulcher*, comparing growth rates of individuals settled inside a group (dominant or subordinate) or unsettled fish (aggregation) of different behavioral types (bold-shy continuum) under a feeding regime where food could not be monopolized. Controlling for other factors, we found no effect of the behavioral type on the growth rates of dominants and subordinates in either sex. In contrast, bold female aggregation fish were significantly growing faster in length compared with shy female aggregation fish, whereas no such effect was detected in male aggregation fish. These growth rate differences were largely matched by differences in feeding rates, but locomotion appeared more important in determining growth than feeding rate. Our results show that differences in social status may need to be taken into account when testing for correlations between behavioral type and growth in vertebrates, and cautions that growth adjustments may get obscured due to correlated changes in other costly behaviors, like locomotion. *Key words*: animal personality, behavioral syndromes, Cichlidae, dominance, status-dependent growth. [*Behav Ecol*]

INTRODUCTION

Individuals in vertebrate populations often exhibit consistent differences in behavioral traits, where each individual can be characterized by his or her particular trait combination (so called “behavioral type” Sih et al. 2004) and the across-individual correlations in behavioral traits are described variously as behavioral syndromes, coping styles, animal personality, or temperament (Wilson 1998; Réale et al. 2007; Sih and Bell 2008). Theoretical models have shown that behavioral syndromes can be generated and maintained through the coevolution of individual behavioral traits (like risk proneness) with individual life histories (like habitat selection Wolf et al. 2007). Recently, Stamps (2007) suggested that food intake and consequently also growth are important components of individual-specific life histories and therefore are likely to be affected by differences in behavioral types. Indeed, evidence for a correlation between behavioral type and growth and/or food intake has been found in 16 different animal species, with particular strong evidence in fish (with “bold” individuals gaining more food and growing faster than “shy” individuals: Biro and Stamps 2008). However, it is unclear whether these correlations only arise under certain testing situations (e.g., food distribution, social context, competition regime, Adriaenssens and Johnsson 2009). For instance, Riebli et al. (2011) showed recently that shy fish outgrow bold fish under a certain social context only (when living mixed with both shy and bold fish), whereas, for instance, shy and bold fish do not differ in growth rates when kept in unmixed groups nor when kept singly (Schürch and Heg 2010a).

A first major point of concern is whether and how food accessibility might influence the relationships between behavioral type, food intake, and growth. For instance, in many laboratory or seminatural settings food enters the system in a predictable way, for example, because food enters the system in a single pulse (e.g., 1 feeding per day) or at a predictable location (e.g., at the upstream part of the system, where the food then flows downstream, see examples in Biro and Stamps 2008). In such situations, individuals of a certain behavioral type (e.g., aggressive, dominating individuals) can easily monopolize the food entering the system. This feeding regime often does not match the natural situation of the focal species in question. A second major point of concern is that behavioral type–dependent food intake and accordingly growth adjustments are often studied under artificial settings (e.g., enclosures, tanks, laboratory), which results might not match the natural settings, as major selective pressures favoring certain behavioral traits or maintaining variation in behavioral traits might go unnoticed. Both concerns will be tackled by us in our experimental design (see below).

Behavioral type–dependent growth adjustments would be particularly interesting to study in a cooperatively breeding species, where the resulting body size differences may affect group membership and eviction of subordinates by dominants from groups (Balshine-Earn et al. 1998), dominant–subordinate interactions and growth (Heg et al. 2004; Hamilton and Heg 2008; Heg 2010), and group structuring (Schürch et al. 2010). Recently, a behavioral syndrome has been described in the cooperatively breeding cichlid *Neolamprologus pulcher* (bold–shy continuum, Bergmüller and Taborsky 2007), which remains stable over life (Schürch and Heg 2010a) and may have consequences for group living in this species (e.g., dominant–subordinate eviction rates and reproduction: Schürch and Heg 2010b; cooperation: Heg et al. 2009 and Schürch et al. 2010). Previous work did not find a relationship between behavioral type and growth in *N. pulcher* held singly and tested more than 6 months from immaturity to maturity (Schürch and Heg 2010a). In this

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paper, we explore how behavioral type may affect growth rate and food intake in *N. pulcher*, taking into account that these cichlids typically show status-dependent and strategic growth in males but not females (see references above and Taborsky 1984; Bergmüller et al. 2005). We released 72 differently sized fish of both sexes, pretested for their behavioral type, in batches of 6 fish every third day in a large octagonal tank containing 24 breeding patches, and we allowed them to compete for group membership (this procedure was followed 3 times, giving 216 fish tested in total, see Schürch et al. 2010; Heg et al. 2011). *Neolamprologus pulcher* feeds on zooplankton flowing through their breeding habitat, and we simulated this situation using 4 feeding stations and a current distributing the food through the whole tank, so food monopolization was not possible, like in nature (Gashagaza 1988; Heg et al. 2004; Bruinjes et al. 2010). We determined their food intake, social status (dominant, subordinate, or aggregation fish Taborsky and Limberger 1981), and growth at the end of the trial. We tested the hypothesis that behavioral type predicts growth rate (bold fish growing faster than shy fish Biro and Stamps 2008), controlling for the effects of social status, sex, and their interaction. We then evaluate whether differences in feeding rate might have caused these effects, controlling for the possibility that individuals might also differ in energetically costly behaviors shown (activity and locomotion).

MATERIALS AND METHODS

Experimental setup

The experiment was conducted inside a large 8000-l octagonal tank ("ringtank") and monitored by D.H. and R.S., who were blind to the behavioral types of the individual fish. All *N. pulcher* used in this experiment were laboratory-reared descendants of fish caught near Mpulungu, Zambia (in 1996 and 2006), at the southern end of Lake Tanganyika. The ringtank contained 24 breeding patches (each patch with 12 pot halves and a shelter between 2 stone slabs), where 72 fish could build cooperative groups as follows (3 trials were conducted, giving $3 \times 72 = 216$ individuals tested in total, rotating the location of the 24 patches between trials). During each trial, a large male (mean \pm standard deviation [SD], standard length [SL] mm 55.4 ± 3.7 , range 48.2–64.1, $n = 39$) and large female (53.9 ± 4.6 , 48.0–66.2, $n = 33$), a medium male (40.8 ± 3.1 , 32.8–46.4, $n = 33$) and medium female (40.4 ± 3.6 , 33.2–46.0, $n = 39$), and a small male (28.8 ± 3.9 , 18.4–35.7, $n = 36$) and small female (30.6 ± 4.9 , 20.3–42.0, $n = 36$) were released inside the ringtank at randomly chosen different sides of the tank (day 0). Every third day, this procedure was repeated, until 72 fish were released (last release on day 33, giving 12 sets of 6 fish released). Cichlids were individually marked with fin clips taken from the dorsal and anal fin (up to 2 positions per individual, unique per size class), individual body measurements taken (body size SL in 0.1 mm and body mass in 1 mg accuracy), and sexed by inspection of the gonadal papilla. Individuals were resexed at the end of the experiment when most individuals had reached mature size (>30 mm SL), and sexing was more reliable.

Cichlid food flakes Tetramin were provided through 4 automated feeders (EHEIM 3582 Twin), supplemented daily with *Artemia* spp. eggs. Food biomass (Tetramin and *Artemia*) was progressively increased with the increase in fish numbers inside the tank: for the automated feeders by increasing the number of rotations per feeding. A large filter, pumping 35 l/min, and 4 additional smaller pumps placed directly before the feeders, created a water current at the surface, thereby distributing the food through the whole tank, ensuring feeding locations could not be monopolized. The flakes and *Artemia*

eggs were distributed quickly horizontally and vertically due to the strong current. Two times per week, fish were additionally provided with fresh food (shrimps, mosquito larvae, *Daphnia*, and *Artemia*), which we evenly distributed in the whole tank. Water temperature (mean \pm SD: $27.01^\circ\text{C} \pm 0.18$, range: $26.7\text{--}27.3^\circ\text{C}$, measured every third day, $n = 39$) and illumination cycle (lights on from 08:00 to 21:00 h) were kept constant in a climate-controlled room. On day 40, all individuals were removed from the ringtank, sexed, and body measurements were taken to determine growth. Growth rate was calculated as the percentage daily change: (daily change SL/initial body length SL) $\times 100\%$ and (daily change mass/initial body mass) $\times 100\%$; where daily change is postexperiment SL or mass minus preexperiment SL or mass, divided by the number of days between the 2 measurements. Note that the latter decreased for individuals released later in the experiment.

Assessment of behavioral type

All behavioral tests were conducted by S.R., who was blind to the sex, social status, and treatment of the individuals tested. Exploration propensity was assessed inside a 400-l tank ($130 \times 65 \times 65$ cm, 5 cm sand layer). At one short side, the tank contained a home compartment of $30 \times 65 \times 65$ cm with a pot half, separated from the exploration compartment by an opaque partition. The fish were transferred to this home compartment and allowed to acclimatize for 10 min. The opaque partition was removed, and the fish were allowed to explore the exploration compartment containing 10 pot halves for 5 min (the distribution of these pots was varied, so individuals never experienced the same pattern when tested again). The following parameters were assessed: 1) latency until entering the exploration compartment (s), 2) latency until entering the first exploration pot (s), 3) time spent in locomotion (s), 4) frequency of entering any exploration pot, 5) frequency of entering a 5 cm radius around any exploration pot, and 6) number of different exploration pots entered (1–10).

Boldness was assessed inside the 40-l home tank of each individual ($50 \times 30 \times 30$ cm), containing a pot half 20 cm from the rear end. A novel object was placed at the front side and this induced the fish to hide inside their pot half. Novel objects used were red-and-black plastic beetle, mixed colored stone bird, a white funnel, a dark-blue globe, a white cross, or a blue plastic device. All novel objects were about equally sized and individuals never experienced the same novel object twice. Recording for 5 min started immediately and the following 2 parameters were recorded: 1) the latency to leave the pot half and approaching the object (s) and 2) estimated shortest distance to approach the object (0–30 cm, with 0 indicating touching the object).

Aggressiveness was assessed inside the 40-l home tank of each individual (see above). A mirror (46×15 cm) was placed at the long side of the tank, which induced the individuals to hide inside their pot half. Recording for 5 min started immediately and the following parameters were recorded: 1) time spend hiding inside their pot (s), 2) frequency of restrained aggression (slow approach to the mirror, fin spreading display, head down display, s-bend display), and 3) frequency of overt aggression (fast approach to the mirror and all contacts with their mirror image includes biting, ramming, mouth-fighting, tail beating).

The 3 behavioral tests were conducted in randomized order for each individual within 1 day and repeated the next day (again randomized). The 216 focal individuals were tested on day $t - 2$ and $t - 1$ before release into the ringtank and again on 2 consecutive days after the experiment (on days 40–52, third and fourth test series).

Behavioral recording inside the ringtank

The location (patches and pots visited), social status (dominant, subordinate, or aggregation), and group membership (pairs, and the identity of the dominants assisted by the subordinates) was determined for each individual daily from day 0 (1st set released) to day 39 (6 days after the last 12th set was released) by D.H. The social status acquired at the end of the trial on day 39 entered the analyses.

Ten-minute focal observations of each individual present in the ringtank were made by R.S. and D.H. on days 11–12 (observation 1, $n = 72$ individuals), days 23–24 (observation 2, $n = 144$ individuals minus 1: we lost one observation), and days 35–37 (observation 3, $n = 216$ individuals); the individual order of observation was randomized. Note that the sample sizes gradually increased due to the addition of focal fish inside the ringtank every third day. We recorded the feeding rate (number of bites/10 min); general “activity” (a summation of all behaviors performed by the focal fish which are known to be energetically costly in these cichlids and involve active movements: aggression, submission, affiliation, and territory maintenance, see Grantner and Taborsky 1998) and a proxy of locomotion (number of movements between different patches, abbreviated “number of patch changes” throughout). Because aggregation fish were less likely to visit any patch compared with the dominants and subordinates (i.e., group members defended one to several patches), and every focal fish may swim over a patch without actually entering the patch, all number of patches changed were calculated regardless of whether the patch was actually entered or not. Table 1 gives an overview of all the parameters recorded for each of the 216 focal individuals.

Statistical analysis

Statistical analyses were conducted using SPSS 17.0. To summarize the many variables of the 3 behavioral tests (exploration propensity, boldness, aggressiveness), we extracted one principal component using a categorical principle component analysis CatPCA (Norusis 2007). All exploration, boldness, and aggressiveness traits loaded highly on one component only (eigenvalue: 6.65, percentage variance explained: 60.5%, see Appendix), low component values indicating shy, less explorative, and aggressive individuals, high component values indicating bold, highly explorative, and aggressive individuals (shy–bold continuum, Schürch et al. 2010). Repeatability of this component across the 4 tests was high 0.80 and

significantly different from 0 (Schürch et al. 2010). We averaged the components of the 2 pretests for each individual and refer to this average principal component as the individual’s “behavioral type.”

The focal individual feeding rate ($\log[\text{feeding rate} + 1]$ transformed), activity, and number of patches changed as assessed during observation 1, correlated with the same focal’s behaviors as assessed during observation 2 (Pearson’s $r = 0.40, 0.32, 0.37$; $P < 0.001, 0.007, 0.001$, respectively; $n = 71$). Similar correlations were found between observation 1 and observation 3 ($r = 0.42, 0.42, 0.40$; all $P < 0.001$, $n = 72$) and also between observations 2 and 3 ($r = 0.49, 0.77, 0.71$; all $P < 0.001$; $n = 143$). Therefore, only the behavior at observation 3 was considered for the remainder of the analyses, that is, when all 72 ($\times 3 = 216$) individuals were present inside the ringtank.

All effects of the focal’s behavioral type on the focal’s percentage growth (separate for SL in millimeters per day and body mass in milligrams per day, normal distributions) or feeding rate (poisson distribution) were corrected for random trial (1–3), fixed set (covariate, 1–12, 1 = 1st released on day 0, 12th = last released on day 36), initial body size (covariate, SL millimeters for growth SL, and body mass milligrams for growth mass) effects, and related to the fixed effects of behavioral type (covariate CatPC), social status (dominant, subordinate, or aggregation fish), sex effects (male or female), and their interactions. Percentage growth per day was analyzed using General Linear Mixed Models (GLMM) (entering trial as random effect) with backward deletion of nonsignificant terms, the scaling parameter was adjusted using the deviance method. Note that we also analyzed the same models with absolute growth rate (SL millimeters per day or mass milligrams per day) as the response variables, but as they gave exactly the same patterns of significance and nonsignificance of terms, they are not presented here. Similarly, feeding rate was analyzed using a log link in Generalized Estimating Equations (GEE), entering trial as subject (random) effect, again with backward deletion of nonsignificant terms, the scaling parameter was adjusted using the deviance method. Lower order interactions were retained whenever higher order interactions were significant. Note in particular that “set” had significant effects on growth (see Results, which is similar to the day of release into the ringtank for each focal individual and so the time spent in the ringtank growing), but that the 2-way interactions between set and other independent variables were never significant in any of the models reported ($0.18 < P < 0.87$).

Table 1
Parameters recorded for each focal cichlid

Parameter	Description	Testing days ^a	Test tank
Behavioral type tests (5 min per test)			
Exploration propensity	Exploring 10 novel pots	$t - 1, t - 2$	40 1
Boldness	Approach of novel object	$t - 1, t - 2$	40 1
Aggressiveness	Attacks toward mirror	$t - 1, t - 2$	400 1
Sex	Male or female	$t - 3, 40$	
Body size (accuracy)	SL (0.1 mm), mass (1 mg)	$t - 3, 40$	
Social status	Dominant, subordinate, aggregation	39	Ringtank
Set	1–12 (released into the ringtank: 1 = days 0–12 = day 33)	t	Ringtank
Behavioral observations (10 min)			
Feeding rate	Number of bites	11–12, 23–24, 35–37	Ringtank
Activity	Summed frequency of aggression, submission, affiliation, territory maintenance	11–12, 23–24, 35–37	Ringtank
Number of patch changes	Number of movements between different patches	11–12, 23–24, 35–37	Ringtank

^a Day 0: first 6 individuals released into the ringtank (6 individuals present), day 39: last observation day inside the ringtank (72 individuals present), day t = day of release into the ringtank of the particular focal individual.

Table 2

Effects of behavioral type, social status, and sex on % daily growth and feeding, corrected for effects of body size and set

Parameter	% Daily growth SL				% Daily growth mass			Feeding rate	
	df	error df	<i>F</i>	<i>P</i>	error df	<i>F</i>	<i>P</i>	χ^2	<i>P</i>
Intercept	1	146.7	293.3	<0.001	20.0	349.3	<0.001	399.7	<0.001
Behavioral type (Bt)	1	196.4	2.0	0.16	200.3	3.5	0.061	0.4	0.51
Social status	2	200.2	0.6	0.56	201.1	2.3	0.098	49.0	<0.001
Sex	1	200.1	7.8	0.006	209.2	11.3	0.001	0.2	0.63
Bt × social status	2	200.3	0.8	0.43			ns	1.4	0.50
Bt × sex	1	200.4	3.1	0.08			ns	16.0	<0.001
Social status × sex	2	200.2	0.1	0.90			ns	32.3	<0.001
Bt × social status × sex	2	200.2	3.1	0.044			ns	9.8	0.008
Body size ^a	1	201.7	149.6	<0.001	209.3	173.6	<0.001	31.4	<0.001
Set	1	200.0	19.2	<0.001	209.0	37.3	<0.001	1.7	0.19

Results of 2 GLMMs for growth and 1 GEE on feeding rate (log link), all 3 models corrected for random trial effects ($n = 216$). Depicted are the degrees of freedom (df), error df, the *F* or Wald χ^2 value, *P* value, and coefficient \pm SE of the estimates. ns, not significant.

^a Initial body length (SL millimeters) for growth SL and feeding rate, initial body mass (milligrams) for growth mass.

To test whether differences in growth rate might come about by differences in feeding rate, controlling for energetically costly behaviors (activity and number of patch changes), we analyzed the daily percentage change in SL or mass and related these to feeding rate, activity, and number of patch changes in 2 GLMMs (entering trial as random effect).

RESULTS

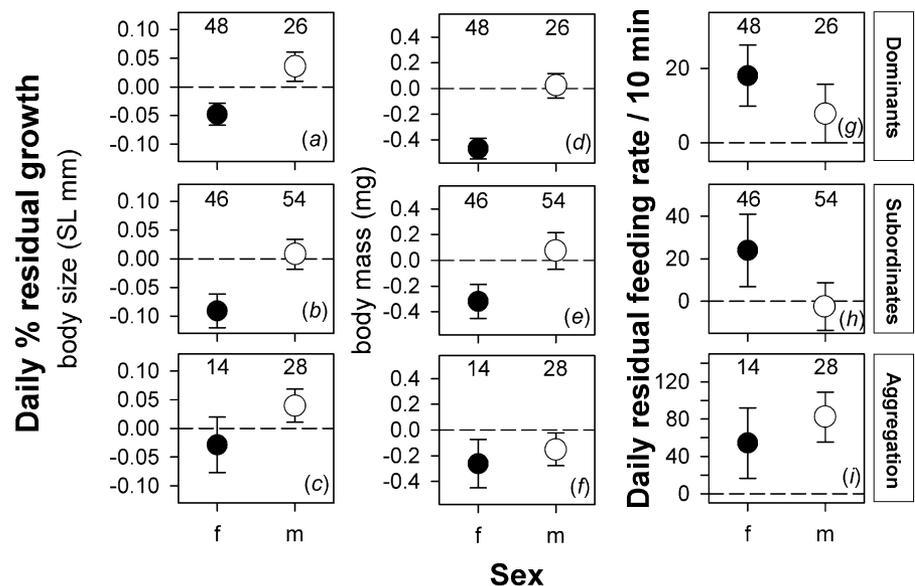
Corrected for other effects (Table 2, growth rates expressed as percentage per day), cichlids showed highly significant decreased growth rates with their initial body size in length (coefficients \pm SE: -0.0200 ± 0.0016) and in mass (-0.00041 ± 0.00003), and males were growing significantly faster than females overall (Figure 1). Feeding rate also declined with initial body size (-0.0314 ± 0.0056). Cichlids released later in the experiment showed significantly reduced growth rates (Table 2, SL: -0.0156 ± 0.0036 , mass: -0.0947 ± 0.0155), suggesting fish needed time to acclimatize to the SL tank. Social

status did not affect growth rates, although it tended to affect growth in body mass (Figure 1d–f). In contrast, social status and the interaction between social status and sex significantly influenced the feeding rates of the fish: 1) aggregation fish were feeding more (Figure 1i) than all other fish (Figure 1g,h, note the difference in the scale of y axes) and 2) males were feeding less than females (Figure 1g,h), but the reverse was true in the aggregation fish (Figure 1i).

Behavioral type did not affect the growth rates of dominants and subordinates (Figure 2, Table 2), although bold fish in general tended to grow faster in mass than shy fish (Table 2, $P = 0.061$). In contrast, boldness had a positive effect on the growth rate in SL (Figure 2c) and feeding rate (Figure 2i) of female aggregation fish (Table 2). The significant 2-way interactions and the one 3-way interaction for growth rates in SL and feeding were not significant for mass, although the direction of the 3 slopes (growth rate SL, growth rate mass, feeding rate) were similar for each status and sex combination (Figure 2), except for subordinates (Figure 2), suggesting that not only energy income (feeding) but also energy spent

Figure 1

Daily % residual growth in (a–c) SL, (d–f) mass, and (g–i) residual feeding rate depending on the sex (white circles: males; black circles: females) for (a,d,g) dominants, (b,e,h) subordinates, and (c,f,i) aggregation fish. Residuals after correcting for intercept, body size, and set effects (see Table 2). Depicted are means \pm standard error of the mean with sample sizes. Note the different y axes scaling comparing (g, h, i).



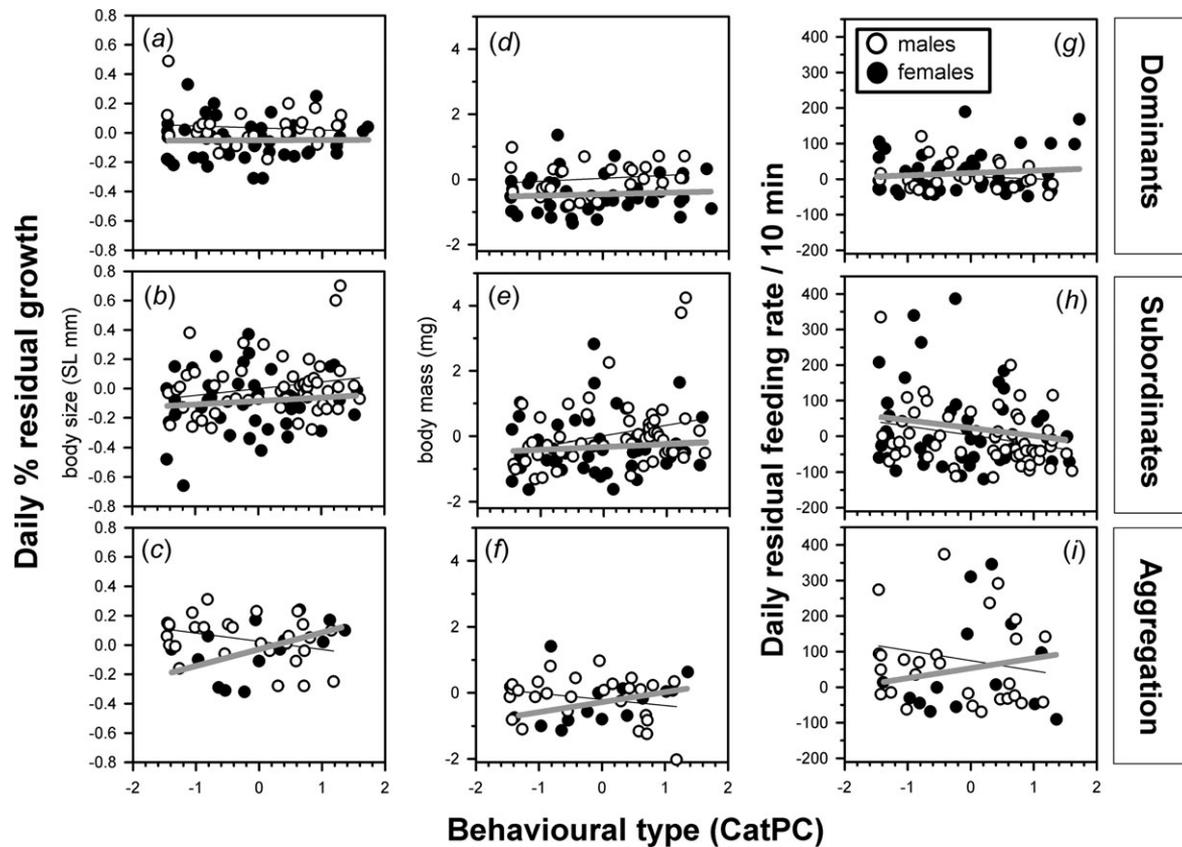


Figure 2

Daily % residual growth in (a–c) SL, (d–f) mass, and (g–i) residual feeding rate depending on the behavioral type and sex (white circles, thin lines: males; black circles, gray lines: females) for (a,d,g) dominants, (b,e,h) subordinates, and (c,f,i) aggregation fish. Residuals after correcting for intercept, body size, and set effects (see Table 2). Lines are simple regression lines per social status and sex combination (for sample sizes, see Figure 1).

(energetically costly behaviors) need to be taken into account. To explore in which sex and social status combinations behavioral type had a significant effect on growth rates, we also ran the 2 models of Table 2 for each combination separately (2 growth rates \times 2 sex \times 3 status = 12 GLMMs, effect of behavioral type corrected for set and body size and random trial effects). For growth rate in SL, only female aggregation fish showed a significant positive effect of behavioral type ($F_{1,8.3} = 41.8$, $P < 0.001$), whereas helper males showed a positive tendency of behavioral type ($F_{1,49.1} = 2.9$, $P = 0.096$), and all other combinations showed no effects of behavioral type ($0.14 < P < 0.79$). For growth rate in mass, again only female aggregation fish showed a significant positive effect of behavioral type ($F_{1,10.0} = 6.4$, $P = 0.03$), whereas again helper males showed a positive tendency of behavioral type ($F_{1,50.0} = 3.9$, $P = 0.053$), and all other combinations showed no effects of behavioral type ($0.39 < P < 0.94$).

Indeed, differences in feeding rates did not translate directly into differences in growth rates (see, e.g., discrepancies between Figures 1g–i vs. Figure 1a–f) because fish also showed large differences in energetically costly behaviors (mean activity \pm SD: 30.6 ± 25.3 , range: 0–119; mean number of patch changes \pm SD: 13.1 ± 13.2 , range: 0–127; $n = 216$). To appreciate these differences, the average distance between the centers of 2 neighboring patches in our ringtank was approximately 75 cm, so the focal individual changing patches 127 times swam about 95 m within 10 min (or the average individual $13.1 \times 0.75 = 9.8$ m, 5% percentile = 0 m, 95%

percentile = 26.3 m). A GLMM ($n = 216$, corrected for random trial effect) on growth rate in SL showed a significant effect of the number of patches changed (Figure 3a, coefficient \pm SE: -0.0035 ± 0.0014 , $F_{1,209.8} = 6.1$, $P = 0.014$), whereas the effect of feeding rate was in the predicted direction but not significant (0.00037 ± 0.00021 , $F_{1,99.5} = 3.2$, $P = 0.077$), and activity was also not significant ($F_{1,12.4} = 1.4$, $P = 0.27$). Similarly, the number of patches changed also affected the growth rate in mass (Figure 3b, GLMM, corrected for random trial effect, $n = 216$, coefficient \pm SE: -0.0115 ± 0.0058 , $F_{1,210.5} = 3.9$, $P = 0.050$) but not feeding rate ($F_{1,80.7} = 1.1$, $P = 0.30$) and activity ($F_{1,9.2} = 0.8$, $P = 0.40$). Note that behavioral type did not correlate with activity (Pearson's $r = -0.073$, $P = 0.28$, $n = 216$) and also not with the number of patch changes ($r = 0.015$, $P = 0.83$, $n = 216$).

DISCUSSION

Contrary to earlier studies, we found only limited effects of male social status on male growth in *N. pulcher* (Heg et al. 2004; Bergmüller et al. 2005), which is most likely due to earlier studies testing for the effect of social status in single isolated groups, whereas we used a seminatural setting (although the absence of female status-dependent growth matches earlier studies: Hamilton and Heg 2008; Heg and Hamilton 2008; Heg 2010). In our experimental setting, individuals were free to interact with many neighboring groups,

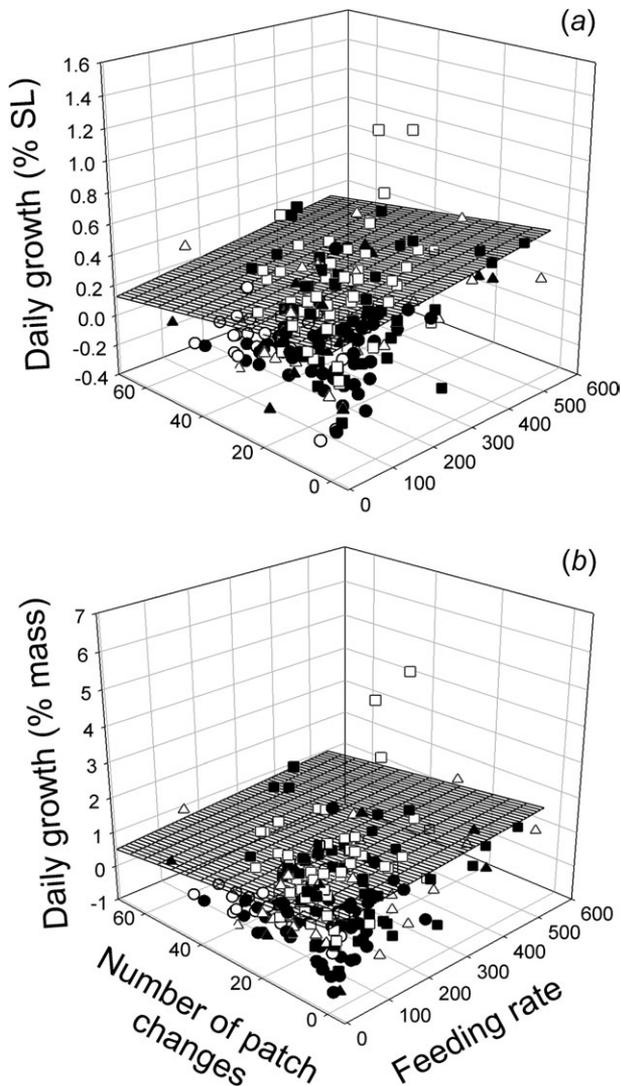


Figure 3
Daily % growth in (a) SL and (b) body mass depending on the feeding rate and number of patch changes (proxy for locomotion), white symbols: males, black symbols: females, with circles: dominants, squares: subordinates and triangles: aggregation fish. For clarity, one extreme data point is not depicted in both panels: a female aggregation fish with feeding rate = 2, patch changes = 127, and % daily growth SL = 0.0928 and % daily growth mass = 0.4119.

and in particular, the number of patches changed as a proxy for locomotion appeared to affect growth much more strongly than the feeding rate. Although the behavioral type appeared to affect the growth rate and feeding rate of female aggregation fish; no such effects were visible in male aggregation fish and dominant and subordinates of both sexes.

So why did only female aggregation fish show a relationship between behavioral type, feeding rate, and growth? The most likely explanation is that bold females target breeding positions in the ringtank, which they will be more likely to acquire when they outgrow their female competitors already settled (Schürch et al. 2010; Heg et al. 2011), whereas shy females also target subordinate positions, which they can only acquire and maintain when they remain substantially smaller than the dominant female already settled (see also Balshine-Earn et al. 1998). Our results cannot be confounded by effects of the time each individual spent

inside the ringtank, as these effects were accounted for in the statistical analyses.

Referring our results back to the review made by Biro and Stamps (2008), which addresses the relationships between behavioral type, growth, and food intake, we have the following discussion points. First, we have shown that behavioral type did only affect growth for individuals of a certain social status and sex. Second, our measurements were made in a seminatural setting with ample and abundant access to food, food which could not be monopolized by certain individuals. For example, effects of behavioral type and social status on growth might be much more pronounced under food limitation and monopolisability of food (e.g., when bold, highly aggressive individuals can exclude shy, less aggressive individuals from the limited food or the patches containing food). Both points stress the importance of considering the actual testing situation wherein food intake and growth were measured, as Biro and Stamps (2008) stress the importance of conducting similar experiments for different life stages (e.g., juvenile and adult) and different ecological settings. For example, a standardized test situation (e.g., aggressiveness in mirror test) might have little predictable power for what will actually happen in more seminatural conditions (e.g., dominance rank in groups). For a telling example for this context dependency, see van Oers et al. (2005). Third, in a (semi)natural setting behavioral type might not only affect energetically beneficial behaviors but is also likely to affect energetically costly behaviors, for instance, activity and locomotion (Careau et al. 2008). Because bold individuals are typically also more aggressive and exploratory compared with shy individuals, any benefit gained by bold individuals in feeding might be offset by these costs. Indeed, we found a stronger effect of locomotion on growth than feeding itself, which suggest again that the exact setting of any experiment (e.g., small tanks or enclosures vs. large tanks or enclosures) or natural population (e.g., fragmented resources or clumped resources) might affect the relationships found between behavioral type and growth. However, behavioral type did not correlate with activity and locomotion (patch changes) in our study. In contrast, a recent study in great tits *Parus major* showed that fast exploring individuals were also more likely to use feeding stations further away from their natal area than slow exploring individuals (van Overveld and Matthysen 2010).

In conclusion, we found only weak support for behavioral type affecting food intake and thereby growth because the effect appears to depend on the social status and sex of the individuals involved. Our results also urge the need to expand the principle of life-history tradeoffs generating and maintaining differences in behavioral types, to the principle of energy income versus energy use behavioral tradeoffs generating and maintaining differences in behavioral types (Lahti et al. 2002; Careau et al. 2008; Biro and Stamps 2010). It is quite likely that bold individuals have a higher net energy gain than shy individuals in certain contexts (e.g., under food monopolisability or high predation risk, Stamps 2007), whereas the reverse might be true in other contexts (e.g., under abundant food or low predation risk).

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APPENDIX

Result of the categorical principle component analysis on the behavioral variables recorded, for the 3 behavioral tests combined: exploration propensity, boldness, and aggressiveness. Loadings, the eigenvalue, and the explained variance are given for the extracted PC. Also given are the descriptive data for the first test series results for the $n = 216$ individuals entering the habitat saturation experiment. For more details, see Schürch et al. (2010)

Behavioral test and variables	Tests ($n = 970$) PC loadings	Descriptives ($n = 216$ individuals) Mean \pm SD (range)
Exploration test		
Latency entering exploration compartment (s)	-0.81	201.37 \pm 103.25 (0–300)
Latency to first pot (s)	-0.86	235.89 \pm 87.12 (23–300)
Time in locomotion (s)	0.79	77.41 \pm 59.27 (0–266)
No. in a pot	0.85	2.18 \pm 3.29 (0–15)
No. near a pot	0.87	3.45 \pm 5.03 (0–26)
No. of different pots	0.85	1.33 \pm 1.93 (0–8)
Boldness test		
Latency approach (s)	-0.69	156.54 \pm 119.79 (0–300)
Shortest distance (cm)	0.73	23.74 \pm 8.47 (0–30)
Aggression test		
Time hiding (s)	-0.74	219.80 \pm 102.71 (0–300)
No. restrained aggression	0.74	14.41 \pm 20.59 (0–130)
No. overt aggression	0.58	4.48 \pm 10.90 (0–67)
Eigenvalue	6.65	
% Variance explained	60.54%	

CatPCA cannot work with 0 values, so we added a constant of 1 to all original dependent behavioral data for the principal component analysis only.

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