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Resource heterogeneity but not inbreeding affects growth and grouping behaviour in socially foraging juvenile cichlid fish

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Abstract

1. Spatial food distribution determines resource profitability, defensibility and encounter rate of foragers. Clumped food distribution can promote aggressiveness and resource monopolisation, in turn increasing within-group variation in food intake and growth. However, the effects of food distribution may depend on foraging strategies. Little is known about the impact of spatial food heterogeneity on growth and grouping behaviour in social foragers in the absence of monopolisation.

2. Social foraging is present in many fishes, particularly at early juvenile life stages when fish are especially sensitive to environmental variation. Here, a heterogeneous food distribution may impair foraging success and growth and juveniles may increase sociability to attain social information about food resources.

3. We examined the impact of the spatial distribution of food as well as inbreeding on growth and social behaviour in juveniles of the cichlid fish *Pelvicachromis pulcher*. Inbred individuals often show poorer performance than outbred individuals (inbreeding depression), but inbreeding effects can be environment dependent. In the experiment, inbred and outbred fish were reared in a split-clutch design either under homogeneously distributed or spatially clumped food conditions for 8 weeks starting 1 week after juveniles could actively feed. We documented growth and performed a shoaling assay and a sociality test (choice between a large vs. a small shoal) after 6 weeks.

4. Spatial food distribution did not affect within-group body length variation, but individuals reared under clumped food conditions were smaller. Shoals of the different feeding conditions differed in social behaviour. Shoals of the clumped treatment group showed higher variation in inter-individual distances compared to shoals of the homogeneous treatment group. Furthermore, focal fish of the clumped treatment adjusted their association preference to the position of the groups' largest individual. We did not find significant inbreeding or environment-dependent inbreeding effects regarding growth or social behaviour.

5. Our study suggests that a clumped food distribution can impede localisation of food resources and thus growth in juvenile social foragers. Accordingly, in

heterogeneous environments, the use of social information may be highly relevant to increase individuals' foraging success potentially explaining orientation on successful foragers, that is, large individuals. Inter-individual variation in juvenile's social behaviour may precede variation in food monopolisation capability and in growth emerging at later life stages.

KEYWORDS
nutritional ecology, phenotypic plasticity, resource variation, social behaviour, social foraging

1 | INTRODUCTION

Environments constantly change and thereby shape organisms' evolutionary adaptations (reviewed in Chevin et al., 2010; Freudiger et al., 2021). The nutritional conditions within habitats determine species' abundance and drive interspecific interactions (reviewed in White, 2008), as well as intraspecific food competition (Goldberg et al., 2001) and are assumed to affect the development of foraging behaviour and social dynamics within species (reviewed in Lihoreau et al., 2015).

The spatial distribution of food can alter resource exploitation efficiency (Gliwicz & Maszczyk, 2016; Klaassen et al., 2006; Vahl et al., 2005) and competitive interactions within species (reviewed in Grant, 1993). Spatially restricted resources are more easily defendable, as individuals need to defend smaller areas (reviewed in Grant, 1993). Thus, clumped food resources may be monopolised by single or a few individuals, resulting in an uneven access to food (Kim et al., 2004; reviewed in Ward et al., 2006). In accordance, studies showed higher encounter rates of competitors (Trevail et al., 2019) but fewer individuals foraging simultaneously at clumped food patches (Kim et al., 2004), increased aggression and higher body size variation within groups that received spatially clumped food compared to groups receiving homogeneously distributed food (Goldberg et al., 2001; Grant & Guha, 1993; Kim et al., 2004). Furthermore, heterogeneously distributed resources may require individuals to spend more time locating food (Trevail et al., 2019).

Effects of spatial food distribution may vary depending on foraging strategies, which often change with life stages. In many species, social foraging prevails at early juvenile stages, while aggressive defence behaviour develops only later in life. Juvenile individuals are especially sensitive to environmental variation and population dynamics, in turn, are affected by juvenile mortality (reviewed in White, 2008). Therefore, studying the impact of changing environments on larvae or juvenile individuals is of great importance (Morimoto et al., 2018). However, studies examining the effects of spatial food distribution in social foragers in the absence of resource monopolisation and at early life stages in particular are scarce (but see Hernández-Reyes et al., 2017). Furthermore, the impact of resource heterogeneity on social behaviour irrespective of life stage received less attention although social behaviour is an important trait that can buffer environmental effects (e.g. de Zwaan et al., 2019; Groenewoud & Clutton-Brock, 2021).

Inbreeding, that is, mating among genetically related individuals, can affect growth, morphology and survival (reviewed in Hedrick & Garcia-Dorado, 2016). The strength of inbreeding depression, that is, the reduced fitness of inbred offspring can be environment dependent, which has been found in a variety of animal species (reviewed in Armbruster & Reed, 2005). Inbreeding depression is often magnified in stressful environments (Gallardo & Neira, 2005). Inbreeding may also alter the expression of social behaviour, which is, however, less well studied (Mattey et al., 2018). Therefore, for a holistic ecological approach, it is important to consider inbreeding consequences for life-history traits, morphology and behaviour in the context of changing environments. The ratio of the costs and benefits of inbreeding defines the limits for the evolution of inbreeding avoidance, tolerance and preference (Kokko & Ots, 2006; Szulkin et al., 2013; Thünken et al., 2007).

Here, we examined the impact of spatial food distribution and inbreeding on growth and social behaviour (i.e. sociability, shoal size preference and shoal density) in *Pelvicachromis pulcher* during early life stages when juveniles live in shoals. Juveniles were reared in a split-clutch design receiving either spatially limited (*clumped*) or homogeneously distributed food for a period of 8 weeks, starting 1 week after juveniles could actively feed. The effects of spatial food distribution on juvenile performance may depend on the ability to monopolise food resources. At early life stages, *P. pulcher* forage in dense shoals showing no overt aggression (R. F. Schons and T. Thünken, personal observation). Given that individuals are not able to defend resources at this age, we expect no resource monopolisation. Accordingly, we do not expect increased body size variation within groups of the *clumped* treatment. Instead, we predict that shoals receiving the *clumped* feeding treatment show poorer growth because they encounter food patches less frequently. Hence, juveniles of the *clumped* feeding treatment may depend stronger on social information compared to individuals receiving the *homogeneous* treatment and thus should show stronger sociability and stronger preferences for large shoals. In contrast, avoidance of the large shoal would indicate competition avoidance. Furthermore, resource heterogeneity could lead to more variable shoal densities when certain individuals searching for food and depart from the shoal. With respect to inbreeding, we expect that inbred fish show poorer performance especially under the challenging condition of the clumped food distribution.

2 | MATERIALS AND METHODS

2.1 | Experimental animals

Pelvicachromis pulcher is a biparental, cave breeding African cichlid fish, which inhabits rivers and streams (Scherer et al., 2020). Fish used in this study were F2-generation inbred or outbred *P. pulcher*, bred under standardised conditions in the laboratory of the Institute for Evolutionary Biology and Ecology, University of Bonn. In all, 20 inbreeding and 20 outbreeding pairs were formed. The breeding tanks (50 × 30 × 30 cm, length × width × height, l × w × h, water depth: 25 cm) were equipped with a sponge filter, a 10 cm long string of *Ceratophyllum demersum* and *Lemna minor*; the bottom was covered with sand (2.55 kg). A half coconut shell served as breeding cave. The water temperature was 25 (±1) °C and breeding tanks were illuminated in a 12:12 light:dark cycle (L 36 W/11-860 Lumilux plus eco daylight by Osram). If a pair had spawned, eggs were carefully removed from the cave, transferred to 1-L plastic tanks and maintained at 22 (±1) °C water temperature. Approximately 70% of the water was replaced by 1- to 2-day aged tap water, 6 days a week. At the age of 7 days, a 1–2 cm long piece of *Taxiphyllum* spec. was added and the juvenile fish were fed with pellet food (0.25 pellets/fish; Rift Lake Red Cichlid Pellets S by Vitalis Aquatic Nutrition) plus 2–3 drops of living *Artemia salina* nauplii 6 days a week until aged 15 ± 1 days.

At the age of 15 ± 1 days, when clutches were split and assigned to the treatment groups, both groups did not significantly differ in within-group coefficient of variation of standard length (SL CV, for information on calculation see below) nor mean standard length (mean standard length: LME, $N_{homogeneous} = 26$, $N_{clumped} = 27$, $F = 0.507$, $p = 0.483$; SL CV: LME, $N_{homogeneous} = 26$, $N_{clumped} = 27$, $F = 1.219$, $p = 0.277$), nor did inbred and outbred individuals (mean standard length: LME, $N_{outbred} = 30$, $N_{inbred} = 23$, $F = 0.038$, $p = 0.848$; SL CV: LME, $N_{outbred} = 30$, $N_{inbred} = 23$, $F = 0.088$, $p = 0.772$).

2.2 | Feeding regime

At the age of 15 ± 1 days, juveniles were assigned to the treatment groups using a split-clutch design. Clutches bigger than 16 fish were split into two groups of eight individuals. One group of each clutch was assigned to the *homogeneous* feeding treatment and the other one to the *clumped* feeding treatment. When clutches consisted of less than 16 individuals, only one group of eight fish was created and randomly assigned a treatment group. In total, 53 groups of 8 individuals were generated out of 28 different clutches, of which 26 groups were assigned to the homogeneous feeding treatment (11 inbred and 15 outbred groups), while 27 groups were raised under the clumped feeding treatment (12 inbred and 15 outbred groups).

Each group was photographed within the plastic tanks (see above) with a water depth of 1.5 cm using a DSLR camera (D5000 by Nikon) with a macro lens (AF-S Micro Nikkor 105 mm 1:28G by Nikon). Subsequently, groups were transferred to the experimental tanks (30 × 20 × 20 cm, l × w × h) which were equipped with

autoclaved sand (255 g) and an airstone for oxygen supply. Tanks were filled with tap water and 2.5 ml of water purifier (Biotopol by JBL) and 5 ml of bacterial starter (Denitrol by JBL) were added. After their introduction, each group was fed with four food pellets and two drops of living old *Artemia salina* nauplii. From the following day on, experimental fish were exclusively fed with the pellet food according to their assigned feeding treatment. The ration was raised by 0.5 pellets/fish every 14 days, starting with 0.5 pellets/fish, using the age of 15 days as starting date for the calculation of food amounts.

The food ration was adjusted whenever a fish had died. When group size fell below 5, these groups were discarded from the experiment, which happened five times. In the *homogeneous* feeding treatment, the daily amount of food was provided equally distributed throughout the tank. This was achieved by dropping one-quarter of the daily food ration into each corner of the tank. In the *clumped* feeding treatment, food was provided in one corner of the tank and was dropped through a green, flexible plastic tube (22 × 1 cm, length × diameter) to avoid spreading. The corner in which the food was provided was randomly determined daily to avoid conditioning the experimental fish to food provision in a specific corner. The tube which was used to provide food in the *clumped* treatment was presented to *homogeneous* groups in a similar manner directly before food provisioning to create an equal disturbance. Approximately 30% of the water was replaced by 1- to 2-day aged tap water weekly.

2.3 | Documentation of growth

Juveniles were photographed to document their body length at the age of 57 ± 2 days, subsequently after the sociability experiments (*measurement 1*) and at the age of 70 ± 7 days (*measurement 2*). For *measurement 1*, each individual was photographed within a petri dish (diameter: 8.5 cm) right after the shoaling assay or the shoal choice experiment, using a DSLR camera (D5000 by Nikon) with a macro lens (AF-S Micro Nikkor 105 mm 1:28G by Nikon). For *measurement 2*, all members of a group were photographed simultaneously within a 1-L plastic tank filled with water from their experimental holding tank (water depth: 3 cm) to minimise handling.

2.4 | Social behaviour

To investigate the effects of the feeding treatments and inbreeding on the social behaviour, two experiments were carried out 42 ± 1 days after groups had entered the feeding treatment (i.e. at the age of 57 ± 2 days). At this time, individuals had a standard length of 1.20 ± 0.10 cm (M ± SD) and sexes could not be visually determined.

2.4.1 | Shoaling assay

Each group consisting of ≥6 fish was used for a shoaling assay. Two identical experimental setups allowed to carry out two trials

simultaneously. Using 1-L plastic tanks, group members were carefully transferred into opaque white plastic buckets (33 × 27.5 cm, height × diameter), filled with 2.6 L of 1- to 2-day aged tap water (water temperature: 22 ± 1°C) which served as experimental arenas. Trials were recorded using two digital cameras (2k resolution, 30 frames per second; Hero 6 Black by GoPro), each mounted above one of the buckets at 30 cm distance from the water surface. A water depth of 4 cm was chosen to minimise errors due to vertical swimming, which could not be measured. After starting the videos, fish were placed into the centre of the experimental arena. We stopped the recordings after 30 min and carefully removed the individuals from the experimental arena using a dip net. Groups consisting of six individuals were photographed (procedure described above) and released into their holding tank. After each trial, the buckets were thoroughly rinsed with tap water to remove olfactory cues. Groups of 7–8 individuals entered the shoal choice experiment subsequently.

2.4.2 | Shoal choice experiment

Seven individuals of a group were used for the shoal choice experiment. The non-participating individual of groups of 8 was chosen randomly, photographed (see above) and released into the holding tank after the shoal assay. The stimulus shoals consisted of two ('small shoal') and four fish ('large shoal'), respectively. The mean standard lengths of the two stimulus shoals did not significantly differ (paired t test, $N = 38$, $t = 0.453$, $p = 0.653$). Two trials were carried out simultaneously in two identical setups. The experimental tanks (50 × 30 × 30 cm, l × w × h) consisted of three compartments, separated by perforated acrylic glass plates (30 × 19.5 cm, l × h; hole diameter: 1.5 mm), which enabled visual and olfactory contact: A centre compartment (30 × 30 cm, l × w) for the focal fish and two side compartments (30 × 10 cm, l × w) for the stimulus shoals. Within the focal fishes' compartment, two regions (30 × 6 cm, l × w) in front of each acrylic glass plate were defined as association zones and marked by black lines. The tanks' inside was lined with dark grey PVC plates. To control for side effects, the compartments housing the small and large shoals were switched after each trial.

The experimental tanks were filled with 18 L of 1- to 2-day aged tap water (water temperature: 22 ± 1°C, water depth: 13 cm). Stimulus shoals were placed in each of the shoaling compartments using a dip net. After 5 minutes of acclimatisation time for the stimulus shoals, the focal fish was placed into a transparent cylinder (diameter: 10 cm) within the centre compartment for another 5-min acclimatisation period. Subsequently, the cylinder was gently removed by hand. The experimental fish were recorded for 35 min using two digital cameras (resolution: 1,920 × 1,440 p; 30 frames per second; Hero 6 Black by GoPro), each fixed to a stand centrally above tanks at 24 cm distance to the water surface. After the trials, the experimental fish were transferred back into the group tanks. The experimental tanks were rinsed with tap water after each trial to remove olfactory cues.

2.5 | Data analysis

2.5.1 | Size measurements

A photo was selected of each individual (*measurement 1*) or group (*measurement 2*). The group IDs were obliterated to enable blind measurements. Individuals' standard length was measured using the software ImageJ (version 1.53e) and the scale paper as reference. The mean of SL was calculated as a proxy for the groups' average growth. The size variation within groups was investigated using the coefficient of variance of standard length (SL CV), which is robust against differences in the mean and was calculated for each group as follows:

$$SL\ CV = \frac{SD\ of\ SL}{mean\ SL}$$

Additionally, the SL of the smallest and the largest fish of each group were identified for *measurements 1* and *2*.

2.5.2 | Shoaling assay

To achieve better comparability, only groups consisting of eight individuals entered the analysis of the shoaling behaviour. After 8 min serving as acclimatisation time, one image was extracted every 30 s for 8 min using the program VirtualDub (version v1.10.4). The inter-individual distances (IID) were measured between all combinations of two individuals (i.e. 28 measurements per photo), using the straight-line tool in ImageJ and fixing the line at the middle of the respective two fishes' heads. Means of shoals' IID were calculated for the individual photos as well as for the entire 8 minutes to investigate shoal density. Variance in IID within shoals was calculated as coefficient of variance (IID CV) for each shoal as follows:

$$IID\ CV = \frac{SD\ of\ IID}{mean\ IID}$$

2.5.3 | Shoal choice experiment

Videos of the shoal choice experiments were analysed using the software BORIS (Friard & Gamba, 2016). The time spent in each of the preference zones by the focal fish was measured from entering to leaving a zone with the entire body. To investigate general sociability, the total shoaling time was calculated as the sum of times spent in both preference zones. A preference index for the time the focal fish spent in either preference zone (association preference) was calculated using the following equation:

$$Association\ preference = \frac{time\ in\ large\ shoal's\ zone(s) - time\ in\ small\ shoal's\ zone(s)}{time\ in\ large\ shoal's\ zone(s) + time\ in\ small\ shoal's\ zone(s)}$$

Positive values indicate a preference for the large shoal, while negative values indicate a preference for the small shoal.

TABLE 1 Linear mixed-effects models calculated for measurement 1. As random factors, clutch ID nested in family combination were included in each model. The degrees of freedom always differed by one during stepwise model reduction. Significant *p*-values are printed in bold ($p < 0.05$)

Dependent variable	Explanatory variable	F	p
SL mean	Feeding treatment × breeding type	0.016	0.901
	Group size	0.036	0.850
	Breeding type	0.040	0.843
	Feeding treatment	12.161	**0.002**
SL of smallest fish	Feeding treatment × breeding type	0.856	0.366
	Breeding type	0.015	0.904
	Group size	2.433	0.128
	Feeding treatment	5.327	**0.031**
SL of largest fish	Group size	0.115	0.737
	Feeding treatment × breeding type	1.688	0.206
	Breeding type	0.030	0.863
	Feeding treatment	20.073	**<0.001**
SL CV	Group size	0.456	0.504
	Feeding treatment × breeding type	2.014	0.171
	Breeding type	0.200	0.662
	Feeding treatment	0.872	0.362

Furthermore, the position of the largest individual of a group was identified (i.e. whether it was the test fish or part of the small or the large stimulus shoal). Due to technical issues, the standard lengths could not be assigned to the experimental fishes' positions in two trials. These were excluded from statistical analyses concerning individuals' positions.

2.6 | Statistical analysis

Statistical analyses were performed using the software R (version 4.0.3, R Core Team, 2020). Normal distribution was tested using Shapiro–Wilk normality tests. Data significantly differing from normality were Box-Cox transformed; thereafter they met the assumptions of normality. Backward stepwise reduction of linear mixed-effects models (LME) was performed using the 'step' function of the 'LMERTEST'-package (Kuznetsova et al., 2017). Non-significant explanatory variables were removed from the models in order of their statistical relevance. Tests of significance were *F* tests, based on Satterthwaite's with Kenward–Roger approximation. In all models, clutch nested within family combination of the parents was used as random factor. Pairwise post-hoc group comparisons were analysed using the 'EMMEANS'-package (Piepho, 2004).

2.6.1 | Growth

The (interactive) effects of the feeding treatment and inbreeding on growth were examined applying different LMEs. The groups' mean SL, SL CV, the size of the smallest or the largest fish in a group at *measurement 1* or *measurement 2*, respectively, were used as dependent

variables. To correct for varying group sizes due to mortality, the group size at the respective time point was included as covariate.

2.6.2 | Shoaling assay

To examine the (interactive) effects of feeding treatment and inbreeding on shoal density, we fitted two LMEs with mean IID or IID CV as dependent variables. The groups' mean SL or SL CV, respectively, were included as covariates.

2.6.3 | Shoal choice experiment

To examine shoal size preference, we performed an intercept model with the association preference index as dependent variable. Groups' mean SL and group size were added as covariates. The clutch nested within family combination was used as random factor in this model. The total shoaling time could not successfully be transformed to normal distribution and also the residuals of the best explaining models were not normally distributed; thus, Wilcoxon tests were applied to investigate differences between the feeding treatment groups and the breeding types.

To investigate the effects of the largest individuals' position within the experiment, an LME was calculated for the association preference as dependent variable and the feeding treatment, inbreeding, group size and position of the largest fish as well as pairwise interaction terms of all factors as explanatory variables. Post-hoc group comparisons were performed to investigate differences in association preference between groups. Furthermore, the association preference was tested for deviation from zero in separate intercept models for each group. Trials in which the focal fish itself was the largest fish of the group were excluded from this analysis.

3 | RESULTS

3.1 | Growth

The feeding treatment affected standard length (SL). Juveniles reared under clumped feeding conditions were smaller than juveniles reared under homogeneous feeding conditions after 42 ± 1 (measurement 1) and 55 ± 8 (measurement 2) experimental days (Tables 1 and 2; Figure 1). The SL CV was not significantly affected by feeding treatment at both time points (Tables 1 and 2; Figure 1). Neither inbreeding nor the interaction between inbreeding and feeding treatment significantly affected any of the size variables (Tables 1 and 2). Group size positively correlated with groups' mean SL at measurement 2 (Table 2).

3.2 | Shoaling assay

Feeding treatment did not significantly affect mean inter-individual distances (Table 3) but the coefficient of variance of inter-individual distance was higher in groups of the *clumped* feeding treatment than in groups of the *homogeneous* treatment (Table 3; Figure 2). Neither inbreeding nor the interaction between inbreeding and feeding treatment significantly affected any of the density variables (Table 3).

3.3 | Shoal size choice experiment

In general, focal fish preferred to associate with the large shoal (intercept model, $N = 40$, $t = 3.058$, $p = 0.005$, Figure 3). Neither the feeding treatment, inbreeding nor the interaction between the two factors significantly affected shoal size preference. However, the position of the largest fish affected shoal size preference of focal fish in the clumped feeding group but not in the homogeneous feeding group. In the *clumped* feeding group, the preference for the large shoal was increased when it included the groups' largest fish, which was not the case when it was included to the small shoal (Tables 4 and 5; Figure 3). In the homogeneous feeding group, the position of the largest fish did not significantly affect shoal size preference.

4 | DISCUSSION

We investigated the impact of the spatial food distribution and (environment dependent) inbreeding on growth and different aspects of social behaviour (sociability, shoal size preference and shoal density) in juvenile *Pelvicachromis pulcher*. Juveniles that received a clumped spatial food distribution for 6 weeks were significantly smaller compared to individuals of groups reared under a homogeneous food distribution, whereas variation in body length did not differ significantly between feeding treatment groups. Additionally, the smallest and the largest individuals of a group were smaller when receiving the *clumped* feeding treatment, which confirms that differences are found uniformly throughout group members rather than being caused by extreme individual values. The differences in the groups' mean size and the size of the largest fish persisted after 8 weeks.

In contrast to other studies investigating spatial clumping of food at later juvenile, subadult or even adult life stages in fishes (e.g. Grant & Guha, 1993; Hansen et al., 2016; Kim et al., 2004), the treatments' application in the present study started approximately 1 week after the experimental fish could actively feed. In periodically conducted observations, we never observed any food monopolisation or overt aggressive behaviour (R. F. Schons and T. Thünken, personal observation). As social foragers moving

TABLE 2 Linear mixed-effects models calculated for measurement 2. As random factors, clutch ID nested in family combination were included in each model. The degrees of freedom always differed by one during stepwise model reduction. Significant *p*-values are printed in bold ($p < 0.05$) and tendencies in italics ($0.05 < p < 0.1$)

Dependent variable	Explanatory variable	F	p
SL mean	Feeding treatment × breeding type	0.187	0.670
	Breeding type	0.008	0.931
	Group size	4.365	**0.043**
	Feeding treatment	5.876	**0.023**
SL of smallest fish	Group size	0.167	0.685
	Feeding treatment × breeding type	1.757	0.197
	Breeding type	0.171	0.686
	Feeding treatment	2.428	0.132
SL of largest fish	Feeding treatment × breeding Type	0.230	0.637
	Breeding type	0.002	0.962
	Group size	3.494	*0.069*
	Feeding treatment	8.904	**0.007**
SL CV	Group size	0.531	0.471
	Feeding treatment × breeding type	0.614	0.442
	Breeding type	0.259	0.618
	Feeding treatment	1.309	0.265
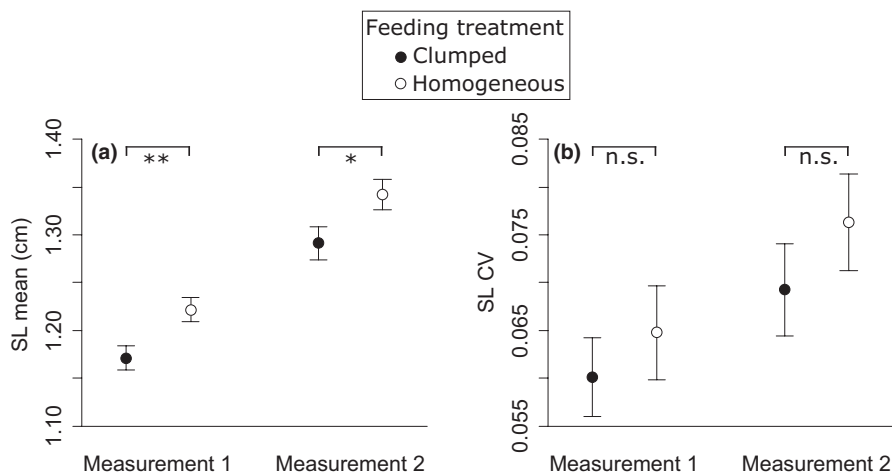
FIGURE 1 Shown are plots of mean values of (a) groups' mean standard length (SL mean) $\pm SE$ and (b) within-group coefficients of variation of standard length (SL CV) $\pm SE$ at measurements 1 and 2. Filled circles show means of groups that were raised under the clumped feeding treatment and blank circles represent means of groups that received the homogeneous treatment. $**p < 0.01$, $*p < 0.05$, n.s. $p > 0.05$

TABLE 3 Linear mixed-effects models for the shoaling assay including the groups' mean SL. As randoms factor, clutch ID nested in family combination were included in each model. The degrees of freedom always differed by one during stepwise model reduction. Significant p-values are printed in bold ($p < 0.05$)

Dependent variable	Explanatory variable	F	p
mean IID	Feeding treatment × breeding type	0.157	0.697
	Breeding type	0.991	0.335
	Feeding treatment	1.802	0.196
	Mean SL	1.806	0.193
IID CV	Feeding treatment × breeding type	0.134	0.717
	Mean SL	0.460	0.502
	Breeding type	0.690	0.412
	Feeding treatment	5.152	**0.033**
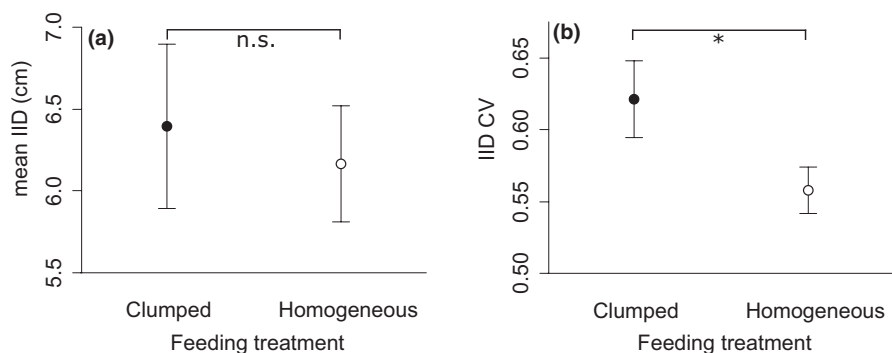
FIGURE 2 Shown are plots of mean values for (a) the mean inter-individual distance (mean IID) $\pm SE$ and (b) the coefficient of variation of inter-individual distance (IID CV) $\pm SE$ for groups of fish raised under the clumped (filled circles) and homogeneous feeding treatment (blank circles). $*p < 0.05$, n.s. $p > 0.05$

through the tank in dense shoals, juvenile *P. pulcher* may encounter clumped food patches less often because shoals seem to detect food rather randomly. Accordingly, larger groups have been shown to find food faster (Day et al., 2001), resulting in an increased food intake (Hamilton & Dill, 2003). The positive correlation between body size and group size in the present study highlights the importance of social foraging at this juvenile stage (see also Hesse & Thünken, 2014).

Small body size can be associated with reduced fitness. Size-selective mortality can act on smaller members of a population because they lack energy reserves (Moss et al., 2005) and are more vulnerable to predation (reviewed in Sogard, 1997). Moreover, smaller individuals are more likely to be targeted by conspecifics stealing resources from other group members (Phillips et al., 2018)

and hungry fish perform risky behaviours more often (Balaban-Feld et al., 2019). Even if individuals were able to compensate body size at later life stages, for example, if food availability improves (Jespersen & Toft, 2003), the poor condition experienced during early life may still result in decreased offspring production (Auer et al., 2010; Vega-Trejo et al., 2016b).

The experimental fish preferred to shoal with the larger shoal, which confirms the results of previous studies on other fishes (e.g. Thünken et al., 2014; Varma et al., 2020). The large shoal preference was not affected by the feeding treatment. However, the preference of focal fish reared under the *clumped* feeding treatment was influenced by the position of the groups' largest fish: focal fish significantly increased their association preference for the large shoal when it contained the largest individual of their group. In focal fish

receiving the *homogeneous* feeding treatment, we did not find this effect. The condition of individual fish appears to affect large shoal size preferences in juvenile *P. pulcher* reared under limited food distribution. Under these conditions, associating with well-conditioned individuals might imply benefits because larger individuals forage more efficiently and may contribute valuable foraging information to conspecifics (reviewed in Ward et al., 2006, 2020). The use of social information was documented in various fish species (Ward et al., 2011; Webster & Laland, 2012), can be transmitted actively via
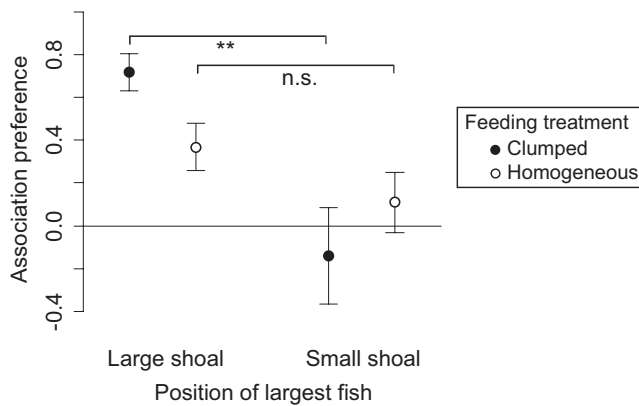
FIGURE 3 Shown are plots of mean values $\pm$ *SE* of the association preference of the focal fish, depending on the position of the groups' largest fish within the experiment and separated for the feeding treatment groups clumped (filled circles) and homogeneous (blank circles). **$p < 0.01$, n.s. $p > 0.05$

behavioural display or inadvertently via chemical cues (reviewed in Gil et al., 2018) and can increase foraging success for less successful foragers (reviewed in Bijleveld et al., 2010). Furthermore, individuals may benefit from inadvertent social information by following successful foragers to food patches (reviewed in Bijleveld et al., 2010). Our result adds to the increasing number of studies showing that large association preferences are more complex than assumed (e.g. Cote et al., 2012, reviewed in Biro & Stamps, 2008). Consequently, several environmental factors seem to drive association preferences and performance of fish shoals, rather than the group size as the sole criterion, which is in line with findings of previous studies (Armstrong et al., 2019; Fischer & Frommen, 2013).

In the shoaling assay, we did not observe a reduction in shoal density in juveniles receiving the *clumped* feeding treatment, which contradicts our expectation of enhanced competition avoidance in this treatment group. In line with the absence of size variation and the non-differing shoal size preferences, this might indicate that food competition did not vary to a great extent between the feeding treatment groups. However, shoals reared under the *clumped* feeding treatment showed higher variance of inter-individual distances compared to groups of the *homogeneous* treatment. This confirms the expectations, since an increased variance of inter-individual distances can reflect the formation of sub-groups or individuals moving further away from the shoal, which might indicate competition avoidance or increased foraging effort. Perceived competition affected kin-shoaling preference in closely related *Pelvicachromis taeniatus* (Thünken et al., 2020). For juvenile *P. pulcher*, leaving their shoal

TABLE 4 Linear mixed-effects models calculated for the shoal choice experiment. As random factors, clutch ID nested in family combination were included in each model. The degrees of freedom always differed by one during stepwise model reduction. Significant *p*-values are printed in bold ($p < 0.05$)

Dependent variable	Explanatory variable	F	p
Association preference	Feeding treatment × breeding type	0.114	0.739
	Feeding treatment	0.095	0.762
	Breeding type	0.213	0.649
	Group size	0.668	0.420
	Mean SL	1.769	0.192
Association preference	Feeding treatment × group size	0.082	0.777
	Group size	0.637	0.432
	Feeding treatment × breeding type	2.093	0.166
	Breeding type	0.679	0.425
	Feeding treatment × position largest fish	5.954	**0.024**

TABLE 5 Results of post-hoc pairwise group comparisons of association and interaction preferences shown in the two feeding treatment groups. Significant *p*-values are printed in bold ($p < 0.05$) and tendencies in italics ($0.05 < p < 0.1$)

Dependent variable	Pairwise comparison group 1	Pairwise comparison group 2	t	p
Association preference	*clumped*—largest fish in large shoal	*homogeneous*—largest fish in large shoal	1.981	*0.060*
	clumped—largest fish in small shoal	*homogeneous*—largest fish in small shoal	−0.998	0.330
	clumped—largest fish in large shoal	*clumped*—largest fish in small shoal	3.402	**0.002**
	homogeneous—largest fish in large shoal	*homogeneous*—largest fish in small shoal	0.685	0.499

is highly risky under natural conditions because they experience high predation pressure due to their small body size. Nonetheless, more risky foraging might be necessary for juvenile *P. pulcher* under challenging environmental conditions as simulated by the *clumped* feeding treatment. The higher behavioural variation among shoal members of the *clumped* feeding treatment groups might be a first indicator for the development of individual foraging efforts potentially resulting in resource monopolisation by these individuals. Thus, variation in more flexible behavioural traits may precede variation in access to food resources and thus growth.

Our findings are generalisable to other socially foraging animals that do not aggressively defend and monopolise food resources, which may especially occur in early life stages when aggressive behaviour has not yet developed. Beyond that, our study has more general implications for other systems. First, it is important to examine the effects of environmental variation across different life stages because individual responses may change across lifetime. Second, social and collective behaviour may play a major role for individual fitness in complex (nutritional) environments, which is in line with theoretical predictions (Lihoreau et al., 2017). Because individuals often respond to changing environments in behavioural traits first, the role of behavioural ecology should gain more attention in ecology in general and in biodiversity research in particular (Bro-Jørgensen et al., 2019).

Inbreeding neither affected growth nor any of the behavioural traits investigated. Furthermore, we did not find evidence for environment-dependent inbreeding effects. In line with these results, the closely related species *P. taeniatus* (Moliwe-population) shows no inbreeding depression in juvenile survival and growth (Thünken et al., 2007) nor reproductive performance of young, mature individuals (Langen et al., 2017). However, those fish originated from an isolated, inbred population, where continuous inbreeding has probably purged recessive deleterious alleles. Since microsatellite analyses showed much lower heterozygosity in the *P. taeniatus* Moliwe-population (Langen et al., 2011) than in the founder laboratory generation of the individuals used in the present study (Barbara Schiffer, SV, Ulrike Scherer, Julia Schwarzer, TT, unpublished data), purging is rather implausible to cause the absence of inbreeding depression. More likely, inbreeding depression might appear in future inbreeding generations due to increasing homozygosity and continuous mutations generating recessive deleterious effects (reviewed in Hedrick & Garcia-Dorado, 2016).

In conclusion, this is one of the few studies examining the effects of spatial distribution of food shortly after hatching. The effects differed from those revealed by other studies starting the food manipulation at later life stages in fishes (Jacobson et al., 2015; Kim et al., 2004). We show that the spatial food distribution did not affect variation of body size within groups. However, individuals reared under clumped food conditions were smaller, which may impair individuals' survival at this sensitive life stage. Furthermore, they preferred shoals with large individuals suggesting orientation at successful foragers. Finally, shoals of the clumped feeding group showed higher variation in shoal density potentially promoting a change in

foraging mode from collective to individualistic strategies. Thus, our study indicates that variation in spatial food distribution affects the development of fitness-related morphological and behavioural traits. In future research, we aim to further investigate the impact of spatial food distribution on ornament development and mate choice as well as on trade-offs among fitness-related traits, which are sensitive to environmental variation (Meuthen et al., 2018; Vitt et al., 2020).

CONFLICT OF INTEREST
We declare that we have no competing interests.

AUTHORS' CONTRIBUTIONS
T.T. conceived the idea of the project; R.F.S. and T.T. designed the experimental methodology supported by S.V.; R.F.S. collected and analysed the data; R.F.S. and T.T. wrote the manuscript supported by S.V. All authors contributed critically to the drafts and gave final approval for publication.

ETHICAL NOTE
This research was performed in accordance with the laws, guidelines and ethical standards of Germany, where the research was performed and conforms to Directive 2010/63/EU.

DATA AVAILABILITY STATEMENT
Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.51c59zw93 (Schons et al., 2021).

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