



## Behavioural types and ecological effects in a natural population of the cooperative cichlid *Neolamprologus pulcher*

Fardo Witsenburg<sup>a,b,c</sup>, Roger Schürch<sup>a,d</sup>, Oliver Otti<sup>a,e</sup>, Dik Heg<sup>a,\*</sup>

<sup>a</sup> Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern

<sup>b</sup> Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, The Netherlands

<sup>c</sup> Department of Ecology and Evolution, University of Lausanne, Switzerland

<sup>d</sup> Department of Evolution, Ecology and Organismal Biology, The Ohio State University, U.S.A.

<sup>e</sup> Animal and Plant Sciences, University of Sheffield, U.K.

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The ecological relevance of behavioural syndromes is little studied in cooperative breeding systems where it is assumed that the behavioural type might influence individual decisions on helping and dispersal (e.g. shy, nonaggressive and nonexplorative individuals remain philopatric and helpful, whereas bold, aggressive, explorative individuals compete for vacancies outside their group and disperse). We measured the behavioural type of 19 subordinates in the cooperatively breeding cichlid fish *Neolamprologus pulcher* in their natural environment by quantifying six behavioural traits up to four times ('trials') in three different contexts, by presenting them with a conspecific intruder, a predator or nothing inside a tube. We found only moderate within-context repeatability (intraclass correlation coefficients) of the focal individual's behaviour, except for attacking either the conspecific or the predator inside the tube. The focal individual's attack rate of the tube was also positively affected by its group size. Averaging traits per context removed the between-trial variation, and consequently the across-context repeatability was very high for all six traits, except for territory maintenance. Trait values depended significantly on the context, except for territory defence. Consequently, individuals could be classified into different behavioural types based on their reaction towards the tube, but surprisingly, and opposite to laboratory studies in this species, ranging propensity and territory maintenance were not included in this behavioural syndrome. We suggest that more studies are needed to compare standardized focal personality tests (e.g. exploration propensity) with actual behaviour observed in nature (e.g. ranging and dispersal).

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Individuals in a wide range of animal taxa vary consistently in their behavioural (Wilson 1998; Sih et al. 2004b), physiological (Koolhaas et al. 1999) and neurological (Miczek et al. 2002; Øverli et al. 2007) reactions to different environments or stimuli, such as novel environments (Verbeek et al. 1994), stressors (Boissy 1995; Weinstock 1997), predators (Magurran 1993; Sih et al. 2003; Dingemanse et al. 2009), mates (Both et al. 2005; Johnson & Sih 2005) and group members (Armitage 1982; Korzan & Summers 2007). A 'behavioural type' is the collection of consistent behavioural trait values for one individual (Sih et al. 2004a; Réale et al. 2007; Sih & Bell 2008). A correlation of these individual behavioural traits at the population level is defined as a behavioural

syndrome: 'a suite of correlated behaviours reflecting between-individual consistency in behaviours across multiple situations' (Sih et al. 2004a, 372).

Alternative life history strategies with equal lifetime fitness might select for specific behavioural trait combinations best adapted to different strategies (Wolf et al. 2007, 2008). Essentially, animals differing consistently in their behaviour are predicted also to differ consistently in their life histories; thus, certain behavioural types can be found at certain locations on two or more dimensional life history trade-off curves (Walters et al. 1992; Réale et al. 2000; Boon et al. 2007; Stamps 2007; Schürch & Heg 2010a), for instance the trade-off between current and future reproduction.

The causes and consequences of behavioural syndromes have been well studied in fish (e.g. Huntingford 1976a; Wilson et al. 1993; Budaev 1997a; Sneddon 2003; Moretz et al. 2007; Brown et al. 2007b; Schürch & Heg 2010a). Owing to their indeterminate growth and strong between-population differences in their

\* Correspondence: D. Heg, Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland.

E-mail address: [dik.heg@iee.unibe.ch](mailto:dik.heg@iee.unibe.ch) (D. Heg).

environment (e.g. predation risk: Rodd et al. 1997; Brydges et al. 2008; Magnhagen & Borcharding 2008), fish are particularly likely to show growth-dependent life history trade-offs generating behavioural syndromes (Chiba et al. 2007; Stamps 2007; Biro & Stamps 2008). This body size-dependent expression of behavioural types in fish has been found in several studies (Brown & Braithwaite 2004; Schürch & Heg 2010a; but see De Kerckhove et al. 2006).

Behavioural types also affect sociality in various and often intricate ways, or rather they may interact and modify each other (Budaev 1997b; Magnhagen 2007; Webster et al. 2007; Pike et al. 2008; Harcourt et al. 2009). Less well explored are the effects of behavioural types on sociality in a cooperatively breeding species (but see Bergmüller & Taborsky 2007; Schürch & Heg 2010a, b). In such species, smaller subdominant group members ('helpers') assist the larger dominant breeding pair in raising their offspring (Taborsky & Limberger 1981; Heg & Bachar 2006), but subordinates may also engage in reproduction themselves (Dierkes et al. 1999; Heg & Hamilton 2008; Stiver et al. 2009). Cooperatively breeding animals are particularly likely to show variation in behavioural types generated by life history trade-offs (West-Eberhard 1975; Armitage 1991). For instance, extending the reasoning of Biro & Stamps (2008), risk-prone subordinates leave home as soon as possible and do not help, whereas risk-averse subordinates stay at home and help, which should scale on the bold–shy continuum (Réale et al. 2007) and social behaviours such as dominant–subordinate aggression and expulsion (Schürch & Heg 2010a, b). Indeed, cichlids (see references above) and other species (Heinsohn & Packer 1995; Arnold et al. 2005; Starks & Fefferman 2006) show consistent variation in cooperative propensity.

We investigated behavioural types in a natural population of the cooperatively breeding cichlid *Neolamprologus pulcher*. Previous work has described the bold–shy continuum in this species (Bergmüller & Taborsky 2007; Schürch & Heg 2010a) in a laboratory population raised from a parental population obtained from the same study site as our current study site. Here we aimed at finding a similar behavioural syndrome in a wild population and how this relates to the ecology of this cooperatively breeding species. We measured behavioural traits of focal subordinate individuals in three different contexts in the field (predator exposure, conspecific intruder exposure and control). Using this setting, we tested: (1) for consistency within and across contexts of behavioural traits; (2) whether behaviour is additionally modified by ecological factors; and (3) whether the bold–shy continuum in the field is similar to the one found in the laboratory. Finally, we discuss how well standardized laboratory-based personality tests predict similar behaviours measured in nature.

## METHODS

### *Study Species and Site*

We studied two colonies of *N. pulcher* 400 m offshore at Kasakalawe point, near the Zambian town of Mpulungu at the southern tip of Lake Tanganyika (8°46.849' S, 31°04.882' E). At this site, *N. pulcher* breeds at a depth of 9–13 m on a rocky or pebbled substrate interspersed with sandy stretches (Heg et al. 2008). Throughout the study period (30 September 2007 to 7 December 2007) preparations and observations were done by SCUBA diving.

*Neolamprologus pulcher* is one of the 19–21 cooperatively breeding cichlid species in Lake Tanganyika (Heg & Bachar 2006). A dominant male breeds with one to several females within a defended territory, consisting of a few stones providing shelters (Taborsky & Limberger 1981; Limberger 1983). A colony consists of

many of these clustered territories that share common boundaries (Heg et al. 2008). The breeding pair receives help from sexually mature helpers that themselves usually refrain from breeding but instead help in fanning the eggs, protecting fry, cleaning and digging out shelters and maintaining the territory (Taborsky 1984; Balshine et al. 2001; Heg et al. 2005). Dispersal to other groups occurs mainly within the same colony, but some large males disperse further away to other colonies (Stiver et al. 2004, 2007) and both sexes may inherit the territory from the dominant same-sex group member, if he or she disappears (Balshine-Earn et al. 1998; Stiver et al. 2006; Fitzpatrick et al. 2008).

For all 124 breeding groups within the study site, the family compositions were assessed and their exact location determined. In 30 groups we caught one individual helper fish each, using a transparent acrylic glass tube and hand net. We did not catch these individuals randomly but selected a priori similarly sized individuals, thus minimizing the sampling bias for bold behavioural types and easy to catch individuals (Biro & Dingemans 2009). These 30 helpers were measured for body size (standard length SL mm, to the nearest 0.5 mm using a measuring board), sexed by visually examining their gonadal pore and individually marked with fin clips. All catching and handling of the fish was done while SCUBA diving by R.S. The caught fish were released immediately after marking and were not disturbed for the next 24 h. It was necessary for most helpers to be re-marked once during the testing period, using the above-described protocol. When all the observations had finished, the majority of these individuals were recaptured and measured a third time.

To assess whether the frequency of interactions with conspecifics, heterospecific shelter competitors and predators depended on the densities of these opponents around the focal individual's territory, we mapped the breeding territories of all fish occurring in the study area and counted the individuals per territory (usually only a breeding pair). For this purpose we laid a 22 × 12 m grid made of rope with 2 × 2 m squares over the study area. The local conspecific density was calculated from the territorial mapping and number of fish present per territory in a 1 × 1 m square around each focal individual's territory. The local heterospecific shelter competitor density was obtained by summing the numbers of *Julidochromis ornatus*, *Neolamprologus caudopunctatus*, *Neolamprologus modestus*, *Telmatochromis temporalis* and *Telmatochromis vittatus* around the focal individual's home territory in a 1 × 1 m square. The local predator density was measured by observing every 2 × 2 m square of our grid in the study area for 90 s and counting the individuals for the 21 fish species that were present (conducted by O.O.). These counts included predators, heterospecific shelter competitors and other fish (see Heg et al. 2008 for a list of all the species occurring in the area), but only data on the (roaming) predators were used, since for the territorial, and thus stationary, competitor species the mapped data (see above) proved to be more accurate. These data were used to calculate the local predator density for every focal individual's territory in a 2 × 2 m square around the home territory (by adding the numbers of eels from the family Mastacembelidae, catfish *Synodontis* spp., and the cichlids *Altalamprologus calvus*, *Gnathochromis pfefferi*, *Lamprologus callipterus*, *Lamprologus lemairii*, *Lepidiolamprologus elongatus*, *Lepidiolamprologus attenuatus*, *Lobochilotes labiatus*, *Neolamprologus sexfasciatus*, *Neolamprologus tetracanthus* and *Perissodus microlepis*). The 2 × 2 m square around each territory overlapped with parts of the four grid squares for which we had counts of predators around the territory. Therefore, the predator density of the 2 × 2 m square around territory *i* was calculated as  $N_i = \sum_{k=1}^4 N_k \times p_{ki}$ , where  $N_k$  is the number of predators in square

$k$  and  $p_{ki}$  is the proportion of overlap of square  $k$  with the square of territory  $i$ .

## Experiment

### Experimental design

From the 30 marked fish, 19 individuals were selected for focal observations, based on equal sex ratios and spaced throughout the colonies (from rim to centre). The focal fish were caught one to three times (once:  $N = 1$ ; twice:  $N = 3$ ; thrice:  $N = 15$ ) and did not change in body size during this short study period, so the body sizes were averaged per individual for the remainder of the analyses. Body length of these focal fish ranged from 41.7 to 47.5 mm in males (mean  $SL \pm SD = 43.9 \pm 1.92$  mm;  $N = 9$ ), and from 35.3 to 48.3 mm in females (mean  $SL \pm SD = 44.4 \pm 3.6$  mm;  $N = 10$ ). Males and females were of similar sizes (ANOVA:  $F_{1,17} = 0.16$ ,  $P = 0.70$ ). To test for consistency in behaviour within and across different contexts, these helpers were exposed to three different contexts, by presenting a transparent acrylic glass tube in the middle of the focal individual's territory. In the first context the tube contained a conspecific intruder (mean  $SL \pm SD = 45.3 \pm 3.5$  mm, range 38–54 mm, 18 males, 43 females, 6 of unknown sex,  $N = 67$  presentations), in the second context the tube contained the natural piscivore predator *L. elongatus* (mean  $SL \pm SD = 79.3 \pm 7.0$  mm, range 59–95 mm, all unknown sex,  $N = 68$  presentations), and the third context was an empty tube. The conspecific intruder and the predator were caught outside the study area and kept in underwater cages between trials for up to 2 (*N. pulcher*) and 4 days (*L. elongatus*).

### Behavioural observations

After placement of the transparent tube in the focal individual's territory, all behaviours performed by the focal fish (including aggression towards the tube) and its location were recorded for 10 min. All observations were conducted by F.W. (sitting 1–2 m away from the focal territory). One to two minutes after the observer had spotted the marked individual at the site, he placed the transparent tube in the territory and immediately started recording: (1) feeding (each bite was counted); (2) territory maintenance (carrying sand in the mouth and spitting it away from the shelter or digging away sand from the shelter by tail beating); (3) aggression (included overt aggression: biting, ramming, chasing, charging; and restrained aggression: spreading fins, spreading gills, head down); (4) affiliation (slow approach or joining a conspecific) and submission (tail quivering or zig-zag swimming with a conspecific). For (3) and (4) we also noted the opponent of the focal individual (conspecific, heterospecific shelter competitor, predator or the individual in the tube). Similarly, if behaviours (3) or (4) were directed towards the focal individual, this and the actor of the behaviour were noted (abbreviated as 'received' throughout). All behaviours were scored as frequencies per minute the focal individual was within sight.

The location and movements were recorded by noting each visit to a conspecific or heterospecific territory within the study area, where the focal individual was on the territory and if it also entered the shelter. This allowed us to calculate the average distance moved (average of all movements from territory  $i$  to another territory  $j$ ), the total movement (summing the distances of all movements), the maximum distance moved away from the home territory (all in cm), the number of different territories visited (where the minimum is 1: the focal individual's territory), and the total number of territory visits (where each territory visit is counted). Movements were not corrected for the time the focal individual was in sight, since

none of these parameters depended on the proportion of time the focal individual was in sight (regression analyses: all  $P > 0.5$ ).

The three different contexts (conspecific, predator in the transparent tube, empty) were presented consecutively in random order within one trial, resulting in  $3 \times 10$  min of observations for one trial. If the focal individual had gone too far from the territory to see the tube, the observer would wait to place the new tube until it had returned to the territory. These three contexts were presented four times (trials) to each of the 19 focal helpers with intervals of 5–18 days between the trials (mode 8 days). Four focal males disappeared during the study period. Therefore, 15 focal helpers received four trials, one focal helper received three trials (left the territory permanently before the empty tube and conspecific in tube could be presented in the last trial), two focal helpers received two trials, and one focal helper received one trial only. We performed a total of 202 tests ( $15$  individuals  $\times 3$  contexts  $\times 4$  trials = 180,  $1$  individual  $\times 3$  contexts  $\times 3$  trials = 9,  $2$  individuals  $\times 3$  contexts  $\times 2$  trials = 12, and  $1$  individual  $\times 3$  contexts  $\times 1$  trial = 3, total = 202).

### Ethical Note

The conspecific fish and predators used for the presentations inside the transparent tube were released after the experiment near to their catching site and did not show any abnormal behaviour after they were released. The holding period of these fish was kept to a minimum, to avoid the fish having problems in re-establishing themselves at their catching site. This study was licensed under the Ministry of Agriculture & Cooperatives of Zambia, and complies with the laws of that country.

### Statistical Analysis

All analyses were performed in SPSS 17.0 (Norušis 2007). The frequencies of behaviours per minute shown and received, and the movements, were summarized using a categorical principal component analysis CatPCA ( $N = 202$ , see the Appendix, Meulman & Heiser 2005). CatPCA allows for spline transformations of the majority of the continuous variables and the inclusion of otherwise rare behaviours (i.e. received behaviours in our case) by interval transformations not amendable in a standard PCA; it also amends the potential nonlinear relationships between the correlated variables that occur when using transformations (e.g. frequencies cannot go below zero and ranging distance might exponentially approach a certain maximum threshold, all of which are complications not amendable in a normal PCA, which assumes all variables, in principle, may vary between minus and plus eternity and show linear relationships). Concerning the latter point, the CatPCA uses an algorithm to search for the optimal combinations of transformations for each variable leading to the best correlation structure (Meulman & Heiser 2005).

As expected, the empty tube was ignored by 18 of the 19 focal fish (only approached aggressively once by one focal helper, showing gill spreading), so therefore aggression towards the tube could not be entered into the CatPCA and needed to be analysed separately. Feeding rate and territory maintenance had intermediate loadings on two different CatPCs, and therefore also had to be analysed separately (see Appendix). The CatPCA extracted three components with eigenvalues larger than 1 and with a Cronbach's  $\alpha$  of 0.94 for the total eigenvalue of 7.555, indicating that a substantial and consistent proportion of variation was explained by these three principal component scores: (1) 'ranging propensity' (with high loadings of all movement parameters); (2)

'conspecific interactions' (with high loadings of aggression, affiliation/submission towards conspecifics); and (3) 'territory defence' (with high loadings of aggression towards heterospecific competitors and predators); see the Appendix. These three CatPCs were used for the analyses and explained 58.1% of the variance (see Appendix).

However, since the 202 observations contain repeated measures of the same individuals over three contexts, which may be problematic (see Budaev 2010), we validated this CatPCA model using two methods. First, we reran the CatPCA model 100 times, each time drawing 50 observations out of the 202 observations. The eigenvalues of the CatPCA scores were significant in each of the 100 models and comparable to the overall CatPCA containing all 202 observations (means  $\pm$  SD, range): ranging propensity ( $4.89 \pm 0.18$ , 4.44–5.27), conspecific interactions ( $1.96 \pm 0.19$ , 1.61–2.54) and territory defence ( $1.57 \pm 0.15$ , 1.22–1.99). Second, we reran the CatPCA model for each of the three contexts separately (empty tube, conspecific or predator in tube), and compared their three principal component scores pairwise with the three principal component scores obtained from the overall model (containing data of all three contexts). Note that the focal fish did not receive submission from the predator inside the tube, so this parameter had to be removed from the CatPCA for this context. Overall, scores obtained from a CatPCA per context (empty tube:  $N = 67$ ; conspecific intruder:  $N = 67$ ; predator:  $N = 68$ ) matched the CatPCA scores obtained over all three contexts together well ( $N = 202$ , Pearson correlations for ranging propensity, conspecific interactions and territory defence, respectively): empty tube context score versus all three contexts score ( $r_{65} = 0.996$ , 0.824, 0.652, all  $P < 0.001$ , respectively); conspecific intruder context score versus all three contexts score ( $r_{65} = 0.976$ , 0.520, 0.315,  $P < 0.001$ ,  $< 0.001$ , 0.009, respectively); predator context score versus all three contexts score ( $r_{66} = 0.992$ , 0.957, 0.696, all  $P < 0.001$ , respectively).

Consistency within the contexts was analysed using variance component analysis of the four trials of the 15 individuals per context, using the RELIABILITY procedure in SPSS. SPSS reports the absolute agreement intraclass correlation coefficient, which is a measure of average consistency of the measures (also known as 'repeatability', ranging between 0 and 1) of the behaviour, in other words whether the trials are able to reach absolute agreement on the behavioural traits of the focal individual. Significance is tested against the null hypothesis of no agreement (repeatability = 0) using  $F$  tests. Consistency across contexts was analysed similarly on the averages per context per individual ( $N = 19$ ). Correlations between behavioural traits were analysed using Pearson correlations.

Furthermore, we tested for modifying effects of the focal individual's body size and sex (as previously described: Taborsky 1984, 1985; Stiver et al. 2005; Brintjes & Taborsky 2008; Schürch & Heg 2010a) and densities of fish (Heg et al. 2008) on the six behavioural traits separately, using general linear mixed models (GLMM), with the fixed effect of context, and random effect of the focal individual identifier. Owing to the limited sample size ( $N = 202$ , but only for  $N = 19$  individuals), interactions were not tested (note that the main effects were only determined once per focal individual). Per trait we tested for those parameters that are likely to affect the focal individual's behaviour: (1) feeding rate, log (feeding rate + 1) transformed before analyses: (a) focal group size (number of group members  $> 25$  mm SL) and (b) conspecific density (i.e. potential food competitors); (2) territory maintenance: (a) focal group size (i.e. owing to potential load-lightening effects, Balshine et al. 2001; Brouwer et al. 2005); (3) aggression towards the tube with either conspecific or predator: (a) focal group size (i.e. owing to potential load-lightening

effects or joint territory defence); (4) ranging propensity: (a) predator density (i.e. predation risk may curb movements away from protective shelter inside the focal individual's group, Heg et al. 2004a); (5) territory defence: (a) heterospecific and (b) predator density (i.e. territory defence is expected to increase if densities are higher); (6) conspecific interactions: (a) group size and (b) conspecific density (i.e. interactions are expected to increase with increasing number of conspecifics in the neighbourhood).

The sex (male, female or unknown) and size of the conspecific intruder inside the tube did not affect the focal individual's aggression shown towards the tube ( $N = 67$  presentations, GLMM corrected for random individual identifier effect, effects of: focal body size:  $F_{1,46.5} = 1.0$ ,  $P = 0.31$ ; intruder body size:  $F_{1,45.3} = 1.0$ ,  $P = 0.32$ ; focal body size\*intruder body size:  $F_{1,45.7} = 1.2$ ,  $P = 0.28$ ; focal sex:  $F_{1,34.6} = 0.04$ ,  $P = 0.84$ ; intruder sex:  $F_{2,57.2} = 0.04$ ,  $P = 0.96$ ; focal sex\*intruder sex:  $F_{2,57.5} = 1.0$ ,  $P = 0.38$ ), so the analyses were not corrected for these effects. Similarly, the size of the predator inside the tube did not affect the focal aggression shown towards the tube ( $N = 68$  presentations, GLMM corrected for random individual identifier effect, effects of: focal body size:  $F_{1,53.9} = 0.05$ ,  $P = 0.83$ ; intruder body size:  $F_{1,53.3} = 0.03$ ,  $P = 0.87$ ; focal body size\*intruder body size:  $F_{1,53.1} = 0.03$ ,  $P = 0.87$ ), so again the analyses were not corrected for these effects.

Finally, to evaluate the variation in behavioural types, we needed to compare behavioural measures that are independent of each other. Therefore, we assessed the behavioural types of the focal individuals by comparing their ranging principal component when the tube was empty as a measure of ranging propensity (as the tube was empty the focal fish were not distracted by attacking the tube and could show their natural exploration behaviour), their aggressive reaction to the conspecific intruder inside the tube as a measure of aggression propensity (as intruders were similar in size to the focal individual tested and therefore may pose a threat to the focal individual's current position within his/her group), and their aggressive reaction to the predator in the tube as a measure of boldness (as attacking a predator exposes the focal individual to predation risk, where *N. pulcher* group members typically show risk avoidance: Heg & Taborsky 2010). All measures were averaged over the trials per individual; the latter two were log (aggression + 1) transformed before the Pearson correlation analyses.

**Table 1**

Behavioural consistency within contexts ( $N = 4$  tests per context of 15 individuals) and across contexts ( $N = 19$  individuals, traits averaged per context before analyses)

Behavioural trait	Within contexts			Across contexts	
	Empty	Conspecific	Predator	Consistency	Difference ( $F$ )
Feeding rate†	0.319	0.386	0.248	0.828***	17.3***
Territory maintenance†	0.099	-0.123	0.590*	0.132	12.0**
Aggression towards the tube†		0.521*	0.649**	0.649**	3.7*
Ranging propensity‡	0.428	0.714***	0.282	0.832***	5.3**
Territory defence‡	0.352	0.125	0.310	0.624**	1.5
Conspecific interactions‡	0.361	0.434	0.594*	0.804***	7.7**

The table gives the average measures intraclass correlation coefficients ('repeatability'). Asterisks represent their associated  $P$  values, which tested whether the coefficients are significantly different from 0. Also given are the  $F$  values testing for the significance of differences across contexts ( $df = 2$ , except for aggression towards tube:  $df = 1$ ).

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

† In frequencies per minute within sight. Note that aggression towards the empty tube was virtually absent and not used for the analyses.

‡ Categorical principal components.

## RESULTS

### Consistency within Contexts

The aggression towards the tube containing a conspecific intruder or predator that we experimentally invoked appeared highly repeatable (Table 1). In contrast, the other five behavioural traits not under our experimental control (feeding, territory maintenance and the three extracted components; see the Appendix) showed overall low levels of within-individual consistency (Table 1,  $N = 15$ ). The low repeatability in these traits suggests a high liability to day-to-day variation. In the empty tube context, none of the five traits showed a significant repeatability (Table 1, although ranging propensity approached significance:  $P = 0.08$ ), indicating that individuals react rather randomly to the tube's presence in their territory. In the conspecific intruder context, ranging propensity showed a significant repeatability, and in the predator intruder context, territory maintenance and conspecific interactions showed a significant repeatability (Table 1).

### Consistency across Contexts

For the analysis of the consistency across contexts, the behavioural traits were averaged per individual over all the test trials to remove the daily variation in their traits (this also allowed us to incorporate the four individuals for which we did not have a complete trial record, so  $N = 19$ ). All traits, except territory maintenance (Fig. 1b, which had also the lowest within-context repeatability in two contexts), showed a high and significant repeatability (Fig. 1a–f, Table 1). Focal individuals that attacked the predator inside the tube at high frequencies also attacked the conspecific intruder inside the tube at high frequencies (Fig. 1c, note the one outlier which was nevertheless tested in four trials: removing this outlier resulted in a consistency of 0.597, which remained significantly different from zero:  $P = 0.004$ ).

### Differences between Contexts

The individual fish significantly changed five of their six behavioural traits measured between the three different contexts (Fig. 2, Table 1,  $F$  tests): focal fish fed at a higher rate when the tube presented was empty (Fig. 2a), showed hardly any territory maintenance when the transparent tube contained a predator (Fig. 2b), attacked the conspecific inside the tube more than the predator inside the tube (Fig. 2c), showed less ranging behaviour when a conspecific was in the tube (Fig. 2d), and was involved in fewer conspecific interactions in the predator context and more interactions in the conspecific context (Fig. 2f). The only trait not showing significant differences between contexts was territory defence (Fig. 2e, last column Table 1).

### Modifying Effects

We detected three modifying effects of the focal individual's body size, its sex or densities of fish on the behavioural traits (Table 2). As in the previous analyses, context had an effect on all behavioural traits, except territory defence (Table 2), so these were corrected for. Group size had a significant positive effect on the aggression towards the conspecific or predator inside the tube ( $P = 0.033$ , coefficient  $\pm$  SE =  $0.049 \pm 0.021$ ; note that the effect of sex tended towards significance:  $P = 0.064$ , coefficient  $\pm$  SE =  $-0.119 \pm 0.059$  less aggression by the females than the males). Group size ( $P = 0.013$ , coefficient  $\pm$  SE =  $0.233 \pm 0.081$ ) and focal individual's sex

( $P = 0.034$ , coefficient  $\pm$  SE =  $0.462 \pm 0.198$  for females, 0 for males, the reference category) both significantly affected the conspecific interactions (Table 2).

### Correlations between Behavioural Traits

The CatPC analysis indicated that correlations between behavioural traits were rare, since all movements, territory defence, territory maintenance and conspecific interactions loaded onto a different component (i.e. correlations between the traits loading on different components were very low, ranging between Pearson  $r_{200} -0.148$  and  $+0.221$ , see Appendix).

The correlations between feeding rate, territory maintenance or aggression towards the tube and the principal components are indicative of trade-offs between behavioural traits: attacking the tube was significantly negatively related to feeding rate, ranging propensity and territory defence; whereas all other correlations were weak and nonsignificant (Table 3).

### Behavioural Syndrome

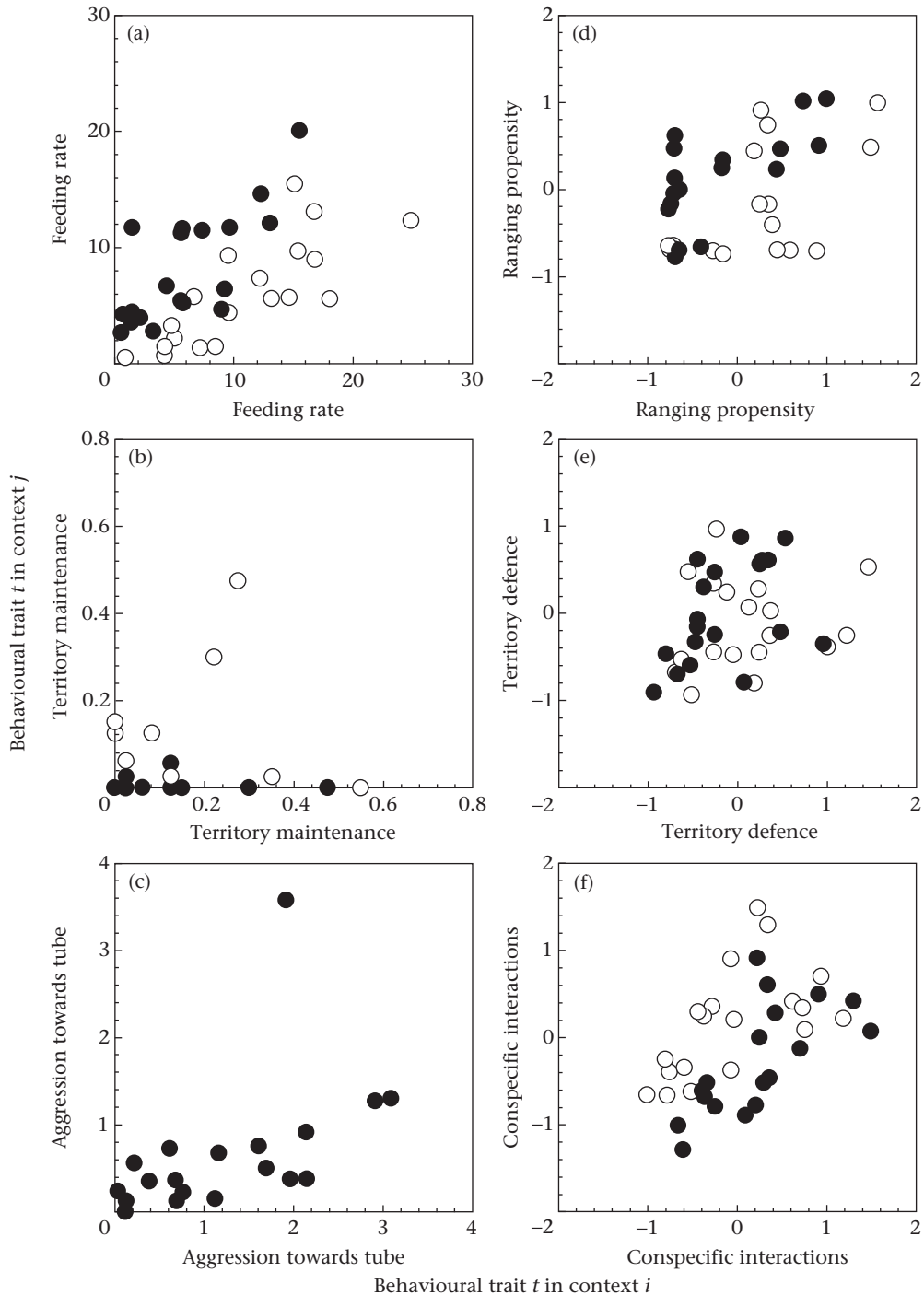
As the negative correlations between traits are suggestive of trade-offs (Table 3), we compared independent tests to score the behavioural type of the focal individuals. Ranging propensity was not correlated with any other trait (versus aggression propensity:  $r_{17} = -0.29$ ,  $P = 0.23$ ; versus boldness:  $r_{17} = -0.42$ ,  $P = 0.077$ ). In contrast, both aggressive propensity and boldness were strongly correlated ( $r_{17} = 0.61$ ,  $P = 0.006$ ). Finally, we compared the growth potential of each focal fish with the three above-mentioned measures, using feeding rate in the empty tube context as a proxy for growth potential. Feeding rate (log + 1 transformed) correlated significantly with ranging propensity ( $r_{17} = 0.48$ ,  $P = 0.036$ ), but not with aggression propensity ( $r_{17} = -0.06$ ,  $P = 0.82$ ) and boldness ( $r_{17} = -0.22$ ,  $P = 0.36$ ).

## DISCUSSION

We explored the natural variation in behavioural type of a cooperatively breeding species in ecologically relevant contexts. We found little within- but high across-context repeatability and could only partially reproduce the behavioural syndrome found in previous laboratory studies in this species (Bergmüller & Taborsky 2007; Schürch & Heg 2010a, b).

### Repeatability Within and Across Contexts

We found that the behavioural consistency within contexts was low (compare Bell et al. 2009: average repeatability from a meta-analysis was 0.30) and significant for only a few traits in a single context (see Table 1). Moreover, behaviour was never consistent in the empty tube context, which can be considered as the least invasive manipulation. This suggests that daily variation in ecological conditions was mostly responsible for the observed variation in behaviour, for example feeding behaviour may be induced by zooplankton blooms (high densities of zooplankton passing through the colonies with the current; Gashagaza 1988), territory maintenance may be induced by the need to remove sand from the shelters after recent storms, and territory defence may be induced by groups of predators or competitors entering the territory. In contrast, aggression towards the conspecific intruder or predator inside the tube were both significantly consistent (within and across contexts), and correlated highly with each other (Huntingford



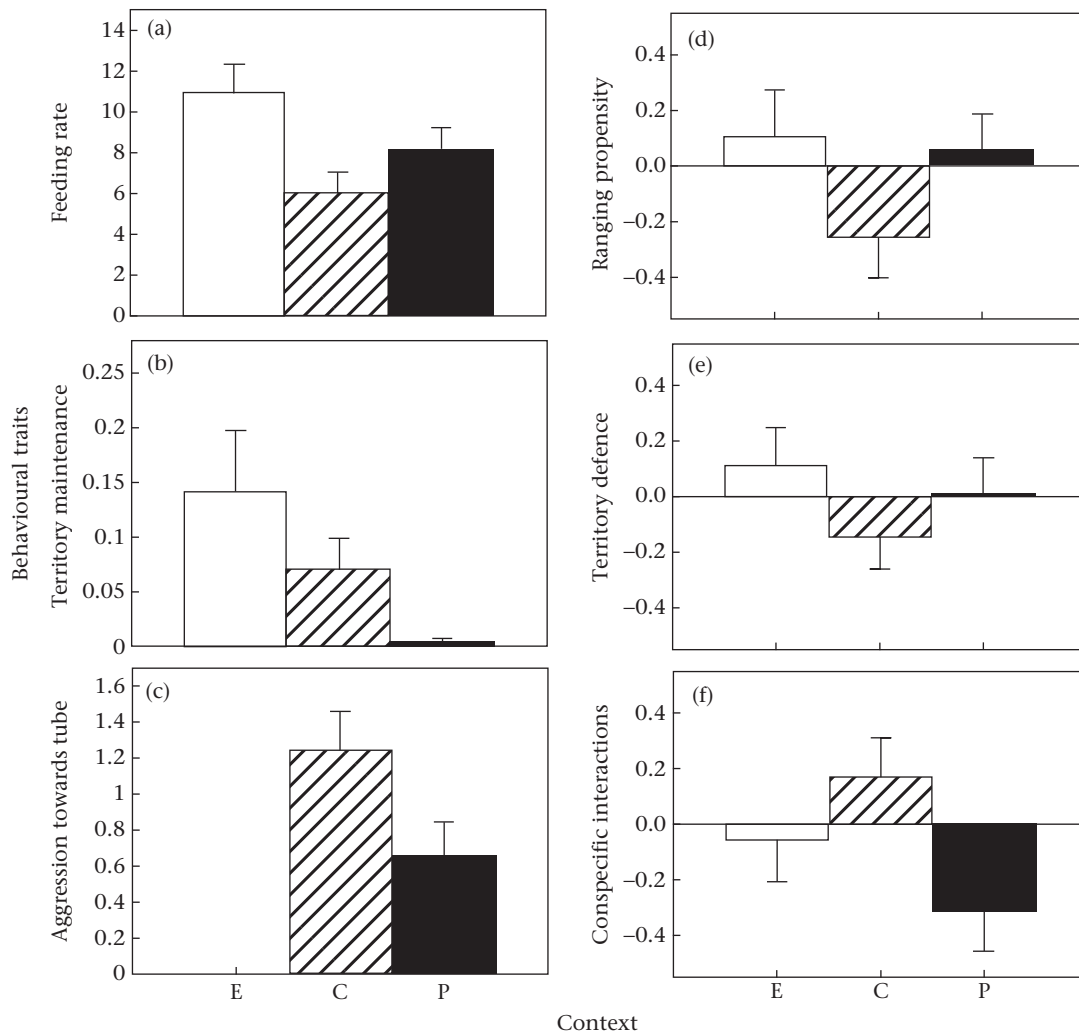
**Figure 1.** Consistency in behavioural traits across contexts ( $N = 19$  individuals, data averaged per individual per context). White circles: conspecific in tube context (Y axes  $j$ ) versus empty tube context (X axes  $i$ ); black circles: predator in tube context (Y axes  $j$ ) versus conspecific in tube context (X axes  $i$ ). The measures in (a)–(c) are frequencies per minute in sight and (d)–(f) are categorical principal components (see [Appendix](#)).

1976a, b). Our experimentally induced aggression against the intruder in the tube is highly repeatable and therefore seems less liable to daily variation than the other measured behavioural traits.

Averaging traits per context removed this daily variation, increasing the across-context consistency to a high and significant degree for all traits, except territory maintenance. Results on within- and across-context repeatability in other species are

ambiguous. Some studies found patterns similar to the present study (Sih et al. 2003; Ward et al. 2004), whereas others found opposite patterns (Coleman & Wilson 1998; Wilson & Stevens 2005), that is, high within-context repeatability (Salonen & Peuhkuri 2006).

We also found significant variation within traits between contexts, indicating that behaviour is context dependent and individuals adapt their behaviour to environmental cues, in this



**Figure 2.** Behavioural traits across contexts ( $N = 19$  individuals, data averaged per individual per context). Depicted are means  $\pm$  SEM for the empty tube context (E, white bars), conspecific in tube context (C, hatched bars) and predator in tube context (P, black bars). The measures in (a)–(c) are frequencies per minute in sight and (d)–(f) are categorical principal components (see Appendix).

case, the state of the breeding territory. Notably, individuals showed more aggression towards a conspecific inside the tube than towards the predator inside the tube. This suggests that the predator is viewed as a personal threat to survival (Heg et al. 2004a).

Finally, we found only limited evidence for modifying effects on the behavioural traits. Focal individuals were selected from a small size range of subordinate fish of both sexes, so not surprisingly body size did not affect the behavioural traits. The sexes did not differ in their behavioural traits, although females tended to show less aggression towards the tube (which matches studies in other fish: Holder et al. 1991; Brown et al. 2007a, but see Schürch & Heg 2010a). Ranging propensity was similar in both sexes which is consistent with a genetic analysis revealing that within-colony dispersal does not differ between the sexes (Stiver et al. 2007). Group size also positively influenced the focal individual's attack rate of the tube. This may be the result of joint territory defence, which reduces individual risk (see also Heg & Taborsky 2010). Since larger groups facilitate more interactions with family members, it was not surprising that group size positively influenced the number of conspecific interactions. Also, the sex of the focal individual was important in determining the

number of interactions. Females interacted more with conspecifics than males. We do not readily have an explanation for this observation.

We have to acknowledge that only 19 individuals were tested, which limited the scope of statistical analyses one could perform (e.g. using mixed GLM to estimate the variance components and structural equation modelling: Dingemans et al. 2010). A larger sample size of a wider size range of *N. pulcher* in the field (as age and therefore body size may affect exploration propensity in males: Schürch & Heg 2010b), and more standardized testing of boldness, aggression and exploration in field settings as has been done in the laboratory (Schürch & Heg 2010a), may yield more accurate estimates of repeatability and trait correlations.

#### Behavioural Syndrome

The behavioural syndrome discovered under laboratory settings (Bergmüller & Taborsky 2007; Schürch & Heg 2010a) was only partly recovered under field settings. Behavioural traits loaded on three principal components and we found evidence for some behavioural traits being traded off against each other (e.g. fish that

**Table 2**  
Tests for modifying effects of the focal individual's body size (SL mm), sex (male or female) and densities of fish (group size, conspecific, heterospecific or predator density) on the focal individual's behaviour, corrected for fixed context effects (tube empty, with conspecific, with predator) and random focal individual identifier effects ( $N = 202$ : 1–4 tests per context of 19 individuals)

Parameter (range)	df	Feeding rate <sup>†</sup>		Territory maintenance <sup>†</sup>		Aggression towards tube <sup>†</sup>		Ranging propensity <sup>‡</sup>		Territory defence <sup>‡</sup>		Conspecific interactions <sup>‡</sup>	
		Error df	F	Error df	F	Error df	F	Error df	F	Error df	F	Error df	F
Intercept	1	14.1	5.6*	14.1	2.6	13.6	0.7	14.4	0.001	14.5	0.1	13.4	6.4*
Context (empty, conspecific, predator)	2	182.0	7.4***	183.2	3.6*	115.1	10.1**	180.9	3.7*	182.3	1.3	181.4	5.3**
Body size (35.3–48.3)	1	14.0	1.7	14.1	2.8	13.6	0.4	14.2	0.01	14.1	0.02	13.2	2.6
Sex (female, male)	1	14.9	0.7	16.0	0.02	14.8	4.0	14.7	0.9	14.9	0.2	14.2	5.5*
Group size (3–9)	1	14.2	1.3	17.5	0.4	15.8	5.4*					13.4	8.2*
Conspecific density (0–38)	1	17.6	0.3									18.1	3.2
Heterospecific density (5–147)	1									13.6	2.8		
Predator density (0.5–3.7)	1							14.4	0.7	13.6	0.2		

The table shows the results of six GLMM (one per behavioural trait): the *df*, error *df*, the *F* value and the significance.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

<sup>†</sup> In frequencies per minute within sight; feeding rate, aggression towards tube and territory maintenance were  $\log(\text{trait} + 1)$  transformed before analyses. Note that aggression towards the empty tube was virtually absent and not used for the analyses; therefore for context  $df = 1$ .

<sup>‡</sup> Categorical principal components.

spent more time attacking the tube spent less time feeding, exploring and defending the territory). Indeed, such trade-offs must be expected to occur, as individuals are time limited and cannot perform all 'tasks' simultaneously (Sih et al. 2004b). Nevertheless, aggression towards the conspecific correlated positively with aggression towards the predator (boldness), as did aggressiveness (either against a conspecific or in a mirror test) and boldness (approach of a novel object) in the laboratory (Bergmüller & Taborsky 2007; Schürch & Heg 2010a). In the field, ranging propensity tended to correlate negatively with these two traits, contrary to the findings on exploration propensity in the laboratory (Bergmüller & Taborsky 2007; Schürch & Heg 2010a) and in other species (e.g. Bell 2005). If ranging is a good predictor of dispersal, this negative correlation would be consistent with the trade-off between helping and dispersal (Bergmüller et al. 2005a, b), that is, helpers that invest more at home explore the environment less for other breeding groups to join or for a suitable habitat to establish their own territory.

However, the ranging behaviour might also be helpful to the group, by gathering information on, for example, zooplankton blooms or potential predators. In that case, the negative correlation between aggression against a conspecific or predator and ranging propensity could point at task differentiation in the breeding group (Arnold et al. 2005), consisting of brood care, predator mobbing or information gathering. Territory maintenance was a completely inconsistent trait and seemed not to interact with any of the other behavioural traits measured. This might reflect the dual nature of this behaviour, because territory maintenance may serve to enlarge shelter(s) privately used by the focal fish, or may serve to enlarge shelters used by multiple group members, including the breeding shelter (e.g. during the pre-spawning period). More controlled tests of the investment in territory maintenance are necessary in the field (e.g. Heg & Taborsky 2010).

Differences in growth rates have been proposed as the underlying physiological trait responsible for consistent correlated variation in behaviour (Stamps 2007) and we used feeding rate as a proxy for growth potential to test this idea. However, despite feeding rate showing a high across-context repeatability, it was positively related only to ranging propensity (as found in some other fish species: Ehlinger 1990; Iguchi et al. 2001), and not to aggression propensity or to boldness, contrary to some other studies in fish (Magnhagen & Staffan 2005).

#### Measurement Considerations

The CatPC analysis derived measures for exploration propensity (which included distances moved and patches visited), conspecific interactions (which included aggression, affiliation and submission to, and received from, conspecifics) and territory defence (which included aggression to, and received from, predators and heterospecific competitors). All traits encompass the major behaviours *N. pulcher* shows under natural conditions (e.g. Heg & Taborsky 2010), so we were confident we had a succinct description of individual behavioural tendencies for our analyses.

It is important to realize what exactly is measured (Bell 2007): how similar are our tools for behaviourally typing our individuals to those of other studies and how well do laboratory tests reflect tests under more natural conditions (Wilson et al. 1993)? Most studies introduce the caught individual to a completely new enclosed environment to measure exploration propensity (Dingemans et al. 2003; Wilson & Stevens 2005) and so may include components of boldness. In contrast, ranging in the field was measured in a familiar environment (assuming the fish regularly make visits to other territories: Bergmüller et al. 2005a), where fish expose themselves to predation risk when leaving the territory (e.g. Heg et al. 2004a). Therefore, it would be helpful to conduct an exploration test in the field similar to the one performed in the

**Table 3**  
Pearson correlations between behavioural traits ( $df = 200$ )

Behavioural trait	Territory maintenance	Aggression towards tube	Ranging propensity <sup>†</sup>	Territory defence <sup>†</sup>	Conspecific interactions <sup>†</sup>
Feeding rate <sup>‡</sup>	–0.061	–0.361***	0.105	0.037	–0.062
Territory maintenance <sup>‡</sup>	—	–0.117	–0.037	–0.039	0.015
Aggression towards tube <sup>‡</sup>	—	—	–0.245***	–0.152*	0.081

\* $P < 0.05$ ; \*\*\* $P < 0.001$ .

<sup>†</sup> Categorical principal components.

<sup>‡</sup> In frequencies per minute within sight and  $\log(\text{trait} + 1)$  transformed before analyses.



laboratory, as has been done for great tits, *Parus major* (Verbeek et al. 1994).

What we measured exactly is also a valid question for the aggression measurements. The predator *L. elongatus* inside the tube was attacked less than a conspecific intruder and can be regarded as a personal survival threat (Heg et al. 2004a). One could argue that it is an altruistic act of the focal individual to attack this predator. Similarly, Balshine-Earn et al. (1998) considered these attacks as helping effort. Attacking the similar-sized conspecific inside the tube carries fewer personal risks (no retaliation was possible, but focal fish may expose themselves to predators by doing so) and may not be helping behaviour at all: these intruders may be perceived as a threat to the focal individual's personal dominance position (Heg et al. 2004b; Fitzpatrick et al. 2008; Mitchell et al. 2009). Still, both of our aggression measurements were taken on the territory. Individuals that cared less about the fate of the territory might therefore have reacted less intensively overall, which might explain the negative correlation between attacking the tube and ranging propensity. Differentiating helpful behaviours from selfish acts could ultimately be considered impossible.

### Conclusions

We have shown high across-context repeatability in behavioural traits in a social cichlid species. Notably, we have found a correlation between aggression towards a conspecific intruder and aggression towards a predator. This suggests that highly aggressive subordinates are willing to defend their interests inside their focal group, and less aggressive individuals are looking for outside options. However, contrary to expectation, less aggressive subordinates did not range more than highly aggressive individuals, although (1) the correlations were in the predicted direction and (2) ranging propensity correlated negatively with aggressiveness across all contexts. The most parsimonious explanation is that exploration propensity measured under laboratory settings (which may involve components of boldness) do not scale one-to-one to ranging behaviour actually shown under natural settings, which may be modified by individual experiences acquired during an individual's lifetime and trade-offs.

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## APPENDIX

**Table A1**

Result of the categorical principal component analysis on the behavioural variables recorded, for the three contexts combined: empty tube, tube with conspecific intruder, tube with predator

Parameter	PC loadings (N=202)			Descriptive data (N=19 individuals)	
	Ranging propensity	Conspecific interactions	Territory defence	Mean±SD	Range
Feeding rate*				8.32±4.68	1.38–17.26
Territory maintenance*				0.07±0.10	0.00–0.33
Aggression towards tube*					
Empty				0.0013±0.0057	0.00–0.03
Conspecific				1.24±0.95	0.05–3.10
Predator				0.66±0.79	0.00–3.57
Maximum distance (cm)	<b>0.978</b>	–0.029	0.026	42.28±35.25	0.00–101.46
Mean movement (cm)	<b>0.978</b>	–0.015	0.019	33.68±26.37	0.00–74.34
Total movement (cm)	<b>0.982</b>	–0.022	0.035	106.8±107.99	0.00–371.89
Number of different territories visited	<b>0.893</b>	–0.045	0.116	1.35±0.36	1.00–2.17
Total number of territory visits	<b>0.917</b>	0.082	0.068	1.79±0.99	1.00–4.75
Heterospecific competitors*					
Aggression	–0.032	0.091	<b>0.687</b>	0.06±0.05	0.00–0.23
Aggression received	0.176	–0.274	<b>–0.392</b>	0.01±0.02	0.00–0.08
Predators*					
Aggression	–0.086	–0.125	<b>0.716</b>	0.03±0.04	0.00–0.12
Aggression received	–0.053	–0.074	<b>0.337</b>	0.005±0.007	0.00–0.02
Conspecifics*					
Aggression	–0.031	<b>0.702</b>	0.021	0.10±0.06	0.01–0.23
Aggression received	0.231	<b>0.677</b>	–0.205	0.07±0.06	0.00–0.19
Conspecifics*					
Affiliation and submission	–0.167	<b>0.569</b>	0.143	0.09±0.10	0.00–0.46
Affiliation and submission received	0.060	<b>0.434</b>	–0.028	0.007±0.008	0.00–0.02
Eigenvalue	4.642	1.578	1.336		
% Variance explained	35.7	12.1	10.3		

Loadings, the eigenvalue and the explained variance are given for the extracted PC. Sample sizes are  $N = 1-4$  tests times three contexts per individual ( $N = 202$  of, in total, 19 individuals). Also given are the descriptive data (means of the means per individual). CatPCA cannot work with zero values, so we added a constant of 1 to all original dependent behavioural data for the principal component analysis only. Feeding rate loaded with 0.179, 0.217 and 0.492 on the three components, respectively and was therefore removed from the CatPCA. Territory maintenance had the low loadings of  $-0.093$ ,  $0.067$  and  $0.051$ , respectively and was likewise removed from the CatPCA. Bold type indicates factors with high loadings.

\* In frequencies per minute within sight.