



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

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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

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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

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