Animal Behaviour 84 (2012) 925–936

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Thomas Riebli[a,*], Michael Taborsky[a], Noémie Chervet[a], Nadine Apolloni[a], Yvonne Zürcher[a], Dik Heg[a,b]

[a] Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland
[b] Department of Clinical Research, Clinical Trials Unit, University of Bern, Bern, Switzerland

ARTICLE INFO

Article history:
Received 3 August 2011
Initial acceptance 31 October 2011
Final acceptance 27 June 2012
Available online 11 August 2012
MS. number: 11-00617R

Keywords:
behavioural syndrome
body condition
cichlid
growth
Neolamprologus pulcher
personality
resource allocation
social context

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

Suites of correlated behavioural traits that remain consistent within individuals but differ between individuals (Sih et al. 2004a, b) have been referred to as coping styles, personality, temperament or behavioural types and have been described in various animal species (Budaev 1997; Réale et al. 2000; Øverli et al. 2004; Dingemanse et al. 2007; see also for a review: Gosling & John 1999). Individual behavioural types are known to affect for instance dominance (e.g. Riebli et al. 2011), risk taking (e.g. van Oers et al. 2005), feeding rate (e.g. Bergvall et al. 2011), mate choice (e.g. Schuett et al. 2010), reproduction (e.g. Both et al. 2005) and helping behaviour (Bergmüller & Taborsky 2007). However, the impact of different personalities on dominance status and on social behaviour in general has not received as much attention (Armitage 1986a, b; McGuire et al. 1994; Bergmüller et al. 2007; Magnhagen 2007; Schürch & Heg 2010a, b). In contrast, other potential correlates of animal personalities (i.e. life history consequences) have been studied in a wide variety of animal species ranging from wild to captive and domestic to laboratory species (reviewed in Smith & Blumstein 2008). Especially within social groups, differences in intrinsic aggressive propensity might predict effects on both social repulsion (e.g. aggression directed towards group members, escalated fighting for dominance with group members, eviction of group members) and affiliation (e.g. tolerance and support of mates, subordinates and offspring inside the group). Physical attributes such as body size or mass have been repeatedly shown to influence substantially the outcome of competition for dominance (Otronen 1988; Huntingford et al. 1990; Olsson 1992; Faber & Baylis 1993), but the influence of behavioural idiosyncrasies on such competition is much less clear. It has been suggested that life history traits such as body weight or size, which can be summarized as resource-holding potential, might be correlated with consistent behavioural properties (Hurd 2006). Indeed, it has been demonstrated that differences in intrinsic levels of aggression may significantly influence life history traits and Darwinian fitness such as growth rates, food intake and the outcome of competition for dominance (Stamps 2007; Biro & Stamps 2008; Adriaenssens & Johnsson 2011; Riebli et al. 2011). Thus, an important aim of this study was to test for potential effects of intrinsic behavioural

---

* Correspondence: T. Riebli, Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland.
E-mail address: thomas.riebli@iee.unibe.ch (T. Riebli).

0003-3472/$38.00 © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2012.07.017

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

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

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

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

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

METHODS

Study Animals and Laboratory Conditions

Focal individuals used in this study were laboratory-reared offspring of wild-caught *N. pulcher* from the southern end of Lake Tanganyika (near Mpulungu, Zambia). They were kept in four 400-litre storage tanks without breeding shelters at a water temperature of 27 ± 1 °C. The chemical attributes of the water closely matched the values of Lake Tanganyika (Taborsky 1984). Each tank contained mixed-sex groups of about 50 individuals of only small (less than 45 mm standard length) or of only large fish (more than 45 mm standard length). To reduce aggressive interactions, plastic bottles were provided at the water surface serving as refuges for expelled individuals. The light regime was 13:11 h light:dark. All fish were fed four times a week with commercial dry food (Tetramin) and twice a week with frozen fresh food (consisting of daphnia, *Artemia salina* and chironomid larvae).

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