Animal Behaviour 128 (2017) 117–124

Contents lists available at ScienceDirect

Animal Behaviour

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

Different or alike? Female rainbow kribs choose males of similar consistency and dissimilar level of boldness

U. Scherer*, M. Kuhnhardt, W. Schuett

Zoological Institute, Biocentre Grindel, University of Hamburg, Hamburg, Germany

ARTICLE INFO

Article history:
Received 16 November 2016
Initial acceptance 27 December 2016
Final acceptance 29 March 2017

MS. number: 16-01004R

Keywords:
antipredator behaviour
assortative
behavioural compatibility
cichlid
mate choice
Pelvicachromis pulcher
personality
risk taking
sexual selection
side bias

Although the existence of consistent between-individual differences in behaviour ('personality differences') has been well documented during the last decade, the adaptive value of such behavioural limitations remains an open field for researchers of animal behaviour. Personalities clearly restrict individuals in their ability to adjust their behaviour to different conditions. However, sheer costs of flexibility cannot explain the polymorphism created by personality variation. In a correlative approach, we here tested whether mate choice might act as a major driving force maintaining personality variation in the monogamous, biparental rainbow krib, *Pelvicachromis pulcher*. We personality-typed all males and females for their boldness (activity under simulated predation risk) and allowed females to choose between two males that differed in their boldness (behavioural level and consistency). Prior to the choice, females were allowed to observe both males, expressing their natural boldness towards a video-animated natural predator. Both sexes showed personality differences in boldness over the short and long term. Furthermore, when removing side-biased females, we found a disassortative mating preference for the behavioural level and an assortative preference for behavioural consistency in boldness. These preference patterns might facilitate effective parental role allocation during offspring care and/or provide genetic benefits. Our results suggest that sexual selection plays an important role in the evolution of personality differences.

Individuals must cope with a wide array of environmental challenges. Therefore, flexibility in the expression of behavioural responses towards different and changing conditions should be favoured by selection (Sih, Bell, & Johnson, 2004). Yet, individuals often show considerable consistent between-individual differences in behaviour over time and/or contexts (Boissy, 1995). Such personality differences are common throughout the animal kingdom (reviewed in Gosling, 2001; Kralj-Fišer & Schuett, 2014) and have been shown for various behavioural traits, such as activity pattern, aggressiveness, exploratory tendencies, boldness and fearfulness (reviewed in Dall, Houston, & McNamara, 2004; Gosling, 2001; Sih, Bell, Johnson, & Ziemba, 2004). Personality traits are moderately heritable (Ariyomo, Carter, & Watt, 2013; Patrick, Charmantier, & Weimerskirch, 2013; Reif & Lesch, 2003; van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005) and have fitness consequences (e.g. Ariyomo & Watt, 2012; Dingemanse & Réale, 2005; Smith & Blumstein, 2008), suggesting they are not merely nonadaptive noise that surrounds an adaptive optimum (Wilson, 1998). Nevertheless, underlying mechanisms that generate and maintain behavioural polymorphisms are largely unclear and many aspects of the growing body of theoretical frameworks have yet to be empirically tested (reviewed in e.g. Schuett, Tregenza, & Dall, 2010; Wolf & Weissing, 2010).

Recently, Schuett et al. (2010) pointed out that sexual selection may be important in generating and maintaining personality variation although this possibility has rarely been tested (but see e.g. Montiglio, Wey, Chang, Fogarty, & Sih, 2016; Schuett, Dall, & Royle, 2011; Schuett, Godin, & Dall, 2011). According to the proposed framework (Schuett et al., 2010), personalities are expected to play an important role in mate choice when a potential mate's behavioural phenotype is either associated with good/compatible genes that increase offspring fitness (Dingemanse, Both, Drent, & Tinbergen, 2004; Ihle, Kempenaers, & Forstmeier, 2015; Mays & Hill, 2004) or provides nongenetic benefits increasing the reproductive success through parental ability and/or behavioural compatibility between mates. While mate choice for genetic quality and parental ability should favour interindividual agreement in the preference for a behavioural trait, mate choice for genetic or behavioural compatibility should depend on an interaction

---

* Correspondence: U. Scherer, Zoological Institute, Biocentre Grindel, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany.
E-mail address: u.k.scherer@gmail.com (U. Scherer).

http://dx.doi.org/10.1016/j.anbehav.2017.04.007
0003-3472/

between male and female genotypes or phenotypes (Schuett et al., 2010). Thus, mate choice for compatibility would lead to interindividual differences in mating preferences, creating either an assortative or disassortative mating pattern (Schuett et al., 2010).

Few studies have investigated the effect of personality traits on mate choice (reviewed in Schuett et al., 2010) and some have only assessed the behaviour of the chosen but not the choosing sex (Godin & Dugatkin, 1996; Ophir & Galef, 2003). The few studies considering a potential interplay between male and female personality during mate choice have often found assortative mate choice for various behavioural traits, in correlative (Gonzaga, Carter, & Buckwalter, 2010; Kralj-Fiser, Sanguino Mostajo, Preik, Pekar, & Schneider, 2013; Mascie-Taylor & Vandenberg, 1988; Montiglio et al., 2016) or experimental settings (Schuett, Godin, et al., 2011), and an increased reproductive success of assortative pairs (e.g. Ariyomo & Watt, 2013; Schuett, Dall, et al., 2011). However, in studies that found increased success of assortative pairs, personality data were often obtained after pairing (Both, Dingemanse, Drent, & Tinbergen, 2005; Harris & Siefferman, 2014; Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016), which did not allow the authors to determine whether mate choice was affected by individual personalities or whether behavioural similarity was achieved after pairing in highly successful pairs (Laubu et al., 2016). Indirect evidence that disassortment for personality can sometimes be beneficial is provided by van Oers, Drent, Dingemanse, and Kempenaers (2008), who found that assortative pairs of great tits, *Parus major*, had higher rates of extrapair paternity. Generally, positive assortment for genotypic or phenotypic traits is far more prominent in the animal kingdom than evidence for disassortment (reviewed in Jiang, Bolnick, & Kirkpatrick, 2013).

Personality traits consist of two measures: the behavioural level and the degree of behavioural consistency. Although there is considerable variation in within-individual behavioural consistency (Dingemanse, Kazem, Réale, & Wright, 2009) the effect of such individual differences in consistency on mate choice has rarely been considered (Schuett, Dall, et al., 2011). Behavioural consistency might be sexually selected for if it reflects individual quality (i.e. consistency is costly under changing conditions) or if choosing a predictable (i.e. consistent) mate provides reliable information about future parental care behaviour prior to mating (Dall et al., 2004; Royle, Schuett, & Dall, 2010; Schuett et al., 2010). For example, a female might be able to predict a male's ability to protect prospective offspring from the consistency in boldness expressed prior to mate choice.

In the present study, we investigated the influence of male and female boldness (propensity to engage in risky behaviour; Wilson, Clark, Coleman, & Dearstyne, 1994) on female mate preference in a socially monogamous, biparental cichlid from West Africa, the rainbow krib, *Pelvicachromis pulcher*. In this species, pairs are highly territorial: they defend territories and offspring aggressively against conspecifics and heterospecifics. Therefore, we assumed individual boldness to be a trait that these fish are likely to consider during mate choice. Furthermore, boldness has been shown to affect foraging success (Dyer, Croft, Morrell, & Krause, 2008), egg fertilization rates (Ariyomo & Watt, 2012), dominance (Dahlbom, Lagman, Lundstedt-Enkel, Sundstrom, & Winberg, 2011), survivorship (Smith & Blumstein, 2010) and parental care effort (Budaev, Zworykin, & Mochek, 1999) in other fish species. We measured male and female boldness (activity under simulated predation risk) repeatedly to test for personality differences. During mate choice experiments, females were first allowed to observe a bolder and a shyer male expressing their natural boldness towards a predator animation. Subsequent female mating preference for the two males was assessed in a standard mate choice scenario. We considered both aspects of male and female personality: the behavioural level and behavioural consistency of each individual.

We expected female preferences to depend on both the behavioural level and behavioural consistency, with our predictions being guided by Schuett et al. (2010). For the behavioural level, we expected that if mate choice is based on male (parental or genetic) quality, females should show a general preference for either bold or shy males (e.g. Godin & Dugatkin, 1996; Kortet, Niemelä, Vainikka, & Laakso, 2012). Alternatively, if mate compatibility is more important during mate choice, females should not show an overall agreement but also consider their own personality during their choice. Because both rainbow krib parents provide offspring care we considered the second possibility, i.e. mate compatibility, to be more important for mate choice based on boldness. In species with biparental care, an assortative mating preference for certain behavioural traits could reduce sexual conflict over parental investment (Royle et al., 2010) and facilitate offspring care coordination by better synchronization of parental activities (Schuett, Dall, et al., 2011). Depending on the environmental conditions or the biology of the species, disassortative mating might also sometimes have advantages (Schuett et al., 2010). For instance, species that perform several parental activities might also benefit from expressing a disassortative mating preference, facilitating role allocation and specialization during offspring care. Often, a sexual dimorphism in role specialization can be observed with the female providing more direct offspring care and the male defending the territory (e.g. Guerra & Drummond, 1995; Itzkowitz, 1984; Neil, 1984; Richter, Santangelo, & Itzkowitz, 2010; Solomon, 1993). Nevertheless, in many species both partners can or do perform the same behaviours (see Royle, Russell, & Wilson, 2014 for a review on the flexibility of parental care behaviour), and at least partly compensate for their mate's tasks if needed (Itzkowitz, 1984; Lavery & Reebs, 2010; Sasvari, 1986; Storey, Bradbury, & Joyce, 1994) indicating that sex roles might be less fixed. For the behavioural consistency, we followed up two possible mate choice scenarios: a general preference for consistent over inconsistent males, which might indicate predictability of later parental performance, and/or individual quality (Royle et al., 2010; Schuett et al., 2010) or mate choice for compatibility leading to a positive assortative preference (Schuett et al., 2010; Schuett, Godin, et al., 2011).

METHODS

Ethical Note

In consideration of animal welfare, we followed the '3R' framework (Russell & Burch, 1959). To decrease the number of study animals needed we used predator animations instead of live predators and test males for mate choice trials were used twice. During experiments, no animals were harmed or exposed to actual predation risk. Prey fish and predators were kept separately and did not have visual contact during fish maintenance. Permits were provided by the German 'Behörde für Gesundheit und Verbraucherschutz Hamburg'.

Study Animals and Holding Conditions

Study individuals were obtained from a captive breeding stock at the University of Hamburg and local suppliers. Males and females were 1–2 years old and sexually inexperienced. Individuals were maintained in same-sex sibling groups under standardized holding conditions (tanks measuring 100 × 50 cm and 25 cm high and 100 × 50 cm and 50 cm high, 26 ± 1 °C water temperature, aerated and filtered water, weekly water changes, 12:12 h light:dark) and were fed once a day on 5 days a week with *Artemia*.