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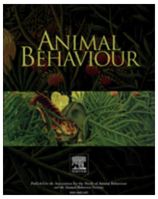

Individual variation in helping in a cooperative breeder: relatedness versus behavioural type

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Helpers in cooperatively breeding groups can vary hugely in the variety and level of care they provide. Several studies suggest that kin selection alone cannot be invoked to explain variation in helping for many species, but there have been few explicit tests of this under controlled conditions. Here, we investigated whether relatedness to the breeding pair or consistent individual differences in behaviours explained variation in helping by the cooperatively breeding cichlid *Neolamprologus pulcher*. We established standardized social groups consisting of a breeding pair and one related ($r = 0.5$) and one unrelated ($r = 0$) helper. Two forms of helping, territory maintenance and territory defence, were measured repeatedly under controlled conditions: helping was variable between, but consistent within, individuals. Furthermore, there was some evidence that helpers that carried out more maintenance also performed more defence. Contrary to the kin selection hypothesis, relatedness did not predict the amount or variety of helping executed. Risk responsiveness, activity levels and aggressiveness were repeatable within individuals, so constituted 'behavioural types' (or personality traits), but were uncorrelated with each other. More aggressive, risk-prone or more active helpers participated in more territory defence than submissive, risk-averse or inactive helpers. Risk-prone individuals contributed more to territory maintenance than risk-averse helpers. Overall, differences in behavioural type, rather than relatedness, explained most variation in helping behaviour in *N. pulcher*. This study highlights the importance of considering consistent individual differences in behaviour for predicting participation and performance in complex social interactions.

Helpers in cooperatively breeding groups can assist breeders by, for example, provisioning young, defending against predators and conspecific intruders, maintaining nests and caring for eggs (Taborsky & Limberger 1981; Stacey & Koenig 1990; Emlen 1991). Individuals can vary in terms of who they help, and also in the variety and level of care provided (Heinsohn & Legge 1999; Arnold 2000). The presence of helpers within a group has been found to boost the reproductive success and reduce the workloads of the breeders, and improve survival rates of both breeders and offspring (Taborsky 1984; Emlen 1991; Balshine-Earn et al. 2001; Brouwer et al. 2005). Helpers suffer costs, including lost mating opportunities, energy expenditure and injury risk (Taborsky 1984; Grantner & Taborsky 1998; Heinsohn & Legge 1999).

The accrual of indirect fitness benefits may offset costs if helpers are related to recipients (Hamilton 1964). Indeed, some studies (Clarke 1984; Reyer 1984; Emlen & Wrege 1988; Komdeur 1994; Stiver et al. 2005; Wright et al. 2010) have found that individuals adjust their helping based on relatedness to the breeders, but others have not (Wright et al. 1999; Clutton-Brock et al. 2001; Canestrari et al. 2005). If most or all individuals within a group are relatives of some degree, then a blanket rule of helping any group member might ensure kin-selected benefits accrue without the need for kin discrimination mechanisms. In many species unrelated helpers are found in groups (Reyer 1984; Magrath & Whittingham 1997; Van Horn et al. 2004; Dierkes et al. 2005; Wright et al. 2010), so direct fitness benefits, for example reduced predation risk and improved foraging opportunities (Hamilton 1964; Taborsky 1984; Heg et al. 2004), may be sufficient to drive selection on helping (Clutton-Brock 2002; Griffin & West 2002). As related helpers receive both direct and kin-selected fitness benefits, they may be expected to help more than nonkin. Similarly, related helpers are predicted to perform more costly or risky tasks, such as intruder defence, than nonkin (Balshine-Earn et al. 2001; Arnold et al. 2005). By contrast, nonkin might focus on low-risk helping such as territory maintenance and brood care. Conversely, if helpers essentially

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have to 'pay to stay' on the territory (Gaston 1978; Balshine-Earn et al. 1998), nonkin should help more than relatives (Kokko et al. 2002), as they are less tolerated by breeders than relatives. Thus, the predictions concerning relatedness and helping are complex.

Factors other than relatedness may also influence the amount and form of help an individual is prepared to, or able to provide: group size, body condition, sex, social status, helper experience and more recently 'behavioural type' (Heinsohn & Legge 1999; Schürch & Heg 2010a). Faced with the same environment or behavioural stimuli, and measured under standardized conditions, individuals of the same species often show 'consistent individual differences' in behaviour (Sih et al. 2004; Bell & Sih 2007). Commonly measured behaviours include: aggression (aggressive–submissive), activity (active–inactive), exploration (fast–slow explorers) and risk responsiveness (risk prone–risk averse, bold–shy or neophobic–neophilic) (Sih et al. 2004; Bell & Sih 2007). When behaviours are consistent within, but vary between, individuals across a range of situations or contexts, they can be defined as 'personality traits' or 'behavioural types' (the latter being the term we use in this paper). As behavioural types appear to have a heritable component (Dingemanse et al. 2002) and may also be programmed by early life experiences, such as social, hormonal, nutritional or maternal effects (Arnold et al. 2007; Arnold & Taborsky 2010; Schürch & Heg 2010a; reviewed by Sih et al. 2004), individuals may become specialized in behaviours that then affect their fitness, such as foraging (Herborn et al. 2010), dispersal (Schürch & Heg 2010a) or helping (Arnold 2000; Bergmüller & Taborsky 2007; Bergmüller & Taborsky 2010; Schürch & Heg 2010b). The definition of behavioural syndromes emphasizes the existence of 'suites of correlated behaviours': that is, correlations between different behavioural types across contexts or situations (Sih et al. 2004).

Neolamprologus pulcher, a cooperatively breeding African cichlid endemic to Lake Tanganyika, lives in social groups consisting of a dominant breeding pair and 1–14 helpers, which vary in size, sex and relatedness (Taborsky & Limberger 1981; Balshine-Earn et al. 2001; Dierkes et al. 2005). Helpers aid breeders by cleaning and fanning eggs, keeping the breeding shelter free of sand and debris, and defending the territory and other group members against predators and intruding conspecifics (Taborsky & Limberger 1981; Taborsky 1984). Helpers may specialize in certain tasks depending on their body size (Bruintjes & Taborsky 2011). As in the wild larger helpers also tend to be less related to the breeding pair than smaller helpers, relatedness can appear to predict the type of helping performed (Dierkes et al. 2005; Stiver et al. 2005). Helping is costly, for example in terms of energy expenditure and growth (Taborsky & Limberger 1981; Taborsky 1984; Grantner & Taborsky 1998; Taborsky & Grantner 1998), but helpers can receive direct fitness benefits through group living, such as improved survival (Taborsky 1984; Heg et al. 2004), enhanced reproductive success via parasitism of the reproduction of the breeders (Dierkes et al. 1999; Heg et al. 2006, 2008) and/or inheritance of the breeding territory (Dierkes et al. 2005; Stiver et al. 2006). Additionally, related helpers are predicted to accrue indirect fitness benefits (Taborsky 1984; Brouwer et al. 2005). Previously, it has been established that juvenile *N. pulcher* can recognize kin via phenotype matching based on chemical rather than visual cues. These full siblings had been reared apart from focal fish, so were unfamiliar to them before the two-way choice trials (Le Vin et al. 2010). So, helpers should be able to assess relatedness to breeders and accordingly adjust their care. However, a previous study of *N. pulcher* uncovered mixed results on the effects of relatedness on helping effort in captivity versus the wild (Stiver et al. 2005). In the field, helpers related to the breeding female and unrelated to the breeding male took part in the most territory defence. In the laboratory, by contrast, helpers unrelated to both breeders carried out the most territory defence and territory maintenance, compared with helpers related to both breeders (Stiver et al. 2005). As that study did not carry out manipulations to standardize helping effort, there was likely to have been variation between groups in the amount of helping required. Recent studies on different populations have also provided evidence for consistent individual differences in exploratory tendency, risk responsiveness and aggression in *N. pulcher* (e.g. Riebli et al. 2010), which can predict helper dispersal, group stability and reproductive decisions (Schürch & Heg 2010a, b). Patterns of correlations between behavioural types and helping differed between studies of the same species (Bergmüller & Taborsky 2007; Schürch & Heg 2010a, b; Witsenburg et al. 2010), which warrants further investigation. Importantly, these studies did not simultaneously assess helper relatedness and behavioural types in predicting helping.

The aim of our experiment was to simultaneously consider the effects of relatedness and consistent individual differences in behaviour on individual helping in *N. pulcher*. We tested *N. pulcher* in a controlled laboratory set-up within standardized social groups that accounted for body size, familiarity and relatedness between individuals. We assessed two helping behaviours in *N. pulcher*: the amount of digging helpers carried out when the breeding shelter was filled in experimentally with sand (territory maintenance), and the level of defence shown against a size-matched conspecific intruder (territory defence). We addressed the following specific questions via experimental manipulations: (1) Is there variability between and temporal consistency within individuals in helping effort? (2) Are territory defence and maintenance correlated within individuals (i.e. are some individuals generally more helpful than others)? (3) Does relatedness to the dominant breeding pair affect the amount or form of helping shown? (4) Do aggressiveness, activity and risk responsiveness show variability among and consistency within individuals? (5) Are different behavioural types correlated, constituting a behavioural syndrome? (6) While controlling for relatedness, does an individual's behavioural type predict the amount or form of helping effort it performs?

METHODS

Adult *N. pulcher* were transported from the University of Bern, Switzerland to the University of Glasgow in February 2007. The fish were a mixture of wild caught ($N = 10$ pairs) and captive bred ($N = 10$ pairs). The wild-caught adults originated in Nkumbula Island, near Mpulungu, Zambia in 2006. The captive-bred adults were the offspring of wild fish caught at Kasakalawe, near Mpulungu, Zambia, in 1996. Captive-bred and wild-caught fish can behave differently, but we found that focal offspring from the two populations did not differ significantly in any of the behaviours analysed below ($P > 0.2$ in all cases; see Appendix). Moreover, microsatellite analyses have shown that the breeding stock fish used in this study were not inbred, with 90% of pairs having a relatedness score of less than 0.125 and 73% being completely unrelated (see Appendix).

Fish were kept in mixed-sex tanks until breeding began in early June 2007. These holding tanks ranged in size from 50 to 250 litres and stocking densities ranged from 3 to 27 individuals. Tanks were provisioned with 1–1.5 cm of coral sand on the base, an airstone, foam filter and several clear plastic tubes suspended at the top of the tank to act as refuges. The water temperature was kept in the range of 26.8 ± 1 °C, pH in the range 8–8.4 and a 13:11 h light:dark cycle. Adult fish were fed once daily with either a commercial dry cichlid food, frozen bloodworm or *Daphnia*.

For breeding, one male and one female were placed into a 80 × 40 cm and 50 cm high 140 litre breeding tank provisioned with 1–1.5 cm of coral sand on the base, an airstone, foam filter, two pieces of plastic guttering pipe and two terracotta flowerpot halves