



RESEARCH PAPER

Variation in Helper Type Affects Group Stability and Reproductive Decisions in a Cooperative Breeder

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Abstract

Recent studies have shown that differences in life history may lead to consistent inter-individual variation in behavioural traits, so-called behavioural syndromes, animal personalities or temperaments. Consistencies of behaviours and behavioural syndromes have mainly been studied in non-cooperative species. Insights on the evolution of cooperation could be gained from studying individual differences in life histories and behavioural traits. Kin selection theory predicts that if an individual's reproductive ability is low, it had to aim at gaining inclusive fitness benefits by helping others. We tested this prediction in the cooperatively breeding cichlid *Neolamprologus pulcher*, by assessing reproductive parameters of adults that had been tested earlier for aggressiveness and for their propensity to assist breeders when they had been young ('juveniles'). We found that juvenile aggression levels predicted the acceptance of a subordinate in the group when adult. Males which were aggressive as juveniles were significantly more likely to tolerate a subordinate in the group when compared with males which were peaceful as juveniles, whereas females which were more aggressive as juveniles tended to expel subordinates more often. Females produced significantly smaller clutches when paired to males which had helped more as a juvenile, despite the fact that adult males hardly provided direct brood care. There was no evidence that females with a high propensity to help when young, produced smaller clutches or eggs when adult, but they took longer to lay their first clutch when compared with females with a low propensity to help when young. These results suggest that variation in behavioural types might explain variation in cooperation, the extent of group-living and reproductive decisions.

Introduction

Since the dawn of kin selection theory (Hamilton 1964), many studies have focused on the degree of relatedness as an important factor in explaining differences in levels of cooperation within (e.g. Stiver et al. 2005) and across cooperatively breeding species (e.g. Griffin & West 2003). However, analyses of within-group kin structure show that in many social systems individuals do not discriminate between

related and unrelated partners in cooperative acts (e.g. Clutton-Brock et al. 2000; Queller et al. 2000), or even preferentially help unrelated recipients (e.g. Dunn et al. 1995; Cockburn 1998). The fact that some individuals provide more help than others irrespective of relatedness (Rabenold 1990; Komdeur & Edelaar 2001a,b) also questions the general importance of kin selection for the evolution of cooperative breeding. Therefore, there is a renewed interest in understanding individual variation in cooperative

propensity by looking at individual differences in costs and benefits of cooperative interactions, rather than relatedness.

Life-history trade-offs affect the costs and benefits of staying within the natal group and engaging in helping activities, versus leaving the group and refraining from helping, and therefore may explain the extent of cooperative breeding in a given habitat. For example, it has been postulated that high juvenile and adult survival may create a surplus of individuals in a given habitat, rendering delayed dispersal more beneficial (Hatchwell & Komdeur 2000; Covas & Griesser 2007). Despite the fact that the life-history hypothesis helped to explain why cooperative breeding may be found in some lineages, but not others (Arnold & Owens 1998), little effort has been made to follow individuals in their life-histories to explain variation in helping behaviour within species. More specifically, it has been argued, that life-history trade-offs lead to polymorphic populations (Rueffler et al. 2004), and eventually to individual differences in risk associated behaviours (Stamps 2007; Wolf et al. 2007).

Probably, the most prominent trade-offs are linked to the cost of reproduction (Harshman & Zera 2007), as well as the trade-off between growth and mortality (reviewed in Lima 1998). These ideas are applicable to cooperatively breeding species as well, but individuals of cooperative breeders have additional life-history options: individuals of cooperatively breeding species do not only have to decide when to start reproduction, and how much to invest into reproduction, but also whether and how much to help, whether to stay in the natal group, disperse to a new group or breed independently (Cahan et al. 2002; Stiver et al. 2005). Therefore, we might expect large adaptive variation in chosen life-history strategies and their associated levels of cooperativeness (Wilson 1998). An early proponent of these ideas was West-Eberhard (1975), who proposed 'aid behavioural syndromes' in cooperatively breeding species. That is, an individual with bad prospects for breeding (e.g. because of small size), could still get kin selected benefits from helping good breeders, even if relatedness is small, because such an individual would not lose as much as an individual with good prospects for breeding. A recent model by Johnstone (2008) supports the idea that the decision of how much help an individual provides to others had to be dependent on its own fecundity. The capability to breed could be genetically determined (e.g. Bongers et al. 1997) or acquired during life-time, e.g. because of strategic niche specialization

(Bergmüller & Taborsky 2007). Eventually, differences in fecundity, or more accurately residual reproductive value, and the propensity to help may result in very different life-history strategies in individuals of cooperatively breeding species: on one extreme, individuals may emphasize selfish reproduction as dominant breeders, on the other end of the spectrum individuals may emphasize helping others in their breeding attempts. West-Eberhard (1975) argued that individuals in cooperative breeders had to tailor their behavioural and reproductive strategies to the respective life-history strategy each individual follows. The theoretical foundations for this notion is still 'under construction', but recent studies find promising results (e.g. Stamps 2007; Wolf et al. 2007), which strengthens the view that life-history trade-offs might induce and maintain behavioural syndromes as commonly found in nature (Sih et al. 2004).

In the present study, we tested for longitudinal effects of the individual's juvenile behavioural type on sociality and reproduction when adult, using the cooperatively breeding cichlid *Neolamprologus pulcher*. Individuals in this species vary in their behavioural types along the bold-shy continuum (Bergmüller & Taborsky 2007) and these differences persist through life (Schürch 2008). Dominance and thus access to reproduction is determined by size in *N. pulcher* (e.g. Heg et al. 2006; Heg 2008; Heg & Hamilton 2008; Heg et al. 2008), but needs to be attained and maintained by aggressive interactions with their subordinate(s) (e.g. Hamilton et al. 2005; Mitchell et al. 2009). However, aggressiveness may have a drawback in a group living context. Aggressive behaviour towards mates may reduce their reproductive capability (e.g. because of costs associated with submissiveness, Grantner & Taborsky 1998), and aggressiveness towards subordinate helpers may lead to helper expulsion (e.g. Dierkes et al. 1999), who then no longer can help, and thus excessive adult aggressiveness may negatively affect adult reproductive output. Such a spillover effect of behaviour from one context to another has for example been demonstrated in a fishing spider (Arnqvist & Henriksson 1997). As an additional confounding factor, males also need to convince females to actually share their precious eggs with them. Thus while for females their own ability to produce gametes is an important factor in current reproductive success, males are limited by the gametes of their partners.

In the current study, we wanted to test whether aggression of young fish and helpfulness of subordinate fish (for the purpose of being brief called

'juveniles' and 'subordinates', respectively) spills over into the breeding context when they attain dominant positions later in life as adults. We tested for three spillover effects. First, we asked whether juvenile aggression predicts aggression towards their mates later in life. Second, we tested whether juvenile aggression predicts aggression towards their subordinate and whether this leads to subordinate expulsion later in life. We expected juvenile aggression to relate positively with (1) aggression towards their mates and (2) aggression towards their subordinate and that this may lead to subordinate expulsion. Third, we were interested in whether helping behaviour predicts reproductive success as an adult. We expected adult females to produce larger clutches for adult males who were selfish as a subordinate, when compared with adult males who were helpful as subordinate. Focal adults were tested using a repeated measures design, so for each focal reproduction in pairs with a helpful adult male and pairs with a selfish adult male could be compared.

Methods

Study Species

The experiment was conducted with artificial groups of the cooperatively breeding Lake Tanganyika cichlid *N. pulcher* (Taborsky & Limberger 1981). Natural breeding groups usually consist of one breeder male and one to several breeder females (Limberger 1983). Males attain breeder status from 50 mm standard length (SL) upwards (standard length is measured as the body length from the tip of the snout to the base of the tail), while females are found in breeding positions from 45 mm SL upwards (Dierkes et al. 2005). The breeders attach clutches to ceilings and walls of breeding shelters where they are tended by the group members. Male and female subordinates (5 mm < SL < 60 mm, Dierkes et al. 2005) assist the breeders, engaging in all tasks relevant to breeding: fanning and cleaning eggs, digging out shelters, cleaning breeding shelters from debris and defending the group against conspecific and heterospecific competitors and predators (Taborsky & Limberger 1981; Taborsky 1984). Breeder males, averaging almost 60 mm in standard length (SL), are larger than breeding females (52 mm SL), and both are larger than the largest subordinate in the group (44 mm SL; Dierkes et al. 2005). Still, subordinates may also take part in spawnings (Dierkes et al. 1999; Heg et al. 2006, 2008; Heg & Hamilton 2008) and feed on eggs (von Siemens

1990), giving rise to potential conflicts within the group.

Tanks were kept in climate controlled rooms at the Ethologische Station, Hinterkappelen, University of Bern. The light regime was held constant at a 13:11 h day:night cycle, and water temperature was held at $26.6 \pm 1.2^\circ\text{C}$. Fish were fed daily *ad libitum* with TetraMin food flakes (Tetra, Blacksburg, VA, USA; on testing days after the tests were completed). The bottom of all tanks used were covered with a 1-cm sand layer.

All experiments were conducted by R. Schürch. In short, 12 male and 12 female fish were tested for juvenile aggressiveness towards a mirror (Fig. 1a) and subordinate helping behaviour (Fig. 1b) following Bergmüller & Taborsky (2007). After these focal males and females had attained adulthood, they were paired (Fig. 1c) according to their own propensity to assist breeders as subordinates in artificial groups (as measured in Fig 1b; see also Schürch 2008) and received a subordinate (sequence 1). This last procedure was repeated (sequence 2, Fig. 1c). All focal and non-focal fish were measured before each test was conducted (standard length SL to the nearest 0.5 mm and body mass in milligram). In between the phases, each focal fish was kept singly in a 'home tank' (25 l, 40 × 25 × 25 cm). After all experiments and observations were carried out, the fish were permanently marked (Biomark, Boise, ID, USA; RFID transponders 8.5 × 2.12 mm; McCormick & Smith 2004) and kept singly for at least a week. Fish were then moved to sex-specific aggregation aquaria. Details of the tests and observations conducted follow in the next paragraphs.

In *N. pulcher*, female reproductive output is determined by her status (dominant or subordinate: Heg 2008) and body size (Heg & Hamilton 2008, Heg et al. 2008), so body size effects had to be accounted for when comparing adult dominant females' reproduction. Male paternity and thus male reproductive success is highly skewed towards the dominant male (Heg et al. 2006, 2008), and therefore in our experiment largely depends on the body size of his mate.

Juvenile Aggressiveness Tests

Twelve juvenile focal males and 12 juvenile focal females were three times tested for aggressiveness in a mirror test (every month) when they were growing towards sexual maturity (21–41 mm SL) as follows (Fig. 1a). Each individual was transferred from their home tank (25 l, 40 × 25 × 25 cm) to a compartment of 30 × 65 × 65 cm inside a 400-l tank

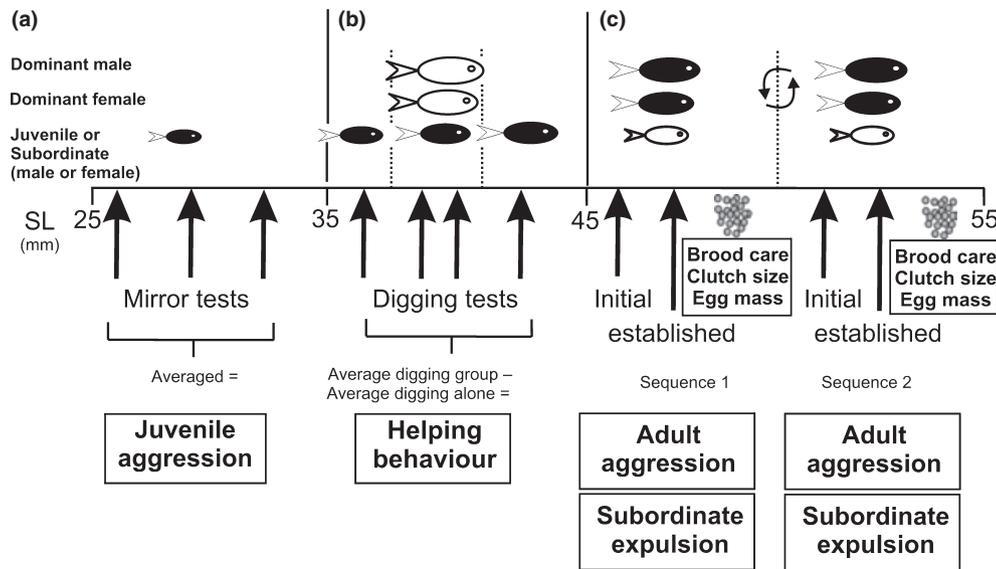


Fig. 1: Experimental history of the focal fish (black), growing from a standard length of ca. 25–55 mm. (a) Juvenile aggression towards a mirror image was assessed three times and averaged (400 l tank). (b) Helping behaviour was assessed as the average of two tests digging sand away from two pot halves when living as a subordinate with a dominant pair (white, ‘digging group’) minus the average of two tests digging sand away from two pot halves when living alone (‘digging alone’) inside the same compartment of the ringtank (130 l compartment, tested before and after the dominants were released). (c) At adulthood focal males and females were paired and given a subordinate (white, sequence 1, 60 l tank). Females were either paired with a selfish or a helpful male [as assessed in (b)]. Adult aggression towards mates and subordinates (direct after release: initial; and when the group had stabilised: established), subordinate expulsion, brood care, clutch size and average egg mass were determined. This procedure was repeated during sequence 2, switching the type of focal male the focal female received, and all pairs received new subordinates. This procedure allowed us to test for spillover effects of juvenile aggression and helping behaviour on adult behaviour (aggression, subordinate expulsion and reproductive behaviour).

(130 × 65 × 65 cm) containing one flowerpot half for shelter, and acclimatized for 10 min. Then a 60 × 15 cm mirror was placed at one 65 cm long-side of the compartment, while the focal fish was hiding inside the flowerpot half. Immediately afterwards, we carried out a 10 min observation, during which we counted the frequency of overt attacks (fast approaches and contacts) towards the mirror image. Aggression towards a mirror has successfully been used in this species (Grantner & Taborsky 1998). Using a mirror further allowed us to test aggression towards a perfectly size matched individual, and to rule out potential winner–loser effects (Oliveira et al. 2005). The three test scores of aggressiveness were averaged to give the ‘juvenile aggressiveness’ score (Fig. 1a). Juvenile aggression was then used to test for spillover effects into adult aggression (see below).

Subordinate Helping Tests

After the completion of the juvenile aggressiveness tests and after the focal fish were larger than 35 mm SL, these 24 focal individuals were tested for their

propensity to assist unrelated dominant breeders in territory maintenance as a subordinate (Fig. 1b, 35–41 mm SL). Note that these focal subordinates were now all sexually mature. Each focal individual was released inside a square compartment (40 × 50 × 65 cm) of the ringtank containing two flowerpot halves (Fig. 1b, see for setup whole ring-tank Heg et al. 2004). On day 3 after release, both flowerpot halves were covered with sand, and thereupon we assessed the frequencies of carrying sand away from the shelters in a 10-min observation for each focal (‘digging alone’). In the evening of the same day, a large male and female was added, who accepted the focal individual as a subordinate in each case successfully. During this period, which lasted on average 78 days, we induced again digging behaviour twice on different days (as above) and assessed the frequencies of carrying sand away from the shelters in a 10-min observation for each focal, these two scores were averaged to give the ‘digging group’ score (Fig. 1b). After this period, the breeding pair was removed and each focal individual was again scored for ‘digging alone’ following the procedure above (Fig. 1b). The helping behaviour score of

an individual focal fish was calculated as the average of the two scores of 'digging group' minus the average of the two scores when 'digging alone' (as assessed before and after the release of the pair to reduce sequence effects). This helping behaviour score was then used to test for spillover effects into adult aggression and reproduction (see below).

Adult Tests

After the completion of the subordinate helping behaviour tests, we allowed the focal fish to grow into adulthood inside their home tanks (42–55 mm SL) and they were then used to create dominant breeding pairs in group trials as follows ($n = 12$ pairs). We ranked the 12 focal breeder males according to their helping behaviour score (see above), classifying the 6 most helpful males as helpful and the remaining 6 males as selfish. These 12 males were randomly paired to the 12 focal females for the first test sequence and released 1 day after a smaller subordinate fish was released inside the tank (see below). For the second test sequence, we reversed the treatment per focal female, so that a female paired to a selfish male (lower rank for helping behaviour) in sequence 1 was paired to a helpful male (higher rank for helping behaviour) in sequence 2 and vice versa (and again the pair was released 1 day after a new subordinate was released inside the tank, see below). This resulted in a paired design from the focal female's perspective, where each female was once paired to a selfish male, and once to a helpful male in random order (Fig. 1c). Each sequence lasted 2 months.

Each group was kept in a 60-l tank ($60 \times 30 \times 33$ cm) with two flowerpot halves that served as breeding shelters, two biological filters (upper left and upper right corners of each tank) and plastic tubes beneath the surface (used for hiding, e.g. in case the subordinate was expelled). One subordinate ($n = 24$, 28–40 mm initial SL, no prior experimental history) was acclimatized per tank for 1 day, before the focal breeding pair was added. The size distributions of the artificial groups were thus within the natural range of size distributions (Dierkes et al. 2005). The measurements taken are described in the next paragraphs.

Helper acceptance

During both sequences, we checked daily for whether the subordinate had been expelled. Expulsion or acceptance of the subordinate was decided

usually early on (from day 2 onwards), however for the data analysis we used whether the subordinate was expelled yes or no from the group on the 8th day since release of the focal pair. Subordinates were judged to be expelled when they were hiding at the provided tubes or filters, and not being allowed elsewhere in the aquarium.

Behavioural observations

We conducted three types of observations (Fig. 1c): (1) an initial aggressiveness observation (during group formation); (2) a later aggressiveness observation (established groups); (3) a brood care observation (established groups). As we sampled levels of focal juvenile aggression by recording the focal's behaviour towards a mirror, we focused our analysis of the focal adult breeder behaviour on behaviours that matched the behaviour towards the mirror. Therefore, we summed the frequencies of ramming and biting into a measure of adult overt aggression in the groups per opponent (focal mate or subordinate, for details of the behaviours see Hamilton et al. 2005; data on other behaviours were available, but not used presently).

The initial aggressiveness score was determined 10 min after the focal pair was released (to allow them to calm down after the handling stress), i.e. to capture aggression during the start of the group formation. Each focal breeder was observed for 10 min, randomizing the sequence for which breeder (focal male or female) was observed first. We recorded all overt aggressive behaviours towards their mate and their subordinate separately. The later aggressiveness observation was determined likewise for 10 min, on day 12 to 38 after release of the focal pair (variation in timing because of observations conducted during the non-breeding phase), when all groups had stabilized (i.e. the pair had either accepted or expelled their subordinate helper, so-called 'established groups').

Brood care observations were conducted on the day each pair had spawned (3–43 days after the focal pair was released to the tank, no evidence of subordinates participating in reproduction detected), after the clutch was complete. Each focal breeder was observed for 10 min, randomizing the sequence for which breeder (focal male or female) was observed first. Brood care was assessed for each pair member as the frequency of egg cleaning (each mouthing movement over the eggs, which removes, e.g. fungi from the eggs) and the duration of egg fanning (focal creates a water current over the clutch by fanning

the pectoral fins, which aerates the eggs). After the brood care observations the flowerpot halve(s) with the clutch was removed (and replaced) and further processed (see below).

Clutch size and egg mass

Each clutch was counted (clutch size), and then the eggs were dislocated and transferred to a Petri dish to determine egg mass as follows. We dried the clutches in an oven at 70°C for 3 days. We weighed dry clutch mass on a Mettler AE100 balance (Mettler-Toledo GmbH, Greifensee, Switzerland) to the nearest 0.1 mg. We calculated average egg mass as clutch size divided by total clutch mass. Some eggs were very fragile and punctured upon dislocation, so had to be discarded. In those cases, average egg mass was determined from the transferred clutch mass divided by transferred number of eggs, and subsequently total egg mass was determined by multiplying the average egg mass with the clutch size.

Statistical Analysis

All observations on adult fish were conducted with the help of the event recorder software JWATCHER (<http://www.jwatcher.ucla.edu/>). Based on personal experience, the 10-minute observation duration was judged to capture the essence of behavioural interactions in small groups as ours (R. Schürch, pers. obs.). To minimize influence of time of day on behaviours, we conducted the observations preferably in the early afternoon, even though diurnal variation in behaviour is not known for these fish in laboratory settings (Taborsky 1982). As we set-up the experiment in a climate-controlled room, seasonal effects can be ruled out.

We investigated a potential spillover of juvenile aggressive behaviour (independent variable) to adult aggressive behaviour (response) by building generalized linear models (GLMM) of the poisson family (Faraway 2006), correcting for the repeated measurements of individuals ($n = 24$) and groups (24 different groups). We built four separate models: aggression towards mate (once for the initial group formation and once for the established group context); and aggression towards subordinate (once for the initial group formation and once for the established group context). For all four models we started with a full model including juvenile aggression, body size (SL), sex and their interactions as effects. We then successively removed non-signifi-

cant effects in a backward model selection process. To illustrate the relationship between juvenile aggression and adult aggression (Fig. 2), we calculated the residuals from the final models' parameter estimates, without accounting for juvenile aggression.

Subordinate expulsion was modelled with generalized linear models (GLM) of the binomial family for focal males ($n = 12$) and females separately ($n = 12$), correcting for the mean aggression of the partners (sequences 1 and 2 combined).

To test whether the helping behaviour predicted adult breeding performance, we built a linear-mixed effect model with total clutch mass as the response variable. Note that only 9 focal females produced clutches during both sequences, reducing our sample size to 18 clutches for these analyses. Continuous helping behaviour scores of males and females were used as the predictors, and we corrected for the repeated measurement of females by adding them as random effects. Since clutch mass is known to depend on female body size (Heg 2008), we had to correct for the body size (SL) of the females as well. The resulting model (model 2 in Table 2) performed not significantly better when compared with the null model (fitted intercept only). This was likely because of the number of parameters involved. Single-term deletion suggested dropping female helping score as a predictor. However, inspection of the resulting model's residuals (model 3 in Table 2) revealed that they had a bimodal distribution. By adding whether the groups accepted the subordinate helper as a predictor to the model, the fit was significantly increased and lead to desired unimodal distribution of the residuals (model 5 in Table 2). Finally, the fit of the model 5 was significantly improved by adding the interaction term helping score of males \times helper acceptance (model 6). To compare the models pair wise during the model building process we used likelihood ratio tests (LRT), calculated from the models' likelihoods (L) as $\chi^2 = 2(\ln L_1 - \ln L_2)$. The difference in the number of free parameters in the two models compared provides the degree of freedom for the test. The test statistic is then evaluated under the assumption of asymptotic convergence to a χ^2 distribution (see e.g. Jacob et al. 2007 for details). There was no sequence effect on clutch mass (LRT: $n = 18$ clutches; sequence (1 or 2): $\chi^2 = 1.887$, $df = 1$, $p = 0.170$).

We used GLMMs of the poisson family to test for a relationship between days to first spawning (response) and the clutch mass produced (independent). By forward selection we noticed that the fit

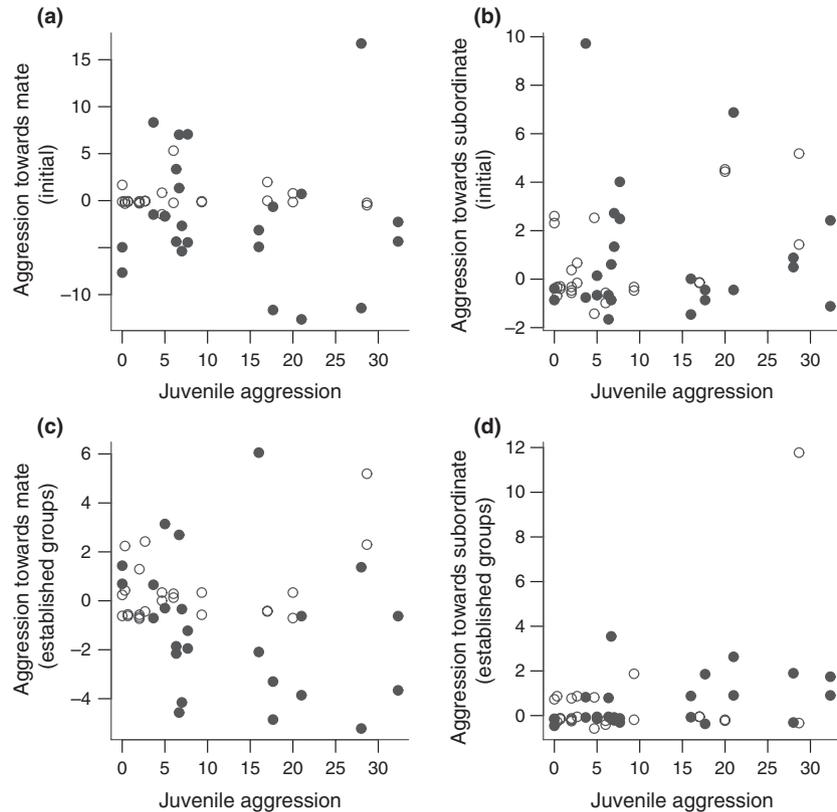


Fig. 2: Juvenile to adulthood spillover effects: the relationship between juvenile aggression and adult aggression towards their (a, c) mate and (b, d) subordinate separately (Fig. 1c); for (a, b) the initial phase of group formation and (c, d) when the group was established. Given are residuals corrected for the effects of body size SL and sex. Note that in (a) juvenile aggression and juvenile aggression \times SL were significant, in (b) juvenile aggression was not significant, in (c) juvenile aggression \times sex and juvenile aggression \times SL, as well as juvenile aggression \times sex \times SL were significant, and in (d) only juvenile aggression was significant (see Table 1 for details).

could be improved significantly when we also added female helper score and an interaction term to the model. We used R version 2.9.1 for all statistical analysis (R Development Core Team 2009). To create the LMM and the GLMMs we used the lme4 package (Bates et al. 2008). For the GLMMs we used the z-test statistics provided and LTR to judge significance of terms, while in the case of the LMM we used LTR. All tests were two-tailed with alpha set at 0.05.

Results

Aggression Spillover and Helper Expulsion

During the initial group formation observations, focal adult males were generally more aggressive towards their mates and subordinates than the focal females were towards their mates and subordinates (Table 1), and aggression towards mates and subordinates significantly increased with focal body size (Table 1), but less so in large focal males (as indicated by the significant interactions between sex \times SL in Table 1). Corrected for these effects, juvenile aggression showed a spillover effect in adulthood. As expected, juvenile aggression was significantly positively related to adult aggression towards their mates

(Table 1; Fig. 2a), but contrary to expectation, not related to adult aggression shown towards their subordinates (Table 1; Fig. 2b).

During the established group observations, juvenile aggression only significantly explained aggression towards mates in focal males, depending on their body size (significant interactions in Table 1). Note that the effects were only marginally significant (both $p < 0.05$). Focal females were more aggressive towards the subordinate when compared with the focal males (Table 1) and aggressiveness towards subordinates increased with focal adult body size (Table 1). Corrected for these effects and as expected, juvenile aggression was significantly positively related to focal adult aggression shown towards subordinates (Table 1; Fig. 2d, both in focal male and females).

However, contrary to expectation, focal adult males were significantly more likely to accept subordinates when they had shown high levels of juvenile aggression (Fig. 3a), whereas focal adult females tended to expel subordinates depending on their juvenile aggression levels (Fig. 3b). This indicates that at least in the focal males the spillover from juvenile aggression, to adult aggression towards subordinates, might be used to dominate and accept their subordinate as a helper.

Table 1: Results of four separate generalized linear mixed effect models of the frequency of adult aggressive behaviour (poisson distributed, log-link) towards their mate or subordinate in two time periods separately, in dependence of aggressive behaviour measured in the same focal individuals when juvenile ('juvenile aggression'), focal sex (females as the reference category), and focal body size (standard length, SL mm)

Parameter	Estimate	SE	z	p-value
Aggression towards mate during initial group formation (n = 24)				
Intercept	-19.884	6.663	-2.984	<0.003
Sex	16.415	6.339	2.590	<0.001
SL	0.375	0.133	2.820	<0.005
Juvenile aggression	0.734	0.247	2.973	<0.003
Sex × SL	-0.275	0.127	-2.170	0.03
SL × juvenile aggression	-0.014	0.005	-3.045	<0.003
Aggression towards subordinate during initial group formation (n = 24)				
Intercept	-9.562	6.554	-1.459	0.14
Sex	16.645	7.087	2.349	<0.02
SL	0.184	0.135	1.358	0.17
Sex × SL	-0.315	0.142	-2.227	0.026
Aggression towards mate in established groups (n = 24)				
Intercept	-3.733	6.076	-0.614	0.54
Sex	-1.374	7.147	-0.192	0.85
SL	0.069	0.124	0.556	0.56
Juvenile aggression	-0.763	0.624	-1.223	0.22
Sex × SL	0.045	0.141	0.322	0.75
Sex × juvenile aggression	1.395	0.700	1.992	<0.05
SL × juvenile aggression	0.016	0.013	1.300	0.19
Sex × SL × juvenile aggression	-0.028	0.014	-2.051	<0.05
Aggression towards subordinate in established groups (n = 24)				
Intercept	-10.772	3.679	-2.929	<0.004
Sex	-1.583	0.741	-2.138	0.033
SL	0.190	0.075	2.522	0.012
Juvenile aggression	0.070	0.021	3.329	<0.001

The random factors in all models were individual identity and group identity.

Helping Behaviour and Adult Reproduction

Out of the 12 focal females tested, only 9 females produced a clutch during both sequences, reducing the sample size to a total of n = 18 for the remainder of the analyses. In one group, we missed the spawning of the first clutch (detected after hatching of the fry behind a filter instead of in a flower pot half), and for this group, we used the data of the second clutch.

Depending on whether helpers had been accepted in the group, adult focal females invested significantly more in their clutches when paired to a selfish male (as measured Fig. 1b) compared with when paired to males that had been helpful when subordinate (Fig. 4, final model 6 in Table 2). However, the significant effect of the interaction between helper acceptance and male helping score were because of

one outlier (data point to the right in Fig. 4). If this data point was removed, the interaction was not significant anymore ($\chi^2 = 0.1937$, df = 1, p = 0.66), and female clutch mass depended on male helping score ($\chi^2 = 13.099$, df = 1, p < 0.001) and the effects of helper acceptance ($\chi^2 = 10.239$, df = 1, p = 0.001). The focal female's own helping score measured when subordinate (see Fig. 1b), did not predict the adult female's investment into clutch mass (model 3 in Table 2). We tested whether a higher investment in clutch mass was counter-balanced by a delay in reproduction (excluding the 1 s clutch, n = 17), but instead females shortened days to first spawning when producing big clutches, independent of male helping score, but in interaction with their own helping score (comparison of GLMMs with and without an interaction of clutch mass × female type as a predictor of the latency to produce a clutch, LRT, n = 17 clutches; days to first clutch: $\chi^2 = 12.146$, df = 1, p < 0.001). The parameter estimates ± SE for the final model of latency, and the respective z and p-values were as follows: intercept 2.754 ± 0.217 , z = 12.713, p < 0.001; clutch mass -0.017 ± 0.007 , z = -2.350, p = 0.019; female helping score 0.055 ± 0.016 , z = 3.390, p < 0.001; clutch mass × female helping score -0.002 ± 0.001 , z = -3.573, p < 0.001.

Because focal males did not perform extensive brood care (with one exception), we assessed whether focal females adjusted their care depending on clutch mass. Females did not adjust egg cleaning to the investment into total clutch mass, however there was a tendency that females fanned more for bigger clutches (comparison of GLMMs with and without clutch mass as a predictor, LRT, n = 18 clutches; egg cleaning: $\chi^2 = 0.002$, df = 1, p = 0.96; egg fanning: $\chi^2 = 3.0438$, df = 1, p = 0.08).

Discussion

We showed that juvenile aggression and subordinate helping behaviour in *N. pulcher* spills over from a younger life-stage into the adult breeder context, but not always in the expected direction. First, and as expected, juvenile aggression predicted aggression towards their mates later in life, but only during the early group formation. Second, juvenile aggression predicted aggression towards their subordinate as adults, but only after the group was established. It seems that in the early stage of a new group, establishing the hierarchy is so important for breeder males, that they show very high levels of aggression towards subordinates regardless of their innate

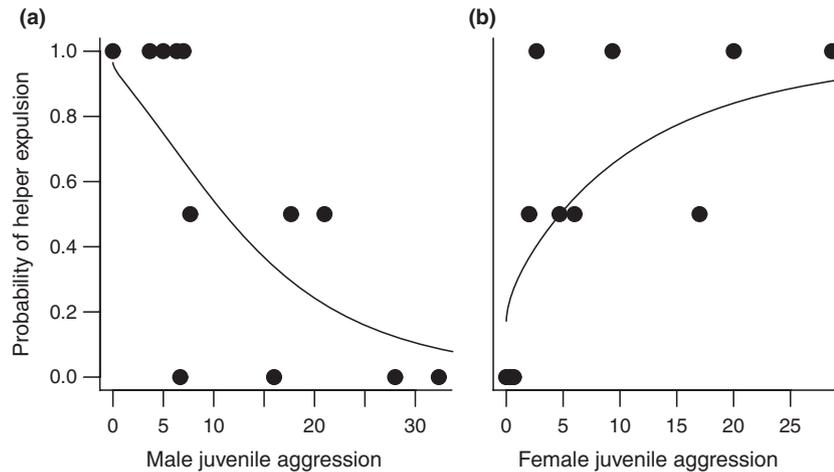


Fig. 3: Juvenile to adulthood spillover effects: the effects of juvenile focal male and focal female aggression (see Fig. 1a) on the likelihood of the focal pair expelling their subordinate (no coded 0 and yes coded 1, see Fig. 1c). Generalized linear models (GLMs) of the binomial family for focal males and focal females separately. Focal males parameter estimates \pm SE (statistics): intercept 1.9015 ± 3.1351 , juvenile male aggression: -0.9956 ± 0.5538 ($\chi^2 = 5.46$, $df = 1$, $p = 0.02$), juvenile partner female aggression 0.5568 ± 0.6606 ($\chi^2 = 0.68$, $df = 1$, $p = 0.41$; mean of two partners). Focal females: intercept 3.7893 ± 3.6504 , juvenile female aggression 0.7232 ± 0.4648 ($\chi^2 = 3.12$, $df = 1$, $p = 0.08$), juvenile partner male aggression -1.5809 ± 1.0876 ($\chi^2 = 3.75$, $df = 1$, $p = 0.05$; mean of two partners). The fitted lines are back transformed from the results of the two GLMs.

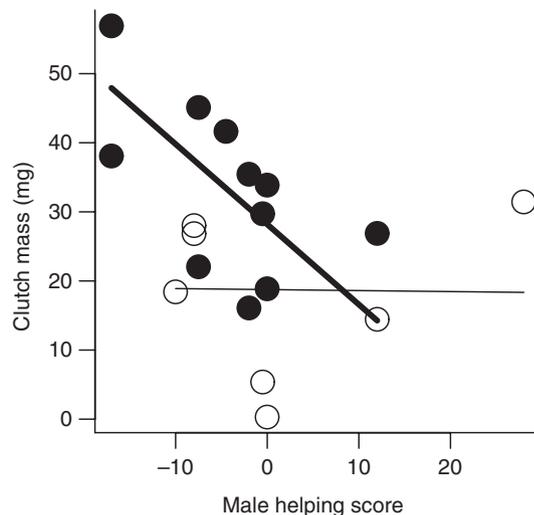


Fig. 4: Focal adult females' investment in clutch mass significantly decreased with the helping score of her mate (as measures when he was a subordinate). There was also a significant interaction between male helping score and whether the pair had accepted their helper (helper expelled: closed circles, thick line; or accepted: open circles, thin line). See Table 2 for statistics.

aggression levels. Contrary to expectation, high juvenile aggression levels did not result in expulsion of the subordinate. Rather, adult males who were aggressive as juveniles were more likely to accept a subordinate, which also suggests that high levels of aggression are needed to force the subordinate into submission. Third, as expected, adult females

invested more in their clutch when paired to adult males who were more selfish as a subordinate, compared with adult males who were more helpful as a subordinate. To our knowledge, this is the first experimental evidence that individuals with poor breeding prospects should have higher propensities to provide help to other individuals (West-Eberhard 1975). There was no relationship between the adult female's clutch size and her helping behaviour as a subordinate. However, also consistent with our expectations, females took longer to produce their first clutch when they themselves had been helpful as subordinates, and the effect was particularly strong when they additionally produced a large clutch (significant interaction between female helping score \times clutch mass on the latency).

Spillovers of aggressive behaviour from one context into another, as we have demonstrated for *N. pulcher* in this study, have also been found in other taxa. The best evidence for spillover of aggression from the juvenile to the adult stage comes from spiders (Arnqvist & Henriksson 1997; Schneider & Elgar 2002). In the fishing spider, females that have been aggressive as juveniles kill their potential mates before copulation and may remain unmated (Arnqvist & Henriksson 1997). However, there is also some evidence for aggression spillover effects in deer (Lingle et al. 2007).

To our knowledge this is the first study demonstrating spillover effects in a cooperative breeder. A theory how behavioural inflexibility might affect

Table 2: Linear mixed effect models of female total clutch mass produced ($n = 9$ females \times 2 clutches = 18), depending on the behavioural type of her mate (measured as a subordinate: helpful vs. selfish) and on subordinate helper acceptance (yes or no)

Model	Fixed effects	Reference model	Effect tested	AIC	χ^2	p
1	Null model			150.77		
2	Male helping score, female helping score, female SL	1		150.55	6.22	0.10
3	Male helping score, female SL	2	Female helping score	148.69	0.14	0.71
4	Female helping score, female SL	2	Male helping score	152.26	3.70	0.05
5	Male helping score, female SL, helper accepted	3	Helper accepted	146.04	4.66	0.03
6	Male helping score, female SL, helper accepted, male helping score \times helper acceptance	5	Male helping score \times helper acceptance	141.55	6.49	0.01

For all log-likelihood ratio tests $df = 1$, except for when comparing model 2 with reference model 1, where $df = 3$, and comparing model 6 with 5, where $df = 2$.

In all models females were used as random effects to account for the repeated measurements. Parameter estimates \pm SE for the final model 6: intercept -59.992 ± 32.441 ; female SL 1.852 ± 0.668 ; male helping score -1.1610 ± 0.341 ; helper accepted -9.443 ± 4.392 ; male helping score \times helper acceptance 1.147 ± 0.410 .

individuals at different life-stages, the social dynamics within groups and especially the reproductive success of individuals is currently lacking. Similar to the fishing spider example, overly aggressive adult females who expel helpers may have reduced fitness in *N. pulcher*, because subordinates have been shown to lessen female workload (Balshine et al. 2001, Heg 2008, Heg et al. 2009), and an increasing number of subordinates leads to higher reproductive output and to longer lived groups (e.g. Heg et al. 2005; Brouwer et al. 2005). In contrast, non-aggressive adult males may have difficulties in forcing smaller fish into submission and rather expel them instead of accepting them and thereby gain a workforce. Whether this effect depends on the sex of the potential subordinates involved remains to be tested in the future, particularly because subordinate males are contenders for reproduction (Heg et al. 2008) and adult males are more aggressive to subordinate males than they are to subordinate females (Mitchell et al. 2009).

In addition to the spillover of aggression, females also adjusted their reproductive effort depending on whether they were paired to males that had been helpful or selfish as young, producing bigger clutches when paired to more selfish males. However, the significant interaction term between male helping scores and helper acceptance indicates that keeping a helper in the group might compensate for this effect (see Taborsky et al. 2007). On the contrary, the interaction seemed to be because of one influential data point, and after removal of this point from the analysis we did not find evidence for such a compensatory effect. Females in *N. pulcher* were shown to adjust investment in clutches already prior to this study. Taborsky et al. (2007) have shown that

females adjust egg size to the numbers of subordinates in the group: the more subordinates the smaller the eggs. Our study now also suggests that females produce a smaller overall clutch mass when there is a helper in the group, and thus yields additional support for their findings. In another study, Heg et al. (2006) have found that clutch size is adjusted to group composition. If large females have large male subordinates in the group, they increase clutch size. Heg et al. (2006) concluded that females increase clutch size to keep such male helpers in the group by conceding reproduction. However, in our case it seemed that females rather expelled helpers actively, instead of trying to accommodate the helpers that were allowed to stay.

Alternatively, differential allocation could either be a consequence of mate choice, that is, females increase investment when paired to a high quality male, or because of compensation of the females when paired to a selfish male (e.g. Burley 1986; Sheldon 2000; Kolm 2001). The experimental set-up does not allow us to distinguish between the two possibilities conclusively. However, in the latter case one would expect the workload of females to be reduced because of the males' help when paired to a helpful male, but adult males almost never cared for eggs, regardless whether they had been helpful as juveniles or not. As a consequence, females which invest more into production of the clutch when paired to a selfish male also have an increased workload when providing care. Thus, we suggest that if females adjust their clutch size to a yet unmeasured male quality indicator, this male quality indicator must somehow correlate with his unwillingness to provide help as juvenile.

The clutch mass adjustment by the females depending on their partner's subordinate helping score was substantial (the difference in clutch mass averaging around 15% of the mean clutch mass), and this strong adjustment to males might explain why there was no effect of her own helping score on her clutch mass. However, the number of days it took a female to produce the first clutch depended on an interaction between the clutch mass and her own helping score. Namely, it took females longer to start breeding when producing large clutches and additionally when being more helpful as a subordinate. How these effects affect the females' overall reproductive performance in the long run is impossible to say without conducting long-term experiments. Nevertheless, it is a further hint that females pay an additional cost through a delay in breeding, when producing larger clutches for more selfish males.

The reduced clutch size males obtain as adults when being more helpful as subordinates can be reconciled with kin selection theory, as individuals having an innate good quality should aim at gaining direct benefits as soon as possible and therefore not help, while bad quality individuals had to try to maximize indirect fitness by helping (West-Eberhard 1975; Johnstone 2008). An earlier study has shown that the males' propensity to disperse and the propensity to help are negatively related (Schürch 2008). A field study has shown that dispersal into other families only occurs, when the position in a breeding queue can be improved (Stiver et al. 2004). The present study now shows that males which were more helpful as subordinates will obtain smaller clutches from the females when adult, especially when they cannot keep a helper in the group. Overall, these results are indicative of an 'aid behavioural syndrome', as males which are poor breeders do not disperse but instead help in their current group.

Evidence for such a pattern in vertebrates is so far limited to observational studies. For instance, helpful Seychelles' warblers were never able to obtain a breeding territory for their own, while non-helping individuals often started budding-off territories on their home territory or dispersed to nearby vacancies (Komdeur & Edelaar 2001b). Similarly, stripe-backed wrens that were more energetic as helpers were outlived by siblings of the same sex showing less help (Rabenold 1990). Thus this study shows the first experimental evidence for the relation between reproductive capability and the propensity to help.

At the moment, an extensive theoretical framework for the co-evolution of life histories and aid behavioural syndromes is lacking, but models

suggests that life history and behavioural syndromes can co-evolve in non-social species (Wolf et al. 2007), and that fecundity and selfishness can co-evolve in cooperatively breeding systems (Johnstone 2008). The finding that juvenile aggression affects group stability in adulthood, and that the decision to help may depend on the innate performance as a breeder later, highlights the necessity to incorporate more than just the momentary act of helping in kin selection theory.

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