



The early social environment affects social competence in a cooperative breeder

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Social competence is defined as the ability of an animal to optimize the expression of social behaviour as a function of the available social information. The social environment encountered early in life can affect the expression of various social behaviours later in life. We investigated whether early social experience can affect social competence. In the cooperatively breeding cichlid *Neolamprologus pulcher*, we tested whether individuals reared with older brood-caring conspecifics persistently perform better in a series of tasks (1) simulating different social contexts, (2) assigning individuals different social roles and (3) exposing them to an unknown social situation. Fish that had been reared together with older conspecifics showed more appropriate behaviours both as winners (more aggressive displays) and as losers (more submissive displays) when aggressively competing with peers over a resource, and when trying to be accepted as subordinate group member and prospective brood care helper by an unfamiliar dominant pair (more submissive displays near shelters), a situation they had never encountered before. In both tasks fish that had grown up with older fish were tolerated better by conspecifics than fish reared with same-age siblings only. We detected effects of the early environment on social behaviour in the juvenile and adult stages of the test fish. Our results suggest that growing up in more complex social groups fosters a general social ability (i.e. social competence) in *N. pulcher* that improves their performance across different social roles and contexts, and which may provide fitness benefits.

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Social competence has been defined as the ability of an animal to optimize the expression of its social behaviour as a function of the available social information (Oliveira 2009). Thus social competence involves the capabilities to perceive and process social information, and to behave most appropriately based on this information in a given social context. This concept implies that social competence is a general social ability pertaining to all possible types and contexts of social interactions at all life stages. The existence of such a general ability would be indicated if the performance across different social situations is correlated within individuals, while differing between individuals. An enhanced ability to use social behaviour appropriately and efficiently across social contexts should markedly enhance the Darwinian fitness of individuals, particularly in highly social species, for which almost all activities involve social behaviour.

Several experimental studies have revealed that the social environment experienced during early ontogeny can influence the performance of animals in socially challenging situations such as resource competition (Bastian et al. 2003; Arnold & Taborsky 2010), the efficiency of forming dominance hierarchies (Branchi et al. 2006, 2009), brood care (Margulis et al. 2005) and mating success (White et al. 2010). While most of these studies targeted only one particular social situation, the possibility that early social experience affects the ability to show appropriate behavioural responses across social contexts (i.e. social competence) has not been explored extensively.

Social competence pertains to social behaviour in general, and therefore its study requires an approach that captures the universal nature of this trait. We propose that social competence can only be compared between individuals when their performance is tested in multiple, qualitatively different social challenges and situations. To capture a representative part of the spectrum of possible social interactions we suggest testing individuals (1) in different social contexts (e.g. a contest over a resource with a competitor, cooperating in obtaining a resource, joining an existing hierarchy as subordinate or courting a mate) and (2) in different social roles within the same context (e.g. being the superior or the defeated competitor). (3) To test for the

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persistence of this ability over time we suggest performing challenge tests across different life history stages (e.g. juvenile and adult stages). (4) Finally, to test critically for the general nature of social competence individuals should be exposed to 'novel' social challenges. Ideally, these are challenges belonging to the natural spectrum of a species' social interactions, but a focal test individual should not have encountered this challenge yet during its ontogeny. If consistent variation in social competence exists, one would expect that certain individuals, or groups of individuals with the same social history, would perform better in all of these four classes of challenges. As such, social competence is an individual quality just like, for example, spatial competence (e.g. Jones et al. 2003), with the respective effects on Darwinian fitness. To avoid the danger of circularity in defining what is the most appropriate behaviour in a situation, it is important to define a priori which behaviour of a given species is the most rewarding in a particular challenge based on a thorough knowledge of a species' behavioural biology in a natural context.

We compared the level of social competence between individuals of the cooperatively breeding cichlid fish *Neolamprologus pulcher*. This species lives in social groups of variable size (Balshine et al. 2001; Heg et al. 2005), and offspring of previous clutches and immigrants to the territory join in brood care of the current clutch produced by a dominant breeder pair (Taborsky & Limberger 1981). We predicted that (1) the composition of the social group in which fish grew up would induce persistent modifications of their social performance, (2) growing up in groups with a more complex social structure would result in a better social competence, and (3) individuals with a better social competence would accrue benefits, which are likely to raise their fitness. We performed two experiments with fish that had been reared in two types of social environments, either with or without the presence of older brood-caring fish. We exposed fish of both treatments at two life stages (juveniles and adults) to two challenges belonging to different social contexts. (1) The test fish had to compete with size-matched conspecifics over the ownership of a shelter in a setting in which both opponents had been assigned the role of the resource owner prior to the test. In this symmetric situation, both contestants should defend the shelter by open aggression (in contrast to an asymmetric contest, in which threat displays are sufficient; see Arnold & Taborsky 2010). If more complex family structures indeed induce a better social competence, fish raised with older family members should more often win these contests. Winners should maintain their gained resource by aggressive defence, whereas losers should behave submissively towards the winner to achieve tolerance near the shelter rather than eviction from the safe hiding place. (2) The fish were forced to achieve acceptance in the territory of an unfamiliar pair of larger fish with breeder status. This situation may be encountered by a smaller individual joining a social group as subordinate after dispersal (Stiver et al. 2004), or after a predation event if one or both dominant breeders of a social group were replaced by new dominant individuals (Dierkes et al. 2005; Stiver et al. 2006). In this situation a smaller individual should strive to acquire acceptance by the dominants as a brood care helper to prevent eviction from the territory. Acceptance as helper involves a subordinate being tolerated all over the territory area and being permitted to enter the breeding cavity. None of the experimental fish had ever encountered unfamiliar large dominants before this experiment. Therefore this task represented a novel situation for the fish. In this situation, we predicted that fish raised with older conspecifics would behave more submissively in general, and in particular would show more submissive behaviour towards the dominants in the vicinity of a prospective breeding cavity.

METHODS

Study Species

Neolamprologus pulcher (synonymous with *N. brichardi*; Duftner et al. 2007) is a highly social cichlid endemic to Lake Tanganyika, East Africa living in social groups that defend small territories around breeding cavities (Taborsky 1984). These groups typically consist of a breeding pair, offspring from a recent brood, and 1–14 immature and mature brood care helpers (mean five helpers, Balshine et al. 2001), but some groups have up to 36 helpers (Heg et al. 2005). Often helpers stay in the territories far beyond sexual maturity (Taborsky & Limberger 1981; Dierkes et al. 2005). Smaller helpers predominantly help in cleaning eggs, larvae and the breeding cavity, whereas larger juvenile and adult helpers join in defence against conspecific and interspecific space competitors and predators, and in territory maintenance, mainly digging (Taborsky & Limberger 1981; Taborsky 1984; Brintjies & Taborsky 2008, 2011). Helpers may be related or unrelated to the breeders (Dierkes et al. 2005; Stiver et al. 2005). In a breeding territory, helpers benefit from the defence efforts against predators by the other group members, they have access to high-quality shelters (Taborsky 1984; Balshine-Earn et al. 1998; Heg et al. 2004a), and they may inherit the position of a dominant breeder (Stiver et al. 2004). By contributing to brood care, defence and territory maintenance they avoid being evicted by larger, more dominant group members (Taborsky 1984, 1985; Balshine-Earn et al. 1998; Bergmüller et al. 2005; Bergmüller & Taborsky 2005; Stiver et al. 2005; Heg & Taborsky 2010).

General Housing Conditions

All holding tanks were equipped with a 2 cm sand layer, an internal biological filter, flower pot halves serving as shelters, and two brown PET bottle halves placed closely below the water surface as additional shelters. The light:dark cycle was set to 13:11 h with 10 min dimmed light periods in the morning and evening to simulate the light conditions at Lake Tanganyika. Water temperature was held constant at 27 ± 1 °C and the biochemical parameters were kept close to values of southern Lake Tanganyika (B. Taborsky, unpublished data). Fish were fed ad libitum 6 days a week (5 days commercial flake food, 1 day frozen zooplankton). The experiment was conducted at the Institute of Ecology and Evolution, University of Bern, Switzerland, under licence 40/05 of the Veterinary Office of the Kanton Bern.

Social Experience Treatment

The experimental fish were taken from 24 sib groups that had been derived from 12 clutches in a split-brood design. The detailed procedure and conditions of raising the split broods are described in Arnold & Taborsky (2010). In brief, half of each clutch was raised together with their parents or with their parents and two juvenile helpers for the first 2 months of life (see Appendix Table A1). As the behaviour of young was not influenced by the presence or absence of the two juvenile helpers, we combined these groups for analysis and refer to this social condition as 'raised with older family members' or, in short, as '+F' fish (see Arnold & Taborsky 2010). The second half of each clutch was raised in sibling-only groups, without the presence of adults ('-F' fish). The clutches were split and assigned to either the +F or the -F treatment at day 10 after spawning when the larvae had reached the free-swimming stage. The social experience phase lasted for 62 days when young were still well below 2 cm of standard length (SL) that is, at a size before they start to act as helpers in natural families (Taborsky &

Limberger 1981; Taborsky 1984). Subsequently, the 24 sibling groups (12 of each treatment) were transferred to neutral holding tanks. Overall, the group sizes in the neutral holding tanks varied greatly because of differences in initial brood size (see Arnold & Taborsky 2010), but groups of +F and –F siblings derived from the split-brood design were nevertheless similar at all times, until the end of this study (see Appendix Table A2). At an age of 3 months, four individuals of each group were temporarily removed for 30 h to perform a first social challenge test, an asymmetric competitive situation (see Fig. 1 in Arnold & Taborsky 2010 for timeline of that study). In this test we checked whether and how the social treatment affected the ability of test fish to show appropriate social behaviour shortly after the social experience phase. Results of this test were reported in Arnold & Taborsky (2010). Briefly, as shelter owners, +F fish showed more threat display, while in the role of an intruder they more often behaved submissively, than fish raised without adults. Contests were terminated earlier only when both opponents were +F fish.

Experiment 1: Symmetric Competition over Shelter

In contrast to the asymmetric test situation created by Arnold & Taborsky (2010), in which one contestant was assigned to be owner of a shelter before a trial and a second fish was assigned to be an intruder, the first social task of this study simulated a symmetric conflict over the possession of a shelter. We used a small clay flower pot half with a 5 cm outer diameter that could be efficiently defended by a small fish against potential intruders and therefore was suitable as a shelter for the experimental fish. Throughout their ontogeny, fish had been kept in tanks equipped with flower pots of various sizes so that they should have been experienced with conflicts over access to shelters at the onset of this experiment (familiar social challenge task). All trials were performed over a period of 10 days, when the fish were between 142 and 338 days old. We selected pairs of size-matched contestants (mean absolute length difference: 0.9 mm SL, range 0–2.5 mm SL; mean relative length difference: 3.0%, range 0–8.3%) that were unfamiliar with each other. As a second criterion, we also balanced the relative position of contestants in the social hierarchy they held in their home tanks. In *N. pulcher*, social rank is determined by body size (Heg et al. 2004b; Hamilton et al. 2005). Before a trial we recorded whether a given experimental fish was among the largest third of fish (rank class 1), the medium-sized third (rank class 2) or the smallest third (rank class 3) of fish in a home tank. Fish of all rank classes took part in the experiment (overall mean rank class: 2.071; mean difference between the rank class of contestant pairs 0.029). We tested 17 pairs of sibling +F and –F fish, 12 pairs of unrelated –F fish and six pairs of unrelated +F fish. Members of each pair of contestants were marked by removing a third of one dorsal fin ray. During this experiment almost all tested fish were still in the juvenile stage (only four individuals were just above the size at maturation of *N. pulcher* (3.5 cm SL; Taborsky 1985)). Therefore, we could not match the fish for sex, as most of them were still too small to be sexed.

Experimental tanks (30 × 20 cm and 20 cm high) were divided in half by an opaque PVC slate. Both compartments were equipped with a flower pot half (5 cm diameter) placed directly adjacent to the central divider of the tank. These flower pots were sufficiently small to serve as a shelter for the test fish (in contrast to the flower pots of experiment 2, see below). We introduced one member of a contestant pair to each compartment, and allowed the fish to habituate to the set-up for 1 h, during which time the fish occupied the shelters. Then the partition and the two adjacent shelters were replaced with a third shelter of identical size put exactly in the middle of the previous positions of the two shelters, so that both

fish would consider themselves to be the owner of this shelter. Immediately afterwards the behaviour of the two fish was recorded for 15 min by an observer (J.J. or A.T.) blind to the social experience of the fish. All social behaviours were recorded continuously in the sequence of occurrence. For analysis they were combined in the categories 'aggressive behaviour', 'threat display' and 'submissive behaviour' (see Arnold & Taborsky 2010). Additionally, we recorded the position of both fish in the tank every 30 s, distinguishing between three spatial categories: (1) in or near (≤ 3 cm) shelter: a close distance to the shelter indicates ownership of the shelter or tolerance by the shelter owner; (2) close to water surface (≤ 10 cm): fish staying in this category for extended periods are not tolerated and can be considered evicted from a territory; (3) anywhere else in the tank.

As our experiment simulated a symmetric interaction between two shelter owners, there was always an initial contest over the shelter that quickly resulted in one fish being dominant (winner) over the other (loser). Following the approach suggested by Oliveira et al. (2009), we classified as the winner the individual that displayed higher ratios of aggressive relative to submissive behaviour. Subsequently, we tested whether this criterion to classify winners and losers reflects shelter ownership at the end of the trials. Indeed, individuals of a dyad that had the higher aggression-to-submission ratio spent more time in or near the shelter (Wilcoxon signed-ranks test: $Z = 4.24$, $N = 35$, $P < 0.001$) and spent less time near the water surface ($Z = 4.34$, $N = 35$, $P < 0.001$), and thus can be regarded as winners of the resource.

Experiment 2: Integration in a Social Group

The second social task aimed to test how well the test fish were able to integrate into an unfamiliar social group represented by a dominant pair, which is the smallest social unit occurring in nature (Taborsky & Limberger 1981). The members of the pair had held the status of the breeder pair in their tank of origin for at least 6 months (D. Heg, personal communication) and all of them had several helpers in their groups. As no reproduction took place during our experiment, we refer to these fish as 'dominants' or 'dominant pairs'. In this situation the test fish were expected to signal to the dominant pair that they are subordinate and motivated to act as brood care helpers. Our test fish had not acted as helpers and had not encountered unfamiliar dominant breeder fish before taking part in experiment 2 (novel social challenge task).

We performed 20 trials using 10 different dominant pairs and 10 sets of one +F and one –F test fish, respectively. The sets of test fish were matched for sibship, size (mean absolute length difference: 1.1 mm; range 0–2.5 mm SL), sex (seven sets of males, three sets of females) and rank class (mean rank class: 1.85; mean difference in rank class: 0.1; see experiment 1 for explanation of this parameter). In this experiment, all but four test fish had reached adulthood, and in all test fish the sex could be determined unambiguously by inspection of the genital papilla. The trials were done over a period of 8 weeks when the test fish were between 225 and 389 days old. We used the same dominant pair for the two fish of a matched set of sibling fish, thereby controlling for individual differences in the behaviour of the dominant pairs. The exposure sequence of +F and –F fish to the dominant pair was balanced to adjust for potential biases caused by the longer habituation time of the second fish of a set (44 versus 20 h) and possible sequence effects in the behaviour of the dominants.

For the trials we used two 200-litre tanks equipped with sand and six flower pot halves (10 cm diameter) as prospective breeding cavities for the pair. Flower pots of this size are used as standard breeding cavities for *N. pulcher* in our laboratory, as large

dominants can enter and defend them against other fish comfortably. These pots were too large, however, to serve as safe shelters for the test fish, as their large openings allowed the dominants to detect and follow them. This was important, as in this experiment the test fish should seek acceptance in the territory of dominants, rather than considering the shelters as their own private shelter. The tanks also contained two biological filters and three brown, semitransparent PET bottles mounted near the water surface. The filters and PET bottles allowed the test fish to get out of sight from the breeders and thus to hide from their aggressive behaviour. For each trial, we first placed a +F and a matched –F test fish singly in the two 200-litre tanks and let them habituate to the set-up overnight before introducing the dominant pair. Introducing the smaller test fish well before the dominant pair prevents the immediate eviction of the test fish. On the morning of the next day, we introduced an unfamiliar dominant pair to one of the 200-litre tanks. This pair had been temporarily removed from another *N. pulcher* group of our laboratory breeding stock.

Directly after the release of the pair the activities in the tank were recorded for 15 min. The observer (B.T.) was blind to the social experience of the respective test fish. We recorded (1) all social behaviours between the test fish and the pair members, (2) all visits of the test fish to the flower pots, (3) all test fish visits to shelters (filters, PET bottles) and (4) every 30 s we recorded the position of the test fish; at these time points we noted the nearest distance to the next dominant fish, whether it was in the lower, middle or upper third of the water column and whether it was near or in a flower pot or a shelter. Two further 15 min recordings were performed in the same way 3 h and 24 h after the first recording, respectively.

After the third recording the dominant pair was captured and transferred to the second 200-litre tank where three 15 min recordings were done for the second test fish following the same time schedule as for the first test fish. After the end of the third recording of the second test fish the dominant fish were returned to their tank of origin in our breeding stock as quickly as possible to prevent social instability in their original groups.

Ethical Note

The fish were allowed to interact directly with each other during both experiments. We observed carefully whether injuries occurred during the trials, in which case we would have interrupted a trial immediately. This was never necessary, as none of the experimental fish were injured during the trials. Even 'open aggression' almost never involved direct body contact between two fish, because the attacked fish retreated quickly to a shelter or to the water surface, where they were no longer pursued by the aggressor. In those cases of experiment 1 in which aggression involved body contact (biting) this did not result in injuries, probably because of the low impact of bites between the light-weight juveniles. In experiment 2, some of the dominant females displayed an inhibited form of biting (rather a pushing movement), while the attacked helper fish showed submissive tail quivering beneath the female.

Statistical Analysis

The behavioural frequencies of experiment 1 were analysed by nonparametric statistics, as they were strongly zero inflated. Nonparametric statistics were also used to analyse effects of the size differences of contestants, as these differences were strongly skewed towards small values. In experiment 2 the behavioural frequencies shown by the test fish towards the dominant pair, both in the entire tank and in the vicinity of the prospective breeding cavities, were too small to analyse them separately per 15 min recording. Therefore we pooled them across the three recordings. These behavioural data

were also strongly zero inflated and were analysed by nonparametric statistics. Raw frequency data were analysed by Wilcoxon signed-ranks tests whenever sibling pairs were compared (experiment 2). Proportions were compared by Mann–Whitney *U* tests because of missing values when a certain behaviour did not occur at all. Location records (time spent hidden or near water surface) and observations of aggression by dominants towards the test fish were used as measures of tolerance of the test fish by the dominants. These observations were available at sufficiently high frequencies to be analysed separately for each recording. To account for repeated sampling, we fitted generalized estimating equation (GEE) models with test fish ID and dominant pair ID as subject effects and repeats per test fish and repeats per dominant pair as within-subject effects. The occurrence of social interactions including dominance interactions have been shown to depend on the physical distance between the interacting parties in fish (Taborsky et al. 1987) and in other species (de Waal & Luttrell 1988). Therefore we included the mean distance between the test fish and the nearest dominant fish as covariate in these models. The statistical analyses were performed with SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Experiment 1: Symmetric Competition over Shelter

Winning/losing of the contest over shelter

The social treatment did not influence the likelihood of winning (binomial test: $N = 17$, $P = 0.63$). Instead, the larger (Wilcoxon test: $Z = 2.14$, $N = 35$, $P = 0.032$) and heavier ($Z = 2.82$, $N = 35$, $P = 0.005$) individuals within a dyad won the contest over the shelter. In each trial, the dominance of the winner over the loser was established right at the beginning of each contest; therefore a comparison of the time until winning was not possible.

Behaviour of winner and losers

The +F winners showed more open aggression towards losers than the –F winners (Mann–Whitney *U* test: $U = 84.5$, $N_1 = 13$, $N_2 = 22$, $P = 0.044$), whereas there were no differences in threat display ($U = 106.5$, $P = 0.21$) and submissive behaviour ($U = 135$, $P = 0.69$) between winners with different social experience (Fig. 1a). Conversely, the +F losers displayed more submissive behaviour than the –F losers towards their opponents ($U = 61$, $N_1 = 16$, $N_2 = 19$, $P = 0.002$; Fig. 1b). This was not simply because they were more frequently attacked by the winner, as submissive behaviour was also higher in these fish when calculated relative to the aggression received ($U = 61$, $N_1 = 15$, $N_2 = 18$, $P = 0.007$; Fig. 1c). The rates of open aggression ($U = 147$, $P = 0.83$) and threat display ($U = 128.0$, $P = 0.41$) did not differ between losers with different social experience.

Tolerance of losers by winners

When we compared the time spent either in or near the shelter (tolerance; see Methods) or near the surface (eviction), the +F losers spent a larger proportion of this time in the tolerance zone than the –F losers [time near shelter/(time near shelter + time near surface): $U = 77$, $N_1 = 16$, $N_2 = 19$, $P = 0.020$; Fig. 1d].

Experiment 2: Integration into a Social Group

Social behaviour of test fish

Neither threat display, which the test fish showed towards the dominants on rare occasions (Wilcoxon test: $Z = 1.25$, $N = 10$, $P = 0.21$), nor submissive behaviour (Wilcoxon test: $Z = 0.46$, $N = 10$, $P = 0.64$) towards dominants differed between +F and –F fish, when we analysed the overall behavioural frequencies during the trials.

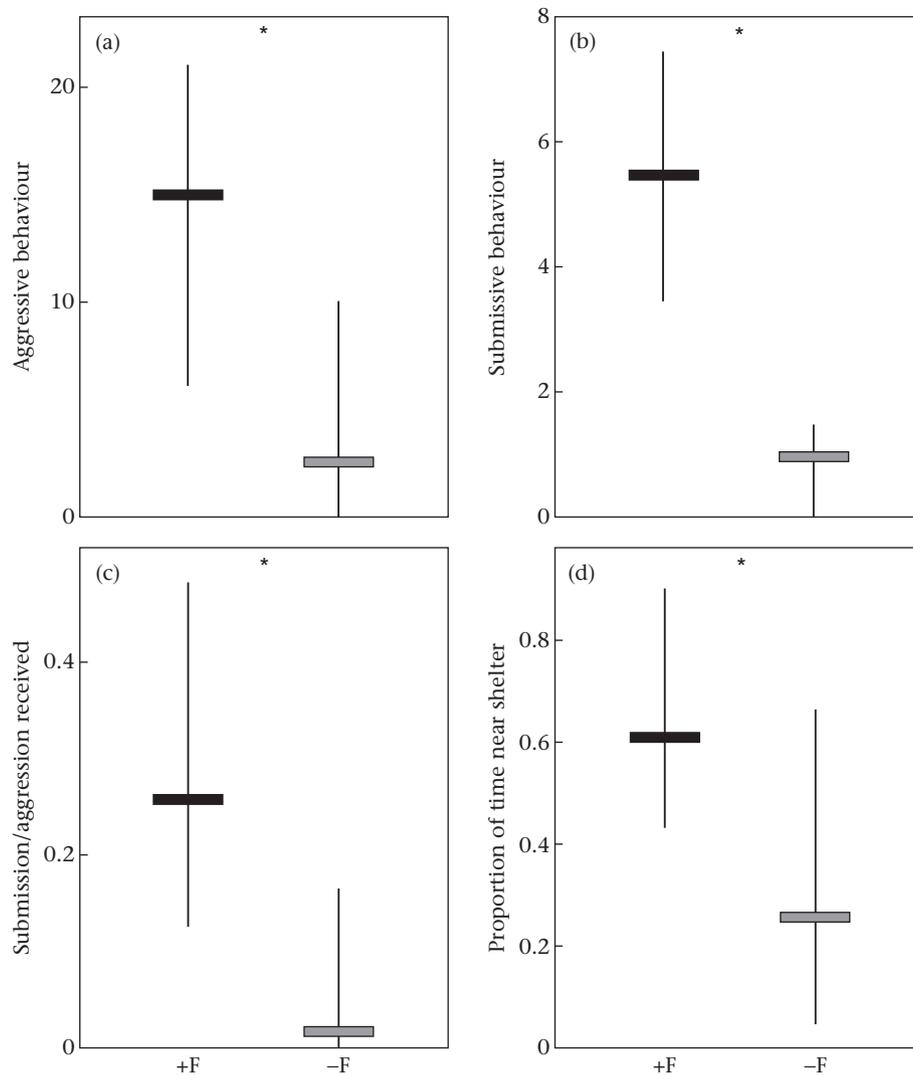


Figure 1. Behavioural frequencies in the symmetric competition experiment (medians and quartiles). Black: fish raised with older conspecifics (+F). Grey: fish raised without older conspecifics (-F). Frequencies of (a) open aggression by winners and (b) submissive behaviours by losers. (c) Proportion of submissive behaviours by losers relative to the number of received aggressive behaviours. (d) Proportion of time losers spent close to the shelter (proportions are based on the total time spent either in or near the shelter or near the surface). Asterisks indicate significant differences ($P < 0.05$).

To be accepted as helpers in a social group, it is particularly important for smaller group members to be tolerated by dominants in the vicinity of the breeding cavity (Taborsky 1984; Heg et al. 2004a). The +F fish showed significantly more submissive behaviour ($Z = 2.37$, $N = 10$, $P = 0.018$; Fig. 2) towards the dominants at the pots than the -F fish. This result cannot simply be explained by a higher preference to stay near the flower pots (and thus a higher random encounter rate with the dominants), as the visit rate of +F fish to the flower pots when no pair member was close to them did not differ between the treatments (Wilcoxon test: $Z = 1.47$, $N = 10$, $P = 0.14$; 59% of 493 total pot visits).

Tolerance by dominants

We predicted that the +F fish would be more readily tolerated by the unfamiliar dominant pair in the experimental tanks. Tolerance by the dominants can be deduced from the spacing pattern of subordinates and from the behavioural interactions between dominants and prospective helpers. We first analysed the position data we had recorded every 30 s during the 15 min recordings. Generally, when a subordinate *N. pulcher* is not tolerated by

a dominant fish, it stays close to the water surface or it remains hidden in a shelter. The -F fish were more often recorded hidden or close to the water surface (i.e. upper third of tank) than the +F fish when either of the dominants was close by, whereas there was no obvious difference in spacing of test fish when the dominants were far away (GEE; see significant interaction term in Table 1, 'Hiding or near surface'; Fig. 3a).

Second, we analysed the frequencies of aggressive displays by the dominants towards +F and -F fish in relation to the distance kept between test fish and dominants. The -F fish were more often target of aggressive displays than the +F fish when dominants were close by, whereas again there was no obvious difference between treatments when the dominants were far away (GEE; see significant interaction term in Table 1, 'Aggression by dominant'; Fig. 3b).

DISCUSSION

Our results show that the social environment experienced during the first 2 months of life had a long-term effect on the social behaviour of *N. pulcher* that had been raised either with or without

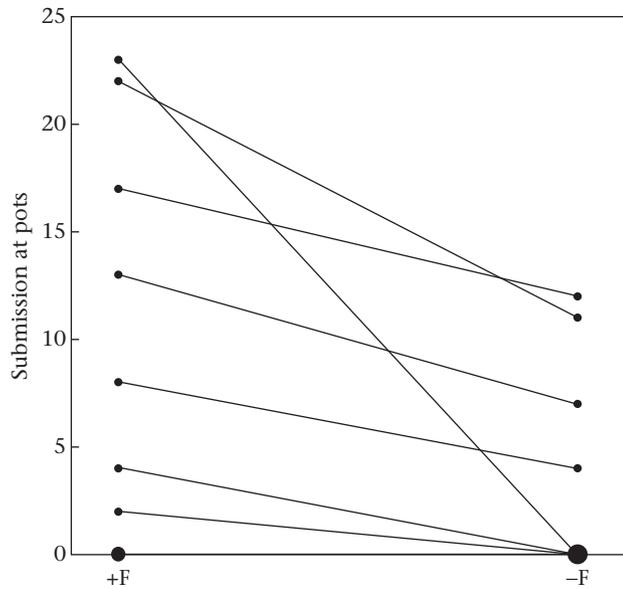


Figure 2. Frequencies of submissive behaviour shown at the flower pots in the social integration experiment (lines connect sibling pairs; enlarged dots represent three and six data points, respectively).

older conspecifics. We detected significant effects of the early social experience in the early juvenile stage, the late juvenile stage and during adulthood (see also Arnold & Taborsky 2010). In all three life stages, fish raised with older conspecifics (+F) showed more behaviours a priori classified as being appropriate in a given situation, whereas the frequencies of other behaviours did not differ. The early-environment effect pertains to different social contexts, namely competition between peers and integration into an unfamiliar social group consisting of a dominant pair. Moreover, the +F fish behaved more appropriately in different roles within a social context (1) when assuming the roles of winners and losers in relation to their body size (this study) and (2) when experimentally assigned the roles of shelter owners and intruders in an asymmetric competition challenge (Arnold & Taborsky 2010). Importantly, we detected the signature of the early environment even in a situation the fish had never encountered before (integration into a social group as a subordinate group member), suggesting that +F fish are better able to generalize across social situations and select a more appropriate behaviour even without a prior opportunity to learn a specific task.

Fish that had been raised with older conspecifics attained benefits during the social interactions, which were likely to raise

Table 1

Effects of social experience (+F or -F) on the frequency of test fish staying hidden or near the water surface and on the aggression by dominant pair members including the mean distances during each 15 min recording between dominants and test fish as covariate

Model comparisons	Wald χ^2	df	P
Hiding or near surface			
Treatment	6.33	1	0.012
Distance	2.75	1	0.097
Treatment*distance	3.91	1	0.043
Aggression by dominant			
Treatment	5.12	1	0.024
Distance	0.66	1	0.42
Treatment*distance	4.09	1	0.048

Generalized estimating equation (GEE) models with test fish ID and dominant pair ID as subject effects and repeats per test fish and repeats per dominant pair as within-subject effects. $N_{\text{treatment}} = 20$; $N_{\text{distances}} = 60$.

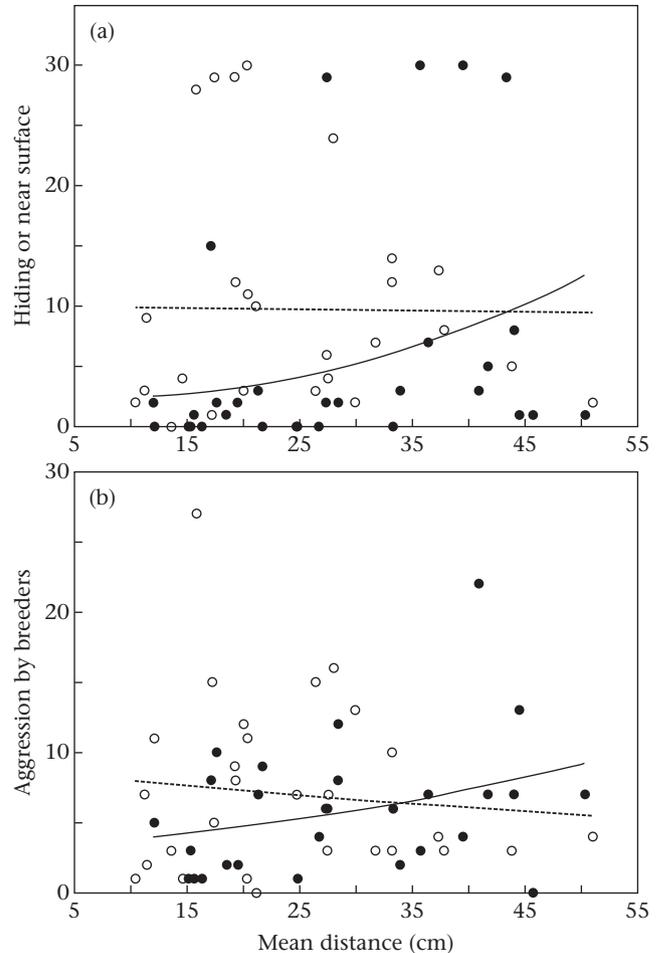


Figure 3. Relationship between the mean distance between test fish and dominant fish during the behavioural recordings and (a) the frequency of test fish staying hidden or near the water surface and (b) the number of aggressive behaviours by members of the dominant pair towards the test fish. Lines show the functions of values predicted by the GEE. Black circles and continuous line: fish raised with older conspecifics. Open circles and dotted line: fish raised without older conspecifics.

their fitness under natural conditions. After losing a contest, the +F fish were more likely to be tolerated by the winner near a shelter than the -F fish. Mature +F individuals were more likely to be tolerated close to the dominant pairs, which is an important precondition for eventual acceptance as helpers. In *N. pulcher* access to shelters and acceptance as a helper in the group territory is crucial for survival (Taborsky 1984; Heg et al. 2004a). Eviction of subordinates from the territory by breeders and by dominant helpers occurs frequently if helpers are not needed or inflict costs on dominants that are not outweighed by benefits (Taborsky 1985; Dierkes et al. 1999), as helpers in *N. pulcher* pay to be allowed to stay in the territory (e.g. Bergmüller & Taborsky 2005; Bergmüller et al. 2005; Heg & Taborsky 2010). Finally, contests were shorter when both opponents were +F fish (Arnold & Taborsky 2010), which hints at an increased efficiency of social interactions that may reduce the energetic expenditure for both opponents and lower the risk of injuries during contests.

Thus groups of individuals raised with older conspecifics show more appropriate social behaviour across the four criteria we proposed should be tested to obtain a representative picture of the social performance of animals. In summary, these findings suggest that +F fish were more socially competent than fish raised without adults, which has also been confirmed by the better outcome of

social challenges for +F fish in different contexts. Notably, in *N. pulcher* –F fish showed fewer of those behaviours classified as appropriate in a given context, but they did not show more of those behaviours classified as inappropriate (e.g. submission by winners of a resource or aggression towards dominant pair members). In contrast, rhesus macaques, *Macaca mulatta*, that had been reared only in the presence of their mother, and thus experienced a less complex social environment during adolescence than individuals reared in natural groups, showed more stereotyped behaviours and more often responded inappropriately towards affiliative displays of their peers later in life (Kempes et al. 2008). Socially deprived macaques behaved more anxiously towards conspecifics, and the authors hypothesized that anxiety might negatively affect the processing of social information. In contrast, +F and –F *N. pulcher* did not show indications of differential anxiety (e.g. no difference in the probability of losing a symmetric contest; no difference in flight behaviour from dominants).

Our results suggest that losers (experiment 1) and prospective helpers (experiment 2) attained a higher level of tolerance by dominants, because they showed more appropriate behaviour. Alternatively, better outcomes of social challenges might have been caused by subtle, nonbehavioural traits that went unnoticed by us and that were also caused by their early social environment. The nature of such hypothetical traits, however, is unclear. In addition, we did find a significant behavioural response of our experimental fish to their rearing conditions, so it seems most likely that the behaviour of dominants was triggered primarily or totally by these behavioural cues.

It is difficult to estimate the fitness effects of the behavioural responses to early social conditions, as other factors confound the outcome of interactions. For example, our prediction that +F fish would win a contest over a resource when the roles are symmetrical (i.e. ownership had been assigned to both opponents) was not fulfilled. Rather, winning and losing were determined by small length and weight differences, which obviously cause sufficient variation in resource-holding power to decide conflict outcomes (Reddon et al. 2011). On the other hand, the fact that +F losers were more likely to be tolerated near a shelter, which can be used to escape in case of danger, may decide their fate in the event of a predator attack (Taborsky 1984). Thus, seemingly small benefits may in fact have a large impact on fitness. In addition, multiple small benefits gained through a better social competence may have a substantial cumulative effect on fitness in such highly social species in which social encounters are very frequent.

We are aware of 10 experimental studies on vertebrates testing for effects of social experience during ontogeny on the performance in social challenge tests later in life (mammals: Bastian et al. 2003; Levy et al. 2003; Margulis et al. 2005; Branchi et al. 2006, 2009; Bester-Meredith & Marler 2007; birds: Adkins-Regan & Krakauer 2000; Bertin et al. 2009; White et al. 2010; fish: Moretz et al. 2007; Arnold & Taborsky 2010). In five of these studies, the challenge tests involved testing for one (different life stages: Bastian et al. 2003; different contexts: Levy et al. 2003; Moretz et al. 2007; social roles, Arnold & Taborsky 2010) or two (different contexts and life stages: Bertin et al. 2009) of the four criteria we proposed for an appropriate assessment of social competence of individuals. All studies detected significant effects of social experience on the outcome of the social tasks. All four studies testing directional predictions for expected behaviours in ecologically relevant test situations (Adkins-Regan & Krakauer 2000; Margulis et al. 2005; Arnold & Taborsky 2010; White et al. 2010) found that individuals that had been exposed to more heterogeneously structured social groups showed more of the expected appropriate social behaviours. Remarkably, those studies testing for nonsocial tasks in addition to social tasks (Levy et al. 2003; D'Andrea et al. 2007; Moretz et al. 2007) suggest that effects on social

performance induced by social conditions during early ontogeny do not necessarily have spill-over effects on behaviours and problem-solving abilities in nonsocial domains. The results of these studies suggest that early social experience does not affect general activity, exploratory tendencies, responses to predators and spatial learning abilities in the respective study species.

While there is good evidence for an influence of ontogenetic social experience on social behaviour later in life, the mechanisms underlying these effects are little understood. Arnold & Taborsky (2010) suggested that rather simple mechanisms might be responsible for the persisting differences in social behaviour of *N. pulcher*. (1) The +F young engaged in more frequent social interactions with their siblings during the social experience phase than the –F fish, offering ample opportunities to learn how to behave appropriately in social encounters with peers (there were no interactions between young and any of the older conspecifics observed; Arnold & Taborsky 2010). Likewise, in brown trout, *Salmo trutta*, the frequent necessity to defend a territory against intruders when growing up in natural streams promotes the ability to solve territorial contests fast and by expressing relatively few energetically costly aggressive behaviours, when compared with hatchery-reared young (Sundström et al. 2003). Possibly, the +F young in our study perceived their environment with guarding adults present as rather safe allowing them to devote more of their time to between-peer interactions rather than to vigilance. (2) Alternatively or in addition, effects on social behaviour might also have been induced passively by the organizational action of water-borne hormones released in the tank water by the older fish (e.g. Earley et al. 2006).

The importance of social competence for the expression of social behaviour has been repeatedly stressed (e.g. Suomi 1997; Kempes et al. 2008; Oliveira 2009). It is surprising that social competence has as yet not received more attention in behavioural biology and that a systematic research focus on this important general ability is hitherto lacking. This strongly contrasts with the social sciences, in which human social competence has been a key research topic for decades (reviewed in Rose-Krasnor 1997; Dirks et al. 2007). The study of animal social competence requires a rather complex and time-consuming experimental approach. We believe, however, that taking this effort is worthwhile especially because substantial, cumulative effects of social competence on fitness are likely, which would otherwise remain undetected. Large fitness effects are expected particularly in species showing many different types of social interactions and acquiring crucial resources with the help of such interactions. Future research should therefore aim to evaluate the relative contribution of social competence to individual fitness, especially in highly social species.

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References

- Adkins-Regan, E. & Krakauer, A. 2000. Removal of adult males from the rearing environment increases preference for same-sex partners in the zebra finch. *Animal Behaviour*, **60**, 47–53.
- Arnold, C. & Taborsky, B. 2010. Social experience in early ontogeny has lasting effects on social skills in cooperatively breeding cichlids. *Animal Behaviour*, **79**, 621–630.
- Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, **9**, 432–438.

- Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N. 2001. Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, **50**, 134–140.
- Bastian, M. L., Sponberg, A. C., Sponberg, A. C., Suomi, S. J. & Higley, J. D. 2003. Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology*, **42**, 44–51.
- Bergmüller, R., Heg, D. & Taborsky, M. 2005. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society B*, **272**, 325–331.
- Bergmüller, R. & Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement. *Animal Behaviour*, **69**, 19–28.
- Bertin, A., Hausberger, M., Henry, L. & Richard-Yris, M. A. 2009. Adult:young ratio influences song acquisition in female European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology*, **123**, 195–203.
- Bester-Meredith, J. K. & Marler, C. A. 2007. Social experience during development and female offspring aggression in *Peromyscus* mice. *Ethology*, **113**, 889–900.
- Branchi, I., D'Andrea, I., Fiore, M., Di Fausto, V., Aloe, L. & Alleva, E. 2006. Early social enrichment shapes social behavior and nerve growth factor and brain-derived neurotrophic factor levels in the adult mouse brain. *Biological Psychiatry*, **60**, 690–696.
- Branchi, I., D'Andrea, I., Gracci, F., Santucci, D. & Alleva, E. 2009. Birth spacing in the mouse communal nest shapes adult emotional and social behavior. *Physiology & Behavior*, **96**, 532–539.
- Bruintjes, R. & Taborsky, M. 2008. Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. *Animal Behaviour*, **75**, 1843–1850.
- Bruintjes, R. & Taborsky, M. 2011. Size-dependent task specialization in a cooperative cichlid in response to experimental variation of demand. *Animal Behaviour*, **81**, 387–394.
- D'Andrea, I., Alleva, E. & Branchi, I. 2007. Communal nesting, an early social enrichment, affects social competences but not learning and memory abilities at adulthood. *Behavioural Brain Research*, **183**, 60–66.
- Dierkes, P., Taborsky, M. & Kohler, U. 1999. Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. *Behavioral Ecology*, **10**, 510–515.
- Dierkes, P., Heg, D., Taborsky, M., Skubic, E. & Achmann, R. 2005. Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecology Letters*, **8**, 968–975.
- Dirks, M. A., Treat, T. A. & Weersing, V. R. 2007. Integrating theoretical, measurement, and intervention models of youth social competence. *Clinical Psychology Review*, **27**, 327–347.
- Duftner, N., Sefc, K. M., Kobl Müller, S., Salzburger, W., Taborsky, M. & Sturmbauer, C. 2007. Parallel evolution of facial stripe patterns in the *Neolamprologus brichardi/pulcher* species complex endemic to Lake Tanganyika. *Molecular Phylogenetics and Evolution*, **45**, 706–715.
- Earley, R. L., Edwards, J. T., Aseem, O., Felton, K., Blumer, L. S., Karom, M. & Grober, M. S. 2006. Social interactions tune aggression and stress responsiveness in a territorial cichlid fish (*Archocentrus nigrofasciatus*). *Physiology & Behavior*, **88**, 353–363.
- Jones, C. M., Braithwaite, V. A. & Healy, S. D. 2003. The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, **117**, 403–411.
- Hamilton, I. M., Heg, D. & Bender, N. 2005. Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. *Behaviour*, **142**, 1591–1613.
- Heg, D. & Taborsky, M. 2010. Helper response to experimentally manipulated predation risk in the cooperatively breeding cichlid *Neolamprologus pulcher*. *PLoS One*, **5**, e10784.
- Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. 2004a. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society B*, **271**, 2367–2374.
- Heg, D., Bender, N. & Hamilton, I. M. 2004b. Strategic growth decisions in helper cichlids. *Proceedings of the Royal Society B, Supplement*, **271**, S505–S508.
- Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. 2005. Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, **142**, 1615–1641.
- Kempes, M. M., Gulickx, M. M. C., van Daalen, H. J. C., Louwerse, A. L. & Sterck, E. H. M. 2008. Social competence is reduced in socially deprived rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, **122**, 62–67.
- Levy, F., Melo, A. I., Galef, G., Madden, M. & Fleming, A. S. 2003. Complete maternal deprivation affects social but not spatial learning in adult rats. *Developmental Psychobiology*, **43**, 177–191.
- Margulis, S. W., Nabong, M., Alaks, G., Walsh, A. & Lacy, R. C. 2005. Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Animal Behaviour*, **69**, 627–634.
- Moretz, J. A., Martins, E. P. & Robison, B. D. 2007. The effects of early and adult social environment on zebrafish (*Danio rerio*) behavior. *Environmental Biology of Fishes*, **80**, 91–101.
- Oliveira, R. F. 2009. Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, **49**, 423–440.
- Oliveira, R. F., Silva, A. & Canario, A. V. M. 2009. Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish. *Proceedings of the Royal Society B*, **276**, 2249–2256.
- Reddon, A. R., Voisin, M. R., Menon, N., Marsh-Rollo, S. E., Wong, M. Y. L. & Balshine, S. 2011. Rules of engagement for resource contests in a social fish. *Animal Behaviour*, **82**, 93–99.
- Rose-Krasnor, L. 1997. The nature of social competence: a theoretical review. *Social Development*, **6**, 111–135.
- Stiver, K. A., Dierkes, P., Taborsky, M. & Balshine, S. 2004. Dispersal patterns and status change in a co-operatively breeding cichlid *Neolamprologus pulcher*: evidence from microsatellite analyses and behavioural observations. *Journal of Fish Biology*, **65**, 91–105.
- Stiver, K. A., Dierkes, P., Taborsky, M., Gibbs, H. L. & Balshine, S. 2005. Relatedness and helping in fish: examining the theoretical predictions. *Proceedings of the Royal Society B*, **272**, 1593–1599.
- Stiver, K. A., Fitzpatrick, J. L., Desjardins, J. K. & Balshine, S. 2006. Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour*, **71**, 449–456.
- Sundström, L. F., Löhmus, M. & Johnsson, J. I. 2003. Investment in territorial defence depends on rearing environment in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, **54**, 249–255.
- Suomi, S. J. 1997. Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin*, **53**, 170–184.
- Taborsky, M. 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour*, **32**, 1236–1252.
- Taborsky, M. 1985. Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. *Behaviour*, **95**, 45–75.
- Taborsky, M. & Limberger, D. 1981. Helpers in fish. *Behavioral Ecology and Sociobiology*, **8**, 143–145.
- Taborsky, M., Hudde, B. & Wirtz, P. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. *Behaviour*, **102**, 82–118.
- de Waal, F. B. M. & Luttrell, L. M. 1988. Mechanisms of social reciprocity in 3 primate species: symmetrical relationship characteristics or cognition. *Ethology and Sociobiology*, **9**, 101–118.
- White, D. J., Gersick, A. S., Freed-Brown, G. & Snyder-Mackler, N. 2010. The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds. *Animal Behaviour*, **79**, 385–390.

Appendix

Table A1

Timeline of the ontogeny of –F and +F sibling groups from which the experimental fish were derived

Age (days)	Social condition
–10 to 0	With older conspecifics and all siblings
0 to 62	+F fish with older conspecifics and half of siblings –F fish with half of siblings only
62 to 321 (227, 391)	+F fish with half of siblings only –F fish with half of siblings only

Day 0 refers to the onset of the social experience treatment. Means and ranges (in parentheses) of ages are provided if not all fish had the same age at a given stage.

Table A2

Composition of sibling groups when social tasks were performed

Age (days)	Task	Sibling group size	
		–F	+F
97	Asymmetric competition	See Arnold & Taborsky (2010)	
246 (142, 338)	Experiment 1	9.4 (2, 30)	8.3 (4, 19)
319 (225, 389)	Experiment 2	8.3 (2, 22)	7.6 (3, 19)

Means and ranges (in parentheses) of ages and group sizes are provided. Single fish were temporarily removed from their holding tanks for each task as indicated in the Methods. The group sizes of +F and –F siblings were not significantly different (Wilcoxon signed-ranks test: experiment 1: $Z = 0.65$, $N = 12$ pairs of sib groups, $P = 0.51$; experiment 2: $Z = 0.65$, $N = 10$ pairs of sib groups, $P = 0.51$) and positively correlated (Spearman rank correlations: experiment 1: $r_s = 0.67$, $N = 12$, $P = 0.013$; experiment 2: $r_s = 0.70$, $N = 10$, $P = 0.023$).