Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*

Roger Schürch[a,b] and Dik Heg[a]

[a]Department of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50A, CH-3032 Hinterkappelen, Switzerland and [b]Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 318 West 12th Avenue, Columbus, OH 43210-1293, USA

Many studies have found that seemingly unconnected behaviors are correlated into behavioral syndromes. These behavioral syndromes may be the consequence of interindividual variation in life-history strategies. Only few studies have investigated the role of behavioral syndromes in cooperatively breeding species, despite the fact that one would expect particular large variation in behavior due to the wealth of life-history decisions a cooperative breeder faces. In a longitudinal study, we repeatedly tested individuals of the cooperatively breeding cichlid *Neolamprologus pulcher* for exploration, boldness, and aggression and tested whether these behaviors were sex specific; whether they were interrelated; and whether they were connected to growth and to 2 major life-history decisions, helping, and dispersal. In both sexes, explorative behavior was correlated over time, even though after sexual maturity males increased their exploration rate. In both sexes, exploration, boldness, and aggression correlated when mature, and in females, helping behavior was part of the syndrome. No relationships with growth were detected. Helping and dispersal were related to each other in males, whereas females hardly dispersed. We suggest that the differences in the life histories between males and females (male dispersal vs. female philopatry) lead to the differences in behavioral types observed and also to the differences in the stability of the behavioral syndromes between the sexes. The links between dispersal and helping in males and the behavioral types and helping in females highlight the necessity to study multiple traits to understand the evolution and maintenance of variation in cooperative behavior. *Key words:* behavioral syndrome, Cichlidae, cooperative breeding, life history, *Neolamprologus pulcher*, ontogeny. *[Behav Ecol 21:588–598 (2010)]*

I n recent years, findings in noncooperatively breeding species have suggested the use of a new approach to study the interplay between behavioral traits and life-history decisions. Among many taxa, consistent individual variation has been found in explorative behavior (Verbeek et al. 1994; Fraser et al. 2001; Dingemanse et al. 2002; van Oers et al. 2005), boldness (Wilson et al. 1993; Verbeek et al. 1996; Sinn and Moltschaniwskyj 2005), aggressiveness (Bakker 1986; Verbeek et al. 1996; Sinn and Moltschaniwskyj 2005), and risk taking (van Oers, Drent, de Goede, et al. 2004) over time and across contexts. Additionally, these behaviors are often correlated to each other, resulting in behavioral syndromes or animal personalities (Sih, Bell, Johnson 2004; Sih, Bell, Johnson, et al. 2004). The relative inflexibility of these correlated suites of behaviors may generate trade-offs: For example, Sih et al. (2003) have found that salamander larvae could adjust their behavior toward predatory cues only to some degree, leading to a trade-off between growth and predation rate.

Theoretical work indicates that different life-history decisions may coselect for different behavioral types, leading to behavioral syndromes: Individuals that focus on future reproductive output should be consistently more risk-averse compared with individuals, which emphasize current reproduction (Wolf et al. 2007). Similarly, Stamps (2007) suggests that correlations between behavioral traits will depend on the effects of the traits on growth and mortality. Subordinates in group-living animals face such trade-offs (e.g., Cahan et al. 2002): They can derive benefits

from investing in their current group (e.g., subordinate reproductive participation, kin selection, inheritance of the dominant position) or they can derive benefits from investing in obtaining immediately an own dominant breeding position somewhere else (e.g., dominant reproduction after successful dispersal). On top of this, intrinsic differences in the potential to breed as a dominant individual could also lead to distinct behavioral types (West-Eberhard 1975; see also Johnstone 2008), where it pays subordinates with bad breeding prospects to provide help to others, even if relatedness is relatively small.

After this reasoning, we here address 2 intriguing core issues in behavioral syndrome research. First, is an individual's behavioral type fixed throughout life or is it rather affected by his or her state (sensu Houston and McNamara 1999)? Second, what are the social consequences of individuality? If behavioral types are not fixed throughout life, but every individual follows roughly the same developmental trajectory, distinct behavioral types might appear due to comparing individuals from different life stages. Thus, in fact, each individual might actually show the same behavioral type if compared during the same life stage (e.g., all individuals become bolder when growing older due to, e.g., experience effects). The ontogeny of individuality has been well studied in domesticated animals (reviewed in Carere et al. 2005) but less so in other animals (e.g., Francis 1990). We suggest that ontogenetic effects may be particularly important in species with indeterminate growth. In fish, for example, it might pay younger smaller individuals to be shy and avoid predators, as opposed to older larger individuals that might be better off by being bold and competing for reproduction.

Behavioral types might also be affected by state, and distinct behavioral types might appear due to comparing individuals from different states, whereas in fact, individuals from the same state show the same behavioral type (e.g., males are bolder and

more aggressive than females because they need to defend a mating territory). Effects of state(s) on the behavior of animals are reported throughout behavioral ecology research (e.g., Boyd 2000; Godfrey and Bryant 2000; Frommen et al. 2007) but have been poorly addressed in a behavioral syndrome context. Any state variable that is likely to affect the animal's (adaptive) behavior in general is also likely to affect its scores in standardized personality tests, and they might include for instance effects of age, sex (both as argued above), and size (e.g., larger individuals or individuals in better body condition are more successful in competition and therefore also are more bold and aggressive).

Adding to the second point, an individual's behavioral type might also affect his or her social behavior in many ways, for example, how and where it engages in competition, behavior toward mates, decisions on group membership, and its willingness to cooperate. The interplay of behavioral types and sociality have been addressed in various animal species (e.g., Verbeek et al. 1996; Budaev 1997; Sih and Watters 2005; Cote and Clobert 2007; Webster et al. 2007; Pike et al. 2008; Magnhagen and Bunnefeld 2009), but only few studies have addressed the effects in a cooperatively breeding species (e.g., Arnold et al. 2005; Bergmüller & Taborsky 2007). This is unfortunate because based on the life-history trade-offs specific to cooperative breeders as mentioned above, it is quite likely that not only individuals show distinct behavioral types but also these differences have strong effects in how they behave socially. Specifically, we hypothesized that subordinates may be coselected for behavioral types lying between the 2 following extremes. On the one hand, subordinates might be philopatric throughout life (no dispersal) while queuing for a breeding position in their natal group. In that case, they would need to reduce their eviction rate from the group by appeasing dominants, for example, by showing a reduced growth rate and a high propensity to help (Heg, Bender, et al. 2004; Bergmüller and Taborsky 2005). This would be a low-risk strategy because these subordinates do not need to explore the environment for breeding vacancies. Benefits can be derived by helping relatives (Brouwer et al. 2005), reproductive participation (Heg 2008; Heg and Hamilton 2008; Heg et al. 2008), and future inheritance of the territory (Komdeur and Edelaar 2001; Stiver et al. 2007). At the other end of the spectrum, subordinates might try to disperse to a breeding vacancy or to setup their own breeding territory as soon as possible. This would be a high-risk strategy because exploration of the environment to detect suitable spots for territories or breeding vacancies might be associated with predation risk (Heg, Bachar, et al. 2004), and competition for vacancies might lead to injuries. In support of this idea, the propensity to take risks in birds correlates with the exploration–boldness–aggression syndrome (van Oers, Drent, de Goede et al. 2004). To be successful in such competition, these subordinates may need elevated growth and aggression rates, leading to conflicts with the dominants and hence, the risk of eviction from the group (Dierkes et al. 2005). Costs may be reduced by denying help to other group members (Grantner and Taborsky 1998). Subordinates showing the high-risk strategy derive benefits from reproduction as a dominant relatively early in life compared with the low-risk philopatric subordinates. In an evolutionary sense, the resultant lifetime fitness payoffs might be equal between subordinates of the different types or, in the case of intrinsic differences, might be the maximum obtainable given their phenotype. Note that subordinates along such a continuum between the 2 extremes face different levels of competition and conflict with group and nongroup members and put different emphases on the lifetime benefits derived at home versus the lifetime benefits derived from breeding independently. If this hypothesis holds true, correlations between helping behavior, dispersal propensity, growth, exploration, boldness, and aggres-

siveness should be detectable among subordinates in cooperative breeders. We tested these ideas in a longitudinal study in the lab using the cichlid *Neolamprologus pulcher*.

In an earlier study on the cooperatively breeding cichlid *N. pulcher*, Bergmüller and Taborsky (2007) have already found consistent individual variation in helping, exploration, boldness, and aggression in the short term. However, the ontogeny, potential differences between the sexes, and their relationships to helping, dispersal, and growth could not be investigated. In *N. pulcher*, the sexes differ in their life histories. Whereas females queue for breeding positions, males usually disperse (Stiver et al. 2004, 2006; Dierkes et al. 2005), and males may also change their growth rate according to the size of the dominant male (Heg, Bender, et al. 2004). Because of the differences in the life histories of males and females, we hypothesized that we would find also sex differences in behavioral types in addition to variation within the sexes. Namely, males should be more explorative than females, and in consequence, risk-associated traits such as boldness and aggression may also differ between the sexes, particularly at maturity.

MATERIALS AND METHODS

Study species and holding conditions

For our study, we used the cooperatively breeding cichlid *N. pulcher*, a substrate breeding fish endemic to Lake Tanganyika, where it lives in depths of 3–45 m (Taborsky 1984). Breeding groups occupy small territories ranging from 775 to 10 100 cm² (Balshine et al. 2001). Clutches are spawned to ceilings and walls of breeding shelters where they are tended by individuals of the group. Groups usually consist of one breeder male and one to several breeder females (Limberger 1983). Subordinates of both sexes may be found in the territory of the breeders, engaging in all tasks related to breeding: fanning and cleaning eggs, digging out shelters, cleaning breeding shelters from debris, and defending the group against conspecific competitors, interspecific competitors for shelters, and predators (Taborsky and Limberger 1981; Taborsky 1984). On the other hand, subordinates may also take their share of group reproduction (Heg et al. 2006; Heg and Hamilton 2008) and feed on eggs (von Siemens 1990), giving rise to potential conflicts within the group.

Individuals between 21 and 29 mm were selected from different rearing groups of our breeding stock population, which are descendants of wild caught fish from Kasakalawe, Zambia (lat 8°46.849′S, long 31°04.882′E, collected in 1996). The focal fish were transferred singly to small acrylic glass housing tanks (20 l) equipped with a 1-cm sand layer and a flowerpot half as a shelter, thus minimizing external interference. Sex of fish could only be determined during the course of the experiment when the fish became sexually mature; nevertheless, there were no size differences between the sexes in the beginning (Welch 2 sample *t*-test, $N_{\male} = 15$, $N = 21$, $t = 0.65$, degrees of freedom [df] $= 33.67$, $P = 0.52$).

The fish were fed daily ad libitum with TetraMin food flakes, and excess food of the previous day was removed. The light regime was held constant at a 13:11 h day:night cycle, and temperature was held at 26.6±1.1 °C in a climate-controlled room.

After at least 3 months and when fish were at least 35 mm, single focal individuals were moved to the ring tank and integrated as subordinates to a breeding pair, thus creating an artificial group. After the "helping" and dispersal tests (see below), fish were again housed singly in the acrylic glass tanks.

Standardized personality tests

For a period of 6 months, every 30 days, the fish were tested for the propensity to explore, their boldness toward a novel object,

and their aggression levels in a 400-l aquarium with a 3-cm sand layer on the ground (Figure 1a). All observations were conducted by R.S. Subsequent to the tests, fish were weighed (to the nearest 0.1 mg) and their standard length (SL) measured (to the nearest 0.5 mm) before they were returned to the housing tanks.

Exploration

Fish were transferred to a small compartment (ca. 1/5) of a 400-l aquarium. This compartment provided shelter (1 flowerpot half) and was separated from the rest of the aquarium by an opaque plastic partition that could be easily removed (Figure 1a). The bigger compartment of the aquarium was equipped with 10 flowerpot halves to provide an "open field" to explore. After 10 min of acclimatization in the small compartment, the plastic sheet was removed, and the fish was allowed to explore the open field. The focal individual was observed for the subsequent 10 min, and it was counted how many pots the fish visited. After the observation period, the fish, if necessary, was gently guided back to the small compartment and the opaque partition was reinstalled. The exploration test paradigm closely follows the paradigm developed for other vertebrates (e.g., great tits Verbeek et al. 1994).

Boldness

After another 10 min of acclimatization, a "novel object" was presented to the fish within the home compartment (Figure 1a) to record the latency of the fish to first approach the object (0.1 s accuracy) and the closest distance (in cm) the fish approached the novel object during a 5-min observation. Novel objects were ranging in size between the focal's size up to approximately 5 times its size (model bird, beetle kitchen magnet, screw driver, blue clamp). The choice of the objects was randomized, and there was no difference in objects regarding shortest distances focals approached (Kruskal–Wallis rank sum test, $P = 0.12$). The boldness test paradigm closely follows the paradigm developed for other vertebrates (e.g., great tits Verbeek et al. 1994).

Aggression

After removal of the object, a mirror was placed in the compartment without further acclimatization, and aggressive reactions were observed during a 10-min focal observation (Figure 1a). Mirrors have previously been used to elicit agonistic behavior in *N. pulcher* (Grantner and Taborsky 1998). Aggressive behaviors scored were restraint aggression (spread fins and slow approaches toward the mirror), and overt aggression (fast approaches and contacts) toward the mirror (Hamilton et al. 2005).

Growth

Growth rate in SL was calculated after the Blumberg curve of growth (Skubic et al. 2004), averaging the growth rates of the first 2 monthly intervals into growth rate before maturity and the last 2 intervals into growth rate after reaching maturity.

Artificial groups

After the fish reached 35 mm SL and were at least 3 months old, 34 focal fish were integrated as the only subordinate helper of a breeding pair (68 breeders), following the procedure of Taborsky (1984). Artificial groups were setup in an octagonal ring tank (7800 l; Figure 1b,c), where a group was housed in 1 of 32 compartments separated by transparent acrylic glass sheets, enabling the fish to see their neighbors (for a similar setup, see Bergmüller, Heg, Taborsky 2005). Each compartment was equipped with
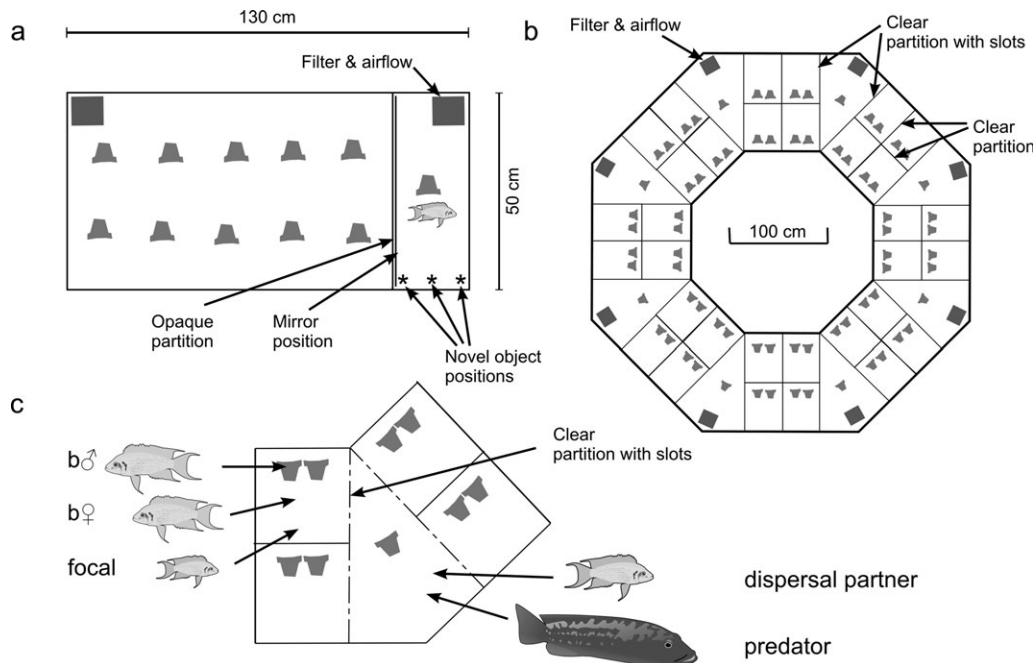

Figure 1
The experimental setup used during the longitudinal study. (a) The 400-l aquarium for the standardized personality tests (exploration test, novel object test, and aggression test; see text for details). (b) The 7800-l ring tank used to setup artificial groups. (c) Detail of the ring tank. The home compartment was used for the focal territory maintenance test (twice with and twice without breeders), predator defense test (once with and once without breeders), and dispersal test (slots opened; once with and once without dispersal partner). The wedge-shaped compartment contained no fish, a dispersal partner (opposite sex of focal fish), or a predator (*Lepidiolamprologus elongatus*), depending on test.

a 3-cm sand layer and 2 flowerpot halves. The focal subordinates were introduced to the compartments first, and the breeders were kept in separate isolation nets (16 × 12.5 × 13 cm). After 3 days, the breeders were released into the compartments.

In the artificial groups, the focal fish were tested for their propensity to help in 2 tasks that are generally assumed to be helping behaviors (e.g., Balshine-Earn et al. 1998): territory maintenance and defense against predators (Figure 1c). Furthermore, fish were tested for their propensity to disperse (Figure 1c).

After all tests were done, breeders were removed and the focal subordinates remained in the compartment for approximately 1 week for final testing (see below).

Territory maintenance
To stimulate territory maintenance activity, sand from the floor was shoveled into the 2 shelters within the group's compartment (Figure 1c). We did this with an acrylic glass shovel to disturb the focal fish as little as possible. After 10 min acclimatization to the new situation, 10 min focal observations were done, counting events of carrying sand away. In total, focals were tested 4 times for their propensity to perform territory maintenance. To assess the focal subordinate's innate propensity to perform territory maintenance, focals were tested once before the breeders were added to the focal's ring tank compartment and once after breeders were removed from the compartment (tests 1 and 4). To assess the propensity to help, the same tests were conducted twice while the focal was assisting breeders (tests 2 and 3). The interval between tests was on average 24 days.

Predator defense
The propensity of the focal subordinates to defend against a predator was assessed during a predator presentation test. We introduced an individual *Lepidiolamprologus elongatus* (Cichlidae) into an empty corner compartment of the ring tank. *Lepidiolamprologus elongatus* is one of the main predators in the field (Heg, Bachar, et al. 2004). Before, the other groups' compartments were shielded from view with opaque plastic partitions (Figure 1c). Thus, the predator only had visual contact with the focal subordinate's group. We counted frequencies of overt aggression (fast approaches, bent bodies, tail beats, see, e.g., Hamilton et al. 2005; Desjardins et al. 2008) of the subordinates during a 10-min focal observation. The observation was started immediately after the predator was set into the corner compartment. To keep incidents of stressful handling of the *L. elongatus* as low as possible, focals were only tested once with breeders present, and once without breeders present, with an average interval of 8 days between tests.

Dispersal test
To assess the propensity of subordinates to disperse, we allowed them to disperse through slots to the neighboring corner compartment (Figure 1c). The slots were too small to fit the breeders, and hence, only the subordinates could disperse (for a similar setup, see Bergmüller, Heg, Taborsky 2005). The corner compartments were equipped with 1 flowerpot half. Each focal individual was tested once with a potential breeding partner of the opposite sex in the corner compartment and once without (average interval between the 2 tests: 11 days). The slots were opened for 3 subsequent days, and the position (home/dispersal compartment) of the focal individual was checked 3 times per day during this period. The fish that visited the compartment usually stayed, and we therefore counted a single visit during the 3 days as dispersal. This seems also justified as fish dispersing in the experiment of Bergmüller, Heg, Taborsky (2005) usually started to breed shortly after successful dispersal.

The experiment was authorized by the Amt für Landwirtschaft und Natur of the canton of Bern (experiment no. 40/05) and complied with the legal requirements of the country.

Statistical analysis

During novel object tests 3 and 4, the fish were presented with an old object from the tests 1 and 2. However, because the boldness scores of these last 2 trials did not differ from the first 2 trials (Welch 2 sample *t*-tests, $N = 36$, $P > 0.6$ in both cases), we concluded that the fish had not memorized the objects, and we included them in the average boldness scores.

Data gathered on personalities (exploration, boldness, aggression) all showed inflation with zeros due to fish not reacting at all. How to deal with zero inflation in longitudinal data analysis is still debated (e.g., Martin et al. 2005; Min and Agresti 2005). To avoid this problem, we averaged data of the first 3 months and the second 3 months into a single value each. Because most of the fish reached sexual maturity around this borderline, we will refer to the combined data for the first 3 months as premature, whereas the second 3 months will be named mature (size at maturity ranges 35–40 mm; Taborsky 1982, 1985).

We averaged the data of the territory maintenance test for both contexts, with (tests 2 and 3) or without breeders (tests 1 and 4), respectively. One male hardly grew and was therefore not used in an artificial group and the resulting analysis; it was excluded from analysis of growth, territory maintenance, defense against a predator, and dispersal. One artificial group broke up, and for the focal female in that group, data on predator defense are missing, and another female was not tested in the artificial group because of space and time constraints (note the differences in sample sizes, e.g., in Tables 1 and 2). Only a subset of 13 males and 15 females was tested for dispersal.

All analysis were conducted using nonparametrical procedures in R2.9.1, except 1) to test for differences in means between the sexes (Welch 2 sample *t*-test, following Ruxton 2006; see also, e.g., Sokal and Rohlf 1981, p. 409), 2) for the analysis of the dispersal data where we built a generalized linear mixed model of the binomial family, and 3) we also built a generalized linear model to assess whether male dispersal with a potential mate present was related to sand carrying (territory maintenance).

We had unequal numbers of males ($N = 15$) and females ($N = 21$), but the statistical power to detect correlations was quite similar between the sexes (males: Spearman's $\rho_{(\beta = 0.2)} = 0.67$; females: Spearman's $\rho_{(\beta = 0.2)} = 0.58$; Zar 1999, p. 398). To compare correlation coefficients of both sexes, we applied the procedure outlined in Sokal and Rohlf (1981, p. 588), adapted for Spearman's rank correlations according to Fieller et al. (1957).

RESULTS

With the exception of helping behavior and dispersal, the sexes had equal variances for all behaviors tested (Fligner–Killeen tests, all $P > 0.05$).

Consistency of behavior over time and different contexts

Exploration
Even though males increased their exploration rates considerably (Figure 2a), premature and mature exploration rates, measured as number of flowerpot halves visited, correlated for both sexes (Figure 3a and Table 1). There was no sex difference in the correlation coefficients (Table 1). The increase in male exploration rate results in significant differences between premature and mature exploration rates in males and mature male and female exploration rates (paired

Table 1

Consistency of behavioral traits

	Males		Females		Comparison		Sexes pooled	
	N	ρ	N	ρ	Z	P	ρ	P
Consistency over time (before vs. after reaching maturity)								
Exploration (number of pots visited)	15	0.52[a]	21	0.69[a]	−0.691	0.25	0.59	<0.001
Boldness (closest distance to a novel object)	15	−0.09	21	0.45[a]	−1.515	0.07	0.19	0.26
Restraint aggression (toward mirror)	15	−0.04	21	0.04	−0.214	0.42	0.02	0.92
Overt aggression (toward mirror)	15	0.60[a]	21	0.35	0.843	0.20	0.43	0.01
Consistency across contexts (alone vs. as a subordinate in a group)								
Sand carrying	14	0.55[a]	20	0.66[a]	−0.427	0.34	0.60	<0.001
Defense against predator (restraint aggression)	14	0.43	19	0.65[a]	−0.754	0.26	0.58	<0.001
Defense against predator (overt aggression)	14	0.48	19	0.74[a]	−1.074	0.14	0.57	<0.001

The table shows Spearman's rank correlations between behavioral traits before and after reaching maturity for the standardized tests (consistency over time, see text for details) or correlations between different contexts (in group vs. alone) for the "helping" behaviors. We present correlations for males and females separately, a test whether males and females differ in their correlation coefficients, and a pooled test for both sexes.

[a] Significant correlations.

Wilcoxon's signed rank test, premature-♂–mature-♂: $N = 15$, $T_+ = 10$, $P = 0.03$; Welch 2 sample t-test, $N_\male = 15$, $N_\female = 21$; mature-♂–mature-♀: $t = 2.47$, df = 24.82, $P = 0.02$).

Boldness
Boldness toward novel objects, measured as closest distance to the object, correlated in females before and after reaching maturity but not in males (Figure 3b and Table 1). A comparison of the correlation coefficients showed a tendency that the sexes indeed differed in their consistencies. Females also stayed further away from the novel object when they were mature (Figure 2b; paired Wilcoxon's signed rank test, premature-♀–mature-♀: $N = 21$, $T_+ = 34$, $P < 0.01$). For males,

no such effect could be found (paired Wilcoxon's signed rank test, premature-♂–mature-♂: $N = 15$, $T_+ = 52$, $P = 1$). Regardless of maturity, we did not find a difference between the sexes (Welch 2 sample t-tests, $N_\male = 15$, $N_\female = 21$; premature-♂–premature-♀: $t = 0.91$, df = 23.23, $P = 0.37$ and mature-♂–mature-♀: $t = -1.17$, df = 26.26, $P = 0.25$).

Aggression
Aggression toward the mirror was consistent in males' overt aggression but not in females. Comparing the correlation coefficients of the sexes for overt aggression showed no difference, and the correlation test for the pooled data indicated that individuals of *N. pulcher* are consistent in their overt aggression

Table 2

Correlations between behavioral traits (Spearman's rank correlation)

	Males		Females		Comparison		Sexes pooled	
	N	ρ	N	ρ	Z	P	ρ	P
Before maturity								
Exploration—boldness	15	−0.42	21	−0.51[a]	0.30	0.38	−0.47	<0.01
Exploration—aggression	15	0.81[a]	21	0.59[a]	1.22	0.11	0.66	<0.001
Boldness—aggression	15	−0.36	21	−0.75[a]	1.56	0.06	−0.55	<0.001
Exploration—sand carrying[b]	14	0.21	19	0.62[a]	−1.27	0.10	0.43	0.01
Exploration—defense against predator[b]	14	0.01	20	−0.08	0.24	0.41	−0.07	0.69
Boldness—sand carrying[b]	14	−0.45	19	−0.17	−0.81	0.21	−0.29	0.10
Boldness—defense against predator[b]	14	−0.08	20	0.03	−0.29	0.38	0.04	0.84
Aggression—sand carrying[b]	14	0.02	19	0.44	−1.13	0.13	0.27	0.12
Aggression—defense against predator[b]	14	−0.15	20	0.12	−0.67	0.25	−0.03	0.87
After reaching maturity								
Exploration—boldness	15	−0.63[a]	21	−0.57[a]	−0.22	0.41	−0.68	<0.001
Exploration—aggression	15	0.69[a]	21	0.59[a]	0.42	0.34	0.67	<0.001
Boldness—aggression	15	−0.90[a]	21	−0.69[a]	−1.58	0.06	−0.81	<0.001
Exploration—sand carrying[b]	14	−0.06	19	0.48[a]	−1.47	0.07	0.14	0.45
Exploration—defense against predator[b]	14	−0.08	20	0.31	−1.00	0.16	0.11	0.55
Boldness—sand carrying[b]	14	0.18	19	−0.43	1.63	0.05	−0.11	0.55
Boldness—defense against predator[b]	14	0.28	20	−0.12	1.02	0.15	0.11	0.54
Aggression—sand carrying[b]	14	0.09	19	0.23	−0.37	0.36	0.15	0.41
Aggression—defense against predator[b]	14	−0.09	20	0.13	−0.55	0.29	−0.05	0.76

The table shows Spearman's rank correlations between behavioral traits. We present correlations for males and females separately, a test whether males and females differ in their correlation coefficients, and a pooled test for both sexes. For details on the different behaviors, see text. Exploration, number of pots visited; boldness, shortest distance to novel object; aggression, overt aggression toward mirror; sand carrying, frequency of sand carrying; defense against predator, overt aggression toward predator.

[a] Significant correlations.

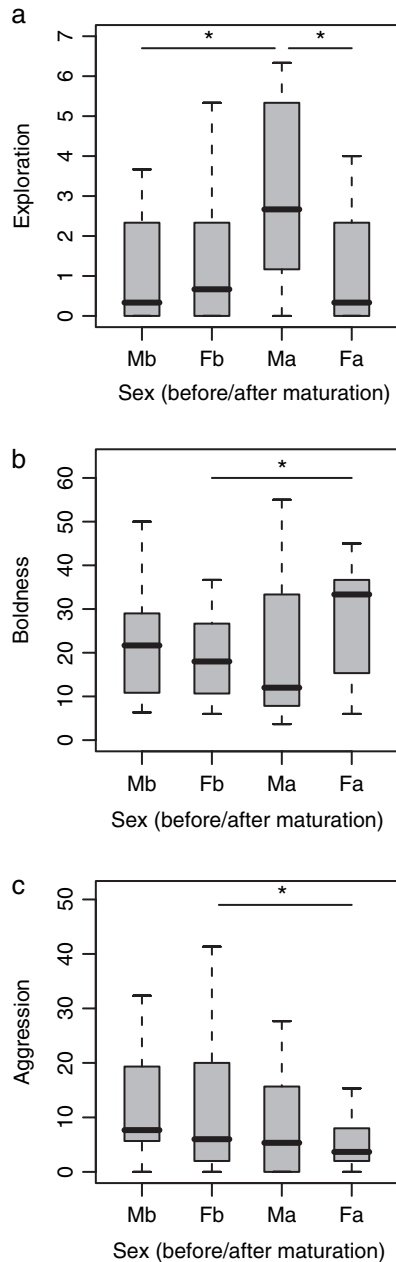[b] Measured as a subordinate inside group.

Figure 2
Box plots for behaviors of males and females before and after reaching maturity. The whiskers extend to the most extreme data points. For statistical details, see the text. Exploration, number of pots visited; boldness, shortest distance to novel object; aggression, overt aggression toward mirror. *denotes significant differences (M, males; F, females; b, before, a, after maturity).

levels (Figure 3c and Table 1). We did not find any indication that restraint aggression levels were consistent, neither in males nor females (Table 1). Therefore, we only proceeded with analyses of overt aggression to reduce the number of multiple comparisons. Males did not reduce the overt aggression toward the mirror significantly over the course of time; in females, this effect was significant (Figure 2c; paired Wilcoxon's signed rank tests, premature-♂–mature-♂: $N = 15$, $T_+ = 92$, $P = 0.073$ and premature-♀–mature-♀: $N = 21$, $T_+ = 145$, $P < 0.046$). The sexes did not differ in their levels of overt aggression toward the mirror (Welch 2 sample t-tests, $N_♂ = 15$, $N_♀ = 21$; premature-

♂–premature-♀: $t = 0.003$, df $= 33.97$, $P = 1.0$ and mature-♂–mature-♀: $t = 1.10$, df $= 20.76$, $P = 0.28$).

Territory maintenance and predator defense
Territory maintenance, in the form of carrying sand away from the breeding shelter with versus without breeders present, correlated in both sexes, and there was no significant difference in correlation coefficients in regard to sex (Figure 3d and Table 1). Even though many males did not perform territory maintenance at all when the breeders were present, this did not result in a significant difference in frequencies of sand carrying between the sexes when breeders were present (Welch 2 sample t-tests, $N_♂ = 14$, $N_♀ = 20$; alone: $t = -1.528$, df $= 31.87$, $P = 0.14$ and in group: $t = -1.217$, df $= 29.28$, $P = 0.23$). Only females were consistent in their aggressive behaviors against a predator (Figure 3e and Table 1); however, there was no significant difference in correlation coefficients, and the pooled sexes were consistent in their restraint and overt aggression toward the predator (Table 1). Both sexes seemed to decrease predator defense when breeders were present; indeed, overt aggression was significantly lower in the group context (paired Wilcoxon's signed rank tests, ♂: $N = 14$, $T_+ = 104$, $P = 0.001$ and ♀: $N = 19$, $T_+ = 142$, $P = 0.01$).

Correlations between traits

Exploration, boldness, and aggression
Before reaching maturity, we found that in males, only exploration rates and overt aggression toward the mirror were correlated significantly, whereas there did not seem to be much of a connection between exploration and boldness (Figures 4a,b and Table 2). For females, the picture was very different: both before and after reaching maturity, exploration rate significantly correlated with boldness as well as with overt aggression toward the mirror (Figures 4a–c and Table 2). When formally comparing the sexes, we did not find a difference in correlation coefficients (Table 2). For the pooled sexes, we found that exploration, boldness, and aggression correlated significantly, both before and after reaching maturity (Table 2).

Standardized tests and helping
Helping in the form of sand carrying when the focal was a subordinate in a group was significantly correlated to exploration rate in females (Figure 4d and Table 2). For males, no such correlation could be found. However, the sexes did not differ significantly in their correlation coefficients, and for the pooled sexes, helping behavior measured when mature was significantly correlated to this syndrome before maturity but not after reaching maturity (Table 2). Interestingly, male sand carrying activity, whether breeders were present or not, was tightly linked to aggression against predators when in a group (Spearman's rank correlation, ♂ sand carrying alone: $N = 14$, $ρ = 0.80$, $P < 0.001$ and ♂ sand carrying in group: $N = 14$, $ρ = 0.77$, $P = 0.001$). For females, this relationship was statistically a tendency at best if only sand carrying in the group context is considered (Spearman's rank correlation, ♀ sand carrying alone: $N = 19$, $ρ = 0.10$, $P = 0.67$ and ♀ sand carrying in group: $N = 19$, $ρ = 0.41$, $P = 0.08$; Figure 4e).

Life-history traits

Dispersal
Of 13 males tested, 7 males dispersed when there was a mate present, whereas only 3 males dispersed when no partner was there (2 males dispersed in both contexts). Of 15 females tested, in both situations, the same 3 individuals dispersed. A generalized linear mixed-effect model revealed that an
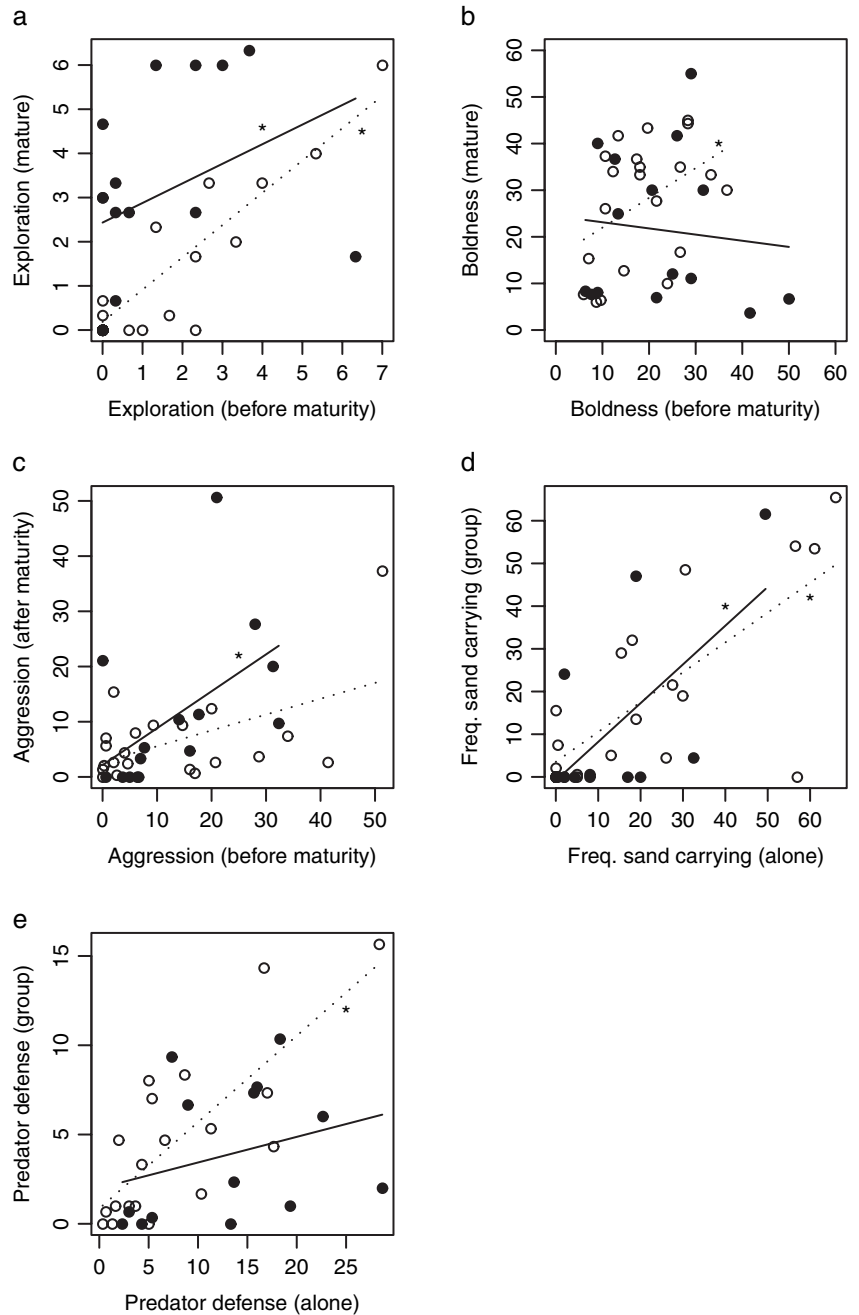
Figure 3
Consistency of behavior in standardized personality tests over time and consistency in digging and predator defense across contexts for males (solid circles and solid lines) and females (open circles and dashed lines). For statistical details, see Table 1. Exploration, number of pots visited; boldness, shortest distance to novel object; aggression, overt aggression toward mirror; frequencies of sand carrying, carrying sand away from breeding shelter; predator defense, overt aggression toward predator. *denotes significant correlations.

interaction between focal sex and presence of a mate might predict the probability of dispersal (analysis of variance to compare both models: full model, log likelihood = −29.529 and model without interaction term, log likelihood = −30.876, $P = 0.10$), but the limited sample size prevented further analysis.

Growth
Growth rate before and after reaching maturity was negatively correlated in males but not in females (♂: $N = 14$, $\rho = -0.56$, $P = 0.04$ and ♀: $N = 21$, $\rho = 0.36$, $P = 0.12$). Males grew significantly faster compared with females before maturity, but they did not significantly do so after reaching maturity (Welch 2 sample t-tests, $N_\male = 14$, $N_\female = 21$; premature-♂–premature-♀: $t = 5.45$, df $= 23.18$, $P < 0.001$ and mature-♂–mature-♀: $t = 1.79$, df $= 22.78$, $P = 0.09$)

Life-history decisions and behavioral traits

The rare events of dispersal in females prevented us from relating dispersal to the behavioral traits. Because males mostly dispersed when a potential mate was in a compartment, we checked whether dispersal to a breeding vacancy could be related to helping with territory maintenance or the propensity to explore. Males that showed more sand carrying when breeders were present were less likely to disperse compared with males that carried less or no sand away from shelters (Figure 5; $N = 13$, $\chi^2 = 7.44$, $P = 0.006$). To see whether growth rate could be related to certain behavioral types, we tested whether it was related to the behavior during standardized tests or sand carrying, but no such correlations existed (Spearman's rank correlations, standardized tests: ♂: $N = 14$, $-0.31 < \rho < 0.28$, all $P > 0.28$ and ♀: $N = 19$, $-0.25 < \rho < 0.32$, all $P > 0.16$; sand carrying: ♂: $N = 14$, $\rho = 0.16$, $P = 0.59$
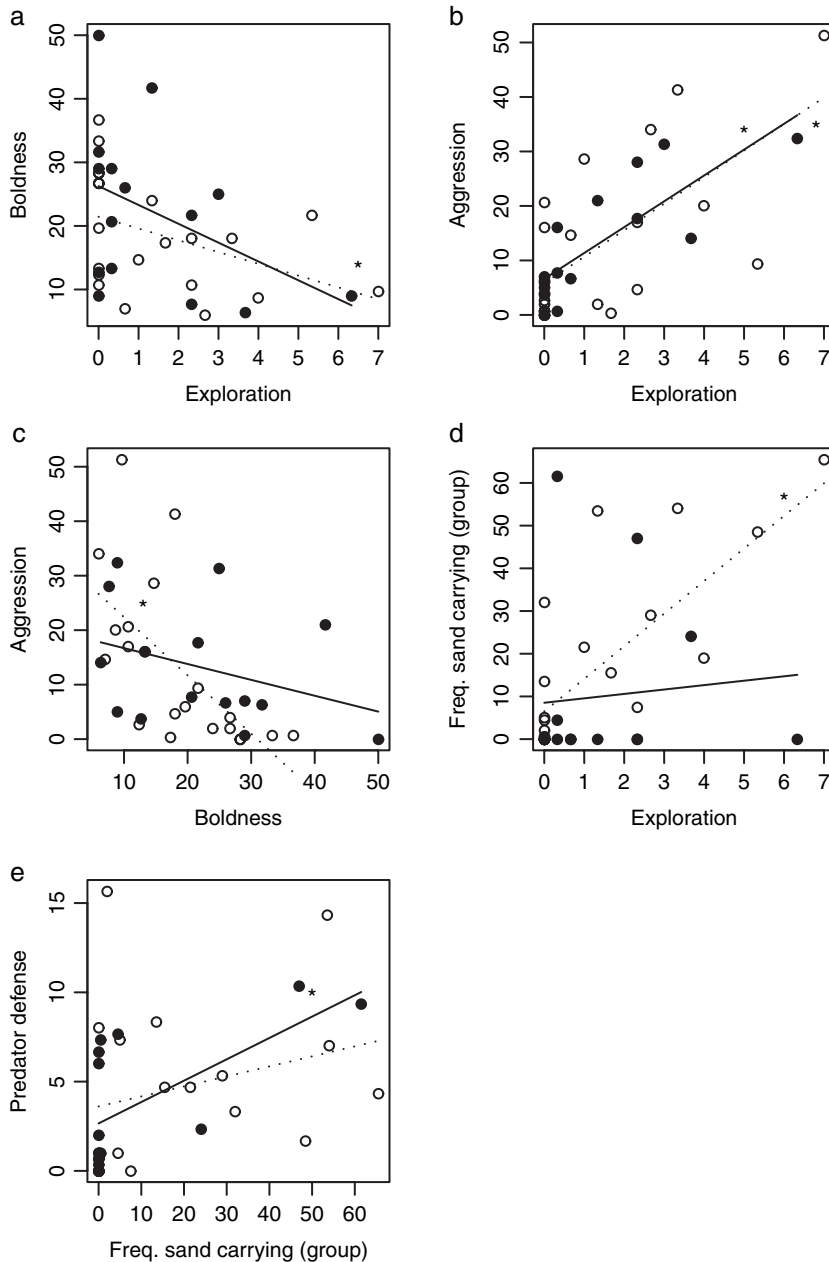
Figure 4
Correlations between various behaviors for males (solid circles and solid lines) and females (open circles and dashed lines) (a–d) before maturity and (d and e) when assisting breeders. See Table 2 for details on statistics. Exploration, number of pots visited; boldness, shortest distance to novel object; aggression, overt aggression toward mirror; frequencies of sand carrying, carrying sand away from breeding shelter; predator defense, overt aggression toward predator. *denotes significant correlations.

and ♀: $N = 19$, $\rho = 0.01$, $P = 0.96$). There were also no significant correlations between the behavior during standardized tests and body size (SL) in any of the single trials (Spearman's rank correlations, ♂: $N = 14$, $-0.42 < \rho < 0.18$, all $P > 0.11$ and ♀: $N = 21$, $-0.29 < \rho < 0.41$, all $P \geq 0.06$). However, if we combined all tests (pseudoreplication), there was a significant correlation between SL and exploration in males (Spearman's rank correlations, ♂: $N = 14$, $\rho = 0.21$, $P = 0.045$ and ♀: $N = 21$, $\rho = -0.03$, $P = 0.72$), supporting the increase in exploration propensity in males through ontogeny reported above (Figure 2a).

DISCUSSION

We investigated consistent individual differences in the propensity to explore, boldness toward novel objects, and aggression levels in the cooperatively breeding fish *N. pulcher*, and we confirmed the existence of an exploration–boldness–aggression syndrome in this species (Bergmüller & Taborsky 2007). Our study was novel because we additionally 1) studied changes throughout ontogeny and 2) related these to patterns of helping, dispersal, and growth.

We found that differences in exploration and aggression persisted throughout ontogeny in both sexes, whereas boldness toward novel objects seemed to be consistent only in females. These behavioral traits were also interrelated to each other into a behavioral syndrome. We additionally found that territory maintenance and defense against predators, 2 behaviors regarded as helping in subordinate fish, were consistent across context, that is, whether the fish were solitary or subordinates in a group. The consistencies of behaviors across time or context confirm findings in various taxa (e.g., Verbeek et al. 1994; Arnqvist and Henriksson 1997; Coleman and Wilson 1998; Wilson 1998; Vøllestad and Quinn 2003; Dall et al. 2004; van Oers, Drent, de Jong, et al. 2004; Sih, Bell, Johnson 2004; Sih, Bell, Johnson, et al. 2004; Ayre and Grosberg 2005; Carere et al. 2005) as well as the findings of Bergmüller
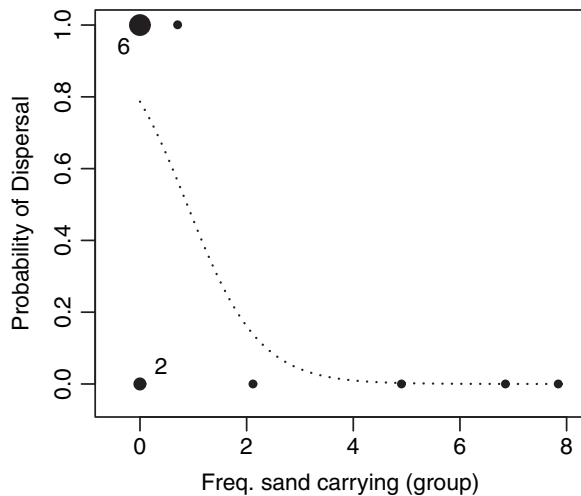
Figure 5
Relationship for subordinate males between frequencies of sand carrying (carrying sand away from breeding shelter) and dispersal. Focals were more likely to disperse when they did not provide help to the breeders by carrying sand away from the shelter. The size of the bubbles represents the number of overlapping data points (with the number indicating how many points are overlapping).

and Taborsky (2007) for *N. pulcher*. However, to our knowledge, this is the first study in a cooperatively breeding vertebrate to report consistency of behavioral traits across an important switch point in ontogeny, namely when becoming sexually mature. Furthermore, the behavioral type was also related to subordinate helping behavior (especially in females) and to subordinate dispersal behavior from a group (only in males because female rarely dispersed). Contrary to one of our predictions, we did not find any relationships between the behavioral type of individuals and their growth rate, nor between helping behavior and growth. Still, the apparent inflexibility in risk-associated and helping behaviors (see also Heg et al. 2009) implies that if we want to understand cooperative propensities of individuals fully, we also have to take into account how the same individuals behave in noncooperative contexts (see also Sih, Bell, Johnson 2004) and how both affect fitness.

We also predicted that males and females might differ in what behaviors are consistent or which behaviors covary. For the behavior toward novel objects, we found a tendency that females were consistent but not males. This tendency was reflected by a tendency for a sex difference in correlation coefficients for boldness and aggression prior to maturity and low correlation coefficients for exploration–boldness as well as boldness–aggression in premature males relative to both males after reaching maturity and females. Similarly, we also found tendencies that the relationship between the exploration–boldness–aggression syndrome and helping might be stronger in females, as correlation coefficients for helping and exploration in males were very low and statistically not different from zero. This result suggests that if there is any relationship in males, it will be weak. Summarizing the general pattern observed, we found a behavioral syndrome involving exploration, boldness, and aggression in both sexes, but it was relatively weak in males when young and got stronger during the course of ontogeny, whereas in females, this syndrome, complemented with helping ("sand carrying"), remained stable throughout ontogeny. Patterns of weakened behavioral correlations at different life stages, as we have found for males, have

also been found in sticklebacks (Bell and Stamps 2004). Although in that study the finding was opposite to ours, as the behavioral syndrome in sticklebacks broke apart at sexual maturity, our finding supports the results of Bell and Stamps (2004) that major transitional periods may affect the correlations of behaviors exhibited.

Note that the isolation in the beginning of the experiment could also have lead to the observed sex differences in behavioral syndromes if the sexes had been affected differently by the isolation. However, other experiments indicated that the behavior of *N. pulcher* is not affected by holding conditions (Rothenberger 2009). Additionally, also the lack of variance may have prevented us from finding a link between helping and exploration in males, but the variance was sufficient to detect correlations between helping and sand carrying when alone and to relate it to dispersal in males.

Male-biased dispersal in our experiment reflects findings from the field that males are the dispersing sex in *N. pulcher* (Stiver et al. 2004; Dierkes et al. 2005). These differences in the propensity to disperse between the sexes could explain why males and females might be different in the ontogeny of the behavioral syndromes observed, even though we can only speculate on what exactly generates this disparity. The main reason for the behavioral syndrome to become visible in males after becoming mature is that they adjust their boldness to match the levels of exploration and aggression, as both exploration and aggression are consistent over time. So, the question is rather why does female but not male boldness match exploration and aggression from the start? Females might be in a competitive situation with their sisters from the beginning on to inherit the breeding position (Dierkes et al. 2005; Stiver et al. 2006) and thus need to have all traits correspond to each other to avoid injuries or fatalities. Males may need to disperse only after reaching a considerable body size (Heg, Bachar, et al. 2004) and might face only mild competition up to that time. On the other hand, the most consistent trait in males, but not females, is aggression: Dall et al. (2004) hypothesized that aggression could have signal value in territorial species and so dispersing males could show how willing they are to escalate a fight over a position in a nearby queue. Thus, the potential reasons why sex differences in life histories of *N. pulcher* should lead to the observed behavioral syndrome pattern are speculative at best and should be investigated further.

Males mostly visited dispersal compartments when there was a potential mate in that compartment. These dispersal events with a breeding vacancy were not related to explorative behavior, as has been demonstrated, for example, in great tits (Dingemanse et al. 2003) and Trinidad killifish (Fraser et al. 2001). Nevertheless, in our study, breeding vacancies were adjacent to the home territory and therefore clearly visible for all males regardless of how explorative they were. In the field, on the other hand, helpers visit other territories ("ranging behavior"), and occasionally switch from their home group to a new group (Stiver et al. 2004; Bergmüller, Heg, Peer, et al. 2005), thereby increasing their social status (Stiver et al. 2004). More explorative individuals are probably more likely to spot such vacancies in queues of neighboring territories (Valone and Giraldeau 1993) and might thus be more likely to disperse. In accordance with this, males, but not females, increased exploration activity during the course of ontogeny. There is also the possibility that the difference between the sexes in exploration after maturity arose because of differences in body size. This is unlikely because size was not correlated with exploration in neither of the sexes in any trial. However, we cannot entirely rule out switch points in ontogeny that males could have reached during our study period but not females. Certainly, additional testing will be necessary

to rule out this alternative and to elucidate the relationship between explorative behavior, ranging, dispersal, and age.

As expected, our data suggest that in males, dispersal is linked to helping (sand carrying). Such a relationship between helping and dispersal has also been found in the Seychelles warbler, where helpful individuals neither disperse nor gain their own territories and must rely on inclusive fitness benefits instead (Komdeur and Edelaar 2001). Although this result is not readily applicable to the females in our study, it stresses the necessity to take all major life-history traits into consideration to understand why individuals consistently differ in the amount of help they provide.

In contrast to one of our expectations, we did not find any relationship between the behavioral types and the growth. Growth did not correlate with the behavior during standardized tests or with helping. Stamps (2007) argues that such correlations might be hard to spot during periods when the juvenile's own behavior has little impact on its growth and mortality, for example, when they are fed or protected by parents. Whether our result is the consequence of the ad libitum food treatment or the absence of predators, which under natural conditions would hinder food uptake of especially the shy individuals, we cannot tell. In the field, fish from medium sizes on (SL ≥ 35 mm) feed in the water column, 50–100 cm above the substrate, and if predators approach, they retreat to the breeding and hiding shelters (Heg, Bachar, et al. 2004, 2005). Thus, there is the potential for a trade-off between growth rate and predation risk mediated through boldness, as has been demonstrated in diverse taxa (e.g., Ydenberg and Dill 1986; Grant and Noakes 1987; Sih et al. 2003; Vøllestad and Quinn 2003). A well-designed field study might be better able to identify this relationship in *N. pulcher*.

In our study, we were able to demonstrate the existence of a behavioral syndrome in *N. pulcher*. The sexes appeared similar in their consistencies, but in 4 of 18 correlations between behavioral traits, we found evidence that the sexes might differ in the strength of the associations. Such syndromes could help explain variation in helping behavior because certain life-history traits may only come as a package and may be mediated through the different behavioral types. We were able to demonstrate a connection between helping and dispersal in males. The stability of the exploration–boldness–aggressiveness–helping syndrome in females needs to be related to their likelihood to inherit the territory or polygynous breeding. Future studies should also investigate whether these individual differences have a genetical basis and to what degree initial choice of a life-history trajectory encourages the development of behavioral types (Stamps 2003; Bergmüller and Taborsky 2007). Ecological studies should elucidate how variation in helping behaviors and their correlated effects might be maintained (Dingemanse et al. 2004; Wolf et al. 2007). Finally, consistent differences between subordinates in cooperative breeders and eusocial insects (e.g., *Apis mellifera capensis*, Moritz and Hillesheim 1985; Hillesheim et al. 1989) may be generated or at least modified by demands imposed on them by the dominant group members and the queen. Both intrinsic differences like temperament and demand may determine the extent of division of labor in group-living animals (Robinson 1992).

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