BEHAVIORAL ECOLOGY

Mismatched partners that achieve postpairing behavioral similarity improve their reproductive success

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Behavioral similarity between partners is likely to promote within-pair compatibility and to result in better reproductive success. Therefore, individuals are expected to choose a partner that is alike in behavioral type. However, mate searching is very costly and does not guarantee finding a matching partner. If mismatched individuals pair, they may benefit from increasing their similarity after pairing. We show in a monogamous fish species—the convict cichlid—that the behavioral similarity between mismatched partners can increase after pairing. This increase resulted from asymmetrical adjustment because only the reactive individual became more alike its proactive partner, whereas the latter did not change its behavior. The mismatched pairs that increased their similarity not only improved their reproductive success but also raised it up to the level of matched pairs. While most studies assume that assortative mating results from mate choice, our study suggests that postpairing adjustment could be an alternative explanation for the high behavioral similarity between partners observed in the field. It also explains why interindividual behavioral differences can be maintained within a given population.

INTRODUCTION

In species with a long-lasting pair bond and biparental care, the reproductive success of a pair is primarily determined by behavioral compatibility between partners (1–4). Because their interactions are repeated, frequent, and stable, compatible partners cooperate more efficiently by synchronizing their activities and coordinating their parental behaviors (2). Synchronized behaviors can be very important, for instance, for defending their territory against intrusion or for pooling nest visits to reduce the likelihood of the nest being detected by predators (5). In zebra finches (*Taeniopygia guttata*) and cockatiels (*Nymphicus hollandicus*), behavioral synchronization between partners is correlated with better reproductive success (2, 5). A key component of behavioral compatibility is the behavioral similarity between partners, which is the tendency for two individuals to behave like each other (2–4). In numerous monogamous species, similar partners were reported to have better reproductive success (3, 6–11); in humans, behavioral similarity was also shown to be related to marital satisfaction and marriage duration (12, 13).

Therefore, individuals are expected to search for a partner that is alike in behavioral traits. In previous studies under controlled conditions in the laboratory and using bird species with biparental care, individuals preferred a partner that was alike in behavioral type (14, 15). However, under natural conditions, finding a similar partner is a complex task. Mate choice implies time and energy costs in searching for potential partners and assessing their behavioral traits. Moreover, individuals must deal with competitors. Thus, for a choosy individual, there is a risk that all potential partners have become mated before it reaches a decision; a high level of choosiness is thus an ineffective strategy to guarantee successful mating (16). Thus, individuals may end up with a mismatched partner if a more similar option is not available. Therefore, there is a possibility for the individuals to make the best of a bad situation by adjusting their behavior to be more like their

partner's after pairing. This pattern of increasing similarity between partners, in one or several traits, is commonly referred to as behavioral convergence (17–19). In a broad sense, behavioral convergence could be either symmetrical (when both partners equally adjust their behavior) or asymmetrical (when adjustment is mainly attributable to one partner) (17, 19). The question of postpairing behavioral convergence is almost exclusively discussed in the psychology literature (17, 18, 20). Yet, studies on humans have yielded inconsistent results because behavioral convergence cannot be easily disentangled from the consequences of the mate choice process (18, 20): for obvious ethical reasons, protocols based on experimentally forced pairs with mismatched partners are complicated to design. Contrary to research on human mating, the question of behavioral convergence and its benefits for monogamous partners have been poorly discussed in animal species. Many studies investigating behavioral assortative mating and its evolutionary consequences implicitly assume that this pattern results from mate choice processes and underestimate alternative possibilities such as postpairing behavioral adjustment (3, 8, 9, 21). Unless the pattern of assortative mating results from mate choice, it does not provide evidence for sexual selection (4, 21, 22).

Across a wide range of taxa, a growing body of evidence supports the existence of consistent interindividual differences in behavioral traits, also named personality, temperament, or behavioral types (23). The correlations between these behavioral traits characterize a behavioral syndrome (24, 25). For instance, the proactive-reactive syndrome is based on the computation of a synthetic behavioral score (mainly defined by individual scores in aggressiveness, boldness, and exploratory tests) that is used to assign each individual to a discrete behavioral type, either proactive or reactive (24). These behavioral types are expected to coevolve with different strategies to cope with environmental or social constraints (25). For instance, in species with parental care, there is a trade-off between direct parental care (oriented toward the young, such as brooding or food provisioning) and nest defense (oriented toward brood predators) (26). The adopted parental style

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is linked to the parent's behavioral type (6, 25). Proactive individuals are better competitors, as they have access to better-quality sites and they usually specialize in aggressive activities such as territorial defense. Reactive individuals are better at adjusting to unstable environments and invest more in nonaggressive activities such as direct parental care (27–29). In the eastern bluebird *Sialia sialis*, pairs of aggressive birds focus more on territorial defense, whereas pairs of nonaggressive birds forage more actively, and both pairs of similar partners (same parental style) are more successful than dissimilar partners (6).

We investigated behavioral matching between partners in a monogamous fish species, the convict cichlid *Amatitlania siquia*. In this territorial species with biparental care, behavioral similarity between partners is likely to be related to the partners' compatibility because partners from successful pairs were more similar in behavioral type than were those that failed to reproduce (8). We formed matched (either proactive-proactive or reactive-reactive) and mismatched (proactive-reactive) pairs. We focused on individual aggressiveness to an unfamiliar conspecific because parental coordination in nest defense is highly relevant to this species. We estimated a behavioral similarity index between the two partners, and we assessed the increase in this index between isolated and pairing contexts and its fitness consequences in terms of reproductive success. We also investigated whether the increase in similarity was attributable to both partners (symmetrical convergence) or only one partner (asymmetrical convergence).

RESULTS

Using repeatable measures of four standardized tests commonly used in fish (aggressiveness, exploration, maintenance activity, and food neophobia), we characterized the proactive or reactive behavioral type (24) of each individual before pairing. Pairs were then formed as matched (either proactive-proactive or reactive-reactive) or mismatched (proactive-reactive) pairs.

Fitness of matched versus mismatched pairs
Within matched pairs, proactive-proactive and reactive-reactive pairs did not differ in fry number (generalized linear model correcting for female body length, $\chi^2_1 = 1.23$, $P = 0.27$) or agonistic behaviors expressed by the partners toward each other (hereafter named intrapair conflicts) ($P = 0.45$). Matched pairs had better fitness than mismatched pairs: they had more fry [mean number, 70.06; 95% confidence interval (95% CI), 31.60 to 112.60 (versus mean number, 38.39; 95% CI, 15.15 to 65.23); generalized linear model correcting for female body length, $\chi^2_1 = 4.522$, $P = 0.033$]. We also recorded fewer intrapair conflicts (frequency of intrapair agonistic behaviors) during the tests between matched partners than during the tests between mismatched partners [mean frequency, 0.007; 95% CI, 0.004 to 0.01 (versus mean frequency, 0.025; 95% CI, 0.01 to 0.043); permutation test, $P = 0.016$; fig. S1], which suggests an overall better compatibility of matched pairs (2). Therefore, we expected mismatched pairs to correct for their dissimilarity to improve fitness.

Behavioral adjustment in mismatched pairs
We evidenced an increase in the behavioral similarity index in mismatched pairs of convict cichlids after pairing (Fig. 1). We also showed that the reproductive success of the pair was significantly predicted by the similarity achieved after pairing (generalized linear model with a
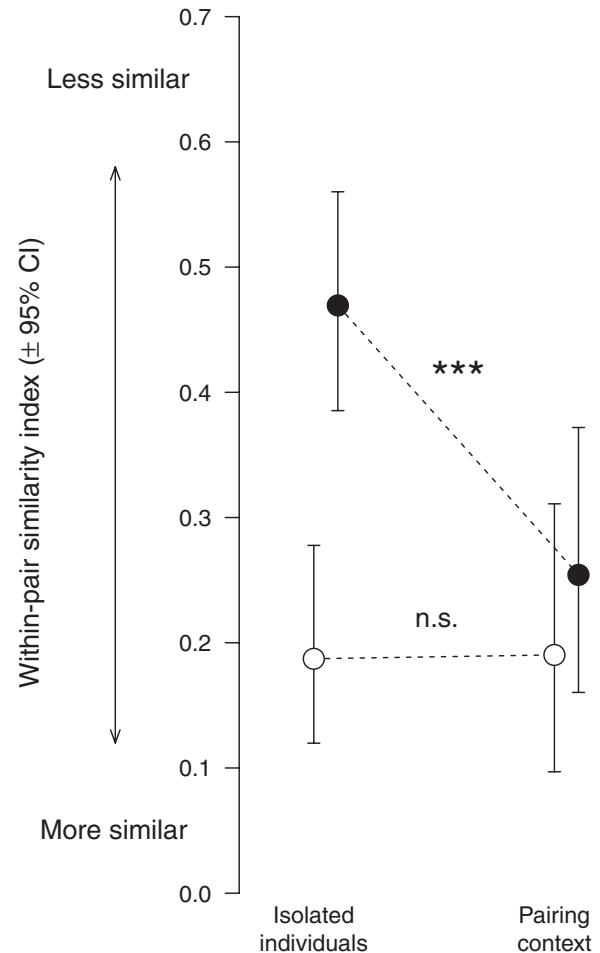

Fig. 1. Change in within-pair behavioral similarity between contexts. The mean behavioral similarity index (± bootstrapped 95% CI) for matched pairs (open circles; $n = 15$) and mismatched pairs (solid circles; $n = 13$) as a function of the context: isolated individuals and pairing context. A significant interaction between the nature of the pair (matched or mismatched) and the context was observed (mixed-effects linear model: $\chi^2_1 = 6.88$, $P = 0.0087$). The similarity index significantly decreased for mismatched pairs (mixed-effects generalized linear model: $\chi^2_1 = 9.07$, $P = 0.0026$), whereas there was no significant difference between contexts for matched pairs ($\chi^2_1 = 0.59$, $P = 0.443$). Between the contexts, only the significant post hoc comparisons were included in the figure (***$P < 0.001$). Mismatched pairs were significantly less similar than matched pairs in the isolated context ($F_{1, 27} = 21.39$, $P < 0.0001$), whereas there was no difference in the similarity index once individuals were paired ($F_{1,23} = 0.0028$, $P = 0.96$). Considering the continuous difference between partners instead of discrete categories (proactive or reactive) leads to consistent results: a larger initial difference in the behavioral score between partners significantly relates to a larger change in similarity ($r = 0.60$, $P = 0.0025$). n.s., not significant.

negative binomial distribution and correcting for female body length, $\chi^2_1 = 14.506$, $P = 0.00014$). The mismatched pairs that became the most similar not only had a larger number of fry compared to the least similar mismatched pairs but also did as well as the matched pairs (Fig. 2). A comparable relationship between behavioral similarity and spawning latency was found ($r = 0.61$; 95% CI, 0.02 to 0.89; range of spawning latency, 1 to 14 days). The least similar mismatched pairs
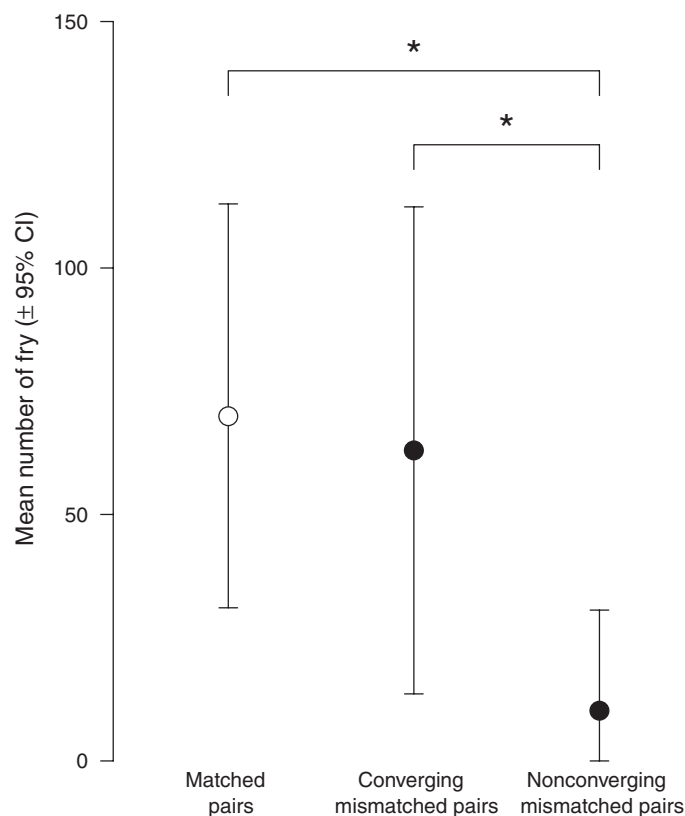
Fig. 2. Reproductive benefits of convergence. Reproductive success was assessed as the mean number of fry (± bootstrapped 95% CI) for matched pairs (open circles) and mismatched pairs (solid circles). To allow for comparison with matched pairs, we dichotomized mismatched pairs into converging pairs (the 50% most similar in the pairing context) and nonconverging pairs (the 50% least similar in the pairing context). Nonconverging mismatched pairs had significantly fewer fry than converging mismatched pairs (permutation test: $P = 0.04$) and significantly fewer fry than matched pairs ($P = 0.04$). Only the significant comparisons were included in the figure (*$P <$ 0.05 after correcting for multiple comparisons).

reproduced later, whereas those that became the most similar reproduced as fast as the matched pairs (fig. S2). However, the benefits of increasing similarity in mismatched pairs were not observed for every component of pair compatibility. Increasing similarity did not significantly lower the frequency of intrapair conflicts between mismatched partners (linear model: $F_{1,10} = 4.53$, $P = 0.06$). This may indicate potential remaining costs of initial dissimilarity between partners.

Proactive versus reactive flexibility

The increasing pair similarity was attributable to reactive individuals that modified their behavior to be more alike their partners, whereas, on average, proactive individuals behaved consistently (Fig. 3). A floor effect—where reactive individuals had a greater scope for change as a result of lower initial aggressiveness—was unlikely because we did not find any change in behavioral response in matched pairs where both partners were reactive (mixed-effects generalized linear model, $\chi^2_1 = 0.29$, $P = 0.59$; for additional details, see figs. S3 and S4). A difference in average flexibility in terms of parental care between the sexes has also been reported in previous studies (4, 30). However, we found neither a significant interaction between sex and context for aggressiveness
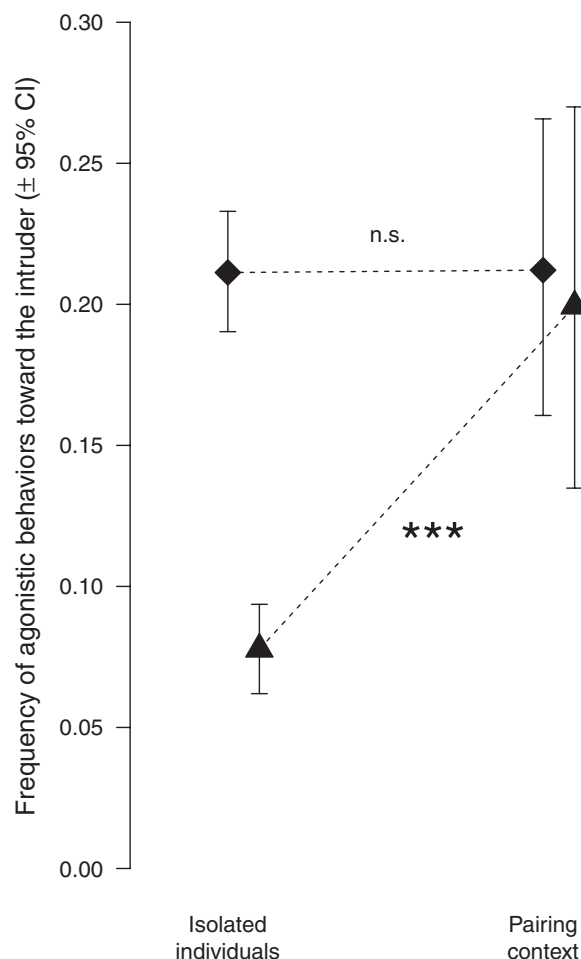

Fig. 3. Proactive versus reactive flexibility in mismatched pairs. The mean frequency of agonistic behaviors (± bootstrapped 95% CI) toward the intruder for reactive partners (triangles) and proactive partners (diamonds) in mismatched pairs as a function of the context: isolated context and pairing context. A significant interaction between behavioral type (reactive or proactive) and context was observed (mixed-effects linear model: $\chi^2_1 = 9.52$, $P = 0.0020$). For reactive fish, aggressiveness significantly increased between contexts ($\chi^2_1 = 11.93$, $P = 0.0006$), whereas it was consistent for proactive fish ($\chi^2_1 = 0.04$, $P = 0.85$). For each given behavioral type, only the post hoc tests between the contexts were included in the figure (n.s.: $P >$ 0.10; ***$P < 0.001$). Reactive and proactive fish significantly differed in the isolated context only ($\chi^2_1 = 39.59$, $P < 10^{-5}$), whereas there was no difference once they were paired ($\chi^2_1 = 0.29$, $P = 0.60$).

toward an intruder ($\chi^2_1 = 1.95$, $P = 0.16$) nor a significant difference between the level of behavioral change in males and the level of behavioral change in females ($\chi^2_1 = 0.003$, $P = 0.96$).

DISCUSSION

Within-pair behavioral similarity is a key component of reproductive success in monogamous species performing biparental care (3, 6–11). Our study experimentally provided evidence for an increase in behavioral similarity between partners after pairing. Among the initially mismatched pairs, those that became most similar achieved higher

fitness than the other mismatched pairs in terms of spawning latency and fry number. In addition, they also did as well as the initially matched pairs. Here, we focused on the pattern of similarity between partners and its short-term consequences on their fitness. We were primarily interested in increasing similarity as a pattern in a pairing context and its link with the reproductive success of the pair, whether or not individuals maintain behavioral adjustment to their former partner. Further work could be required to address the question of the long-term maintenance of this behavioral matching after the fry had hatched and the pair had split.

Our study also provides experimental evidence for a pattern of asymmetrical convergence of one pair member onto the other after pairing. The partners differed in behavioral flexibility in response to the pairing context, with the reactive individuals being significantly more flexible than the proactive individuals. Reactive individuals in mismatched pairs have been observed to change their behavior, resulting in an increase in the similarity of the pairs. This can be interpreted as an adjustment toward their proactive partner and not only as a general increase resulting from the sexual context because reactive individuals, when paired with another reactive partner, did not change their behavior between contexts. This supports previous results reporting that reactive individuals exhibited greater behavioral flexibility in a social context (31). Adult convict cichlids do not form a stable shoal; therefore, social relationships are mainly limited to their sexual partner (32). Thus, in this species, the question of behavioral flexibility in response to the social context is only ecologically relevant to the pairing context. Our results are in line with the request made by Réale et al. (25), Royle et al. (30), Webster and Ward (33), and Réale and Dingemanse (34) that researchers consider the social context when studying the fitness implications of behavioral types. The adaptive value of a given behavioral type cannot be assessed only in an isolated context because it may depend on individuals' ability to adjust to the social environment and on the behaviors of social partners (33, 35, 36). With the hypothesis of social niche specialization, the potential benefits of behavioral adjustment to the social environment have been addressed at the individual level within groups but not in a sexual context (28, 37).

On average, mismatched partners had lower fitness than matched pairs. However, this result should not conceal the fact that there was a difference in success among mismatched pairs as a function of their ability to increase their postpairing similarity. This raises two questions. First, why would not all of the mismatched pairs have increased their similarity? There are possibly strong interindividual differences in flexibility, even within the reactive type (38). In addition, the adjustment by reactive individuals, which increases their aggressiveness, can imply survival costs by exposing them to higher predation risk (39). Under natural conditions, particularly under strong predation pressure, reactive individuals that do not adjust their behavior to their partner's behavior may favor long-term reproductive success at the expense of immediate fitness gain. Among reactive individuals, some low-quality fish may be unable to cope with flexibility costs, and pairing with such an individual negatively affects the reproductive success of the pair. Second, as a result of better reproductive success in matched pairs, one could expect the individuals to search for an initially similar partner, instead of relying on postpairing adjustment. In a free-choice situation with a wide range of variation in partner type, do individuals preferentially mate with a matching partner? Additional experiments should be helpful to further investigate this question. However, finding a matching partner is a complex task that implies non-negligible

sampling costs (energy, time, predation risk, and lost opportunities) and is based on the assumption that it is possible to quickly and accurately assess the behavioral type of a potential partner. In the case of intense competition for access to a partner, it is unlikely that there is still an available matching mate (16). Thus, postpairing adjustment could be a way for mismatched partners to make the best of a bad situation and to ultimately improve their fitness. One individual can therefore limit the cost of searching for a similar partner by quickly pairing with a dissimilar partner, as long as partners manage to increase their postpairing similarity. Because they exhibit greater flexibility, the choosiness of reactive individuals may decrease with the increase in mate competition in the local population, whereas proactive individuals do not adjust their choosiness because of their generally higher competitiveness (29). In great tits and zebra finches, proactive individuals preferred similar partners, but reactive individuals did not exhibit any preference (14, 15). In some circumstances, however, it could be argued that reactive individuals, rather than proactive individuals, may be choosier. If the predation risk is low, reactive individuals may favor reactive mates to limit the intrapair conflicts that occur when they are paired with a dissimilar partner. On the contrary, if aggressiveness toward potential predators is beneficial, then a reactive individual should rather strongly favor proactive mates and then become more like their partner to efficiently deter predators and protect their young.

In our study, the fitness of reactive-reactive pairs did not differ from the fitness of proactive-proactive pairs. It could be explained by the fact that the success of a given pairing combination depends on the environmental conditions in nature. For instance, we did not allow predators to have access to the young. We cannot exclude that, under strong predation pressure, reactive-reactive pairs have higher brood loss as a result of their lower efficiency in deterring predators. Only field comparisons of the fitness of matched and mismatched pairs would disentangle this question. However, some pieces of evidence suggest that reactive-reactive pairs could still perform reasonably well in a natural population with low predation risk. In the trade-off between direct parental care and nest defense (26), partners are likely to benefit from a similar parental style, thus improving their coordination and, subsequently, their fitness (6). Nest defense is not the only component of parental care. Although two proactive partners may efficiently compete for the best territory and quickly chase away predators, two reactive partners focus their effort on direct parental care, such as fanning and provisioning, and may benefit from being well coordinated with regard to parental activities. Thus, reactive matched partners may compensate for their lack of aggressiveness by providing more direct parental care (9).

Here, we highlight the importance of considering postpairing adjustment as a confounding factor in assortative mating studies. The observation of a pattern of assortative mating cannot be used to assume mate choice for similar partners. Hormonal convergence and call convergence during reproduction have been exhibited in monogamous birds (19, 40); therefore, the adjustment of multiple parameters in monogamous partners may be a non-negligible phenomenon. Thereby, behavioral convergence could partly explain the maintenance of different behavioral types within a given population. The literature on assortative mating usually assumes significant evolutionary consequences, through disruptive selection resulting from strong mating preference, which play a key role in speciation as a result of premating isolation (22, 41). Thus, a decrease in the variability of behavioral types

in these divergent populations is expected [(*22*); but see van Oers *et al.* (*42*), who argued that phenotypic variability in offspring is maintained by higher extrapair paternity in similar pairs of birds]. However, our results highlight that elevated behavioral similarity between initially (before pair formation) mismatched partners can result from postpairing adjustment. It is thus theoretically possible to observe a pattern of assortative mating at the population level without assuming any preference based on similarity. The mere observation of a pattern of behavioral assortative mating is not sufficient in itself to conclude on the existence of disruptive sexual selection.

MATERIALS AND METHODS

Profiling of individual behavioral types

All fish were housed in same-sex tanks (52.5 to 96 liters), with 10 fish per tank, at 25° ± 1°C under a 12-hour light:12-hour dark cycle. Fish were fed Tetra Cichlid XL flakes daily. Four to 5 days before the start of the behavioral tests, the fish were isolated in a 20-liter tank (40 cm long by 20 cm wide by 25 cm high). Each tank was equipped with an artificial shelter (8 cm in diameter, typically used in breeding experiments), an air stone, and a gravel substrate. Visual isolation was achieved by separating the tanks with opaque dividers. Animal care and all experimental procedures were approved by the University of Burgundy Ethical Committee.

We characterized the proactive-reactive behavioral type (*24*) of 108 (44 males and 64 females) convict cichlids using four behavioral tests commonly used in fish: aggressiveness, exploration, maintenance activity, and food neophobia (*43*, *44*). For each individual, each test was repeated with a 1-week interval between sessions to assess behavioral repeatability (table S1). Exploration, maintenance activity, and aggression tests were recorded with DFK 21AU04 video cameras (The Imaging Source) connected to the Noldus Media Recorder 2 software (version 2.0.212; Noldus Information Technology).

Exploration. This test closely followed the procedure described by Bergmüller and Taborsky (*45*). The novel environment consisted of a 450-liter tank (150 cm wide by 50 cm deep by 60 cm high) divided into two compartments: a small compartment (40 cm wide) separated from the larger compartment by opaque plastic partitions, equipped with a sliding door. The novel environment contained a gravel substrate, two plastic plants (25 cm high), and six artificial nests (8 cm in diameter, typically used in breeding experiments) to provide shelters to explore. After the fish had spent 5 min to acclimatize in the small compartment, we gently opened the partition between the two parts with a pulley system, and the fish was allowed to explore the large compartment for 15 min. Locomotor activity (swimming distance) was analyzed using automated trajectometry software (EthoVision; Noldus Information Technology).

Food neophobia. The test closely followed the procedure described by Schweitzer *et al.* (*43*). A novel sort of food was presented to the fish at the usual feeding schedule and within the feeding area to record the latency to consume unfamiliar food. If a fish had not eaten after 15 min, a maximum score of 900 s was recorded. Two different novel foods (Tetra Delica Krill Freeze Dried Shrimp or colored pellets) were used in randomized order to avoid familiarization. To ensure uniformity in hunger level, we deprived the fish of food for 24 hours before the test.

Maintenance activity. This test closely followed the procedure described by Bergmüller and Taborsky (*45*). The shelter was covered with gravel and we measured the time that the fish spent to clear the nest for 20 min. The individual was considered as having cleared the nest when it pushed the gravel outside the nest with its tail or with its mouth.

Aggressiveness toward an intruder. We used the procedure described by Schweitzer *et al.* (*43*) to test for aggression. We measured the agonistic responses of each fish to a conspecific intruder by pushing two visually isolated adjacent tanks together and by removing the opaque divider between them, enabling the two fish to interact. For each encounter, we recorded the latency to start an agonistic interaction and the frequency of agonistic behaviors (displays and bite attempts) for 15 min. The focal fish and the intruder were of the same sex and matched for body size. Each individual was only tested once with a given intruder.

Synthetic behavioral score. These aggressiveness, exploration, maintenance activity, and food neophobia measures were repeatable (table S1) and correlated in syndrome (table S2). For each fish, a synthetic behavioral score (*S*) was calculated from these measures using principal components analysis (PCA; fig. S5 and table S3) (*11*, *43*). The first two principal components (PC1 and PC2) of the PCA explained 39% and 25% of the variance, respectively (table S3). For all subsequent analyses, PC1 defined the behavioral scores for each individual. The two sexes were evenly distributed along this score. Behavioral type was then quantified as an individual's behavioral score along a proactive-reactive continuum, with positive values indicating proactive individuals (highly aggressive and explorative individuals) and with negative values indicating reactive individuals (less aggressive and less explorative individuals) (*24*).

Pair formation

Twenty-eight males and females were chosen to form a pair, depending on their behavioral score (figs. S5 and S6) and size (standard body length ± SD: $L_M = 62 ± 12$ mm in males; $L_F = 48 ± 5$ mm in females). Four pairing combinations were thus obtained: eight matched pairs with two reactive partners, seven matched pairs with two proactive partners, six mismatched pairs with a reactive female and a reactive male, and seven mismatched pairs with a proactive female and a reactive male (fig. S6). Within a given sex, individuals from the matched and mismatched pairs did not differ in body length (males: $t = -0.167$; $P = 0.87$; Cohen's $d = -0.068$; 95% CI, −0.90 to 0.79; females: $t = -0.113$; $P = 0.91$; Cohen's $d = -0.045$; 95% CI, −0.76 to 0.88). Matched and mismatched pairs did not differ in body length contrast between the partners, defined as $| L_M - L_F | / (L_M + L_F)$ ($t = 0.13$; $P = 0.89$; Cohen's $d = 0.053$; 95% CI, −0.79 to 0.87). The behavioral score between partners did not significantly differ in matched pairs ($n = 15$; Cohen's $d = 0.03$; 95% CI, −0.72 to 0.75), whereas it was highly contrasted in mismatched pairs ($n = 13$; Cohen's $d = 4.07$; 95% CI, 3.19 to 6.20; fig. S6).

To prevent frequent injury between partners in the case of experimentally forced pairs, we designed a procedure to control for the behavioral type of the partners while letting the individuals choose their partner. We used a 450-liter tank divided into four distinct territories, each freely accessible. Each territory contained an artificial nest, a gravel substrate, a plastic plant, and a rock. For each pairing combination, three (respectively, four) males with a similar behavioral type were first introduced into the tank for 72 hours to let them establish their territory. We then introduced three (respectively, four) females with a similar behavioral type. For example, the introduction of four reactive males was followed by the introduction of four proactive

females to form four mismatched pairs including a proactive female and a reactive male. After the introduction of the females, we allowed the individuals to choose their partners. When a pair was formed in a territory (partner's close proximity to the nest, no agonistic interactions between them, and nest defense toward conspecifics), the pair was moved into a 54-liter breeding tank until the end of the experimental period. Each tank was visually isolated from the other tanks and contained an artificial nest, a gravel substrate, and a heater to maintain the water at 27°C. This procedure was used to provide the individuals the opportunity to choose between several potential partners while achieving the desired pairing combinations (fig. S6). Hence, all of the fish managed to find a partner, and we observed no injury among them.

Maintenance of individual differences and similarity index

The whole range of behavioral tests is a relatively long procedure and is likely to be stressful for fish. Therefore, only one behavioral test, included in the behavioral syndrome, was retained for testing in the pairing context. This allowed us to not only avoid the confounding effects of pairing and reproduction (because pairs can reproduce very quickly after pairing) but also not disturb reproduction and avoid bias in measuring the fitness of the pairs. We focused on individual aggressiveness in response to an intruder because it is highly relevant to parental coordination in territory defense in this species. Aggressiveness was estimated as the response to an unfamiliar juvenile conspecific (standard length ± SD, 55 ± 3 mm; range, 52 to 58 mm), which is a predator for fry in this cannibalistic species (46). The intruder was introduced into the tank in a hermetic clear glass jar for 5 min. The intruders used with the matched and mismatched pairs did not differ in mean body length ($\chi^2_1 = 2.32$, $P = 0.13$). On average, the intruder was 5.4 mm (95% CI, 2.2 to 8.6) smaller than the male partner and 7.4 mm (95% CI, 5.8 to 8.9) larger than the female partner. To allow for comparison, we estimated aggressiveness in both contexts (isolated or pairing) as the frequency of agonistic behaviors (displays and bite attempts) toward the unfamiliar intruder. We also measured the frequency of intrapair conflicts as a cue for pair compatibility (2).

As reported in the literature on the consistency of behavioral type across contexts (24, 25), individuals' behavioral scores measured before pair formation significantly predicted aggressiveness in a pairing context for matched pairs (mixed-effects linear model: $\chi^2_1 = 9.365$, $P = 0.002$, standardized slope ± SE = 0.62 ± 0.19). However, there was no similar relationship for mismatched pairs ($\chi^2_1 = 0.143$, $P = 0.705$, standardized slope ± SE = 0.063 ± 0.18), and this discrepancy between matched and mismatched pairs ($\chi^2_1 = 5.196$, $P = 0.023$) can be explained by a change in behavior in mismatched pairs. We calculated a within-pair similarity index (D) based on the relative difference in the frequency of agonistic behaviors expressed by the male (A_M) and the female (A_F): $D = |A_M - A_F|/(A_M + A_F)$. An index value close to 1 corresponds to dissimilar partners, and an index value close to 0 indicates similar partners. Before pair formation, the mean similarity index was significantly lower than the expected similarity achieved by random pair formation ($D_R = 0.30$, estimated by permutation) for matched pairs ($D = 0.19$; 95% CI, 0.12 to 0.28) and was higher for mismatched pairs ($D = 0.47$; 95% CI, 0.39 to 0.56). The change in the similarity index was used to characterize the pattern of behavioral convergence. Intruder body length had no effect ($\chi^2_5 = 0.0055$, $P = 0.94$) on the similarity index. Moreover, instead of focusing on the discrete categories (reactive versus proactive), we also considered the continuous

difference in the behavioral score between partners: abs($S_M - S_F$). We then calculated the correlation between this measure and the change in the similarity index ($D_p - D_i$) between isolated context (D_i) and pairing context (D_p).

Fitness of the pairs

The breeding tanks were visually inspected twice a day for spawning and hatching. Reproductive success was measured as the spawning latency and the number of fry (counted just after hatching).

Statistical analysis

Repeatability of the behavioral measures was assessed using the intraclass correlation coefficient of Nakagawa and Schielzeth (47). When the data followed a nonstandard distribution, we relied on the repeatability measurement based on rank, and behavioral consistency over time was assessed by Spearman's rank correlation coefficients. Repeatability was achieved for each behavioral test. To analyze the effects of the pairing context on the similarity index and number of agonistic behaviors, we used a mixed-effects model with pair identity and individual identity as a random variable, respectively. We followed a stepwise selection model procedure to identify the best model. For covariates with a significant effect, we performed post hoc pairwise comparisons. To limit the inflation of type I error, we used permutation tests ($n = 10,000$ permutations) (48) in comparing variables with a small sample size.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/2/3/e1501013/DC1

Fig. S1. Frequency of intrapair conflicts.
Fig. S2. Spawning latency (in days) in matched and mismatched pairs.
Fig. S3. Aggressive responses toward the intruder.
Fig. S4. Individual behavioral reaction norm across pairing for reactive individuals.
Fig. S5. Behavioral score.
Fig. S6. Formation of 28 pairs of cichlids based on their behavioral type along the proactive-reactive continuum.
Table S1. Repeatability of behavioral traits.
Table S2. Correlations between the behavioral traits used to define the proactive-reactive behavioral types.
Table S3. Loading of the four behavioral traits on to the three principal components.

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**Mismatched partners that achieve postpairing behavioral
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Mismatched partners that achieve postpairing behavioral similarity improve their reproductive success

Chloé Laubu, François-Xavier Dechaume-Moncharmont, Sébastien Motreuil, Cécile Schweitzer
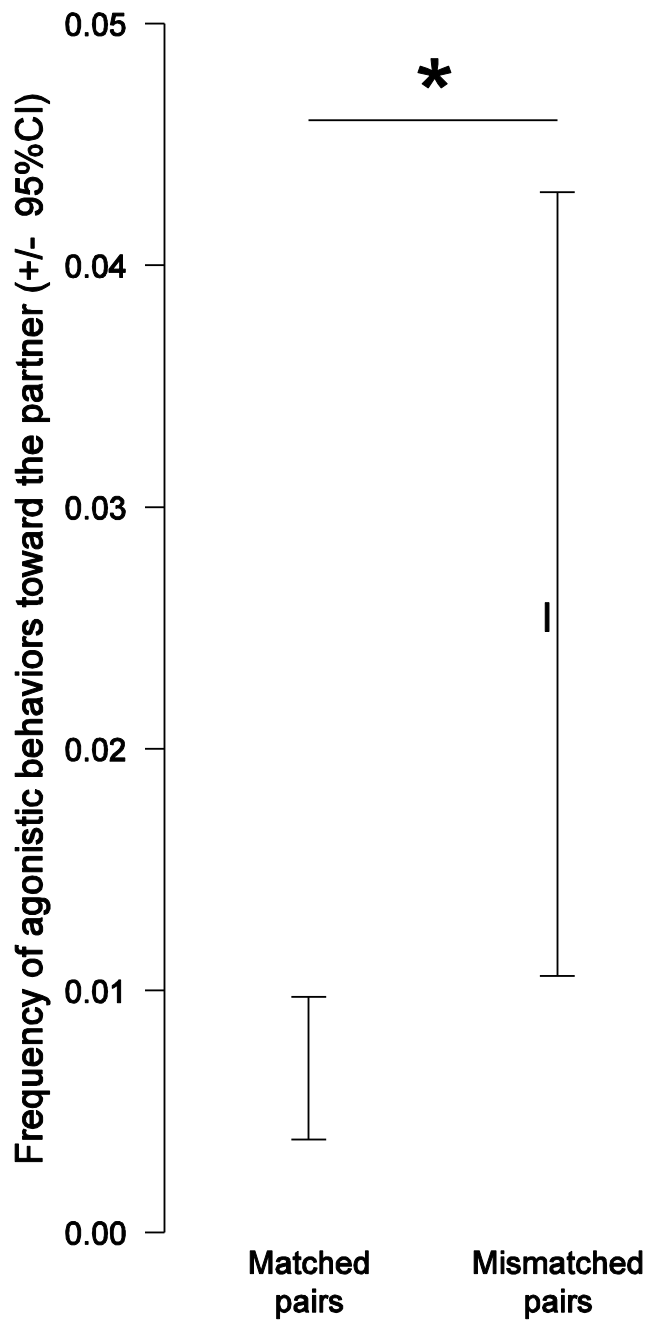
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Fig. S1. Frequency of intrapair conflicts. The mean frequency of agonistic behaviors (± bootstrapped 95% CI) expressed by one of the partners to the other partner for matched (open circles) and mismatched pairs (solid circles). Permutation test: * $p < 0.05$.
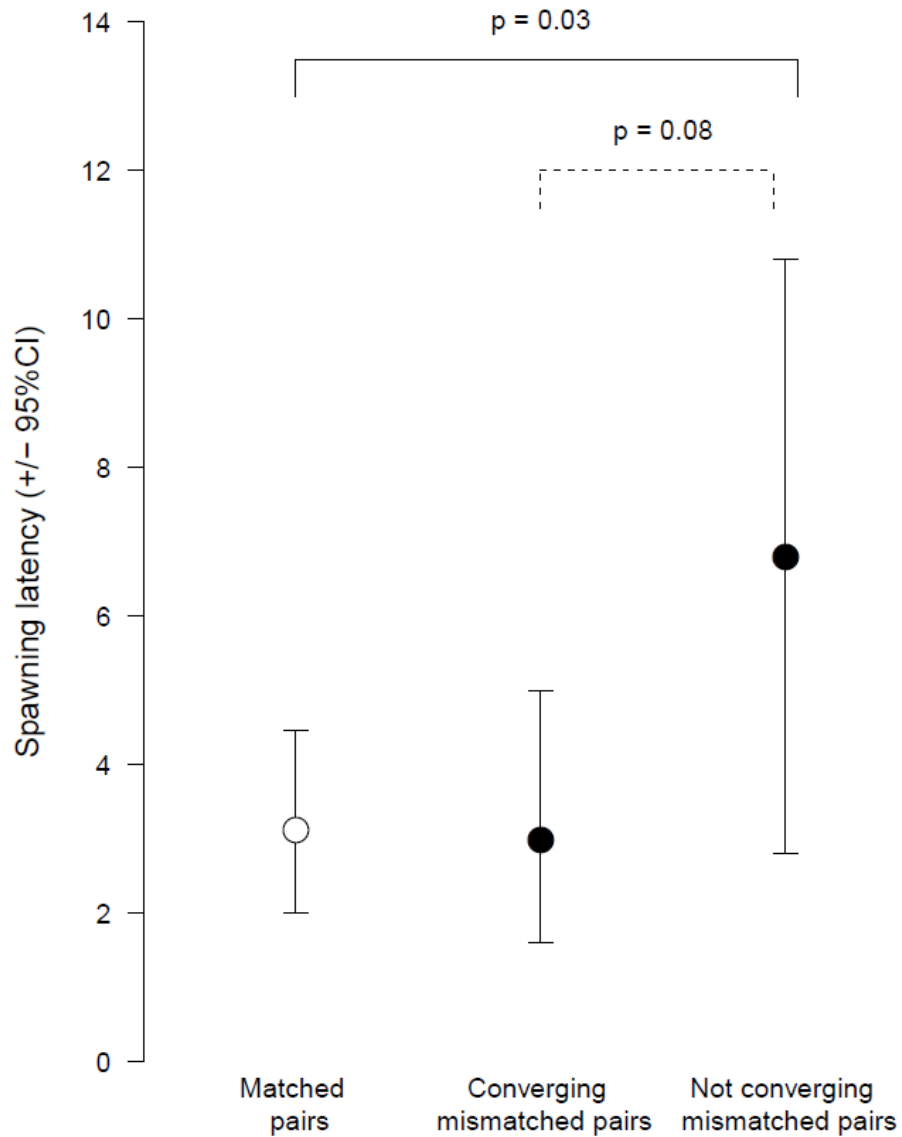
Fig. S2. Spawning latency (in days) in matched and mismatched pairs. Reproductive success measured as the mean spawning latency (± bootstrapped 95% CI) for matched (open circles) and mismatched pairs (solid circles). In order to allow a comparison with matched pairs, mismatched pairs were dichotomized in converging (the 50% most similar in the pairing context) and nonconverging pairs (the 50% least similar in the pairing context). The significant permutation tests and tendencies were included in the figure.
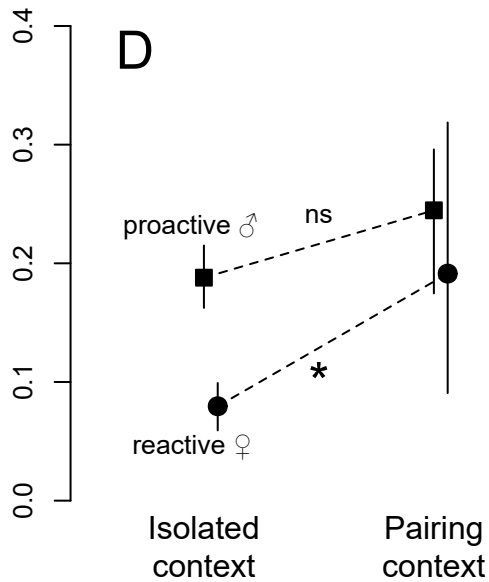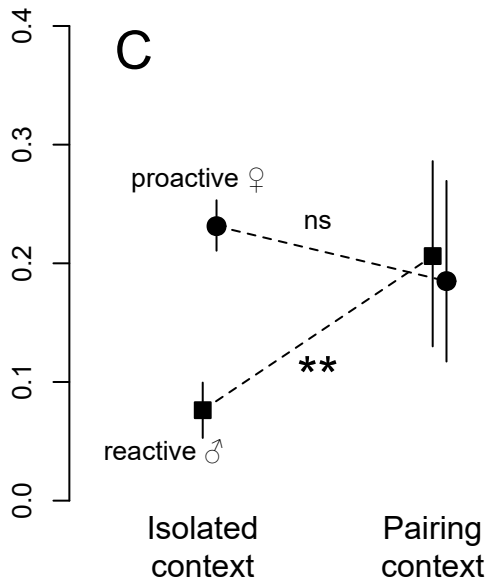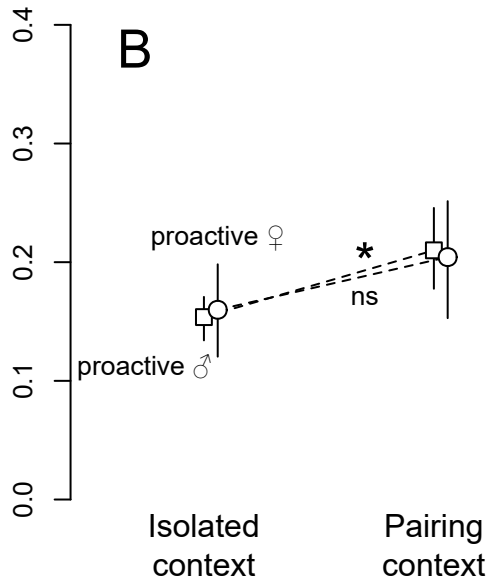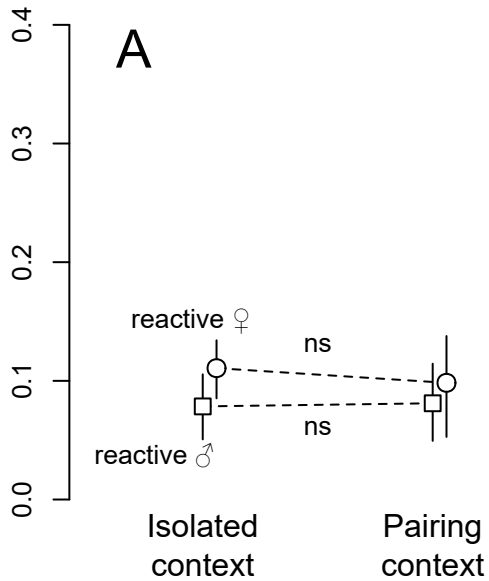
Fig. S3. Aggressive responses towards the intruder.

Mean frequency of agonistic behaviors toward the intruder (± bootstrapped 95% CI) of the male (squares) and female (circles) partners for the four pairing combinations, in the two contexts. Matched pairs (open symbols): (A) two reactive partners, (B) two proactive partners. Mismatched pairs (solid symbols): (C) a proactive female and a reactive male, (D) a reactive female and a proactive male. For a given sex and pairing combination, the comparison of the responses between context was done using paired permutation tests: ns $p > 0.10$, * $p < 0.05$ and ** $p < 0.01$.
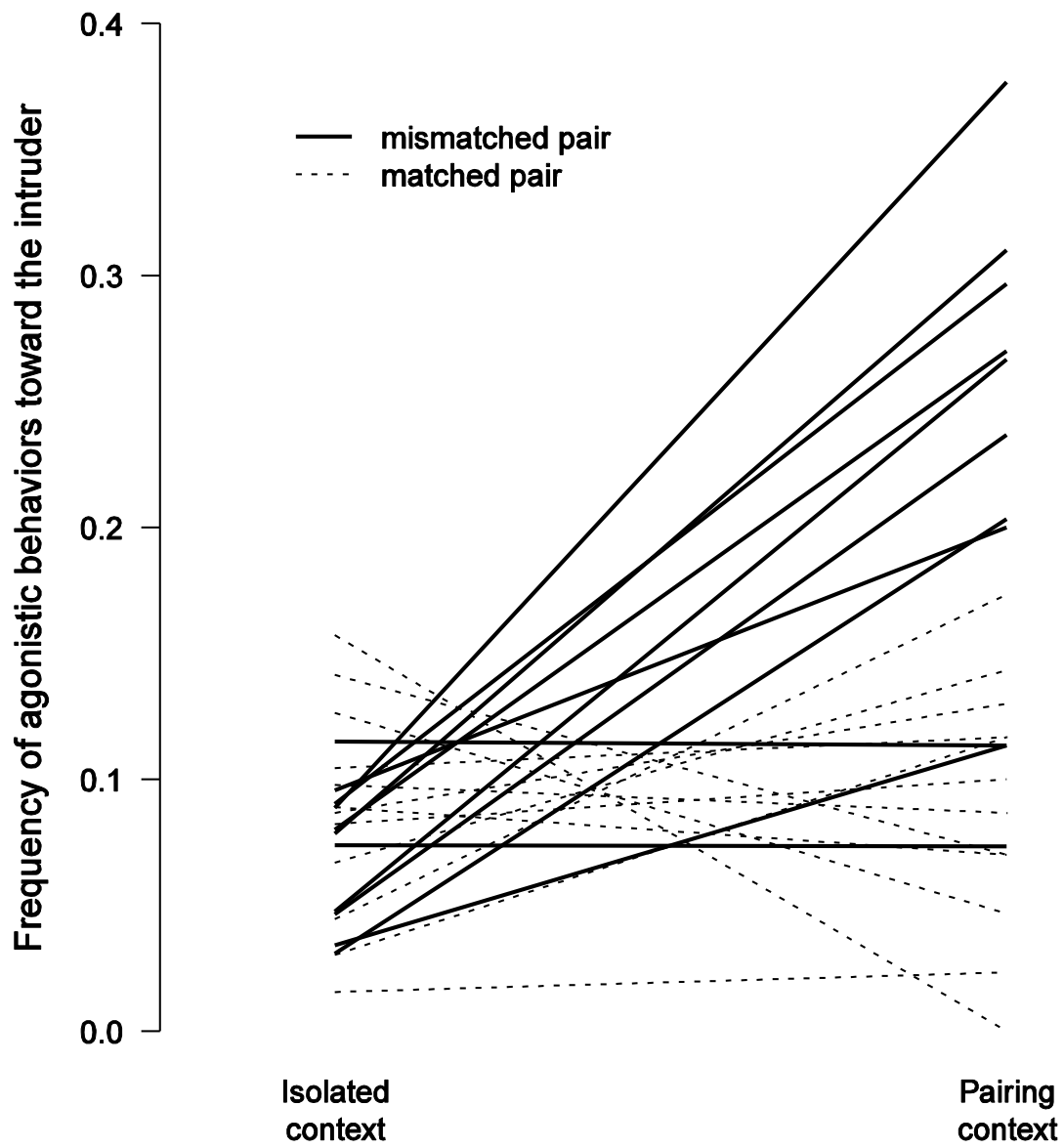
Fig. S4. Individual behavioral reaction norm across pairing for reactive individuals. Reactive individuals in mismatched pairs have been observed to increase their aggressive response toward the intruder between the two contexts (Fig. 3). This can be interpreted as a convergence toward their proactive partner, and not just as a general increase due to the sexual context because reactive individuals in matched pairs did not change their behavior between contexts. In order to illustrate this point, we focused on reactive individuals to compare their behavioral reaction norms for agonistic behaviors toward the intruder as a function of the context: isolated and pairing context. There was a significant interaction between the nature of the pair (matched or mismatched) and the context (mixed-effect linear model: $\chi^2_1 = 9.97$, p = 0.0016). The aggressive responses of reactive individuals were consistent over time in matched pairs (dashed lines, $\chi^2_1 = 0.29$, p = 0.59), whereas they increased in mismatched pairs (solid lines, $\chi^2_1 = 11.9$, p = 0.00055).
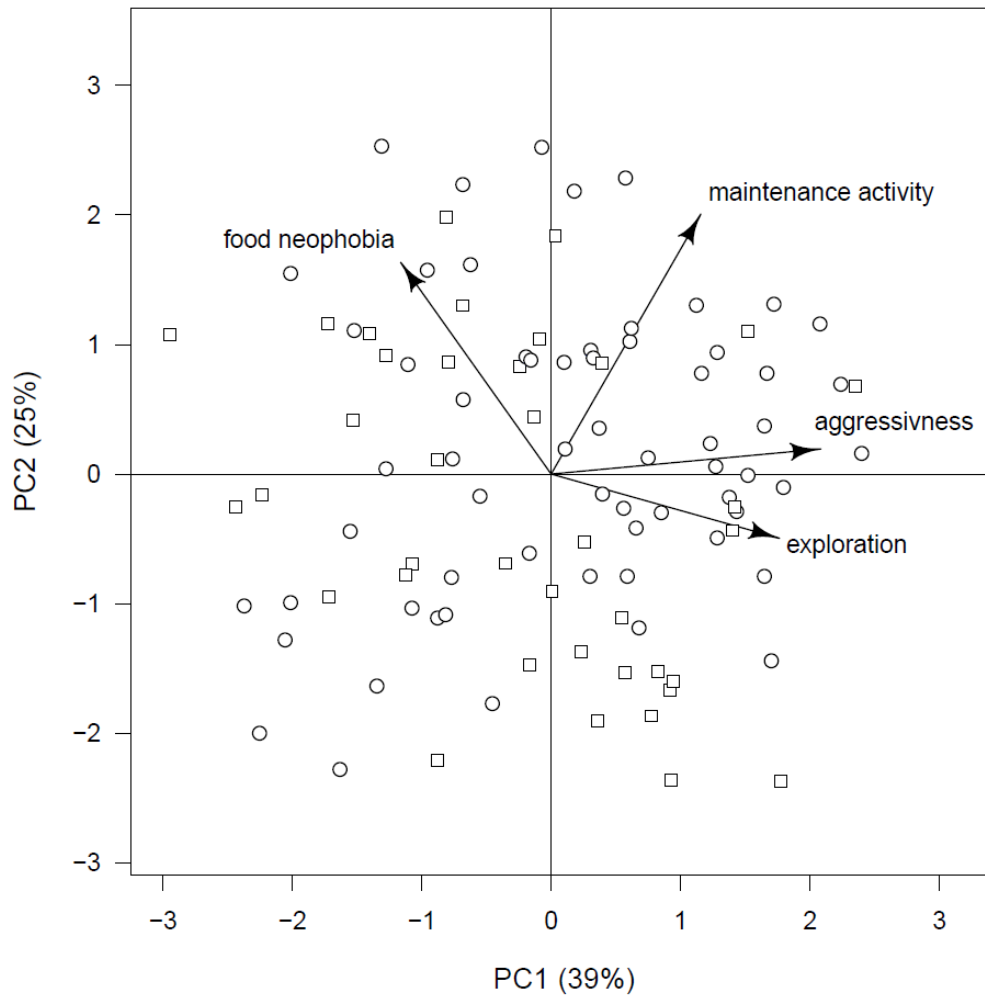
Fig. S5. Behavioral score. Scatter plot of the principal component analysis based on 44 males (squares) and 64 females (circles) profiled in the four behavioral tests. The loadings of the four traits are given in Table S3. The behavioral type of each individual was derived from PC1 score which defined the proactive-reactive continuum with positive values indicating proactive individuals (highly aggressive and explorative individuals) and negative values indicating reactive individuals (less aggressive and less explorative individuals).
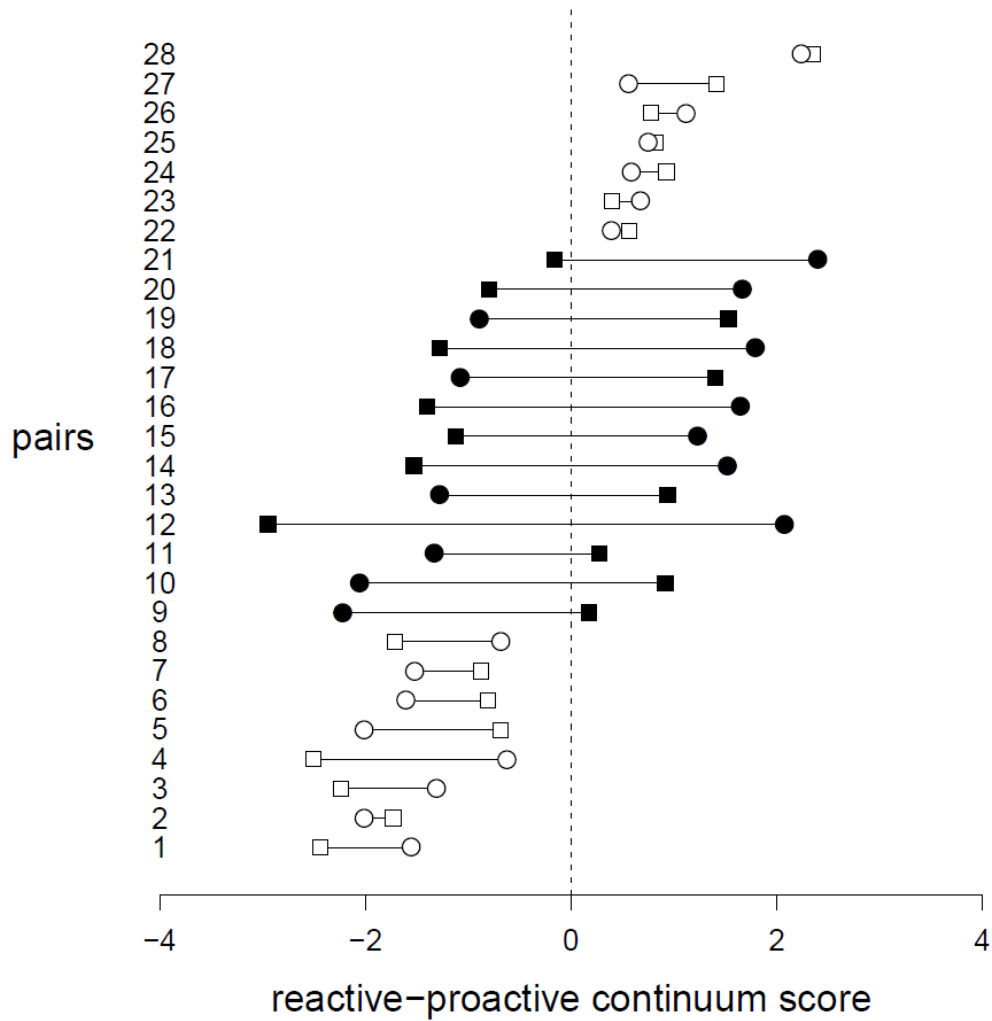
Fig. S6. Formation of the 28 pairs of cichlids based on their behavioral type along the proactive-reactive continuum. Positive scores indicated proactive individuals (highly aggressive and explorative individuals) and negative scores indicated reactive individuals (less aggressive and less explorative individuals). Matched pairs: open symbols, and mismatched pairs: solid symbols.

Table S1. Repeatability of behavioral traits. Repeatability was assessed by the intraclass correlation coefficient and 95% confidence intervals (in brackets) for exploration and aggressiveness. Spearman's rank correlations were used to analyze the two other behavioral traits, and 95% confidence intervals (in brackets) were computed by bootstrapping. The profiling of the behavioral type was based on a larger number of fish (n = 108) than the ones used for the pair formation (n = 56). All behavioral traits were strongly consistent over a one-week interval for the two samples.

Behavioral traits	Repeatability	
	All individuals (n=108)	Pairing individuals (n=56)
Exploration	R = 0.50 [0.37; 0.61]	R = 0.66 [0.53 ; 0.78]
Food neophobia	$\rho = 0.42$ [0.23, 0.59]	$\rho = 0.54$ [0.28; 0.75]
Maintenance activity	$\rho = 0.57$ [0.40, 0.71]	$\rho = 0.59$ [0.33; 0.78]
Aggressiveness	R = 0.24 [0.04; 0.41]	R = 0.39 [0.14; 0.60]

Table S2. Correlations between the behavioral traits used to define the proactive-reactive behavioral types. Spearman correlation (ρ) with 95% confidence interval between the four behavioral traits depending on sex (female F: n=64; male M: n=44). Correlations still significant after correcting for multiple comparisons (following Benjamini-Hochberg procedure, see Schweitzer et al. 2015 (43)) are figured in bold.

	Sex	Food neophobia	Maintenance activity	Aggressiveness
Exploration	M	-0.32 [-0.58, -0.01]	**-0.39 [-0.60, -0.12]**	**0.42 [0.15, 0.63]**
	F	0.09 [-0.19, 0.33]	**0.45 [0.22, 0.64]**	**0.35 [0.10, 0.58]**
Food neophobia	M		-0.05 [-0.30, 0.21]	-0.13 [-0.45, 0.19]
	F		0.19 [-0.06, 0.43]	-0.22 [-0.42, 0.0]
Maintenance activity	M			-0.13 [-0.48, 0.21]
	F			**0.39 [0.17, 0.56]**

Table S3. Loading of the four behavioral traits on to the three principal components. The behavioral score used to characterize the individual behavioral types was derived from the first principal component (PC1).

	PC1	PC2	PC3
Exploration	0.55	-0.19	-0.62
Food neophobia	-0.36	0.62	-0.67
Maintenance activity	0.37	0.76	0.40
Aggressiveness	0.66	0.073	-0.08
Percentage of variance explained	38.6	25.0	21.8
Eigenvalue	1.54	1.00	0.87