Recreational fishing selectively captures individuals with the highest fitness potential

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Fisheries-induced evolution and its impact on the productivity of exploited fish stocks remains a highly contested research topic in applied fish evolution and fisheries science. Although many quantitative models assume that larger, more fecund fish are preferentially removed by fishing, there is no empirical evidence describing the relationship between vulnerability to capture and individual reproductive fitness in the wild. Using males from two lines of largemouth bass (*Micropterus salmoides*) selectively bred over three generations for either high (HV) or low (LV) vulnerability to angling as a model system, we show that the trait "vulnerability to angling" positively correlates with aggression, intensity of parental care, and reproductive fitness. The difference in reproductive fitness between HV and LV fish was particularly evident among larger males, which are also the preferred mating partners of females. Our study constitutes experimental evidence that recreational angling selectively captures individuals with the highest potential for reproductive fitness. Our study further suggests that selective removal of the fittest individuals likely occurs in many fisheries that target species engaged in parental care. As a result, depending on the ecological context, angling-induced selection may have negative consequences for recruitment within wild populations of largemouth bass and possibly other exploited species in which behavioral patterns that determine fitness, such as aggression or parental care, also affect their vulnerability to fishing gear.

recreational fisheries | reproduction | evolutionary change | catchability | angler

Size-selective fishing, or even just an elevated level of fishing mortality, has the potential to induce rapid evolutionary change in a range of production-related traits in fish populations (1, 2). Theoretically predicted and empirically supported fisheries-induced adaptive change involves the modification of life history traits, including reductions in age- and size-at-maturation, increases in reproductive investment, and changes in pre- and/or postmaturation growth rates (1–3). Changes in life history traits in response to fishing often collectively reduce adult size-at-age and fisheries yield and result in fish populations that only slowly rebound from overexploited states (4–7). There is little consensus, however, concerning the prevalence of fisheries-induced evolution and its relevance to management (1, 8–10). Perspectives range from calls for "evolutionarily enlightened management" (11) to positions that argue that evolutionary change induced by fishing is slow, thereby rendering it largely unimportant to fisheries management (9).

One important tool to predict long-term population-level consequences of fisheries-induced evolution involves the construction and analysis of individual-based models (5, 12) or more simplified stage or age/size-structured (7) population models. Suitable models to study the potential for fisheries-induced evolution include ecological feedbacks resulting in density- and frequency-dependent selection that shapes fitness landscapes and evolutionary responses to fishing (7, 10). Many of these simulation models assume that fitness or fitness surrogates scale positively with body size (e.g., an exponential increase in individual female fecundity with size or a decline in natural mortality with increasing body length) (5, 7, 12, 13). Under such model assumptions, size-dependent fishing mortality often means that larger, more-fit individuals are harvested at a higher rate than smaller, less-fit ones. Several empirical studies on wild fish populations, however, have questioned the notion that larger fish generally exhibit higher reproductive fitness (14, 15). As a result, although for many fisheries size-selective exploitation is well established (3–5, 7), there is little empirical evidence from wild populations demonstrating that fishing truly targets reproductively more-fit individuals. One can speculate that certain fishing gear might even target less-fit individuals, that is, those that are either competitively inferior or in poorer condition and therefore more prone to attack fishing lures, more likely to encounter passive fishing gear, or less able to evade actively fished gear such as trawls.

Although size-selective mortality should be common across many fisheries, the relationship between size and capture probability is gear-dependent, and the resulting size-selectivity curves are often nonlinear (16). Moreover, a trait that renders individuals more vulnerable to capture likely also varies across different taxa and/or fisheries. In some fisheries, such as recreational angling, selection seems to operate on angling vulnerability as a complex, heritable trait composed of a range of covarying physiological, behavioral, and life history traits (17, 18), rather than body size per se. In the popular recreational fish species largemouth bass (*Micropterus salmoides*), for example, it has been shown that fish with higher vulnerability to angling also exhibit higher metabolic rates and more intensive parental care (19–21). Likely as a result of greater energetic expenditure, however, the largemouth bass that were genetically predisposed to being vulnerable to capture did not grow better under experimental pond conditions in which food was limited (20, 21). Because more-vulnerable individuals may have particular behavioral phenotypes during mate choice that are desired by females (e.g., higher levels of aggression that presumably indicate a willingness to provide more intense parental care), they may still be reproductively more fit than their less-vulnerable conspecifics, despite their smaller body size. We addressed this hypothesis in the present study.

The largemouth bass is one the most targeted species in North American recreational fisheries (22), making it an ideal study species to examine the consequences to fitness of recreational angling. Nesting male largemouth bass provide extended parental

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care for several weeks, defending eggs and fry against potential egg predators, which makes them particularly vulnerable to angling during the reproductive period (23, 24). This is important because nest defense behavior of males during parental care has been found to be critical for brood survival (24, 25). In addition, although it has been proposed that fisheries-induced selection in recreational angling operates more directly on behavioral and underlying physiological traits than on body size (17), it is most likely that both body size and the type and degree of male parental care behavior are involved in determining the fitness of individual males (13). That is, larger males are expected to compete better for nesting sites, and as a result of male size-based female mate choice, often have higher mating success (26). It is also likely that the most aggressive males provide the most intensive parental care and as a result are the most vulnerable to fishing during the nesting period (23). This would, independent of individual size, result in the potentially most reproductively fit individuals facing the greatest likelihood of capture and subsequent death or in the case of catch-and-release fisheries loss of fitness due to loss of all or some of their brood to egg predators (23–25).

The objective of the present study was to assess the relationship between reproductive fitness and vulnerability to angling, using as a model system male largemouth bass from two experimental lines selected over three generations for differences in their vulnerability to angling (18). Because angling should selectively target those largemouth bass males that are the most aggressive nest defenders and therefore the more likely to attack angling lures [i.e., males from the line of highly vulnerable (HV) fish], we postulated that under identical ecological conditions these HV males should demonstrate higher levels of reproductive success than the less vulnerable (LV) males. We further postulated that females might also differentially allocate more reproductive resources to HV males because they might recognize and preferentially mate with a superior nest defender, as has been observed in a range of other species that provide male parental care (27).

Results and Discussion

Spawning events occurred in each of six experimental ponds over 30 d (April 21 to May 20, 2009), with 45 of the 48 males (94%) receiving eggs during this period. Even though the spawning period lasted more than 4 wk, the majority of males (56%) spawned within the first week. There were no differences in the relative timing of spawning between HV and LV males, but in each pond the larger males of both lines spawned earlier than the smaller males (Table 1), a pattern seen before for largemouth bass (28). In addition, there was a clear effect of male size and selection line on male mating success (i.e., the number of eggs received by a male in his nest during spawning) (Fig. 1*A* and Table 1), with a strong interactive effect between male size and line (Table 1). That is, larger HV males had substantially greater mating success than smaller HV males, as well as both larger and smaller LV males, indicating that females were allocating more eggs to larger HV males.

Even though there was no observed effect of male size on the intensity of the parental care behavior expressed before egg hatching, there were some significant behavioral differences between HV and LV males (Fig. 2*A* and Table 1). HV males spent a greater proportion of time guarding their nests and fanning their eggs, whereas LV males spent a greater proportion of time away from their nests. The resulting parental care behavioral scores were on average 36% lower for LV than for HV males (Fig. 2*A* and Table 1). During this period HV males also showed significantly higher aggression toward potential brood predators (i.e., they were more than twice as likely to hit hookless fishing lures than were LV males) (Fig. 2*B* and Table 1). These findings

Table 1. Parameter estimates of generalized linear mixed models assessing the relationships of selected line, their respective size, and the date of spawning on reproductive, behavioral, and offspring characteristics

Response variable	Variable	Parameter estimate	*SE*	*df*	*t*	*P*
Date of spawning	Intercept	5.1	0.76	5	6.65	0.001
	HV vs. LV	0.1	0.19	5	0.72	0.505
	Male size	–0.01	0.003	30	–4.26	0.0002
No. of eggs received	Intercept	1,561.2	5,151.83	5	0.30	0.774
	HV vs. LV	13,855.9	6,731.72	5	–2.06	0.095
	Male size	16.4	18.09	22	0.90	0.376
	Male size × HV vs. LV	56.6	23.85	22	2.37	0.027
Diligence of parental care	Intercept	3.6	12.32	5	0.29	0.780
	HV vs. LV	11.1	3.32	5	3.36	0.020
	Male size	0.04	0.04	25	0.96	0.348
Anti-predator aggression	Intercept	–0.9	0.83	5	–1.08	0.331
	HV vs. LV	1.1	0.43	5	2.60	0.048
	Male size	0.003	0.003	27	1.13	0.268
Duration of parental care of swim-up fry	Intercept	11.4	8.96	5	1.27	0.260
	HV vs. LV	–24.5	11.55	5	–2.12	0.087
	Male size	–0.01	0.03	19	–0.25	0.802
	Male size × HV vs. LV	0.1	0.04	19	2.25	0.037
No. of offspring in fall	Intercept	0.6	1.89	5	0.32	0.759
	HV vs. LV	–5.3	2.51	5	–2.10	0.090
	Male size	0.01	0.007	33	1.26	0.216
	Male size × HV vs. LV	0.02	0.008	33	2.27	0.030
Size of offspring in fall	Intercept	56.4	3.24	5	17.43	<0.0001
	HV vs. LV	–2.9	0.86	5	–3.33	0.021
	Date of spawning	–0.3	0.17	18	–1.76	0.095

Largemouth bass males selected for high vulnerability to angling (HV) versus males selected for low vulnerability to angling (LV). The LV line is the reference group (= 0) in all models. The units of the response and predictor variables are: time variables in days (day of the first spawning = 1), size variables in mm, and two ordinal scores (diligence of parental care, range 0 to 36; aggression measured as hits to fishing lures ranging from 0 to 15).

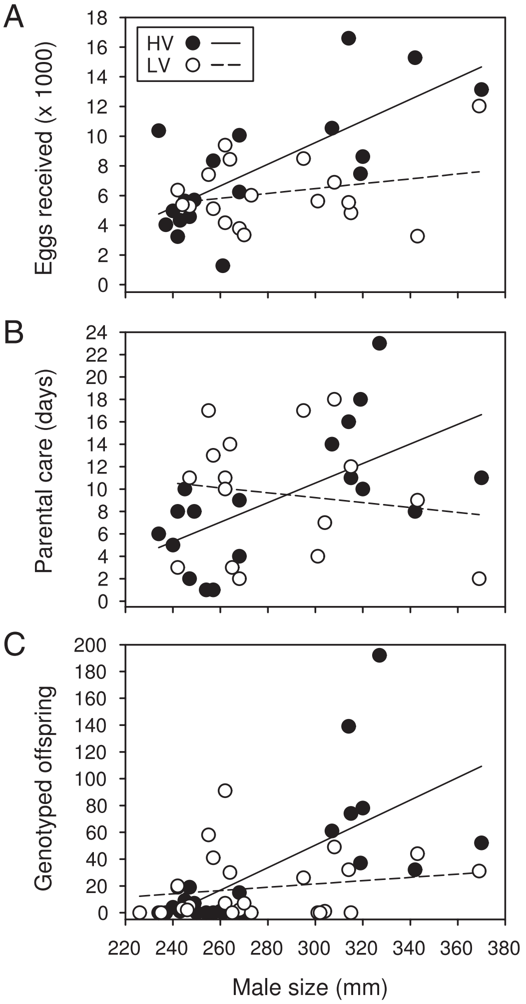

Fig. 1. (*A*) Number of eggs in individual largemouth bass nests of males with high vulnerability to angling (HV, full circles and solid lines) and low vulnerability to angling (LV, open circles and dashed lines), (*B*) duration (days) of parental care (starting at swim-up fry stage) provided by the nest-guarding males, and (*C*) number of genotyped fall recruits across nest-guarding males of different sizes.

are in agreement with earlier work assessing their vulnerability to angling using previous generations of HV and LV largemouth bass (19), indicating consistency of evolutionary differences among generations of fish selected for high and low vulnerability to fishing over three generations, respectively, despite no further selection over two subsequent generations. Finally, larger HV males provided parental care for a longer duration than any of the other males (i.e., smaller HV males, as well as larger and smaller LV males; Fig. 1*B*), as evidenced by the significant interaction between selection line and the covariate male size (Table 1). The shorter duration of parental care seen for the smaller males may reflect their expected lower energy reserves coming out of winter, thereby limiting their ability to sustain parental care activities, a situation that may be particularly acute for smaller HV males because of their higher metabolic rates (19–21). The lower willingness for smaller HV males, as well as smaller and larger LV males, to provide parental care may also be due in part to their lower mating success (i.e., fewer eggs received) after spawning (23). It is also possible that HV and LV males assessed the value of their current vs. future potential broods (29) differently. That is, HV males might have developed a higher level of expected mating success than LV males and as a result chose to abandon larger broods than did LV males.

When the experimental ponds were drained after the first summer growing season, in September 2009, a total of 11,375 juvenile (young-of-the-year) largemouth bass were recovered across the six ponds. Of the 1,200 offspring (200 per pond) randomly subsampled for parentage assignment, 1,189 (99.1%) were assigned to specific HV and LV male parents at a 95% confidence level. Of those 1,189 offspring, 740 (62%) were sired by HV males and 449 (38%) by LV males. The remaining 11 offspring were sired by a wild-type male that was initially mistyped as a female and remained undiscovered until observed guarding fry. Offspring sired by this fish were excluded from further analyses. Both the selected line (HV vs. LV) and size of the male had a significant interactive influence on individual reproductive success in terms of offspring numbers (Fig. 1*C* and Table 1). More specifically, the number of offspring produced by larger HV males was higher than the number of offspring produced by all other males (Fig. 2*C*). Comparison of total lengths of offspring also revealed that HV offspring (51 mm, SD ± 6.2) were, on average, 5% smaller than LV offspring (54 mm, SD ± 5.4) in fall (Table 1), consistent with earlier findings for juvenile HV and LV largemouth bass raised under food-limited pond conditions (20). It is likely that the higher metabolic rates of HV offspring were responsible for their smaller sizes in the present experiment. In addition, because all females used in this experiment were of wild-type origin (i.e., not selected for vulnerability to angling), the fact that our results still revealed an impact of elevated metabolic rates among the offspring of HV males suggests paternal inheritance of at least some metabolism-related aggressive traits (30). Another possible explanation, however, is that HV fish, despite having a higher growth capacity due to

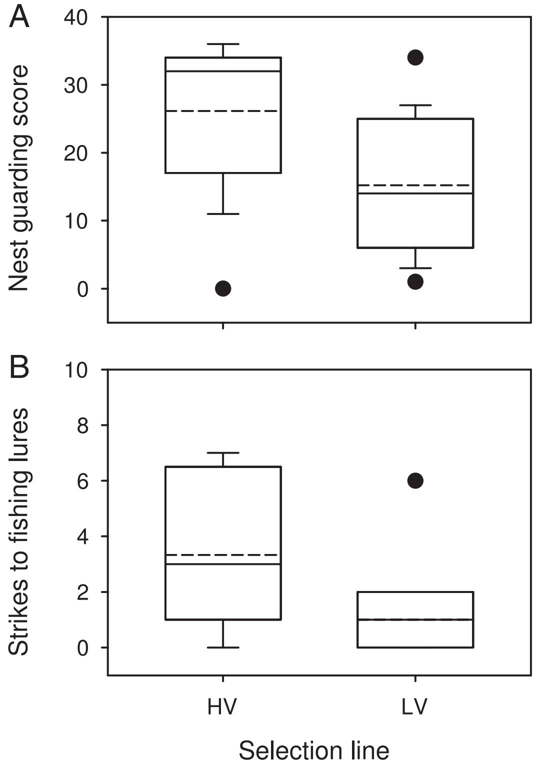

Fig. 2. (*A*) Nest-guarding intensity score and (*B*) aggression score (as measured by hits to fishing lures) for male largemouth bass guarding eggs with high vulnerability to angling lures (HV), and low vulnerability to angling lures (LV). Data are shown as box plot showing the median (solid line) and mean (dashed line).

elevated metabolic rates (21), did not ingest as many food items as LV fish owing to differences in their foraging ecology (31). Moreover, because it has also been shown that general swimming activity of HV and LV fish is similar in ponds (32), when food is limited, HV fish would be expected to pay the costs of increased metabolism and higher aggression, resulting in smaller size-at-age and potentially even an elevated size-dependent over-winter mortality (20, 33). As a result, the different metabolic rates of the HV and LV fish could result in relative survival probabilities for their offspring that vary depending on ecological context (e.g., high and low food availability and/or short or long growing seasons across latitudes). In summary, our findings provide empirical evidence that fish with different vulnerabilities to angling also exhibit differences in reproductive fitness and that in largemouth bass more-vulnerable fish indeed carry a higher fitness potential.

The higher relative fitness of the larger HV males can be attributed to several of their characteristics. First, the largest HV males had the highest mating success among all male classes, probably reflecting differential allocation of eggs via female mate choice, as previously described for a range of species in which male parental care offers key fitness benefits to females (27). The fact that the larger LV males did not receive as many eggs as the larger HV males suggests that compared with LV males, HV males court females more effectively and/or they are more attractive to them. Female mate choice may involve an expectation of the preferred males providing direct, material benefits (such as increased parental care for a female's offspring by more aggressive HV fish) or an anticipation of indirect, genetic benefits, as per the expectations of the "sexy-son" or "good-genes" hypotheses (34, 35). Even though the exact mechanism remains unknown, the result is an elevated reproductive fitness for HV males. Second, the HV males across all sizes were more active in providing parental care to their offspring (i.e., they spent more time fanning eggs and guarding the nest than LV males), and they were more aggressive toward potential predators, which likely contributed to their higher offspring numbers when ponds were drained. Third, the larger HV males provided the longest duration of parental care for the offspring (Fig. 2*A* and Table 1). The duration of parental care has been shown previously to be a key component in determining relative reproductive success among spawning male largemouth bass, reiterating the obligatory need for parental care to allow offspring survival (28).

Our results collectively suggest that in any given population, the largest, most aggressive males may have the greatest potential fitness, yet these males are also the ones that are most vulnerable to angling. As a result, largemouth bass populations subjected to angling harvest during the nesting phase can experience the selective removal of those individuals with the greatest potential for high reproductive success. Even in the absence of harvest, any temporary removal (e.g., an angling event in a catch-and-release fishery) could mean a loss of at least some fitness to egg predators (23, 24). As a result, in response to either harvest or catch-and-release angling, fish in exploited largemouth bass populations would generally be expected to evolve traits that reduce their exposure to fishing gear (i.e., behavioral and physiological characteristics similar to those observed for LV fish). Because those characteristics involve key behaviors that are involved in determining general levels of individual aggression, however, fisheries-induced selection would also be expected to evolutionarily alter parental care behaviors. The result could be a population-wide decrease in average parental care effort, including less time spent fanning eggs and reduced aggression toward brood predators, which could affect recruitment particularly in northern latitudes or populations with overall low productivity (36). The rate and amplitude of such an evolutionary change in these behavior/life history traits and their potential ramifications for recruitment (37) would of course depend upon the amount of harvest mortality, or for catch-and-release fisheries, the intensity of catch-and-release of male bass on nests. The resulting ecological implications for such an affected fish population would certainly be context dependent. That is, negative effects of this fisheries-induced evolution on population-level recruitment in the wild would be expected to be strongest in environments with abundant food resources (i.e., where LV are benefiting less from their lower metabolic rate), with short spawning seasons (i.e., where the opportunity to respawn after brood loss is limited, e.g., in northern latitudes), and with overall high egg predation potential (i.e., where the added wariness/timidity of LV-like fish would result in a greater reduction in fitness due to increased brood predation). In addition, fisheries-induced evolution to LV-like genotypes would almost certainly be accompanied by a concomitant decline in catchability on a population-level scale (18), a scenario that would be undesirable for recreational anglers that value catch rates (38).

Our study shows conclusively that fishing can target those individuals that exhibit the highest reproductive fitness potential, thereby establishing the potential for selection of behavioral traits that help a fish avoid capture, but in the process decrease its parental care abilities. For any species of fish with parental care that is targeted by recreational anglers, that evolutionary scenario may have consequences for the quality of the fishery (7) or for population-level recruitment (36, 37). Because some level of angling for nesting largemouth bass (both catch-and-harvest and catch-and-release) has been occurring in most, if not all, populations in North America for many years, we predict that many populations will show evidence for this fisheries-induced behavioral change; that is, they would already contain fish that are less vulnerable to capture than nonfished populations. Assessing the historical prevalence of such evolutionary changes through a controlled survey of vulnerabilities in the wild, coupled with reciprocal transplant studies using common garden experiments, would constitute a fascinating research approach for the future. If the changes in bass behavior and life history prove to be large enough to reduce recruitment, then management strategies designed to constrain or even remove the underlying selective pressure (angling nest-guarding male largemouth bass) may need to be implemented. Because a great proportion of recreational angling effort in North America is directed at species that provide some form of parental care (e.g., other Centrarchidae, members of the Ictaluridae) (22), the management implications of this study extend well beyond the largemouth bass.

Materials and Methods

The study was carried out at the Illinois Natural History Survey's Aquatic Research Facility at the University of Illinois at Urbana–Champaign, IL (40.07°N, 88.22°W) from April to September 2009, and animal use was approved by the Institutional Animal Care and Use Committee (protocol #10202). Males from two lines of largemouth bass that had previously been artificially selected to exhibit either high or low vulnerability to angling lures over three generations (18) were used as test subjects. Fish from the F5 lines, two generations after selection was halted, were used in the present work. Largemouth bass from both lines, which had been raised in ponds where they fed on natural food (e.g., *Erimyzon sucetta*, *Lepomis* spp., *Rana catesbeiana*), were recovered in April 2009 by draining the holding ponds. Male largemouth bass from the two lines were tagged individually with passive integrated transponder (PIT) tags and given a colored anchor tag inserted in the dorsal musculature to allow visual identification of individuals. After tagging, six replicate 2,500-m^2 earthen ponds were each stocked with four 3-y-old mature males from each line; male size [HV = 277 ± 36 mm total length (TL), mean ± SD; LV = 278 ± 39 mm TL] did not differ across lines (ANOVA $F_{1,41}$ = 0.01, $P = 0.92$) or ponds (ANOVA $F_{5,41} = 0.95$, $P = 0.45$). A total of 42 unrelated wild females collected by boat electrofishing from Lake Mingo (71.7 ha), IL (40.21°N, 87.73°W) were implanted with PIT tags and stocked together with the HV and LV males. Genders were assigned according to the shape and size of their genital opening and the presence or absence of swollen genital papilla (39). Each of the six ponds containing male largemouth bass received seven females; female size (351 ± 68 mm TL) did not differ significantly across ponds (ANOVA, $F_{5,36} = 0.24$, $P = 0.94$). For subsequent genetic analyses fin clips were taken from all adults and preserved in vials containing 95%

ethanol. Each of the six ponds also received ∼500 immature bluegill (*Lepomis macrochirus*) and redear sunfish (*Lepomis microlophus*) to serve as both potential egg predators and forage (23, 24, 33). These fish were obtained from the Kaskaskia Biological Station (38.71°N, 88.75°W) and a local hatchery [Little Grassy Fish Hatchery, Makanda, IL (37.39°N, 89.07°W)]. Sunfish from both sources were equally distributed across ponds.

After stocking of all fish, ponds were snorkeled every day for 6 wk beginning April 20, 2009, to locate males on nests and to identify the start of parental care (defined as the first day that a male largemouth bass was observed with eggs in his nest). To reduce disturbance to nest guarding fish, egg numbers were quantified by digitizing a method previously described for smallmouth and largemouth bass (40, 41). Digital photographs were taken from all discovered nests along with a ruler with 1-cm markings placed on the edge of a nest. Egg numbers were then quantified using the image manipulation software GIMP 2.6.12. All photos were overlaid with a digital grid of 1-cm^2 squares based on the 1-cm markings of the ruler. The total number of eggs was quantified by outlining the egg mass with a digital brush tool and counting the number of eggs in three of the 1-cm cells within the outlined egg mass, with one each from the center of the egg mass, midway to the edge, and the edge. The averages of these egg counts were used with the total number of squares within the outlined egg mass to calculate total egg numbers of nests, as adapted from refs. 40 and 41. Levels of parental care investment among the males of both lines (HV and LV) were assessed from shore by recording standardized nest-guarding behaviors every 10 s over a 2-min observation period between 7:30 AM and 10:00 AM, for a total of 12 distinct observations per individual. Assessments were performed when a male was seen on a nest containing eggs <2 d old. Observations started as soon as males became accustomed to the observer on the shore; i.e., they returned to their nests and resumed parental care activities. Largemouth bass that were positioned on their nest and fanned eggs during the 10-s observation period received a score of 3; males engaged in behaviors to deter nest predators during the observation period were given a score of 2; males simply swimming in proximity to the nest (<2 m) were given a score of 1. Males that remained >2 m from their nests during the 10-s observation period were considered absent from the nest and, therefore, received a score of zero. The highest possible nest guarding intensity score a male could achieve during the entire 2-min observation session was 36. As an additional metric of parental care intensity, the duration of parental care (in days) provided for swim-up fry was recorded for each individual male. Parental care was considered terminated when a male ceased to be observed in proximity to its developed fry. In addition, as an assessment of the aggression shown by males toward potential brood predators, the vulnerability to angling during the nest-guarding period was also quantified. The experimental angling protocol consisted of casting three different hookless fishing lures (a surface popper, a 6-cm white twister jig, and a 12-cm black plastic worm) to each male five times while they were guarding eggs (24). Hooks were removed from all lures so that males could not actually be captured, while permitting responses toward the lures to be quantified. The number of strikes at each lure was summed to generate a total aggression score, with a maximum of 15 strikes per angling session being possible (24). The response to angling by brood-guarding largemouth bass has previously been shown to be representative of nest defense behavior (23).

The six experimental ponds were drained between September 8 and 12, 2009, the total number of largemouth bass offspring determined, and a random subsample of 200 of those offspring collected from each pond. Each offspring was measured for TL, and a caudal fin clip for parentage analyses was collected as described above for the adults. Individual reproductive success of all HV and LV males, determined as the number of offspring produced per each male, was quantified by parentage assignment using microsatellite markers. Amplification of microsatellite DNA was performed by using a two-step multiplex PCR (42). Two sets of distinct DNA microsatellite markers taken from literature were used (43–46). "Multiplex 1" consisted of the microsatellites *MS13*, *MiSaTPW025*, *MiSaTPW038*, and *MiSaTPW068* and "Multiplex 2" of *Lma 10*, *Lma 21*, *Msa 18*, *MiSaTPW011*, and *MiSaTPW107*. DNA was extracted from fin clips by the use of a DNA isolation kit (PEQLAB Biotechnology) according to the manufacturer's protocol. PCR reactions were set up in 15-μL volumes containing 1.5 μL of DNA isolate. The master mix (13.5 μL) contained 3 μL Taq buffer, 1.5 μL (25 mM) MgCl$_2$ and 3 μL (1.25 mM) dNTP, adjusted primer amounts for the five microsatellites per multiplex, and 0.15 μL Taq polymerase (GoTaq Flexi DNA Polymerase; Promega). Sterile water was added for a total reaction volume of 15 μL. Annealing temperatures were optimized for each multiplex and amplifications performed on a Biometra T 3000 thermocycler. The reaction consisted of an initial 3-min denaturation step at 95 °C followed by 15 cycles of a 45-s annealing time (Multiplex 1 53 °C, Multiplex 2 58 °C) and a 30-s elongation period (72 °C) followed by 25 cycles with annealing times of 30 s, extension times of 15 s, and a final extension of 3 min. Microsatellite analysis was performed using fluorescently labeled forward primers (Sigma-Aldrich) and a capillary electrophoresis system (CEQ 8000; Beckmann Coulter). Detected fragments were scored using the CEQ 8000 fragment analysis software (Beckmann Coulter). Any allele resulting in multiple detection failures when performing the fragment analysis was excluded from the analysis and considered a null allele (47). The most likely parent pairs of an offspring were identified using the program CERVUS ver. 3.0 (48), where the typing error probability was set to a level of 0.01%. Candidate parents were determined by calculating the trio logarithm of the odds scores and assessing the trio confidence at a 95% confidence level. Offspring that were not assigned to a parent pair on a 95% confidence level were excluded from further analyses.

Statistical analyses comparing the two lines with respect to behavioral characteristics, mating success, relative reproductive success, and offspring size were subsequently performed using a complete randomized block design with multiple experimental units (male largemouth bass individuals) within a block (ponds) (49) using a mixed model procedure (SAS version 9.1; PROC GLIMMIX; SAS Institute; coding for the modeling approach taken from ref. 50). Ponds were considered to be blocks to account for interpond variance, and the selected line (HV, LV) entered as a fixed factor. To account for possible size-dependent contributions to individual reproductive success, male TL was used as a covariate in the model. To test for offspring size differences among paternal lines, offspring sizes were pooled for individual males, and resulting means were compared across lines using the approach described above. When comparing offspring sizes, the covariate male size was replaced by the day of spawning (starting with 1 for the first nest) to account for differences in offspring age. All initial models contained an interaction term between the main effect (selected line) and the covariate (size). Main effect by covariate interactions were removed from the final models when nonsignificant, indicating homogeneity of slopes (51).

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