

Fisheries-Induced Evolution in Largemouth Bass: Linking Vulnerability to Angling, Parental Care, and Fitness

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Abstract.—Long-term studies in Ontario, Canada on Largemouth Bass *Micropterus salmoides* and Smallmouth Bass *M. dolomieu* have demonstrated that angling nesting males (both catch and harvest and catch and release) can have negative impacts on the reproductive success for the captured individual. They have also demonstrated that within a population, the male bass that provide the best and longest parental care for their offspring are the most capable of having the greatest relative contribution to the year-class. Furthermore, those males are also the most aggressive toward potential brood predators and, hence, the most vulnerable to angling. Based on those relationships, we postulated that angling in general, and especially angling for nesting bass, results in selection against aggressive individuals in a population, and as a result, the angled population evolves to become less aggressive, containing males with diminished parental care attributes, an example of fisheries-induced evolution (FIE). We recognize, however, that some change towards less aggressive behaviors may also result from learning and phenotypic plasticity. Controlled, long-term selective breeding experiments over 30+ years have, however, documented the heritability of vulnerability of bass to angling and, hence, the potential for selection to act on that trait. Reproductive competition experiments further demonstrated that the highly vulnerable strain of bass produced in those selective breeding experiments indeed had greater reproductive success than the less vulnerable strain. Because angling for Largemouth Bass has been occurring for decades, we also postulated that there should be some evidence in the wild of this FIE. In fact, we did find that the level of vulnerability to angling of nesting male Largemouth Bass in lakes that have had little to no exploitation was significantly greater than that observed for nesting males in moderately and heavily angled populations.

Introduction

Fisheries-induced evolution (FIE) is defined as a genetic change over generations in one or more characteristics of a population (e.g., life history, behavior, physiology, and morphology) in response to selection imparted on individuals in that population via fishing (Law 2000; Heino and Godø 2002). Fisheries-induced adaptive change (FIAC) is a more encompassing term describing phenotypic change caused by fisheries that includes both evolutionary change due to selective forces (FIE) and phenotypic

changes due to plastic responses (Laugen et al. 2014). Although we are currently investigating the role that learning can play in changing bass behavior, especially how lure recognition can influence hooking avoidance, in this paper we concentrate on the evolutionary aspects of behavioral change (i.e., the FIE component).

There have been numerous examples reported in the literature of FIE and FIAC resulting from commercial fishing activities, with changes in the size and age at maturation, reproductive investments, growth rate, avoidance of gear, egg size, and

morphological alterations provided as examples (e.g., Law 2000; Stokes and Law 2000; Conover and Munch 2002; Olsen et al. 2005; Kuparinen and Merilä 2007; Uusi-Heikkilä et al. 2008, Conover et al. 2009; Heino et al. 2013). Even though there has been the suggestion that recreational angling can act as an evolutionary force (Lewin et al. 2006), little empirical evidence has been provided to support that suggestion (for an exception, however, see Saura et al. 2010). Some of the best experimental evidence comes from our ongoing studies using two lines of the Largemouth Bass *Micropterus salmoides* selected for differential vulnerability to angling as part of a 30+ year selection experiment (Philipp et al. 2009), and key findings are summarized in this paper.

We hypothesize that FIE in black bass can influence recruitment through selection against the most effective nest-guarding males. That is, angling in general (certainly catch and harvest, but also, to a lesser degree, catch and release) induces selective pressures that will favor less aggressive bass because their chance of being angled is lower than that for more aggressive bass. As a result, in angled populations over time, the level of aggression among the individuals in that population decreases as a result of that selection. Furthermore, because aggression is a behavioral trait that is linked to many aspects of the behavior of a bass and even its life history as a whole, decreased aggression will also result in correlated changes in other traits. One such trait of importance is the parental care behavior of males during the reproductive period. In our hypothesis, males that have been selected for reduced aggression via angling will also show reduced aggression to brood predators and, as a byproduct of that change in behavior, will also demonstrate an overall reduction in parental care vigilance. That is, less aggressive males will provide less effective parental care (fanning eggs and larvae as well as defending their offspring against potential brood predators) than their more aggressive counterparts. Even though the level and duration of parental care has been shown to be important for individual male reproductive success (Philipp et al. 1997; Suski and Philipp 2004; Parkos et al. 2011), under the scenario of continued angling pressure, less aggressive males would have the highest fitness in a fished environment. Under the scenario of no angling pressure (even no angling just during the reproductive period), the reverse becomes true; more aggressive males are favored over their less aggressive conspecifics because the reproductive success of individual males is directly related to the vigilance and duration of their parental care (Parkos

et al. 2011; Sutter et al. 2012). Under our hypothesis, therefore, it is theoretically possible to have a long history of angling result in the evolution of a Largemouth Bass population with such reduced aggression/parental care traits that population-level reproductive success and annual recruitment declines.

To demonstrate and understand the potential for fisheries-induced evolution in bass, our hypothesis must be assessed across the following four criteria. First, the trait of selection interest (vulnerability to angling) must be shown to be heritable and to be altered in the face of the selection pressure. Second, to understand the ramifications of that FIE, we need to know how the selection of that trait impacts other facets of life history, behavior, physiology, energetics, morphology, and so forth. Third, we need to assess how those trait changes affect individual fitness within the population. Finally, to determine the relevance of that FIE to the management of the target species, we need to determine whether or not FIE occurs in wild populations and if it has impacts to population-level processes such as recruitment. The overall purpose of this article is to summarize what we know about angling-induced evolution in Largemouth Bass within the context of these four criteria.

Criterion 1: Evidence for the Heritability of Vulnerability to Angling, a Surrogate for Aggression

A 4-year study was conducted in Illinois at Ridge Lake (an experimental and drainable 15.7-acre fishing impoundment managed by the Illinois Natural History Survey) on the effects of a total catch-and-release regulation on Largemouth Bass catch (Burkett et al. 1986). Access to the site by recreational anglers was controlled and monitored, and a complete creel census of all anglers on the lake was conducted. Creel census data and recovery of the entire population at the end of the study by draining the impoundment provided the total catch history over the duration of the study for every individual bass in that population. Results revealed that although a majority of bass were caught one to three times, about one-third of fish were caught many more times (one more than 20 times) and some not at all during the full study. Two groups of fish (individuals caught five or more times in the last year and fish that were never caught in the entire study) provided the parents that served as the initial P_1 broodstock for a long-term selection experiment that was initiated more than 30 years ago (Philipp et al. 2009).

For that experiment, which was designed specifically to determine the heritability of hook-and-line vulnerability of Largemouth Bass, P_1 adults from Ridge Lake that had been caught at least five times in the last year of the study were allowed to breed together to produce a high vulnerability (HV) line. Similarly, P_1 adults from Ridge Lake that had never been caught throughout the duration of the study were allowed to breed together to produce a low vulnerability (LV) line. Details of the experimental breeding design can be found in Philipp et al. (2009), but they are briefly summarized here to provide context. For each generation in the experiment, after being produced in separate spawning ponds, these ponds were drained and young-of-the-year (YOY) HV and YOY LV bass were recovered. These fish were differentially marked with pelvic fin clips and stocked together in a set of 0.25-acre grow-out ponds (a common garden design). The fish were allowed to grow for three more years, at which time they had reached sexual maturity. At this point, the grow-out ponds were drained, HV and LV fish were recovered, and equal numbers of equal-sized 3-year-old fish were stocked as the only bass in an experimental angling pond. The population was allowed to acclimate to the pond and complete any spawning activity before they were experimentally angled under controlled conditions during mid-June to mid-September. The rate at which each selected line of fish (HV versus LV) was captured and the total number of captures for each selected line were used to calculate the relative vulnerability of the two lines the given generation. That entire process was repeated through three generations (F_3) of selection.

The divergence in the vulnerability to angling between the two lines was immediate and rapid, with the HV fish being captured more quickly and to a much greater extent than the LV bass (Philipp et al. 2009). Specifically, even by the first generation of selection, it only took about half the time for anglers to capture 50% of the HV population as compared to what it took to capture 50% of the LV population in the same pond (Table 1). In addition, the total number

of captures for the HV bass was almost 50% higher than for the LV bass (Table 2). That divergence between the lines continued to increase though the F_2 and F_3 generations (Philipp et al. 2009). The pattern of divergence became particularly interesting when we compared the total catch rate (TCR, total number of captures/h per bass/ha) for each line across all generations, a calculation that standardized catch rates across ponds by correcting for density differences in the three experimental fishing ponds and Ridge Lake. In comparing the TCR for each line across generations (Figure 1), it appears that the cause for the divergence was due substantially more to the loss of vulnerability in the LV line than an increase in vulnerability in the HV line. To calculate the heritability of the complex phenotypic trait, vulnerability to angling, we used the TCR for the fish used as parents of each line and the TCR for their next generation offspring to calculate the selection differential, S , for each generation, as well as the cumulative selection differential, S' , and the response to selection, R , for each round of selection. When R was regressed against S' , the resulting slope gave us a heritability, h^2 , of 0.146. That value is comparable to heritability values calculated for other traits in fish, such as juvenile growth rate or age and size at maturation (Refstie and Steine 1978; Bondari 1983; Dunham and Smitherman 1983). In summary, these experiments documented that vulnerability to angling was a heritable trait in Largemouth Bass, and for subsequent studies we used that trait to serve as a surrogate measure of aggression for this species (Sutter et al. 2012).

Criterion 2: Behavioral, Physiological, and Life History Ramifications of Selection for Vulnerability

Following the heritability studies performed on the P_1 , F_1 , F_2 , and F_3 generations of the HV and LV lines, further selection for vulnerability within the two

Table 1. Half-capture life (the hours of cumulative angling pressure required to capture, for the first time, 50% of the fish from a given group) for each of three generations (F_1 to F_3) of Largemouth Bass selected for high vulnerability (HV) and against low vulnerability (LV) to angling.

Generation (N)	Low vulnerability	High vulnerability	LV/HV ratio
F_1 (120)	65	33	1.97
F_2 (150)	74	34	2.18
F_3 (60)	10	3	3.33

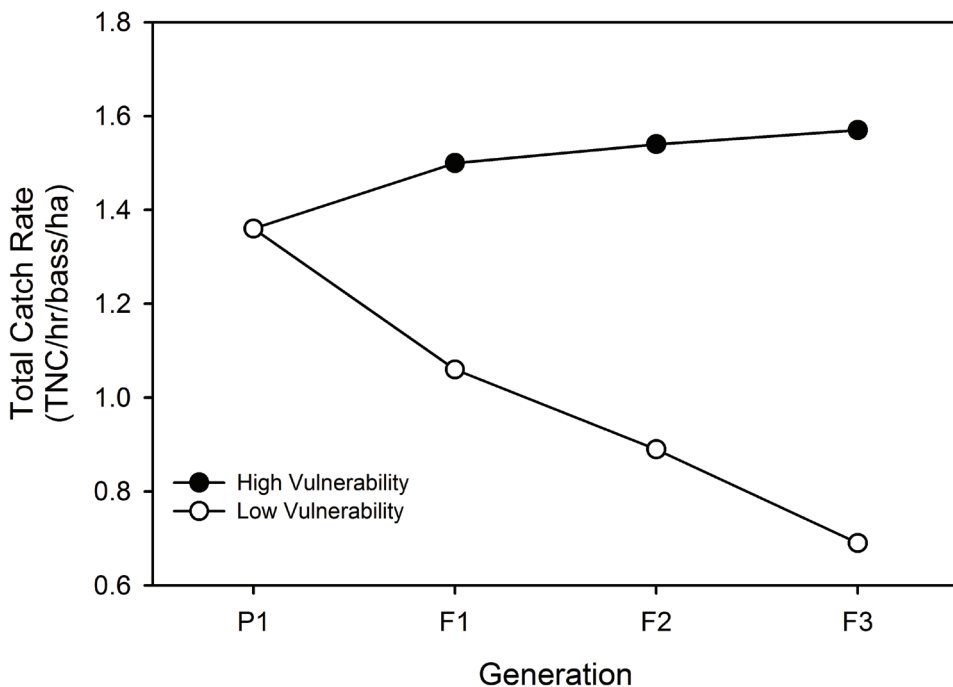
Table 2. Total number of captures for the parental (P_1) stock and each of three generations (F_1 to F_3) of Largemouth Bass selectively bred for high vulnerability (HV) and against low vulnerability (LV) to angling (NA = not applicable).

Generation	Total number of fish in population	Captures of high-vulnerability fish	Captures of low-vulnerability fish	Ratio HV/LV
P_1	3,641	NA	NA	NA
F_1	230	135	95	1.42
F_2	202	128	74	1.73
F_3	68	47	21	2.24

lines was suspended to remove all ecological effects and allow clean comparisons among selection lines under common garden conditions. To that end, F_4 and F_5 generations were produced within each line using a random set of F_3 adults as parents, which allowed us to remove any ecological and parental effects. In an effort to understand the underlying differences between the two selected lines, these unselected F_4 and F_5 HV and LV fish were used over a period of years to assess the physiological and behavioral differences between the two lines in a number of ways.

From a metabolic standpoint, we found the two lines (in the F_4 generation) to be substantially differ-

ent. First, Cooke et al. (2007) showed that the HV fish had higher resting cardiac activities but, at the same time, less cardiac scope (i.e., the range of potential cardiac activity) than the LV fish. From this result, they predicted from modeling exercises that with similar food intake, HV fish would have to consume 40% more food than LV fish to maintain the same growth rate. Redpath et al. (2009) tested that prediction in fish also from the F_4 generation and found that when raised together in common ponds, the LV fish grew 9–17% faster than HV fish, even though the food in the stomach contents of both lines were similar. Further laboratory research revealed

**Figure 1.** Total catch rate (TCR) for high-vulnerability (closed circles) and low-vulnerability (open circles) Largemouth Bass across three generations of selection, compared to the original TCR for the P_1 generation. Total catch rate is calculated as [(total number of captures or TNC)/(number of hours fished)]/(number of bass/ha).

that LV fish had 10% lower standard metabolic rates, 14% lower maximum metabolic rates, and 16% lower metabolic scope (Redpath et al. 2010). In addition, this research demonstrated that it took HV fish twice as long to recover from exhaustive exercise than LV fish, with LV fish showing a much greater capacity for anaerobic activity. As a result, there seems to be a clear metabolic cost to being selected for high vulnerability to angling, but the potential ramifications of this metabolic cost for fitness are unclear. Alternately, even though the higher metabolism of the HV line also suggests that these fish have a greater capacity for growth, they will usually not be able to reap the benefits of that growth potential because food is limited in most situations. In those situations, higher metabolic rate is a cost that decreases somatic growth in HV individuals.

In subsequent studies using these same F_4 generation fish, we found substantial differences in the behaviors of the two selection lines as well, including some differences in foraging behaviors. Although Binder et al. (2012) reported that the daily activity levels and diel patterns of that activity were similar for the two lines during nonreproducing periods in ponds, there were clear differences between the two lines reported for parental care behaviors by male bass. Cooke et al. (2007) first reported that compared to the LV line, HV fish exhibited significantly higher parental care behaviors, including higher fanning and turning rates on the nest, greater in situ swimming speeds, and a higher level of antibrood predator vigilance. In addition, the F_4 HV fish had retained much higher hook-and-line capture rates while guarding broods than LV fish, even after selection was halted for one generation. The bottom line here is that all behavioral assessments point to the HV fish exerting more aggressive parental care than the LV fish, which has obvious potential fitness ramifications.

Criterion 3: Fitness Consequences of Selection for Vulnerability

The linkage between selection for angling vulnerability and parental care vigilance created a mechanism for testing the fitness consequences of that selection. Clearly, anything that reduces the willingness or ability of a male bass to provide parental care for its offspring has the distinct potential for reducing relative fitness as well. Sutter et al. (2012) used male bass from the F_5 generation HV and LV lines to test their relative fitness in a set of experimental ponds.

Although the details of the experimental protocol can be found in Sutter et al. (2012), the highlights of the results of that experiment follow. Using equal numbers and sizes of genetically identified HV males and LV males stocked together in a set of ponds along with wild-type Largemouth Bass females, we compared the ability of males from the two lines to successfully produce surviving offspring. Parental care activities were monitored throughout the period of parental care to determine if the male raised his brood to independence (a successful brood) or abandoned it before independence (an unsuccessful brood). To test the relative vulnerability of each parental male while on its nest guarding its eggs, they were presented with three hookless lures five times apiece, a 4.5-in (115 mm) floating silver Rapala, a 3-in (75 mm) white Twister jig, and a 6-in (150 mm) black Texas-rigged plastic worm, and the number of times each bass hit each lure was recorded.

The results demonstrated clear differences between the two lines on a number of levels. First, the wild-type females preferred to spawn with HV males (i.e., their mating success [number of eggs deposited] in their nests was significantly greater than mating success of the LV males), indicating either that the HV males were more aggressive/better at courting females or that they appeared as more attractive partners or both, leading to a greater allocation of reproductive resources by female bass to HV males than to LV males. That attractiveness of the HV males could be the result of an assessment by the females of their potential direct benefits via expected increased parental care or an assessment of their potential indirect genetic effects as per the sexy son hypothesis (Weatherhead and Robertson 1979) or the good genes hypothesis (Byers and Waits 2006). In addition, once spawning had ceased and parental care had begun, compared to the LV males, the HV males provided more active parental care that was also of longer duration, an important component determining success of a brood in bass (Parkos et al. 2011). When the ponds were drained at the end of summer and the relative contribution of each male to pond's offspring production was assessed using microsatellite-based genetic analysis, the HV males (particularly the larger individuals) contributed disproportionately more offspring than all other males, even when corrected for their higher levels of mating success. This result clearly demonstrated that under conditions of no angling, the previous selection for LV traits produced male bass that were less fit than HV males.

As expected, the males that were the most aggressive toward the hookless lures during the angling trials were the larger HV males (i.e., those males that had the highest mating success), provided the best and longest parental care, and were the most successful at raising offspring to independence, meaning that in a given population of bass, the males that are at the most risk to angling are those males that are also the most likely to produce the bulk of the next year-class. As a result, angling during the nesting period for Largemouth Bass would exert more directional selection against the best dads than angling at any other period of the year.

Criterion 4: Evidence for Historical Angling-Induced Evolution in Wild Populations

The volume of evidence coming from the wide range of experiments summarized above supported our working hypothesis that angling bass (particularly during the spawning season) results in selection for males that are less aggressive towards lures and less vigilant in their parental care activities. Because anglers have been fishing for bass (including nesting bass) in many waters across the country for decades, if that working hypothesis is correct, then one would expect to see some evidence for that angling-induced behavioral change in the wild. Our prediction would be that populations that have experienced high levels of angling (including angling during the spawning season) should contain bass that are less aggressive (i.e., less vulnerable to angling) than populations that have not experienced such high levels of angling, as conceptualized in Figure 2. Our concern is that along with vulnerability to angling, parental care is being coselected, as conceptualized in Figure 3.

To test that prediction, we identified a series of lakes with healthy bass populations that varied in their historical patterns of angling (Table 3). The first class of lakes were unexploited lakes, which were lakes that were closed to the public and therefore had received extremely low to no fishing pressure throughout the year over at least the past 50 years. The second class included seasonally exploited lakes, which were lakes that were open to the public and received moderate angling pressure throughout the year but had protective closed seasons for bass during the spawning season. The third class included totally exploited lakes, which were lakes that received high angling pressure through-

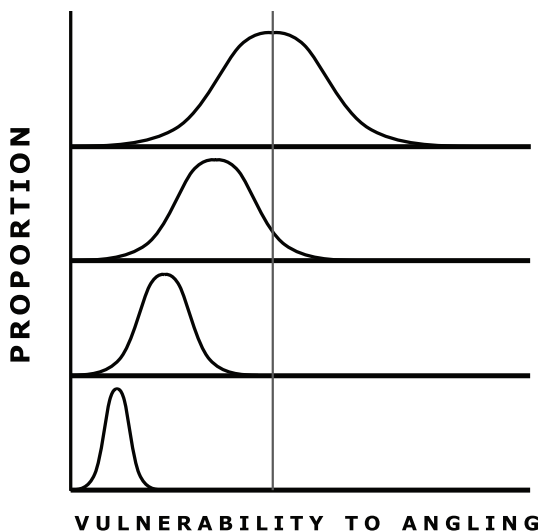


Figure 2. Conceptual model of selection for lower vulnerability to angling. The graph at the top represents the distribution of the trait within the original population with the mean of that trait indicated by the vertical dashed line. Subsequent graphs moving down represent the distribution of the trait within the population after increasing duration of selection.

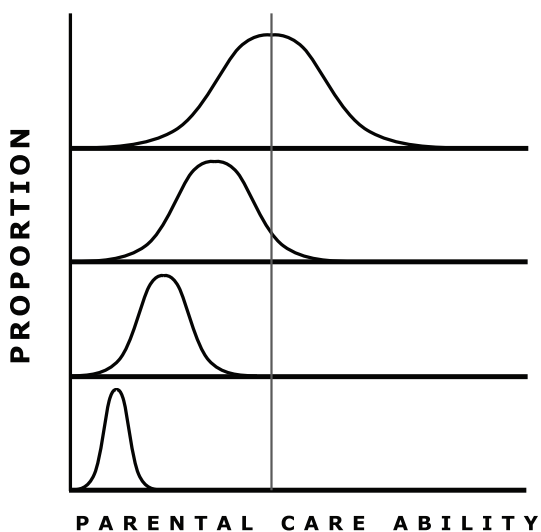


Figure 3. Conceptual model of selection for lower parental care. The graph at the top represents the distribution of the trait within the original population with the mean of that trait indicated by the vertical dashed line. Subsequent graphs moving down represent the distribution of the trait within the population after increasing duration of selection.

Table 3. Lakes tested for vulnerability. Number of nests for each population (i.e., in the lake listed) of Largemouth Bass represents the number of parental males fished using the experimental angling protocol.

Lake group	Name/location	Nests
Unexploited	Long Lake, Ontario (2006)	52
	Long Lake, Ontario (2009)	48
	Mills Lake, Quebec (2011)	46
	Hedge Pond, Illinois (2011)	37
Seasonally exploited	Loughborough Lake, Ontario (2006)	42
	Loughborough Lake, Ontario (2009)	46
	Opinicon Lake, Ontario (2009)	58
	Lake Charleston, Ontario (2009)	44
Fully exploited	Lincoln Trails Lake, Illinois (2006)	35
	Lincoln Trails Lake, Illinois (2009)	42
	Redear Lake, Illinois (2010)	40

out the year and had no closed seasons. All of these lakes had to be clear enough for snorkelers to locate bass nests for experimental angling because fishing for nesting bass allowed us to present a lure or series of lures repeatedly to a known individual in a standardized manner. In this way, we could quantify the vulnerability of individuals and use those data to compare the relative vulnerability of different bass populations.

For this vulnerability test, in each test lake we located between 35 and 58 Largemouth Bass males guarding nests that held unhatched eggs (1–3 d post-fertilization), eliminating any males that had wounds of any kind (including new hook wounds) and any nests that had only few eggs or that had significant amounts of dead eggs. Each nest was marked with a numbered white polyvinyl chloride tag for relocation from a distance. Those nests were revisited by an angler in a boat anchored 10–15 m away from the nest, and each male was then presented with five casts using each of three lures in a set order, five with a 4.5-in (115 mm) floating silver Rapala, five with a 3-in (75 mm) white Twister jig and finally, five with a 6-in (150 mm) Texas-rigged black plastic worm. Each cast landed the lure directly on the nest, and the angler recorded if the male bass hit the lure on that cast or not. If the fish was hooked, it was played until landed and then measured and immediately released. If the fish was not hooked, then the series of casts was continued until either the fish was hooked and landed or it received all 15 casts. Two metrics were used to assess the vulnerability of the males in each population: the percentage of males that hit the first cast (with the Rapala), and the

percentage of males that hit at least 1 of the 15 casts (with the three lures).

The results clearly indicated that the variability in the vulnerability across lake groups was strongly related to angling history (Table 4). Fish from the unexploited lakes behaved as expected from our previous work in the area; about half the males (47–63%) hit the first cast, and all or almost all (95–100%) in every lake hit one of the 15 casts. In the seasonally exploited lakes, 24–41% hit the first cast and 55–86% hit at least one of the 15 casts, indicating that seasonally exploited lakes contained bass that were less vulnerable than bass from unexploited lakes, although hit rates were slightly more variable in seasonally exploited populations. It was the fully exploited lakes that were the most surprising, however, with none or almost none (0–8%) of the male bass hitting the first cast and not very many (3–18%) of them hitting at least 1 of the 15 casts. Snorkelers could even tell the difference between bass in the two extreme groups right away; bass in the unexploited lakes were openly aggressive toward the swimmers, many flaring gills, charging, biting fingers and fins, and even ramming facemasks. None of the males in the fully exploited lakes behaved anywhere near that aggressively. Instead, they backed off their nests and observed the snorkeler from a distance, during which time nest predators (e.g., small Bluegill *Lepomis macrochirus*) were able to enter the nest and prey upon the bass eggs in it. That scenario never happened in the nests of bass in the unexploited lakes group. While the behavioral differences among these lakes were huge, for the three lakes for which we have 2 years of testing the re-

Table 4. Relative vulnerability to angling of bass populations. Percentages given show the range of values for all of the lakes tested in that lake group, as well as for the fifth generation of high-vulnerability (HV)/low-vulnerability (LV) selected bass.

Lake group	Percentage that hit first cast	Percentage that hit any cast
Unexploited	47–63	95–100
Seasonally exploited	24–41	55–86
Totally exploited	0–8	3–18
HV-selected line	36	82
LV-selected line	27	55

sults within a given lake across those 2 years were surprisingly consistent, indicating that the experimental angling approach using individual parental male bass was a legitimate assessment technique (Suski and Philipp 2004). We want to acknowledge, however, that the wild nesting bass in the seasonally and fully exploited lakes had been exposed to angling in previous seasons, whereas the wild nesting bass in the unexploited lakes had not, providing the opportunity for hook avoidance learning to have affected the results. There is no real evidence for hook avoidance learning in bass, but it is known that this species is capable of some learning (Coble et al. 1985). Nevertheless, it is possible that some of the differences in vulnerability observed among the different bass populations in this study may be the result of some hook avoidance learning. In any case, the exact origin of the lower vulnerability (learning versus evolution) notwithstanding, decreases in parental care among male bass in fished ecosystems is likely detrimental to reproductive fitness.

To put these results into perspective, tests on the relative aggression toward fishing lures were done with the HV and LV lines during the reproductive fitness experiment described under Criterion 3 above. Experiments were conducted in the same manner as the trials with the bass in the three lake groups described above. In that pond assessment, 36% of the HV fish and 27% of the LV fish hit the first cast; 82% of the HV fish and 55% of the LV fish hit at least 1 of the 15 casts. Those levels of vulnerability were at the high end and low end, respectively, of the seasonally exploited lakes group. So, even after our directional selection, the HV fish were not as vulnerable as the wild fish from unexploited lakes, indicating that the strong heritability observed in the creation of the HV and LV selected lines may actually underestimate selection forces in situ. More interesting was the fact that even after selection, the LV fish were substantially more aggressive than the bass in

the wild populations from fully exploited lakes. We note, however, that the wild fish and not the experimental HV and LV fish had been exposed to angling during the previous season, again providing the opportunity for some sort of hook avoidance learning to have affected the results.

Conclusions and Future Directions

We have proposed that angling Largemouth Bass may result in FIE. The streamlined version of our working hypothesis proposes that angling elicits selective pressures that favor less aggressive bass. As a result, in angled populations through time, the level of aggression among the individuals in that population will decrease, resulting in a coselected decrease in parental care abilities that will likely affect individual reproductive success. We stated at the outset that to test our hypothesis regarding FIE, it must be assessed across four criteria. We feel that our 30+ years of experimentation has done just that, although we do realize that lure recognition and hence learning to avoid certain lures may also contribute to some changes in behavior over time. We further conclude that this FIE combined with learning responses that result in lure avoidance (i.e., FIAC) will reduce fishing quality by negatively affecting catch rates (Philipp et al. 2009). Whether such evolutionary change affects population-level recruitment is unknown so far and likely to be context dependent (Sutter et al. 2012).

We would like to close by offering our suggestions of what is needed to advance our knowledge in this area. The most important and logical next steps for basic/applied research are to

1. Identify the molecular genetic and neuro-endocrine mechanisms that control the metabolism-behavior-angling vulnerability axis in an effort to understand how that axis influences male parental care activities in bass.

2. Assess how fast vulnerability to angling (and the coselected traits associated with aggression, metabolism, and parental care) can return to preangling values once the selection pressures from angling are removed.
3. Evaluate the relative strength of FIE versus fish learning to avoid capture. We could not fully separate these effects in our past studies, so future studies should quantify the degree of fish learning after exposure to angling.

To help address those proposed next steps (1–3 above), we have bred a sixth generation of these HV/LV bass (Table 5). Not only have we produced another generation of pure HV and LV lines of Largemouth Bass, we have produced both reciprocal F_1 crosses between these two lines ($HV \times LV$ and $LV \times HV$), which have reunited the two selected nuclear genomes equally in each individual offspring. The two lines differ, however, in their

maternal and paternal origins, so they also differ in their mitochondrial DNA (mtDNA) source (HV or LV). In addition, we have also produced a second generation of both of these F_1 crosses, producing two F_2 lines ($HV \times LV \times HV \times LV$ and $LV \times HV \times LV \times HV$). These two lines retain their two different sources of mtDNA (i.e., the first has mtDNA from the HV line and the second has mtDNA from the LV line). Because of recombination and random assortment of chromosomes during meiosis and fertilization, however, the group of individuals in each of these two lines contain a huge spectrum of different nuclear genotypes (i.e., all combinations of genetic variation from the original P_1 population collected from Ridge Lake back in 1979 [Philipp et al. 2009] and likely some new ones). These fish should prove to be extraordinarily valuable tools for the future work needed to address the basic research questions above.

Table 5. History of the breeding to produce the various lines/generations of selected fish used.

Breeding history	
Parents (P_1) from Ridge Lake	
Bass caught a lot	Bass never caught
First generation (with selection)	
High-vulnerability bass	Low-vulnerability bass
Second generation (with selection)	
High-vulnerability bass	Low-vulnerability bass
Third generation (with selection)	
High-vulnerability bass	Low-vulnerability bass
[Fish in first three generations were used for the heritability study]	
Fourth generation (without selection)	
High-vulnerability bass	Low-vulnerability bass
Fifth generation (without selection)	
High-vulnerability bass	Low-vulnerability bass
[Fish from generations 4 and 5 were used for the metabolic, behavioral, and fitness studies]	
Sixth generation (with selection)	
High-vulnerability bass	Low-vulnerability bass
HV mtDNA	LV mtDNA
Crossbreeding to produce F_1 crosses	
$HV \times LV$	$LV \times HV$
HV mtDNA	LV mtDNA
Crossbreeding to produce F_2 crosses	
$(HV \times LV) \times (HV \times LV)$	$(LV \times HV) \times (LV \times HV)$
HV mtDNA	LV mtDNA

4. Assess the level of individual bass vulnerability to angling across our North American bass populations along the historical continuum of selection for vulnerability to angling, and document the genetic basis for the FIE using common garden experiments and reciprocal transplants.
5. Determine if there are any populations that have been so heavily selected that the parental care levels are low enough to endanger lake-wide reproduction and recruitment.
6. Explore fisheries management strategies to reverse the selection toward less aggressive bass.

Addressing these three proposed next steps (4–6 above) will not need the genetic tools of the future described earlier. It will, however, require cooperation between anglers, managers, and scientists working together in the field on real bass fisheries in a joint effort to understand how our shared passion for bass angling is actually impacting bass populations—our shared resource. That effort may take some innovative thinking, stakeholder collaboration, and significant resources but promises cutting edge results that are academically compelling and important for fisheries.

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