Physiological and Behavioral Consequences of Long-Term Artificial Selection for Vulnerability to Recreational Angling in a Teleost Fish

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ABSTRACT

Few studies have examined the physiological and behavioral consequences of fisheries-induced selection. We evaluated how four generations of artificial truncation selection for vulnerability to recreational angling (i.e., stocks selected for high and low vulnerability [HVF and LVF, respectively]) affected cardiovascular physiology and parental care behavior in the teleost fish largemouth bass *Micropterus salmoides*. Where possible, we compared artificially selected fish to control fish (CF) collected from the wild. Although, compared to control fish, resting cardiac activity was ~18% lower for LVF and ~20% higher for HVF, maximal values did not vary among treatments. As a result, the HVF had less cardiac scope than either LVF or CF. Recovery rates after exercise were similar for HVF and CF but slower for LVF. When engaged in parental care activities, nesting male HVF were captured more easily than male LVF. During parental care, HVF also had higher turning rates and pectoral and caudal fin beat rates, increased vigilance against predators, and higher in situ swimming speeds. Energetics simulations indicated that to achieve the same level of growth, the disparity in metabolic rates would require HVF to consume approximately 40% more food than LVF. Selection for angling vulnerability resulted in clear differences in physiological and energetic attributes. Not only is vulnerability to angling a heritable trait, but high vulnerability covaries with factors including higher metabolic rates, reduced metabolic scope, and increased parental care activity. Despite these energetically costly differences, HVF and LVF of the same age were of similar size, suggesting that heightened food consumption in HVF compensated for added costs in experimental ponds. Ultimately, angling vulnerability appears to be a complex interaction of numerous factors leading to selection for very different phenotypes. If HVF are selectively harvested from a population, the remaining fish in that population may be less effective in providing parental care, potentially reducing reproductive output. The strong angling pressure in many freshwater systems, and therefore the potential for this to occur in the wild, necessitate management approaches that recognize the potential evolutionary consequences of angling.

Introduction

The evolutionary consequences of fishing-induced selection pressures are an emerging concern in fisheries science (e.g., Heino and Godo 2002), although such changes have been hypothesized for some time (Miller 1957; Kirpichnikov 1981). Only recently have these evolutionary consequences been considered a potential risk to the sustainability of fisheries resources (e.g., Hutchings 2000; Stokes and Law 2000; Heino and Godo 2002). Reductions in long-term yield, age at maturity, size at age, and other genotypic and phenotypic changes that are of interest to fisheries managers may arise from selective harvest (e.g., Favro et al. 1979; Sheridan 1995; Law 2000; Conover and Munch 2002). Artificial selection can elicit rapid phenotypic changes under controlled conditions in a variety of taxa (Hill

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and Caballero 1992), including genetic changes in wild fish stocks in response to fishing pressure (Reznick et al. 1990). Owing to advancement in theoretical modeling, supplemented with empirical data, it has become apparent that fisheries-induced genetic changes can and do take place at temporal scales that are relevant to fisheries management (Law 2000; Heino and Godo 2002). To date, the majority of research on fisheries-induced selection has focused on commercially exploited marine stocks, assessing the potential ability of these resources to persist under current levels of harvest (e.g., Hall 1999). Recreational angling, however, may provide even stronger selection forces, particularly in inland freshwater systems where fishing pressure can be more intense and more targeted to individuals of certain sizes or sexes (Post et al. 2002; Coleman et al. 2004; Cooke and Cowx 2004, 2006; Arlinghaus and Cooke 2005; Allan et al. 2006; Lewin et al. 2006). Despite high rates of catch-and-release angling in many recreational fisheries (Quinn 1996), substantial mortality (e.g., Muoneke and Childress 1994; Bartholomew and Bohnsack 2005) or sublethal physiological and fitness alterations (Cooke et al. 2002*a*; Cooke and Suski 2005) may occur, leading to opportunities for angling selection to operate even without harvest.

Most previous assessments of fishery-directed selection have focused on alterations in specific sizes, ages, distributions, or sex ratios of fish or on reductions in genetic variability (e.g., Borisov 1978; Ricker 1981; Smith et al. 1991). Undoubtedly, alterations in phenotypic traits can affect sustainability at the population level (Heino and Godo 2002) and may also result in ecosystem effects (Hall 1999). It has been suggested that differential vulnerability to angling reflects learning experiences in response to negative stimuli from previous angling events (Farabee 1970) or variation in the ability to discern natural prey from artificial replicas (see Garrett 2002). Evidence used to support the notion that less vulnerable fish have learned from previous angling experience is derived from the inverse relationship between fishing pressure and both angling vulnerability (Anderson and Heman 1969) and catch per unit effort (Martin 1958). There is also evidence supporting the genetic heritability of vulnerability to angling (Garrett 2002; D. P. Philipp, S. J. Cooke, J. E. Claussen, J. Koppelman, and D. Burkett, unpublished manuscript). Some of these data were assumed to represent different levels of "wariness" (Garrett 2002). An alternative supposition is that this heritable variation in vulnerability to angling may represent behavioral differences in such traits as feeding activity (both spatial and temporal) and food item preference, as well as differences in general levels of aggression (Philipp et al., unpublished manuscript), the latter being a trait that has been shown to be heritable in many different taxa, including fish (Archer 1988). Because aggression is positively correlated with metabolic rate (e.g., Metcalfe et al. 1995; Cutts et al. 1998), we postulate that differential vulnerability to angling may represent selection for opposite extremes of metabolic rates (i.e., low vulnerability corresponds to low aggression and low metabolic rates; high vulnerability corresponds to high aggression and high metabolic rates). If that is true, then we would further predict that differences in metabolic rates alter the energy requirements of differentially vulnerable individuals, further exacerbating this selection (i.e., high-vulnerability fish [HVF] must consume more food because of the cost of high aggression and metabolic rates). Evidence from Atlantic salmon (*Salmo salar*) suggests that although aggressive fish have higher resting metabolic rates, their active metabolic rates do not increase, thus reducing available metabolic scope (Cutts et al. 2002). Similar mechanisms may also occur in fish that are highly vulnerable to angling.

The purpose of this study was to examine the energetic correlates of artificial selection for vulnerability to angling. We used two stocks of a single population of a popular freshwater sportfish, the largemouth bass (*Micropterus salmoides*; Burkett et al. 1984), that had been selected over three generations to exhibit variation in vulnerability to angling (Philipp et al., unpublished manuscript). That study, using the same stocks of largemouth bass that were used as parents in this study, determined that vulnerability to angling in largemouth bass is a heritable trait (Philipp et al., unpublished manuscript). Specifically, using these stocks, we compared resting cardiovascular parameters and response to exercise for the high- and low-vulnerability lines, as well as a control group. Next, we compared the parental care activity of males in the low-and high-vulnerability lines. In largemouth bass, the parental male fish provides extended care for developing offspring to keep the nest region well oxygenated and to defend the brood from potential predators. Previous studies have revealed that parental behavior (e.g., fanning rates, vigilance, time spent on nest) of fish is correlated with reproductive success (Coleman and Fischer 1991; Philipp et al. 1997; Suski and Philipp 2004). Finally, we used bioenergetics modeling to understand the implications of observed differences in activity and metabolic rates for food consumption and growth. This research activity was intended to encompass physiological, behavioral, and energetic perspectives that collectively may directly influence the fitness of largemouth bass selected for different vulnerabilities to recreational angling.

Material and Methods

Study Animals and Artificial-Selection History

This study takes advantage of a long-term artificial-selection experiment that began in 1977 in Ridge Lake, Illinois (D. P. Philipp, S. J. Cooke, J. E. Claussen, J. Koppelman, and D. Burkett, unpublished manuscript). Ridge Lake is an experimental reservoir (6.28-ha surface area) within the Fox Ridge State Park and has been the site of much previous work on various aspects of largemouth bass biology (e.g., Bennett 1954). In the late 1970s, Ridge Lake was the site of a large project evaluating the effect of catch-and-release angling on the fishery for this species (Burkett et al. 1981). From 1977 through 1979, all angled largemouth bass were creeled before release, and the number of times individual fish were captured was recorded (assessed via external tags). In the spring of 1980, Ridge Lake was drained, and largemouth bass size and catch histories were determined (Burkett et al. 1984). Individual fish that were captured once or not at all during the 1977–1979 period were used to establish a line of largemouth bass selected for low vulnerability to angling in experimental ponds in central Illinois. Similarly, individual fish caught four or more times in a single season were used to establish a line of largemouth bass selected for high vulnerability to angling. For the remainder of the experimental period, fish in the two lines were differentiated with opposing pelvic fin clips. Experimental angling and selective breeding were used to further select each of these lines for three more generations, resulting in two lines of largemouth bass bred for different vulnerabilities to angling (Philipp et al., unpublished manuscript).

In 1998, offspring from the third generation of artificially selected high- and low-vulnerability bass were all stocked into a common-garden pond and permitted to grow for 3 yr. Also in the pond were bluegill (*Lepomis macrochirus*), known brood predators of largemouth bass nests (Cooke et al. 2006). No additional experimental angling occurred to identify less and more vulnerable fish, as had taken place during the selection experiment. It was these 3+-yr-old adult fish that we used for our experimentation at the Sam Parr Biological Station in central Illinois.

Cardiovascular Assessments and Bioenergetics Modeling

Fish captured from local reservoirs using electrofishing were transported to the Sam Parr Biological Station for use as control fish (CF). It was not possible to acquire CF that were identical in size (see below) to the LVF (low-vulnerability fish) and HVF individuals. LVF and HVF were collected from the experimental pond via seine net. For the physiological assessments, largemouth bass (CF: $N = 8$, total length $= 247 \pm 12$ mm, mass $= 185 \pm 25$ g; LVF: $N = 10$, total length $= 200 \pm 2$ mm, mass $= 87 \pm 2$ g; HVF: $N = 10$, total length $= 201 \pm 1$ mm, mass $= 90 \pm 3$ g) were held for 48 h before surgery in flow-through tanks (~600 L) at water temperatures of 20° ± 0.3°C. Surgical procedures and the cardiac output apparatus are described in detail elsewhere (Cooke et al. 2003*b*; Cooke and Philipp 2006). Briefly, each fish was anesthetized with 60 ppm clove oil (emulsified with ethanol; 9 : 1 ethanol : clove oil) until the fish lost equilibrium and was nonresponsive. Water containing a maintenance concentration of anesthetic (30 ppm clove oil) was pumped over the gills during surgery. A flexible silicone cuff-type Doppler flow probe (subminiature 20-MHz piezoelectric transducer, Iowa Doppler Products, Iowa City, IA), sized to match the diameter of the vessel, was placed around the aorta and secured with a single suture. The lead wire from the probe was then sutured to the side of the fish in six locations to prevent shifting of the cuff. We used a flowmeter (545C-4 Directional Pulsed Doppler Flowmeter, Bioengineering, University of Iowa, Iowa City, IA) and a digital strip chart recorder (LabVIEW, ver. 4.0.1, National Instruments, Austin, TX) to monitor cardiac variables.

After surgery, individual fish were immediately placed into a 40-L tank (30 cm × 40 cm) and allowed to acclimate to the tank for at least 18 h. The experimental tanks were continuously supplied with water (~50 L h^{-1}) at temperatures within 0.3°C of desired experimental temperatures. To induce exhaustive exercise, fish were chased around the tank by tail-pinching until they were unresponsive and began to lose equilibrium (Kieffer 2000; Cooke et al. 2003*a*, 2003*b*). Cardiac variables were recorded continuously for at least 1 h before the exercise simulation (the resting period), during the exercise simulation, and for at least 5 h after exercise (the recovery period). Human access to the laboratory was restricted during resting and recovery to prevent external disturbance.

After experimentation, fish were euthanized with an overdose of anesthetic (180 ppm clove oil), and a postmortem calibration was conducted to convert Doppler shift (in volts) to actual blood flow (mL min^{-1}; Cooke et al. 2003*b*). Using a constant-infusion pump (Harvard Apparatus, South Natick, MA), anticoagulated pig's blood was perfused through the aorta to calibrate the probes over a range of flow rates encompassing those recorded during the trials. To determine recovery times, traces for cardiac output, heart rate, and stroke volume, adjusted to resting (100%), were plotted for each fish as 60-s means and evaluated visually (Cooke et al. 2003*a*, 2003*b*). A fish was considered to have recovered when values became stable and returned to within 10% of resting values (Schreer et al. 2001; Cooke et al. 2003*a*, 2003*b*; Cooke and Philipp 2006). The maximal disturbance was determined as the greatest observed change in a cardiac variable (either positive, >100% resting, or negative, <100% resting) during the recovery period. Maximum change was substituted for maximum increase when stroke volume decreased.

To examine the effects of differences in resting cardiac output on the respiration rates and growth of the high- and low-vulnerability largemouth bass, we conducted a series of energetics simulations with the software Fish Bioenergetics 3.0 for Windows (UW Sea Grant Institute 1997). We adjusted the respiration component (model 1) of the largemouth bass model parameters developed by Rice (1981) to account for differences observed in resting cardiac output at 20°C between the two groups. For all simulations, we set the initial (day 0) and final (day 20) mass of fish to 100 g and then modeled consumption over that period. The proportion of maximum consumption and the amount of food consumed (in grams) at maintenance rations (zero growth) at 20°C was then determined for each group. It is important to note that we have assumed that cardiac output is directly and proportionately correlated to metabolic rate; although it can be the case (e.g., Webber et al. 1998), this is an assumption for largemouth bass. Indeed, variation in parameters such as oxygen extraction efficiency can alter the relationship between cardiac output and metabolic rate (Thorarensen et al. 1996). Thus, the bioenergetics modeling should be viewed as preliminary until direct respirometry assessments can be completed. To assess whether there were differences in the size (growth) of LVF and HVF, we collected fish from the experimental pond via seine net, measured their total length, and determined their fin clip position before release.

Assessment of Parental Care Behavior

To quantify differences in parental care behavior between the two groups of fish, a snorkeler swam through the holding pond, marked nests with small tiles, identified the stage of offspring development, and determined the fin clip position of the guarding male to identify LVF and HVF. We then used a micro black-and-white high-resolution underwater video camera (AU-120, J. J. Communications. Englewood, NJ) mounted on an aluminum pole to quantify the parental care activities of guarding male fish (Cooke and Bunt 2004). Measurements were all conducted on April 15, 2002, when the developmental stage of offspring was determined to be 1-d-old eggs. Using a pole from shore, the camera was carefully positioned 0.5 m from the nest, on a 45° angle pointing down toward the nest. This technique provides minimal disturbance, and the fish continue to guard the nest. We waited for 5-min to allow the fish to recover from the disturbance of the camera and then began to record the activity of the attending male (Cooke et al. 2006). Video for each of 20 nests (10 HVF, 10 LVF) was recorded using a time-lapse video recorder to yield 10 min of video data. We relied on ambient light to provide illumination for the camera.

Several hours after the video recordings, each fish was angled from the nest using spinning gear, small hooks, and fathead minnows. A single experienced angler was used for this aspect of the experimentation and stood on shore at least 4 m away from the nest. Methods were standardized such that only casts that placed the bait within the actual nest were considered. The purpose of the capture was to verify that the clips identified by the snorkeler or on the video were correct and to quantify the number of casts required to catch nesting fish with different angling vulnerabilities. We assumed that the number of casts required to catch a nesting fish could serve as a surrogate for aggression, similar to Suski and Philipp (2004). All nesting fish that we studied with video were captured using this technique.

We used video transcription protocols established by Hinch and Collins (1991) to quantify nesting activity. We quantified the frequency of two behaviors (turning and departing) that reflect general activity and vigilance. Turning was defined as a change greater than 45° in axial orientation over the nest, and departures were defined as times when the male left the view of the camera. Departing can be indicative of chasing predators in systems where predation levels are high (Cooke et al. 2006), but extended absences can also indicate a general lack of vigilance. Departures were quantified as the amount of time that parental fish were absent from the nest (>1 m from nest edge) during the 10-min observation period. Three measures of swimming activity were collected: (1) nest-departing speeds, indicated by the time required for the male to swim 1 body length; (2) caudal beat frequency, associated with nest departure speed; and (3) caudal and pectoral fin beat frequency of the fish while on the nest. The caudal beat frequency of the fish while on the nest was used to represent the in-place swimming speed of the male.

Statistical Analysis

For all data, normality was assessed using probability plots, and homogeneity of variance was assessed using Levene's test. Where data were normally distributed and variances were homogeneous, data were not transformed, and we used parametric analyses. A one-way ANOVA was used to evaluate differences among the LVF, HVF, and CF lines. When significant differences were noted, the conservative Tukey-Kramer HSD post hoc test was used to determine where pairwise differences occurred (Day and Quinn 1989). For instances where no data on CF existed (i.e., behavioral metrics), we used *t*-tests for normal homoscedastic data and Mann-Whitney *U*-tests for nonnormal heteroscedastic data to compare LVF and HVF lines. All statistical assessments were conducted using JMP 4.0 (SAS Institute). Values reported are means (±SE), with significance evaluated at $\propto = 0.05$.

Results

Physiological and Energetic Assessments

Resting cardiac output and heart rate values for largemouth bass differed significantly among lines (ANOVA, $P < 0.001$), being highest for HVF, lowest for LVF, and intermediate for CF (Tukey HSD, $P < 0.05$; Fig. 1*A*, 1*B*). Conversely, resting stroke volume was similar among all lines (ANOVA, $P = 0.61$; Fig. 1*C*). When fish were exposed to exercise, both cardiac output and heart rate increased, and stroke volume decreased (Fig. 1*D*–1*F*). Neither maximal cardiac output nor maximal heart rate differed across lines ($\mathrm{ANOVA}_{\mathrm{cardiac\ output}}$ $P = 0.68$, $\mathrm{ANOVA}_{\mathrm{heart\ rate}}$ $P = 0.80$). Overall, the maximal change in stroke volume was significant across lines (ANOVA, $P = 0.03$); however, no differences were detected by the Tukey-Kramer post hoc test ($P > 0.05$). The scope for cardiac output was lowest for HVF, differing significantly from that for LVF and CF (ANOVA, $P < 0.001$; Fig. 2*A*). A similar pattern was also observed for scope for heart rate (ANOVA, $P < 0.001$; Fig. 2*B*). Cardiac parameters consistently recovered most slowly for LVF and equally fast for HVF and CF (ANOVA, $P < 0.001$; Fig. 3). Energetics modeling revealed that the differences in resting cardiac output between the HVF and LVF would require the HVF to consume approximately 40% more food to maintain a mass

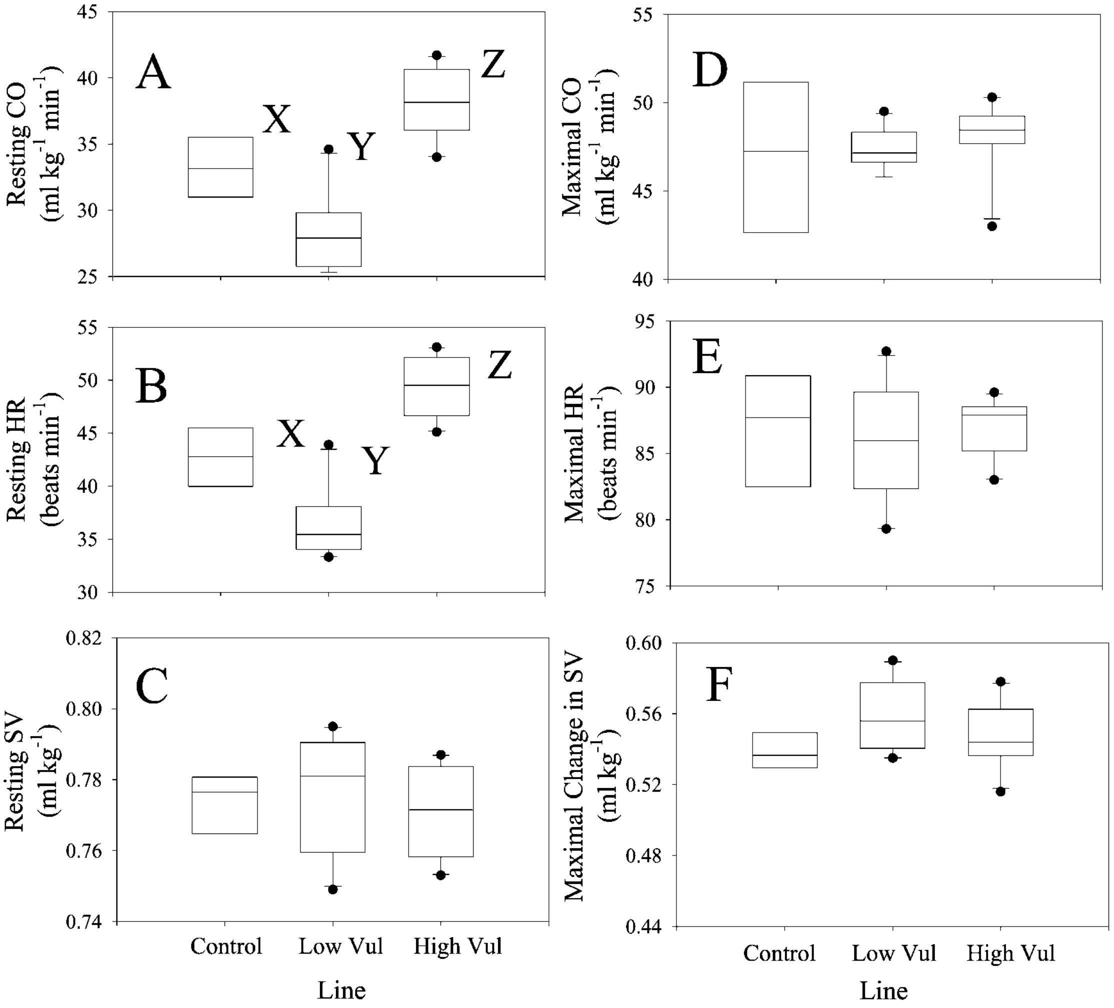

Figure 1. Resting cardiac output (*A*), heart rate (*B*), and stroke volume (*C*), as well as maximal changes in these three parameters (*D*, *E*, and *F*, respectively) for largemouth bass selectively bred for different angling vulnerabilities. "Low Vul" refers to fish bred for low vulnerability to angling, "High Vul" refers to fish bred for a high vulnerability to angling, and "Control" refers to fish that were not exposed to an artificial-selection program and were collected from the wild. Data were collected for control ($N = 8$) and low- ($N = 10$) and high- ($N = 10$) vulnerability groups at 20°C using Doppler flow probes. Dissimilar letters indicate significantly different (Tukey-Kramer HSD test, $P < 0.05$) values among groups for each of the cardiac variables. Resting rates were determined from the 60-min period before exercise. The maximal changes in cardiac variables were determined for the 300-min recovery period after exhaustive exercise.

similar to that of the LVF. Interestingly, there were no significant differences in the total length of LVF ($N = 66$; 200 ± 1 mm) and HVF ($N = 105$; 199 ± 1 mm) that we randomly collected from the ponds using seine nets to assess potential differences in growth (*t*-test, $P = 0.60$).

Parental Care Behavior

During the provision of parental care, nest-guarding male HVF turned on the nest more frequently than did male LVF (*t*-test, $P < 0.001$; Fig. 4*A*). Similarly, while on the nest, both the nesting caudal fin rate and pectoral fin rate were significantly higher for HVF than LVF (*t*-tests, $P < 0.001$; Fig. 4*B*, 4*C*). While on the nest, in-place swimming speeds were also higher for HVF than LVF (*t*-test, $P = 0.02$; Fig. 4*D*). The male LVF tended to leave the nest both more frequently (*t*-test, $P < 0.001$) and for longer periods of time (*t*-test, $P < 0.001$) than did the male HVF (Fig. 4*E*, 4*F*). When the male HVF departed the nest, however, they were typically chasing potential predators and exhibited higher swimming speeds (Mann-Whitney *U*-test, $P = 0.002$) than did the LVF, which were observed to be swimming slowly away from the nest (Fig. 4*G*) and venturing more than 3 m from the nest site. The number of casts required to capture nest-guarding largemouth bass also differed signifi-

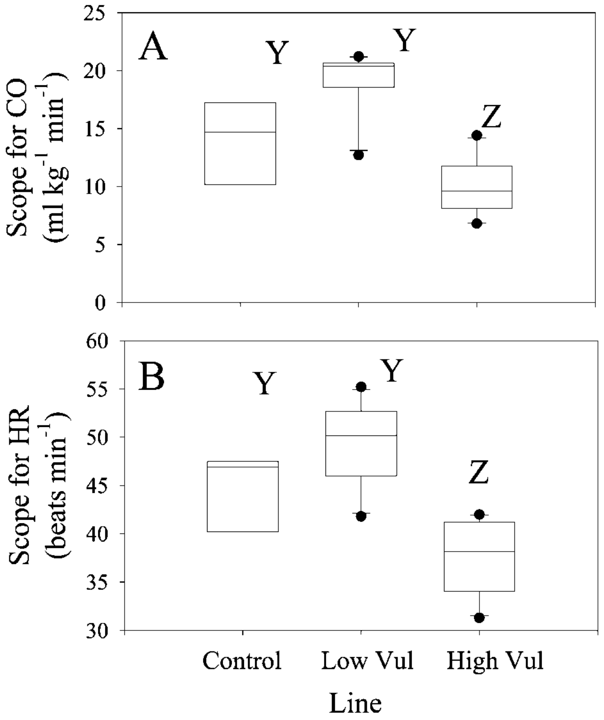

Figure 2. Scope for cardiac output (*A*) and heart rate (*B*) for largemouth bass from different lines: control ($N = 8$), low vulnerability to angling ("Low Vul," $N = 10$), and high vulnerability to angling ("High Vul," $N = 10$). Dissimilar letters indicate significantly different (Tukey-Kramer HSD test, $P < 0.05$) values among groups.

cantly among groups, with male LVF being more difficult to capture (4.3 ± 0.9 casts) than male HVF (1.6 ± 0.2 casts; *t*-test, $P = 0.01$; Fig. 4*H*).

Discussion

The pattern and response of a trait to selection depend on the presence of genetic variation, its mode of inheritance, and genetic correlation with other traits (Trexler 1990). Substantial genetic variation has been observed within and among populations of largemouth bass (Philipp et al. 1983). Depending on the relationship between genotypic and phenotypic variability for the traits under selection, fisheries-induced selection can result in evolutionary changes (Heino and Godo 2002). Although most examples of changes in phenotypic characteristics of populations are related to maturation- and growth-based life-history traits (Ricker 1981; Law 2000), our study documents how selection for vulnerability to angling can directly depress the fitness of individuals in a population as a result of proximal physiological and behavioral alterations. Consistent with our predictions, selection for vulnerability to angling in largemouth bass appears to have the capacity to cause population-level changes in metabolic rates (assessed via cardiovascular physiology) and parental care activity over generations. Because behavioral characteristics can be determined by many loci, it is possible that other life-history characteristics may be inadvertently selected for or against as a consequence of selection for fish with different vulnerabilities to angling, a result with important implications for fisheries management and conservation.

Philipp and coworkers were able to induce significant differences in angling vulnerability through selection for low- and high-vulnerability individuals (D. P. Philipp, S. J. Cooke, J. E. Claussen, J. Koppelman, and D. Burkett, unpublished manuscript). Theirs was the first long-term (i.e., three generations) study to document such changes. Garrett (2002) also examined the effects of selection for angling vulnerability, but that study was confounded by the fact that the founder population was an admixture of two largemouth bass species and their hybrids. As a result, the study by Garrett (2002) primarily highlights the differences in angling vulnerability that can be observed among different but closely related species, as had previously been documented (e.g., Rieger et al. 1978). Because the fish used in our study were all derived from the one founder population, (i.e., they did not include alleles from Florida bass *Micropterus floridanus*; see Philipp 1991), the study by Philipp et al. (unpublished manuscript) was the first documentation of selection for vulnerability to angling within a freshwater fish species.

Our data illustrate that, as a consequence of selecting for vulnerability to angling, selection also occurs on resting cardiovascular variables that can be representative of resting metabolic rates (Farrell 1991; Satchell 1991; Thorarensen et al.

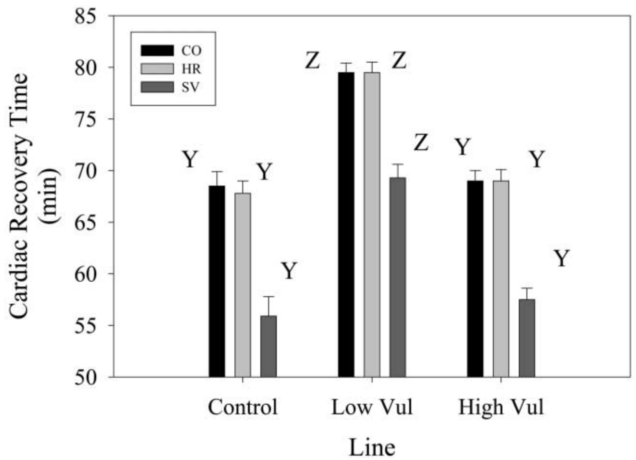

Figure 3. Time required for cardiac variables to return to predisturbance levels after exhaustive exercise (manual chasing) for control largemouth bass ($N = 8$), as well as largemouth bass bred for low vulnerability to angling ("Low Vul," $N = 10$) or high vulnerability to angling ("High Vul," $N = 10$). Values plotted are mean (±SE) recovery times for cardiac output (*CO*), heart rate (*HR*), and stroke volume (*SV*). Dissimilar letters indicate significantly different (Tukey-Kramer HSD test, $P < 0.05$) values in each cardiac variable among treatments.

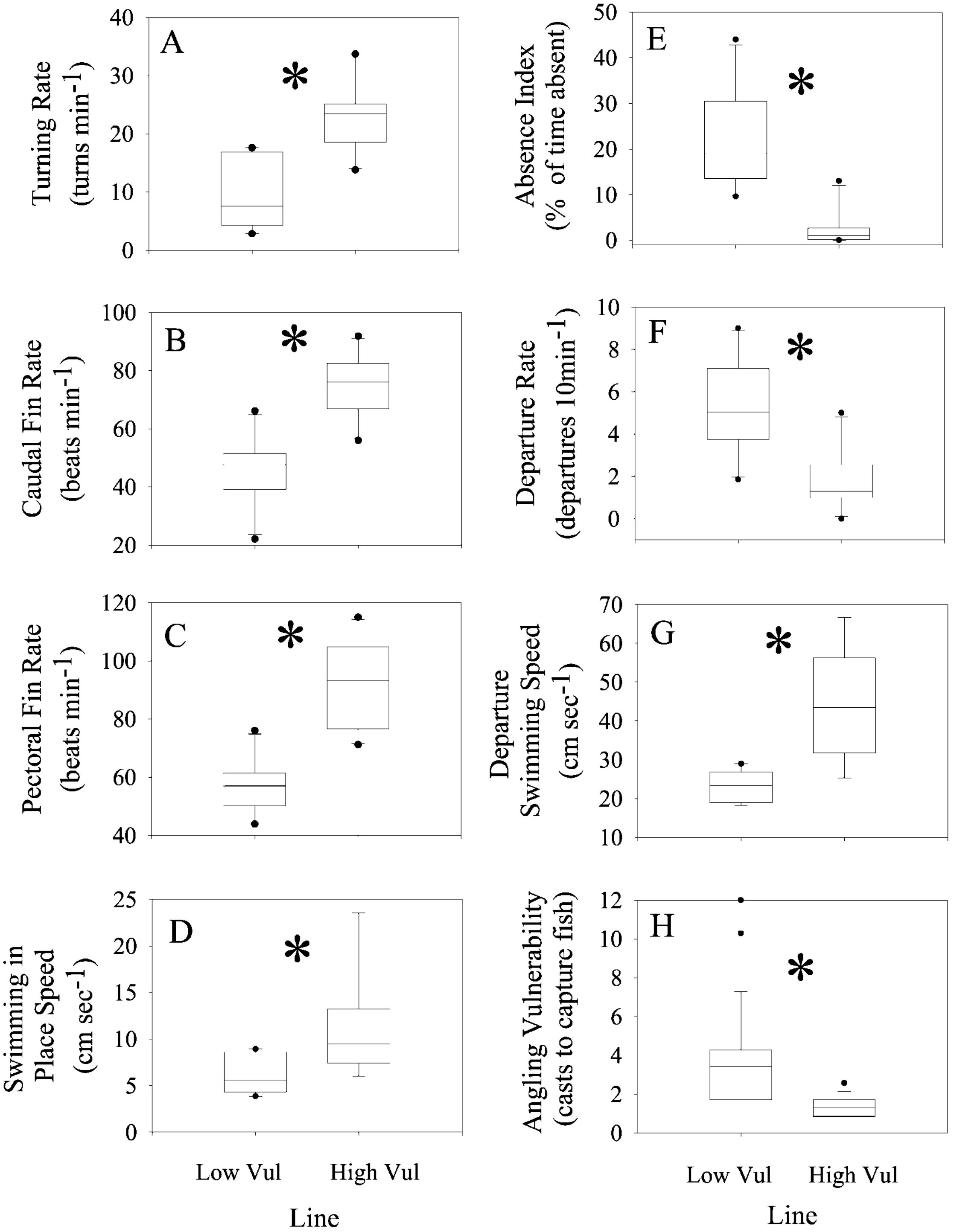

Figure 4. Parental care activity of largemouth bass that were bred for low ($N = 10$) and high ($N = 10$) vulnerability to angling. Turning rate (*A*), caudal fin rate (*B*), pectoral fin rate (*C*), and swimming-in-place speed (*D*) were recorded while largemouth bass were on their nest. Absence index (*E*), departure rate (*F*), and departure speed (*G*) were calculated when the fish departed their nest. Angling vulnerability (*H*) was also determined for nesting bass by evaluating the number of casts required to capture the nesting male. Significant differences between groups are indicated by asterisks (*t*-test or Mann-Whitney U-test, $P < 0.05$).

1996). In our study, although the HVF had resting cardiac output and heart rate values that were higher than values for the LVF and the CF (LVF was lowest), stroke volume did not differ among groups for resting or maximal change. The lack of change in stroke volume is not surprising, in that irrespective of a variety of different stressors and environmental conditions, resting stroke volume in largemouth bass is essentially fixed, except at low water temperatures (Cooke et al. 2003*a*, 2003*b*). It is clear that when Philipp et al. (unpublished manuscript) selected for vulnerability to angling, they also selected for a distribution of resting metabolic rates that was different from the expected distribution of resting cardiac output and heart rates observed in CF. There is clear evidence in several fish species at both the interindividual level (e.g., Cutts et al. 1998) and the interpopulation (Metcalfe et al. 1995) level that various indicators of aggression and dominance are correlated positively with standard metabolic rate (analogous to resting cardiac variables; Satchell 1991). Although having a higher resting metabolic rate can be viewed as energetically costly in terms of expenditures (Priede 1985), if this is correlated with increased aggression toward brood predators, then the fish may benefit in competition for resources and mates.

Although we observed differences in the resting cardiac output and heart rate in differentially selected groups, no such differences were observed in maximal cardiac parameters. It is reasonable to assume that fish with high metabolic rates may compensate for the higher resting rates by pushing their maximal values higher to maintain metabolic scope (Priede 1985). In our study, we did not observe any compensation; consequently, HVF had a decreased scope for cardiac output and heart rate relative to the other two groups. Indeed, similar patterns of individuals with high standard metabolic rates having small metabolic scopes have been observed in Atlantic salmon (Cutts et al. 2002). For this species, Cutts et al. (2002) argue that because aggressive/dominant fish have higher costs of maintenance (see Priede 1985), fish gain an advantage not from increasing metabolic scope and thus capacity for aggressive behavior, but instead by exhibiting aggressive behaviors to gain access to resources required to sustain their higher energetic requirements. It is then clear why fish that are most vulnerable to angling also have higher metabolic rates, need to consume more food, and thus have greater chances of being harvested after attempting to consume an angler's bait or lure.

There is some evidence to suggest that growth rates are more dependent on competitive ability and aggression than on physiological efficiency (Weatherley 1976). In some cases, however, it has been proposed that less aggressive individuals may be more efficient at converting food into somatic growth (Ruzzante and Doyle 1991). In aquaculture scenarios, although less aggressive fish typically exhibit reduced growth relative to dominant individuals, this phenomenon is generally attributed to an inability to acquire food resources (Cutts et al. 1998). In our study, there was no difference in the size of fish when grown in a common-garden experiment. We believe that the apparently similar growth rates are the result of the complex interaction between the higher metabolic demands of HVF, their increased competitive ability, and their need to consume additional resources to compensate for these energetic costs. Food was likely not limiting in the production ponds, allowing all fish to access adequate food resources. Our energetics modeling suggested that the HVF would require ~40% more food to compensate for the increased energetic expenditure. The HVF would, therefore, need to spend more time foraging than LVF, thereby potentially explaining why HVF are be more vulnerable to angling. Although these HVF exhibit a costly strategy that is typical of aggressive individuals (Högstad 1987), it may provide fitness benefits over the LVF, as outlined below. Alternatively, competition for food in the ponds where the common-garden experiment was conducted could have restricted food consumption by the LVF. In larger systems with unlimited food resources, LVF may actually have the potential to grow larger than the HVF, with longer-term fitness consequence for both LVF and HVF. Future work will have to assess growth rates in natural systems to assess trade-offs between energetic and foraging costs under a range of prey resource availabilities or in a laboratory environment with controlled rations.

When fish were chased to exhaustion, we observed differences in recovery rates among groups. Specifically, the LVF took significantly longer to recover after disturbance than did the HVF. This is somewhat surprising because recovery rates after exhaustive exercise are remarkably consistent for largemouth bass across a range of water temperatures (13°–25°C; Cooke et al. 2003*b*). Although recovery rates can vary by type of disturbance (e.g., air exposure vs. exercise; Cooke et al. 2002*a*, 2003*b*) and also among stocks of fish that have been translocated or hybridized (Cooke and Philipp 2006), it is unclear why recovery rates would vary with selection for low angling vulnerability. The most probable explanation is that selection for angling vulnerability results in selection for some other cofactors that impair or delay recovery relative to CF and HVF. Delayed recovery is energetically costly and may limit the ability of individuals to respond to subsequent stressors during this period (Priede 1977). In a selection experiment for stress responsiveness (Øverli et al. 2002), rainbow trout that had low responsiveness (i.e., magnitude and duration of disturbance, as seen in our CF and HVF) also had higher incidences of food intake than did highly responsive fish, illustrating the potential energetic consequences of delayed recovery in the LVF. Furthermore, in rodents, individual differences in aggression reflect heritable means of coping with stress (Benus et al. 1991). When rodents are exposed to stress, aggressive individuals apparently adopt an active response, whereas nonaggressive individuals adopt a passive response. The passive responses may be protracted, leading to delayed recovery rates relative to aggressive individuals (Benus et al. 1991), which may also explain the differences in recovery rates observed here. Other unknown mechanisms affecting recovery rates in the LVF may also exist, but they will require additional work to identify.

Dominance and aggression levels in fish are linked not only to higher metabolic rates and energy requirements but also generally to increased fitness (Archer 1988). Although the specifics vary with mating systems (Trexler 1990), in general, more aggressive individuals will be superior competitors for mating territories, mates, and matings. Furthermore, in instances of parental care, fish with higher levels of aggression should be superior at defending the developing offspring from predators, as has been noted by Suski and Philipp (2004) for largemouth bass. Indeed, our data suggest that LVF had lower nest-guarding activity and vigilance than did the HVF. The caudal and pectoral fanning rates in nest-guarding largemouth bass provide oxygenated water to the developing offspring while also keeping them free of silt and excreted wastes (Cooke et al. 2006). Reduced fanning rates in LVF could contribute to reduced survival of offspring, because there is generally a positive relationship between fanning intensity and reproductive success (e.g., Ostlund and Ahnesjo 1998). The high turning rates, in-place swimming speeds, and proportion of time spent on the nest for HVF represent activities that are related to the vigilance and ability of the male to detect potential predators. In our study, the HVF departed the nest at higher speeds than did the LVF. We interpret this as the HVF leaving rapidly to charge or chase potential intruders (such as conspecifics and bluegill that were in the pond) that were approaching the nest. This interpretation is consistent with data collected on nest-guarding largemouth bass using activity transmitters, which show that burst swimming was used for chasing potential predators (Cooke et al. 2002*b*). Conversely, the LVF left their nest more frequently and with less speed, suggesting that their departures were not linked to the engagement of potential predators. In addition, by having a significantly higher absence index and a significantly lower pectoral fin rate (and thus egg fanning), the LVF may be reducing the chance of offspring survival. It is important to note, however, that in this study we did not assess offspring survival, and there may be a threshold for fanning above which there is no fitness benefit. Future experiments will have to evaluate such relationships and to assess fitness metrics over longer timescales (i.e., lifetime reproductive output).

When we angled for nesting largemouth bass, the HVF consistently were captured with fewer casts. Although it is difficult to determine whether this reflects increased demand for resources or increased vigilance against potential nest predators, several pieces of evidence suggest that it is the latter. In particular, recent research has revealed that there is a clear relationship between parental aggression (as measured by responses to staged intrusion of model nest predators) and angling vulnerability for largemouth bass (Suski and Philipp 2004). In addition, there is limited evidence that largemouth bass feed opportunistically during the parental care period (Hinch and Collins 1991), and this is therefore regarded as one of the most energetically costly periods in the life of a male largemouth bass (Cooke et al. 2002*b*, 2006).

In a review of fisheries-induced selection, Heino and Godo (2002) suggest that although much of the evidence of evolutionary effects is vague and inconclusive, it is still imperative to recognize that such changes can occur and that management actions should reflect these potential effects. It is clear from Philipp et al. (unpublished manuscript) that angling vulnerability is a heritable trait; however, it is likely pleiotropic and may have a complex interindividual physiological and behavioral basis. Additional research into this conservation topic using ecophysiological approaches will be necessary to better understand the mechanisms involved (Wikelski and Cooke 2006). Furthermore, some of these correlates of angling vulnerability include those related to fitness. We advocate management approaches (i.e., evolutionarily enlightened management; see Ashley et al. 2003) that take into account the possibility that selection from angling can alter the life-history characteristics and fitness of populations (Heino 1998). Empirical examples of such changes in largemouth bass fisheries would usually be masked by stocking additional fish in response to perceived or real instances of decreased abundance (Post et al. 2002; Cooke and Cowx 2006; Lewin et al. 2006). Furthermore, there are few reliable, long-term data sets that monitor the angling effort, catch rates, and population structure of fish communities (Cooke and Cowx 2004). Until such data sets are developed, experimental and manipulative studies, such as what we present here, must be used as indicators as to what may be happening in wild populations.

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