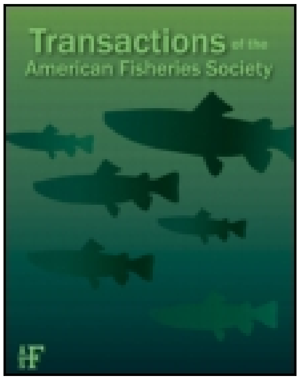

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Largemouth Bass Selected for Differential Vulnerability to Angling Exhibit Similar Routine Locomotory Activity in Experimental Ponds

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ARTICLE

Largemouth Bass Selected for Differential Vulnerability to Angling Exhibit Similar Routine Locomotory Activity in Experimental Ponds

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Abstract

A growing body of work is focused on attempting to understand the biological mechanism(s) by which some fish are highly vulnerable to angling while others are not. We used electromyogram telemetry to monitor routine locomotory activity of artificially selected largemouth bass *Micropterus salmoides* in experimental ponds to test two potential explanatory hypotheses: (1) that the difference in angling vulnerability between high-vulnerability (HV) bass and low-vulnerability (LV) bass is related to a difference in routine activity level between the two groups, and (2) that the difference in vulnerability between HV and LV bass is related to a difference in the diel activity pattern

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displayed by each group (e.g., LV fish are more active at night, a time where there is typically little bass fishing effort). Neither hypothesis was supported by our results. Differences in vulnerability to angling in artificially selected lines of largemouth bass were not related to inherent differences in routine locomotory activity in our ponds. Mean daily activity levels were close to 5% of maximum swim speed in both groups, which we estimated to reflect a mean swimming distance of approximately 5,875 m (range = 1,280–9,670 m) per day. There was also no difference in the diel pattern of activity displayed by the two groups. Both HV and LV bass displayed a significant diurnal activity pattern: 16% and 19% higher activity levels during the day than at night, respectively. These results contribute to the ongoing efforts to understand the behavioral basis of vulnerability to angling in largemouth bas and other fish species.

There is an increasing concern over the potential evolutionary consequences of fishing-induced phenotypic selection (e.g., Policansky 1993; Walsh et al. 2006; Jørgensen et al. 2007; Kuparinen and Merilä 2007; Thériault et al. 2008; Enberg et al. 2009). Indeed, there is now abundant evidence that size-selective harvest in commercial fisheries has contributed to changes in the life history traits of heavily fished populations (for review see Law 2000; Heino and Godø 2002; Jørgensen et al. 2007; Hutchings and Fraser 2008). In addition to size-selectivity that is common in most fishing gear, some fishing gear, especially those gears working passively and depending on active fish movement to encounter the gear, may preferentially catch specific behavioral phenotypes (Heino and Godø 2002). As a result, fishing can also influence the evolution of life history traits through correlated behavioral mechanisms (Lewin et al. 2006; Biro and Post 2008; Uusi-Heikkilä et al. 2008). Moreover, because behavioral traits may have larger heritability compared with life history traits, evolution by means of behavioral selection may occur more rapidly (Uusi-Heikkilä et al. 2008), providing an advantage for behavioral phenotypes less vulnerable to fishing (Cooke et al. 2007; Philipp et al. 2009).

Like commercial fishing, recreational fishing targets a specific suite of behaviors that make some fish more likely to be angled than others. Vulnerability to angling has been linked to personality traits like boldness (Wilson et al. 2011) and aggression (Suski and Philipp 2004; Cooke et al. 2007), and may also be affected by learning and other cognitive abilities (Beukema 1970; Raat 1985; Askey et al. 2006), all of which may influence the fitness of an individual. Although it has largely been ignored, recreational fishing-induced selection, therefore, has the potential to exert strong selective pressure on a population, which will lead to evolutionary adaptations as long as the targeted traits are heritable and not the result of unknown environmental factors.

A long-term artificial selection study by Philipp et al. (2009) on largemouth bass *Micropterus salmoides* provides empirical evidence that vulnerability to angling is a complex heritable trait, exhibiting a realized heritability (h^2) of 0.15. Within just three generations of truncated selection, changes in several physiological and behavioral traits have been noted as correlated responses to selection for vulnerability to angling. For example, age-1 low-vulnerability (LV) bass had a 9–17% higher realized growth rate than their high-vulnerability (HV) counterparts (Redpath et al. 2009), which was later explained by a 10% higher standard metabolic rate (SMR) in HV bass (Redpath et al. 2010). Furthermore, there was evidence of reduced aerobic and anaerobic capacity in the LV bass (Redpath et al. 2010). In addition, Cooke et al. (2007) identified significant differences in obligate parental care behavior exhibited by nesting males, HV males exhibiting more intense parental care and expending more energy in guarding the nest. High vulnerability males were also found to behave more aggressively against potential predators than LV males. Because metabolism and aggression are often correlated (Metcalfe et al. 1995; Ros et al. 2006; Huntingford et al. 2010), the elevated aggression level exhibited by HV males represents a plausible mechanism by which the greater vulnerability to lure-based recreational fishing (which was also used during the selection process; Philipp et al. 2009) can be explained.

One further mechanism that could explain the difference in vulnerability to angling between HV and LV largemouth bass is differences in locomotory activity. This is because vulnerability to lure-based angling should, at least in part, be a function of the probability of encountering the angler's lure. Under the assumption that HV and LV bass both inhabit the same habitats, one would then predict that individuals that are more active should have a higher probability of encountering a lure or bait and thus being captured. Similarly, differences in vulnerability to angling could result from differences in the expression of diel activity, as long as anglers preferentially fish during particular times of the day. In this case, vulnerable fish need not be more active in general but instead are more likely to be active during those times of the day that they are being targeted by anglers. Because most largemouth bass fishing happens during the day, as did the fishing for the selection experiment by Philipp et al. (2009), one would predict HV bass to be significantly more active at day compared with LV bass.

The purpose of this study was to test the hypothesis that the difference in vulnerability to angling between the two artificially selected lines of largemouth bass is due to inherent differences in routine locomotory activity. We employed electromyogram (EMG) telemetry in a 4,000-m^2 experimental pond to compare both the level and diel pattern of activity displayed by individuals from the two selected lines. We made two nonmutually exclusive predictions. First, if the difference in vulnerability to angling between the two lines is related to differences in activity level, then HV bass should display a greater overall level of activity than LV bass. Second, if the difference in vulnerability to angling between the two lines is related to differences in the period during which the fish are most active, then the two groups should display different diel swimming activity patterns.

METHODS

Experimental animals.—This study used a total of 29 adult largemouth bass (15 HV and 14 LV; age 2+, mixed sexes, mean ± SE TL = 337 ± 5 mm, mean ± SE mass = 681 ± 26 g). The fish used in the present study belonged to the F_5 generation (bred in 2007), having experienced three generations of truncated selection according to vulnerability to angling and two further generations without selection. The selection process began in 1977 in Ridge Lake, an experimental reservoir in Fox Ridge State Park, Charleston, Illinois, as described completely in Philipp et al. (2009). Briefly, between 1977 and 1980, all angling in Ridge Lake was controlled and catch histories were maintained for each largemouth bass that was landed. At the end of the 4-year study, the lake was drained and the bass were categorized based on the number of times they had been caught by anglers. Bass that were never caught were used as broodstock to establish an LV line, and bass that were captured four or more times within a single year were used as broodstock to establish an HV line. High vulnerability and LV bass were separately bred in two 800-m^2 brood ponds. The F_1 fish were fin-clipped to identify parental line and experimentally angled, separated into LV and HV groups based on the number of times they were caught, and then bred to establish an F_2 generation. This process was repeated through the F_3 generation.

The F_5 fish used in this study were stocked into 1,200-m^2 ponds at the Sam Parr Biological Station (near Kinmundy, Illinois) approximately 1 year before the current study. High-vulnerability and LV bass (identified by pectoral fin clips) of both sexes were mixed equally into two groups for use in two separate trials for assessment of activity metrics (15 bass in trial 1 and 14 bass in trial 2). The day before each trial began, the holding pond was drained and the bass were moved to 1.25-m-diameter holding tanks to await surgical implantation of the EMG transmitters.

Surgeries began the next morning at approximately 0900 hours. Bass were netted individually from the holding tank and anesthetized in a 50 mg/L solution of clove oil (9:1, clove oil: ethanol). Once stage 4 anesthesia was achieved, the fish was measured for total length and mass, and then transferred to a wetted foam surgical table. The gills of the bass were infused with aerated water containing light anesthetic (20 mg/L solution of clove oil) for the duration of the surgery (4–5 min). The EMG transmitters (Lotek Wireless; model CEMG2-R11-18, 11 × 54 mm, 10 g in air, transmission rate = 30/min) were implanted through a ~3-cm-long incision made just left of the ventral midline of the fish, immediately anterior to the pelvic girdle. The two gold-tipped electrodes (10 mm in length) were inserted parallel to one another (~1 cm apart), into the band of red muscle running along the lateral line using a 12-gauge plunger device. The external antenna wire of the transmitter was fed out through the open incision, which was then closed with four simple, interrupted monofilament sutures. Fish were then transferred back to holding tanks to recover from the anesthetic. All surgeries were performed by a single surgeon to control for surgery effects (Cooke et al. 2003).

We did not attempt to assign a sex to the fish at the time of surgery because the gonads were reduced at this time of the year and were not easily seen through the incision without the risk of causing trauma to the internal organs. We did record a sex for each of the fish in trial 2 at the end of the trial when the transmitters were removed, but, unfortunately, transmitters were removed from the fish in trial 1 before sex could be recorded.

Electromyogram tag calibration.—The EMG tags used in this study transmitted a unitless EMG value ranging from 0 to 50 that can be used to estimate the swim speed of fishes (Cooke et al. 2004; Brown et al. 2007). The caveat is that, although the relationship between EMG value and swim speed is approximately linear (Cooke et al. 2004), the slope and intercept of the relationship varies by tag, fish, and position of the electrodes (Beddow and McKinley 1999; Geist et al. 2002; Brown et al. 2007). For this reason, the EMG tags must be individually calibrated after implantation if the values are to be accurately used to estimate swimming speeds.

Electromyogram tags in this study were calibrated relative to the range of EMG value obtained for each fish. In this way, EMG values were converted to percent of maximum swim speed, rather than an absolute swimming speed, using the equation

$$\%\,\text{max activity} = \left[\frac{(\text{EMG} - \text{EMG}_{\text{min}})}{(\text{EMG}_{\text{max}} - \text{EMG}_{\text{min}})}\right] \times 100,$$

where EMG is the EMG value to be converted, EMG_{min} is the minimum EMG value for a given fish that summed greater than 1% of the total number of EMG values for that fish (assumption was that this value represents the EMG level when the fish were at rest in the pond), and EMG_{max} was the greatest EMG value obtained during a calibration procedure at the end of the trial where the bass were stimulated to burst swim (maximum exertion) while being captured in a dip net and held at the surface for up to 60 s.

This method of calibrating EMG tags could yield biased activity estimates if the variation in minimum and maximum EMG values among individuals is the result of different minimum and maximum swim speeds (i.e., behavioral differences) rather than random differences in tag sensitivity and electrode position. Such bias would be evident from consistently higher mean minimum or maximum EMG values in one experimental group relative to the other. Thus, to validate our use of this calibration technique to compare routine activity between experimental groups, we used two-sample *t*-tests to compare the mean minimum, maximum, and range of EMG values

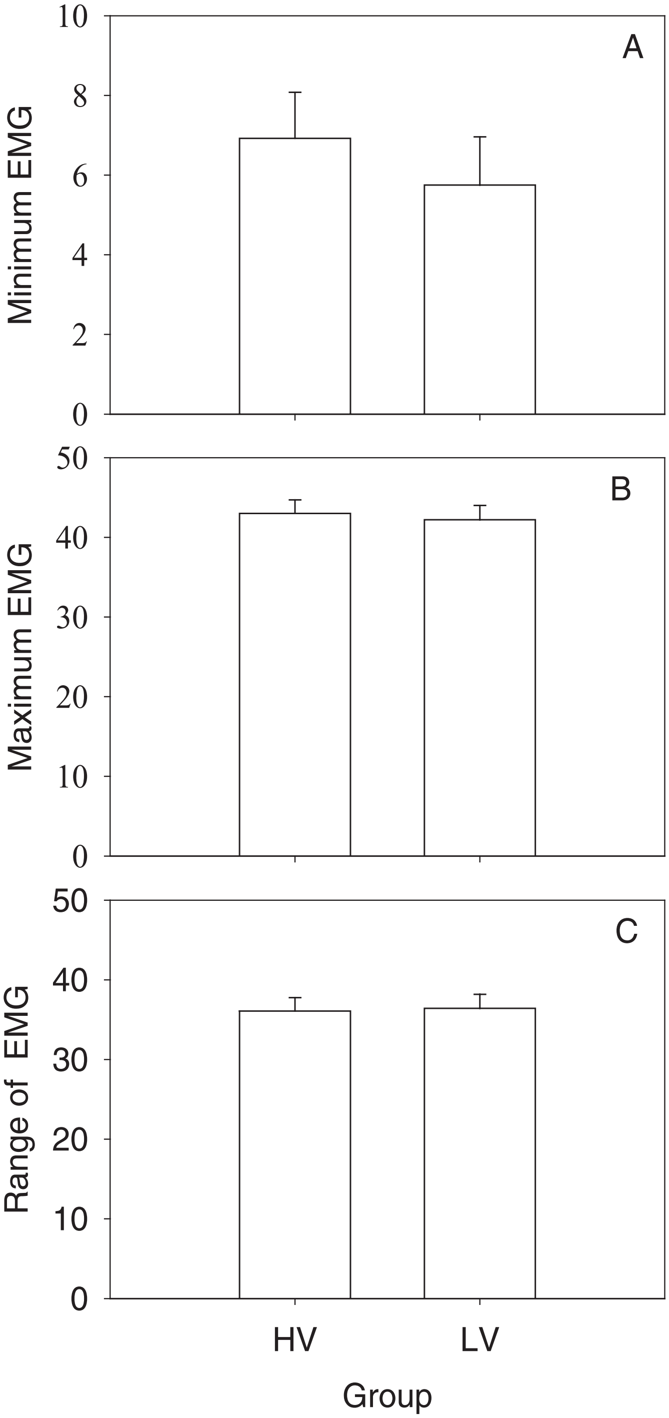

FIGURE 1. (**A**) Minimum, (**B**) maximum, and (**C**) range of EMG values for HV and LV largemouth bass. Bars display mean values ± SE. There was no significant difference in any of these parameters between HV and LV bass (*t*-test: $P > 0.451$ for all comparisons).

between HV and LV fish. No evidence of bias was found among any of the variables (Figure 1; *t*-test: $t = 0.698$, 0.337, and -0.139; $P = 0.492$, 0.739, and 0.451 for minimum, maximum, and range, respectively). As a result, we assume our method to be reliable in terms of comparing among-individual differences in routine locomotory activity level.

Experimental details.—Following implantation and recovery of all fish used in a given trial (mid to late afternoon on the day of tagging), the group was transferred to a 4,000-m^2 experimental pond. A total of two 7-d trials were run in fall 2009. Trial 1 ran from 23 September 2009 to 30 September 2009, and trial 2 ran from 2 October 2009 to 9 October 2009. Water temperatures within the experimental pond ranged from 19°C to 22°C during trial 1, and from 14°C to 18°C during trial 2. In both trials, naturally occurring aquatic invertebrates and stocked free-swimming fathead minnows *Pimephales promelas* and juvenile bluegill *Lepomis macrochirus* acted as a forage base for the bass. The large number of forage fish remaining at the end of the study period when the ponds were drained suggests that food availability was not limited.

A telemetry receiver (Lotek SRX-400 series) and three-element Yagi antenna were placed at one end of the pond to record the transmitted EMG signals. The receiver cycled through the unique tag frequencies, logging tag transmissions for 30 s at each frequency. Given the sample size of 14–15 fish in each trial, this meant that the activity level of each fish was monitored for 30 s about 8 times/h for the duration of the trial. One exception occurred during trial 1: on the night of 26 September 2009, there was a 6-h power interruption that resulted in a loss of records during that period.

After each trial, the experimental pond was drained, and fish were collected and held temporarily in a small raceway near the pond. Each fish individually underwent the calibration procedure described above to determine the EMG value transmitted during maximum exertion (EMG_{max}). Following the procedure, the fish were euthanized and the transmitters were recovered.

Statistical analyses.—Activity records were analyzed over a 4-d period following an acclimation period of 32–34 h. Activity records began at midnight the day after the fish were released and ended at midnight the night the ponds began draining (draining started at ~0100 hours). Two individuals from trial 1 and a third from trial 2 fell victim to predation by resident great blue herons *Ardea herodias* during the study and were consequently eliminated from analysis. A fourth individual from trial 2 was also eliminated from analysis because one of its electrodes became dislodged during the trial.

Two-sample *t*-tests were used to compare the mean length of LV and HV fish and to test for differences in activity level between male and female bass in trial 2 (six males and six females; sex was not recorded in trial 1). Comparison of mean routine activity level between LV and HV fish and between night (1800 to 0559 hours) and day (0600 to 1759 hours) was accomplished using a nested linear mixed model. The model included treatment group (LV or HV), time of day (day or night), and their interaction as fixed effects. Fish identification was nested within trial (random effects) to account for repeated measures, and fish length was a covariate.

All statistics were performed use JMP statistical software (version 4.0.4; SAS Institute, Cary, North Carolina). *P*-values $<$ 0.05 were considered significant, and all means are reported as mean ± SE.

RESULTS

Low vulnerability bass were slightly larger, on average, than HV bass (346 versus 333 mm), but the difference was not significant (*t*-test: $t = -1.788$, $P = 0.087$). There was no relationship between activity level and fish length (nested linear mixed model: $F = 0.1418$, $P = 0.710$), nor was there sufficient evidence to conclude a significant effect of sex on activity level (*t*-test: $t = -1.931$, $P = 0.083$). The latter result, however, may be due to the fact that we only recorded sex for individuals in trial 2 and, consequently, sample size was low for this test.

The activity level of largemouth bass in this study was generally low, relative to their maximum swimming speed. Mean activity levels ranged from 1.1% to 8.3% of maximum swim speed. The overall activity level of HV and LV bass did not differ significantly from one another. Mean activity levels were 5.1 ± 0.5% (median = 4.8%, range = 2.7–8.3%) and 4.3 ± 0.5% (median = 4.0%, range = 1.1–8.0%) of maximum swim speed in HV and LV bass, respectively (Figure 2; nested linear mixed model: $F = 1.055$, $P = 0.316$).

Though activity occurred during both day and night, both groups displayed a significant diurnal activity pattern, activity level during the day being significantly greater than at night (Figure 3; nested linear mixed model: $F = 61.141$, $P < 0.001$). Activity levels tended to peak by a couple of hours after dawn and were at their lowest by approximately 3 h after dusk. High-vulnerability bass were 16% more active in the day than at night (mean difference = 0.75 ± 0.15% of maximum swim speed), and LV bass were 19% more active during the day than at night (mean difference = 0.77 ± 0.16% of maximum swim speed).

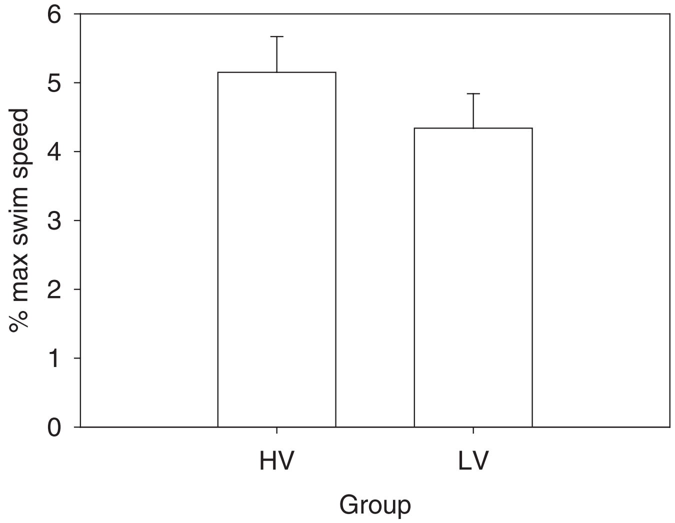

FIGURE 2. Mean activity levels of HV and LV largemouth bass. Bars display mean activity (% of maximum swim speed) ± SE. There was no significant difference in mean activity level between HV and LV bass (nested linear mixed model: $P = 0.316$).

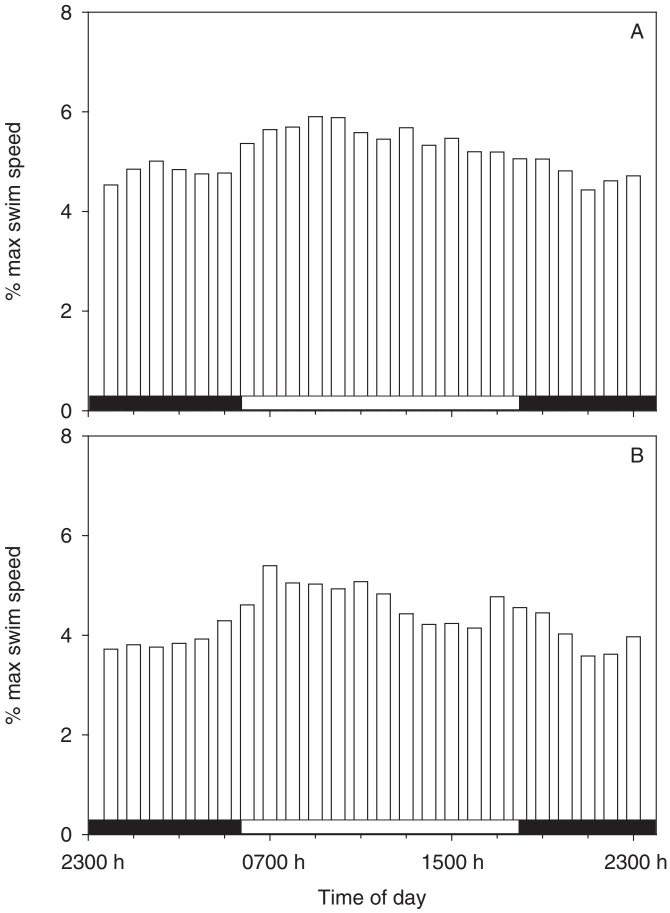

FIGURE 3. Diel activity pattern of **(A)** HV and **(B)** LV largemouth bass. Vertical bars display mean activity level (% of maximum swim speed) over each hour of the day for the duration of the study. Dark horizontal bars identify nighttime hours, and light horizontal bars identify daytime hours. Both groups displayed a significant diurnal activity pattern (nested linear mixed model: $P < 0.001$).

DISCUSSION

Selection for vulnerability to angling in largemouth bass did not result in observed differences in their routine locomotory activity in experimental ponds. We tested two possible explanatory hypotheses related to routine activity: (1) that the difference in angling vulnerability between HV and LV bass is related to a difference in the level of routine activity between the two groups, and (2) that the difference in vulnerability between HV and LV bass is related to a difference in the diel activity pattern expressed by the two groups. Neither hypothesis was supported by our results. High-vulnerability and LV bass displayed equal levels of activity and, while HV and LV bass did each display a significant diel activity pattern, the pattern was the same for both groups.

It is possible that this negative result is due to a reversal of evolutionary change over the two generations (F_4 and F_5) without selection for angling vulnerability. Indeed, genetically based reversal of fishing-induced evolution has been demonstrated in Atlantic silversides *Menidia menidia* (Conover et al. 2009; Salinas et al., in press). The silversides were exposed to size-selective fishing for five generations and then monitored for an additional five generations after selection was halted, at which time there was already evidence of evolutionary changes being reversed (i.e., fish body size was increasing). The authors predicted full recovery from fisheries selection in approximately 12 generations. We believe complete reversal of evolutionary change is unlikely in our study for two reasons. First, as far as we are aware, there are no extrinsic selection factors in the experimental ponds that would cause a rapid shift in activity level. The study by Conover et al. (2009) did demonstrate that phenotypic traits can reverse in the absence of extrinsic selection factors; however, the reversal was relatively slow (only partial reversal over five generations), so complete reversal of phenotypic differences in locomotor activity over just two generations seems unlikely. Second, other phenotypic behavioral differences between these two lines in terms of aggression and nest defense were evident in F_4 generation fish (Cooke et al. 2007; Nannini et al. 2011) and were also present in F_5 fish (Sutter 2010). We therefore conclude that vulnerability to angling is, in fact, not related to inherent differences in routine locomotor activity in largemouth bass held in ponds.

Mean activity level in this study was approximately 5% of maximum (burst) swim speed in both HV and LV bass. Maximum burst speeds of approximately 4 body lengths/s have been observed in free-swimming, similarly sized smallmouth bass *M. dolomieu* (Peake and Farrell 2004). If we assume a similar maximum burst speed for the largemouth bass in this study, then estimated mean swimming speed was approximately 6.8 cm/s and the estimated mean distance traveled each day was approximately 5,875 m (range = 1,280–9,670 m). These values are consistent with values obtained from free-swimming largemouth bass in Warner Lake, near Kingston, Ontario (Hanson et al. 2007). Calculated daily swimming distances for those fish were 7,300 m in April and decreased to 2,700 m by mid-November. Our swimming distance estimate may seem somewhat high relative to the fall value for Warner Lake bass (Hanson et al. 2007), but it is likely that the slight elevation is a result of the warmer water temperatures at our more-southern field site.

The lack of difference in activity level between HV and LV bass is somewhat surprising given the 10% higher SMR and 16% higher metabolic scope for activity previously observed in the HV bass, relative to their LV counterparts (Redpath et al. 2010). Higher metabolic demand in HV bass can come at a cost in terms of growth if food is limited (Redpath et al. 2009) but, contrary to what one might predict, did not appear to support higher activity levels (i.e., foraging activity) in our system. Nannini et al. (2011) hypothesized that the differences in energetic requirements between HV and LV bass influence differences in foraging behavior through the mechanism of varying hunger levels. If this is the case, then one could predict that differences in foraging activity would be greatest when feeding opportunities are limited. In our study, the presence of numerous stocked prey items and limited refuge habitat for prey likely meant that prey were readily available to all bass and, consequently, HV bass may not have needed to maintain higher activity levels to meet their energetic requirements. In addition, swimming could have been restricted in the small ponds or the ponds might not have been large enough to induce a need to search for food, thereby constraining possibilities for activity differences to be expressed. Therefore, while there appears not to be inherent differences in locomotor activity between HV and LV bass, it would be necessary to compare the activity levels of HV and LV fish in a more competitive system before we can rule out the possibility of an indirect relationship between locomotor activity and vulnerability to angling.

High-vulnerability and LV bass both displayed diurnal activity patterns, activity levels during the day being 16–19% higher than during the night. These results are consistent with several previous studies of diel activity in largemouth bass, although the magnitude of the difference between daytime and nighttime activity levels was more subtle in this study than in some others (Warden and Lorio 1975; Reynolds and Casterlin 1976). This result can be attributed to seasonal differences in the expression of diel activity in largemouth bass. Several independent studies have reported seasonality with respect to diel activity in largemouth bass. For example, Demers et al. (1996) found that the elevation of daytime activity in largemouth bass was strongest between July and September, and was reduced in October as water temperature and day length decreased. Similarly, Hanson et al. (2007) observed a clear diurnal activity pattern in free-swimming largemouth bass in April, but not in either January or November.

Our approach with respect to the implementation of EMG telemetry to study the activity of free-swimming largemouth bass produced two limitations that, if addressed in future studies, would allow researchers to take greater advantage of the full benefits of this technology. First, calibrating EMG tags on an absolute scale (such as would be done in a swim tunnel; e.g., Brown et al. 2007) rather than a relative scale (as was done in this study) would increase precision and allow for construction of accurate bioenergetics models for comparing groups of fish. Second, by monitoring the activity of bass in groups, the swimming behavior of individual fish was recorded for only about 4 min/h. Censored behavior of individuals may have limited our ability to detect subtle differences in activity, although this is a limitation with most other telemetry techniques as well. Nonetheless, our approach did have two obvious benefits over traditional position telemetry. First, EMG telemetry can provide more-accurate instantaneous estimates of movement rates than positional telemetry because it is not based on the assumption of linear movement between two points over time (Cooke et al. 2001). Second, activity estimation using positional telemetry requires either that there are several listening stations present, often at a prohibitively inflated financial cost, or that the fish be followed for some time period, which can alter the behavior of the fish and may bias the results.

In conclusion, the behavioral basis of artificial selection for angling vulnerability in largemouth bass seem unrelated to inherent differences in routine locomotory activity. By contrast, angling vulnerability in this species is clearly related to metabolism and aggression (Suski and Philipp 2004; Cooke et al. 2007; Redpath et al. 2010) and may be influenced in part by differences in foraging behavior (Nannini et al. 2011). One possibility that has not yet been tested, however, is that the difference in vulnerability to angling is a result of differences in the spatial ecology (e.g., home range size and preferred habitat) of HV and LV bass. Anglers rarely fish all available habitats but rather target specific habitats that are traditionally known for high angling success. As a result, by selectively targeting specific habitats, anglers might inadvertently select for habitat-related behavioral phenotypes (Árnason et al. 2009; Jakobsdóttir et al. 2011; Parsons et al. 2011). Indeed, in a study of the relationship between boldness and angling vulnerability in bluegill, Wilson et al. (2011) found that bolder sunfish (as determined by a standardized refuge emergence test) were more likely to approach a baited hook from open water, whereas shy sunfish tended to approach the hook from a refuge. If differences in spatial ecology and habitat use were to exist between HV and LV selected bass, these differences could also account for diverging foraging tactics and energetic constraints (Savino and Stein 1989), both of which have previously been observed between these two lines (Cooke et al. 2007; Redpath et al. 2010; Nannini et al. 2011). Research into the spatial ecology of the two lines of bass, therefore, represents a logical next step in discovering the behavioral mechanisms on which this selection regime acts.

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