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The glucocorticoid stress response is repeatable between years in a wild teleost fish

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Abstract Patterns of glucocorticoid (GC) hormone regulation exhibit considerable inter-individual variation that is often examined relative to individual traits and fitness measures. Although stress-induced GC concentrations are repeatable within an individual in captive populations, this assumption remains untested in wild animals in their natural environment across longer time periods. We assessed the repeatability of baseline and post-stress GC concentrations in a wild teleost fish. Largemouth bass (*Micropterus salmoides*) were captured and subjected to a standard stress protocol and then stocked into a small research lake. Upon recapture by angling up to 1 year later ($n = 26$), fish were re-sampled following identical methods. After controlling for a strong effect of water temperature, we confirmed repeatability of post-stress cortisol concentrations despite stress presumed to accompany relocation. We documented no consistency in baseline GC concentrations. This study serves as an important validation for the use of post-stress cortisol concentrations as an individual trait. However, the effect size of repeatability was lower than that found in other taxa. Results also bring forth the reality that environmental variables such as temperature must be considered in studies where these factors can vary, such as when sampling wild animals at liberty.

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Introduction

When an animal is exposed to stress, the resulting suite of physiological, behavioral and cognitive responses are considered as adaptive mechanisms that enable an individual to overcome and recover from the challenge (Wingfield et al. 1998). Glucocorticoids (GCs), the predominant hormones involved in this response are extremely variable among individuals at both baseline (pre-stress) and post-stress concentrations, even under consistent conditions. Although traditionally this variation at the individual level has been considered inherent error in analyses and ignored (Bennett 1987; Williams 2008), more recently, interest has emerged in linking hormonal variation to life-history characteristics. Post-stress GC concentrations are thought to represent the ability of an individual to appropriately respond to a challenge (Breuner et al. 2008), whereas baseline GC concentrations have primarily regulatory and metabolic functions (Mommsen et al. 1999; Landys et al. 2006). As such, the two measures have distinct functions and exhibit differing consequences and correlations (Romero 2004). Across taxa, GC concentrations are thought to mediate behavior (Øverli et al. 2005; Cockrem 2007) and survival strategies (Ricklefs and Wikelski 2002; Hau et al. 2010) as well as fitness and performance measures (Breuner et al. 2008; Bonier et al. 2009). In mammals, distinct stress coping styles have been revealed based on the magnitude of a stress response that encompass a suite of consistent behavioral traits (Koolhaas

et al. 2010). Extending to fish, domestic populations of rainbow trout selectively bred for responsiveness have revealed these coping styles to be associated with recovery of food intake, locomotor activity, aggression and social status (Øverli et al. 2005).

When exploring correlates of GCs, it is typical to sample each specimen for blood cortisol on only one occasion. This methodology follows the strict assumption that hormone titres are repeatable within an individual, and that a value acquired at one time is representative of that individual across all situations. However, if this rarely tested assumption were incorrect, any patterns among individuals with respect to hormonal correlates would be concealed by low consistency within an individual (Romero and Reed 2008). The validity of sampling an individual only once is based on experimentation with laboratory and semi-captive populations that has revealed GC levels and responses to be heritable (Satterlee and Johnson 1988; Pottinger and Carrick 1999; Evans et al. 2006) and repeatable (Cockrem and Silverin 2002; Schjolden et al. 2005; Romero and Reed 2008; Cockrem et al. 2009). However, relationships between behavior and physiology in wild populations are not as clear as those in lab populations, and it is very uncommon to compare replicate samples within a single individual (Williams 2008). To our knowledge, there are only two examples of repeatability of GC responses in wild animals, both in birds. Cockrem et al. (2009) sampled a colony of Adelie penguins (*Pygoscelis adeliae*) and found the corticosterone response to be generally repeatable with similar coefficients of variation among individuals. The second study showed repeatability of fecal corticosterone levels, testosterone levels and individual behavior in a semi-captive population of geese (*Anser anser*) across several seasons (Kralj-Fiser et al. 2007). Other studies exploring intra-individual variability of wild animals brought into captivity have inconsistent results with repeatability being either context- or sex-dependent. For example, Romero and Reed (2008) reported repeatability of baseline GC levels to be dependent on experimental condition. Wada and colleagues (2008) found repeatability of stress responsiveness in wild zebra finches from nestling to adult in females but not in males.

The assumption of repeatability of GC levels remains unexplored over the long term in wild animals in their natural environment, and has not been validated in free-swimming wild fish. The physiological stress response in fish has been reviewed extensively (Wendelaar Bonga 1997; Mommsen et al. 1999; Barton 2002), and thus will not be described in detail here. Briefly, cortisol is the primary GC in fish. Exposure to an acute stressor activates a series of physiological processes that culminate in the synthesis and secretion of cortisol into the blood stream.

As the elevation of circulating cortisol concentrations is delayed from exposure to the stressor by several minutes, proper sampling protocol allows quantification of baseline as well as post-stress cortisol concentrations (Gamperl et al. 1994). In the current study, we assessed the stress response of 50 wild largemouth bass (*Micropterus salmoides*) using a standardized stress protocol, and then stocked them into a private research lake. After a 6-week acclimation period, and then again the following summer, the lake was exhaustively angled to re-capture stocked fish. Upon capture, bass were subjected to the same standardized stress protocol. The results of this experiment provide an analysis of the long-term repeatability of baseline and post-stress cortisol concentrations of a wild fish at liberty.

Methods

Study site and research subjects

All fish were sampled under an Ontario Ministry of Natural Resources Scientific Collection Permit and handled in accordance with the guidelines of the Canadian Council on Animal Care, administered by Carleton University. The study was carried out from June 2009 to August 2010 at the Queen's University Biological Station in south eastern Ontario, Canada. Study animals were taken from Lake Opinicon (788 ha surface area, 44°31′N, 76°20′W) by either electro-fishing ($n = 24$) or angling ($n = 26$). Both methods were employed because as Lake Opinicon is a large lake, electro-fishing is only possible in near-shore shallow areas. Use of both angling and electro-fishing ensured that fish were taken from all habitat types in the lake. Fish were captured between the hours of 5:30 and 8:30 a.m. from June 6th to June 19th, 2009. Upon capture, individuals were treated with a standardized stress protocol modified from O'Connor et al. (2011). A 3-min standardized air exposure stressor began as soon as a fish was hooked (when angled) or netted (when electro-fished). All fish were landed in <30 s and immediately placed in a moistened foam-lined trough. Approximately 1 mL of blood was drawn via caudal puncture using lithium-heparinised 3 mL vacutainers (B.D. Vacutainer, Franklin Lakes, NJ) and 21 gauge, 38 mm needles. Fish were then measured for TL (Total length) and injection-implanted intra-peritoneally with individually-coded passive integrated transponder (PIT) tags (2×9 mm) using a hypodermic needle. Following the standardized stress protocol, fish were placed individually in 50 L coolers filled with lake water for 25 min to allow cortisol levels to peak. A second blood sample was then taken. Blood samples were

held in ice-water slurries for no more than 2 h before being centrifuged at 10,000*g* for 5 min (Compact II Centrifuge, Clay Adams, NJ). Plasma samples were flash frozen in liquid nitrogen and stored at −80°C until analysis. Fish were then held in individual coolers that were continuously re-circulated with fresh lake water and transported back to holding facilities at the Queen's University Biological Station. Fish were held in groups of four in a 100 L tank supplied with constant flow-through lake water to recover from the capture event for 24 h. The following day, fish were stocked into Warner Lake (8.3 ha surface area, 44°31′N, 76°20′W), a research lake that was closed to public angling approximately 8 km from Lake Opinicon. Details regarding lake structure and community can be found in Hanson et al. (2007). Fish were transported in individual coolers and water was replenished at the half-way point. The total transport time was approximate 15 min. Warner Lake experienced a near complete winterkill during the winter of 2007–2008 (O'Connor et al. 2010). Therefore, these stocked fish comprised a large proportion of the largemouth bass population in the lake.

Resampling protocol

A standard angling protocol was employed to recapture fish in late July/early August of 2009 following an acclimation period and in June of 2010. Warner Lake was divided into four sections of approximate equal size based on the natural landmarks. Fishing was conducted by two anglers from a rowboat and occurred for 2 h across four different time periods: dawn (5–7 a.m.), morning (9–11 a.m.), afternoon (2–4 p.m.) and dusk (7–9 p.m.). Lake sections were randomly assigned to time periods while ensuring that the entire lake received equal effort for each time period. Only two people ever fished one section at any given time. Upon capture, fish were exposed to the standard stress protocol as detailed above, identified by PIT tag number, measured for TL, weighed and released back into Warner Lake after obtaining a blood sample for the measurement of post-stress cortisol levels.

To minimize variability in cortisol concentrations due to reproductive status, all fish were sampled following the reproductive period. Bass spawn in the early spring, usually when water temperatures approach 15°C and following spawning, males will guard nests in the littoral zone for several weeks (Scott and Crossman 1998). Timing varies by year and is highly dependent on temperature (Scott and Crossman 1998). Snorkel surveys were conducted in both lakes in which a snorkeler swam the lake perimeter searching for nests to ensure nest guarding was complete. Sampling occurred no sooner than approximately 2 weeks following completion of nest guarding period.

Analyses

Cortisol concentrations were determined using a commercial radioimmunoassay kit (ImmunoChem Cortisol I^{125} RIA kit; MP Biomedicals, Orangeburg, NY) routinely used to quantify cortisol concentrations in fish plasma (Gamperl et al. 1994). Two assays were conducted, one for each year. Intra-assay variability for 2009 was 8.9%, and 11.8% for 2010. Inter-assay variability was 15.2%. Statistical analyses were conducted using SPSS Statistics 19.0 (2010). Residuals were tested for violations of normality using a Shapiro–Wilk goodness-of-fit test and data were log-transformed where necessary. Homogeneity of variance was examined with a Levene's test. We tested for effects of somatic condition, temperature and capture details on cortisol concentrations. Multiple regression analyses assessed relationships between size (TL, total length), condition factor ($K = 10^5 \times$ weight/length^3) and temperature on cortisol concentrations in either lake. Furthermore, as samples were taken from two different lakes with distinct temperature profiles, across different years, months and time periods, we explored differences potentially attributed to these factors using univariate general linear models (GLM) with post-stress and baseline cortisol concentrations as dependent variables and temperature as a covariate. In Lake Opinicon, as electro-fished fish were caught in early June and angled fish in mid-June, interaction effects of capture method × temperature were included in the GLM. In Warner Lake, fish were caught in late July/early August of 2009 and June of 2010 and thus the interaction of year × temperature was also included in Warner Lake GLMs. The GLMs determined if differences in both baseline and post-stress cortisol concentrations could be attributed to (1) capture method in Lake Opinicon, (2) year and time period caught in Warner Lake and (3) relocation to Warner Lake. In all the cases, effects on baseline and post-stress cortisol concentrations were analysed separately as sample sizes differed. Baseline cortisol values identified as outliers (±2 SD of mean) within each lake were excluded as they are likely not representative of a true baseline physiological profile but are elevated due to the uncontrollable events prior to capture. It is common to measure the stress response, the change from baseline to post-stress GC concentrations, but a recent review has suggested that post-stress cortisol concentrations may provide more accurate data interpretation (Romero 2004). As statistical results of these two variables did not differ, only post-stress cortisol levels are presented.

Repeatability of baseline and post-stress cortisol concentrations was assessed with the regression models using a two-tier enter method where we first explored whether the first measured value within an individual predicted the

second measured value, and then whether this relationship could be improved by accounting for the elapsed time between sampling periods. Where temperature was a significant covariate, the regression analyses were conducted on the residuals of the relationship between the cortisol parameter and water temperature. A significant regression between residuals of cortisol × temperature between the two lakes would indicate repeatability.

Results

Post-stress cortisol concentrations exhibited large variability between individuals ranging from 28.26 to 1029.9 ng mL^{-1} (mean 325.63 ± 225.92 ng mL^{-1}). Baseline cortisol concentrations ranged from 0.84 to 12.16 ng mL^{-1} (mean = 3.27 ± 2.55 ng mL^{-1}) when excluding outliers ($n = 4$; mean = 17.56 ± 4.77 ng mL^{-1}) which is comparable to previous studies of non-reproductive largemouth bass in the wild (e.g. O'Connor et al. 2011) and held in a laboratory setting (e.g. Carmichael et al. 1984). There was minimal change from stocking to recapture in size (TL; Opinicon: 361.1 ± 35.2 cm; Warner: 367.1 ± 33.8 cm) or condition factor (Opinicon: 1.4 ± 0.1; Warner: 1.5 ± 0.1). Multiple regression models with condition factor, length and temperature as predictors of cortisol concentrations were significant for baseline cortisol concentrations in both lakes (Opinicon: $R^2 = 0.23$, $F_{(3,27)} = 3.91$, $P = 0.019$; Warner: $R^2 = 0.37$, $F_{(3,27)} = 6.84$, $P = 0.001$) where temperature was the only significant predictor in both cases. Although these same models were not significant for post-stress cortisol overall (Opinicon: $R^2 = 0.15$, $F_{(3,28)} = 1.59$, $P = 0.21$; Warner: $R^2 = 0.21$, $F_{(3,28)} = 2.45$, $P = 0.084$), there was an effect of temperature. Indeed, in both lakes water temperature influenced baseline cortisol levels (Opinicon: $R^2 = 0.29$, $F_{(1,30)} = 12.30$, $P = 0.001$; Warner: $R^2 = 0.35$, $F_{(1,29)} = 15.81$, $P < 0.001$; Fig. 1) and post-stress cortisol concentrations (Opinicon: $R^2 = 0.14$, $F_{(1,31)} = 4.98$, $P = 0.033$; Warner: $R^2 = 0.20$, $F_{(1,30)} = 7.38$, $P = 0.011$; Fig. 1). In all the cases, there was a negative relationship between temperature and cortisol concentrations. GLMs revealed that in Lake Opinicon, neither baseline nor post-stress cortisol concentrations differed with respect to capture method or capture × temperature (Table 1). In Warner Lake, sampling procedures (time of day, year and temperature at which fish was captured) had an effect on baseline but not post-stress cortisol concentrations (Table 1). There was a significant effect of temperature on baseline cortisol levels. Consistent with the regression between baseline cortisol and temperature, concentrations were elevated but temperatures lowered in 2009 (June) compared to 2010 (July/August). Between lakes, results show differences in baseline and post-stress
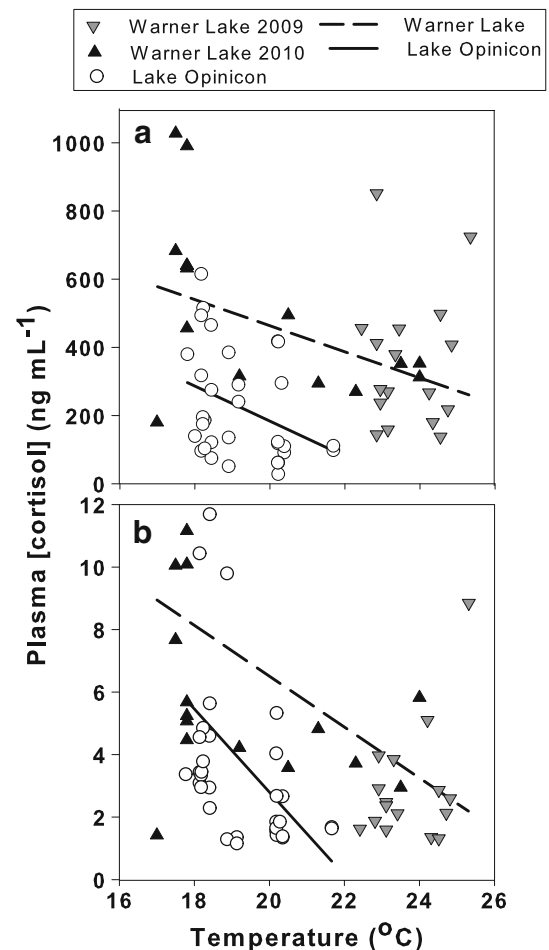

Fig. 1 Correlations between lake water temperature at capture and post-stress cortisol concentrations (**a**) or baseline cortisol concentrations (**b**) in free-swimming largemouth bass (*Micropterus salmoides*) sampled from Lake Opinicon in June 2009 (*open circle*) and from Warner Lake in July/August 2009 (*inverted filled triangle*) and June 2010 (*filled triangle*). The relationships between the stress response and water temperature were similar to those for post-stress cortisol concentrations and thus the data are not shown. Regression line for Warner Lake encompasses values from both years (see text for regression line equations)

cortisol concentrations to be attributed to temperature (Table 1).

Given significant relationships between lake temperature and cortisol concentrations, standardized residuals from the regression of cortisol concentration on temperature for each lake were compared to each other, revealing significant repeatability of post-stress cortisol concentrations ($R^2 = 0.19$, $F_{(1,\ 29)} = 6.57$, $P = 0.016$; Fig. 2) that was not improved by including time between sampling periods (Post-stress: $R^2 = 0.19$, $F_{(2,\ 28)} = 3.22$, $P = 0.055$). Baseline cortisol was not repeatable ($R^2 = 0.062$, $F_{(1,\ 27)} = 1.78$, $P = 0.19$; Fig. 2) and although still not significant, including time between sampling events did improve model fit ($R^2 = 0.16$, $F_{(2,\ 26)} = 2.47$, $P = 0.10$).

Table 1 Results of univariate general linear models (GLMs) testing for effects of sampling procedures on baseline and post-stress cortisol concentrations for largemouth bass (*Micropterus salmoides*) captured from Lake Opinicon by either angling or electro-fishing in June 2009, stocked into Warner Lake ($n = 50$) and recaptured ($n = 26$) by angling across differing time periods in July/August of 2009 or June 2010

GLM	Factors	Baseline cortisol concentration (ng mL^{-1})		Post-stress cortisol concentration (ng mL^{-1})	
		$F_{(DF)}$	P value	$F_{(DF)}$	P value
Lake Opinicon	Model	$2.75_{(3, 28)}$	0.061	$1.80_{(3, 29)}$	0.17
	Capture method				
	Temperature				
	Capture × temperature				
Warner Lake	Model	$3.08_{(6, 25)}$	**0.004**	$1.99_{(6, 25)}$	0.11
	Time period	$1.61_{(3, 25)}$	0.21		
	Year	$0.34_{(1, 25)}$	**0.028**		
	Temperature	$13.16_{(1, 25)}$	**0.001**		
	Year × temperature	$0.35_{(1, 25)}$	**0.036**		
Between lakes	Model	$5.60_{(3, 80)}$	**0.001**	$12.08_{(3, 84)}$	**0.001**
	Temperature	$10.58_{(1, 80)}$	**0.001**	$8.71_{(1, 84)}$	**0.004**
	Lake	$1.54_{(1, 80)}$	0.36	$0.57_{(1, 84)}$	0.45
	Lake × temperature	$2.42_{(1, 80)}$	0.20	$1.60_{(1, 84)}$	0.21

Owing to unequal sample sizes, models were run separately for baseline and post-stress cortisol concentrations, and for effects within Lake Opinicon, within Warner Lake, and between lakes. Both lakes are located in Eastern Ontario. Significant effects are indicated by bold text
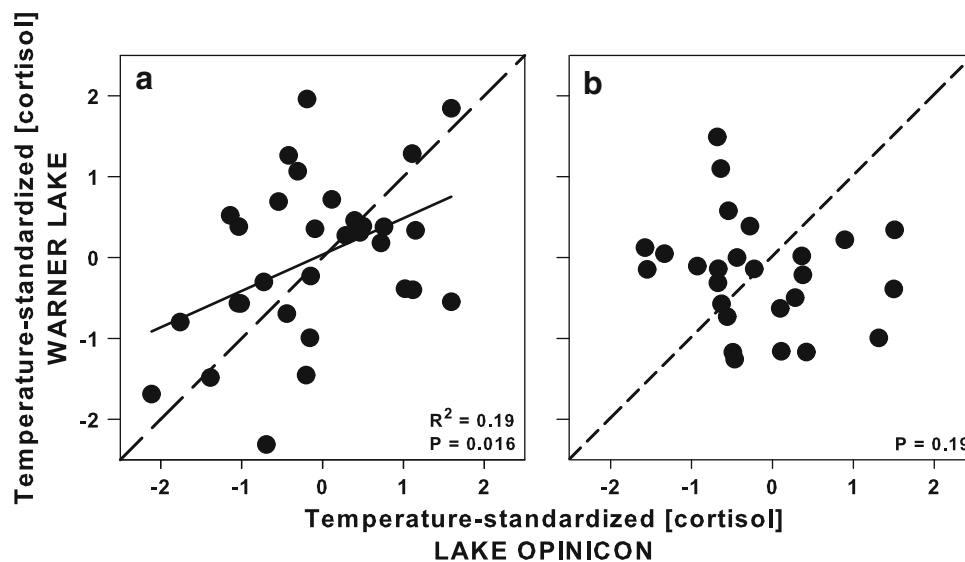

Fig. 2 The repeatability of post-stress cortisol concentrations (**a**) and baseline cortisol concentrations (**b**) within free-swimming individual wild largemouth bass (*Micropterus salmoides*) between sampling from Lake Opinicon (June 2009) and sampling from Warner Lake 6 weeks to ∼ 1 year later (July/August 2009 and June 2010). Regression analyses were conducted using the standardized residuals of the temperature × cortisol relationship for each lake to control for an effect of lake temperature. A significant regression model ($P < 0.05$; see text for regression line equations) indicates that the measured value is repeatable within an individual fish. The *dotted line* represents a hypothetical relationship between lakes given perfect repeatability

Discussion

This study aimed to assess the long-term repeatability of patterns of cortisol responses in a wild teleost fish in a natural environment. Using largemouth bass, we examined the repeatability of baseline and post-stress cortisol concentrations by re-capturing and re-sampling fish across years. Our results confirmed that post-stress cortisol levels in response to a standardized challenge are repeatable within an individual but failed to document temporal consistency within individuals with respect to baseline cortisol levels.

Effect of water temperature on circulating cortisol concentrations

It was necessary to control for the effect of water temperature on cortisol concentrations. Temperature profiles differed considerably between the two lakes; Warner Lake is dark-bottomed, small and shallow resulting in very high summer water temperatures (Hanson et al. 2007), whereas Lake Opinicon is much larger and deeper. All measures of cortisol were elevated in Warner Lake compared to Lake Opinicon, a difference that was attributed to water temperature. However, despite this positive relationship between cortisol measures and water temperature across lakes, post-stress cortisol levels were negatively correlated with temperature within each lake. These results are unexpected and inconsistent with previous studies on *Micropterus* spp. in the same region (O'Connor et al. 2011). In previous research, relationships between the magnitude of the stress response and temperature have been equivocal (Pickering 1992), with no effect of temperature (Barton and Schreck 1987), a positive association (Davis and Parker 1990), or a negative relationship (Strange 1980). Therefore, it seems as if this relationship is context dependent. In this study, samples were collected later in the summer and at warmer temperatures than those in the study of O'Connor et al. (2011). Therefore, acclimation to warmer temperatures in the later summer months may have contributed to the negative relationship between water temperature and cortisol levels. Throughout the spring, water temperatures rise rapidly and O'Connor et al. (2011) reported that *Micropterus* spp. increased their cortisol response to an acute stressor with temperature during this period. Later in the summer, increases in water temperature occur at a much slower pace and temperatures tend to stabilize by mid-July. As the summer progresses, fish may acclimatize to elevated temperatures such that cortisol responses to an acute stressor no longer exhibit the strong temperature sensitivity of the spring.

Are patterns of cortisol regulation repeatable?

We reveal post-stress cortisol concentrations to exhibit significant repeatability within individuals. Moreover, fish were captured in the same year as their relocation to the new lake (with ∼ 6 weeks acclimation time) as well as approximately 1 year later. This time between assessments did not affect consistency within an individual which emphasizes the finding that measures of post-stress cortisol concentrations are indeed an individual characteristic that is repeatable over the long term. However, the regression effect size, essentially the degree of repeatability, was lower than expected and considerably lower than repeatability statistics calculated for captive and wild populations

of birds (e.g. Romero and Reed 2008; Wada et al. 2008; Cockrem et al. 2009). The stress response however, is a dynamic trait influenced by many environmental factors (e.g. temperature) and it is impossible to control for all of these interacting variables. Sex, for example, is known to effect consistency of GCs (Wada et al. 2008) but as sex cannot be externally determined in largemouth bass, was not controlled for in this assessment. Indeed, we did see a large range of variability in post-stress cortisol concentrations when all fish experienced an identical acute stressor. Additionally, there was a change in habitat imposed in this experiment; study fish were relocated to a lake that while still suitable habitat for largemouth bass, differed considerably from their original environment. Along with differences in the physical environment (area, depth, substrate and temperature), Lake Opinicon was populated by a diversity of fish species, whereas Warner Lake exhibited low species diversity and fish numbers; the transferred fish undoubtedly became the largest in the lake. It is therefore likely that inter- and intra-specific competition and interactions would change in this new habitat. Handling, transport and relocation to a novel environment also has the potential to induce chronic stress (Barton and Iwama 1991; Dickens et al. 2010), which in turn can affect subsequent responses to an acute stressor (Schreck 2000). Thus, individual variability in the response to relocation may have contributed to the low effect size. Furthermore, although no significant differences in post-stress cortisol concentrations were detected across months or time periods, cortisol responses in fish are known to vary with both time of day and season (Barton 2002; Pankhurst 2011), potentially explaining some proportion of the variation observed in the regression of cortisol concentrations between lakes.

Baseline cortisol concentrations were not significantly repeatable. Baseline cortisol concentrations play a regulatory role in vertebrates, fluctuating with variability in the environment and modulating physiological and behavioral responses accordingly (Landys et al. 2006). Consistent variability in baseline cortisol concentrations are known to occur in fish [e.g. with feeding schedule (Bry 1982) and diel period (Lankford et al. 2003)]. Thus, a lower degree of repeatability is not unexpected. In great tits (*Parus major*), both baseline and post-stress GC concentrations were repeatable, but the coefficient of variation was greatest for baseline samples (Cockrem and Silverin 2002). There was also a greater effect of temperature on baseline compared to post-stress cortisol concentrations. Collectively, these results suggest that baseline cortisol concentration is not a trait repeatable within an individual but rather a trait that fluctuates with environmental changes. However, there are also problems associated with measuring low cortisol concentrations with a low degree of variability. The total range of variability of post-stress concentrations is

approximately 100-fold greater than baseline cortisol concentrations (all <10 ng mL^{-1}), making it harder to detect a significant regression. Additionally, the impact of assay error becomes greater as values near the detection limits of commercial kits where even small amounts of random variation in assay values could change the relative order among individuals (O'Connor et al. 2011; Romero and Reed 2008).

Conclusions

Post-stress cortisol concentrations, as well as the overall response (change from baseline to post-stress) were found to be repeatable once controlling for temperature. There are methodological implications of these results as most commonly the overall response (change from baseline to post-stress) is used in analyses, especially with mammalian and avian models. However, where baseline physiological state cannot be quantified or sampling an individual multiple times proves difficult, the results of the present study support the use of post-stress cortisol concentrations alone. Our findings also emphasize the importance of considering potential interacting environmental factors such as habitat variability and temperature when conducting analyses of cortisol levels in wild fish.

Most notably, we confirm that the magnitude of post-stress cortisol secretion is a consistent trait within the wild fish; the magnitude of cortisol elevation in response to an acute stressor is an individual and repeatable characteristic over the long term. The time between sampling also had no effect on consistency within an individual. We thus validate the use of this hormone at post-stress concentrations as a potential mediator of life history and reproductive trade-offs in wild fish, as is the case in other taxa (i.e. Wingfield et al. 1995; Angelier et al. 2007; Moore and Hopkins 2009). Further, the correlates of stress responsiveness observed in laboratory populations of fish (i.e. Pottinger and Carrick 2001; Sloman et al. 2001; Øverli et al. 2005) are likely are transferable to wild populations and conserved over the long-term.

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