

Sex-specific differences in cardiovascular performance of a centrarchid fish are only evident during the reproductive period

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Summary

1. Although in birds and mammals sex-specific differences in organismal performance and physiology are well documented, comparatively little is known about the influence of sex or reproductive status on fish performance or metabolism.
2. In this study, the resting cardiovascular performance of male and female Largemouth Bass *Micropterus salmoides* was contrasted across three seasons and different reproductive states including the spring when nesting males provide sole parental care. Doppler flow probes were used to monitor resting cardiac output (Q) and its two components (heart rate, f_H and stroke volume, SV_H).
3. During the spring when Largemouth Bass were engaged in reproduction (at 21 °C), parental male nesting fish had heightened resting cardiovascular rates (both Q and f_H) relative to non-nesting males and females. In the summer at higher water temperatures (24 °C), and in the autumn at water temperatures similar to the reproductive period (21 °C), resting cardiovascular variables were similar between sexes.
4. This study found that there are sex-based differences in fish physiological performance. However, the sex-specific differences were evident only during the reproductive period, and in particular for male fish actively engaged in the nesting phase of parental care, indicating a likely role of the endocrine system.

Key-words: Cardiac output, heart rate, Largemouth Bass, parental care.

Functional Ecology (2004) **18**, 398–403

Introduction

In studies of life history and ecology, some of the most simple and common categorical variables used as factors in analyses are the sex and reproductive status of the organism. Sex can typically be linked to dimorphisms in size, shape, age of maturation, energetics, longevity and behaviour (e.g. Short & Balaban 2003). In addition, physiological characteristics also vary between sexes, although existing studies are typically limited to mammals (Shechtman & Katovich 1993), and in particular, humans (Wells & Plowman 1983; Sanborn & Jankowski 1994). Most of the research on sex-specific physiological differences in lower vertebrates has focused on reptiles (e.g. Cullum 1998; Lailvaux, Alexander & Whiting 2003) with comparatively little effort devoted to understanding the role of sex on the physiology and performance of fishes.

One of the most well-studied and profound sex-specific physiological differences in humans is the cardio-respiratory system (Pate & Kriska 1984; Legato 2000; Kuo & Yang 2002). The cardio-respiratory system is directly linked to energetics and exercise performance. In humans, resting total metabolic rates are typically lower in females (Pate & Kriska 1984) whereas resting heart rates are typically higher (Bazett 1920). These patterns largely reflect differences in physiology (Pate & Kriska 1984; Legato 2000), morphology (Legato 2000), size (Wells & Plowman 1983; Pate & Kriska 1984), and the endocrine system and androgen concentrations (Mooradian, Morley & Korenman 1987). In fish, sex-specific variation in cardiovascular physiology has been documented in only a few instances (reviewed in Burggren 1997). Altimiras *et al.* (1996) observed different patterns of heart rate variability among male and female Atlantic Salmon *Salmo salar* and Davie & Thorarensen (1997) observed differences in atrial inotropic responses among male and female Rainbow Trout *Oncorhynchus mykiss*. However, neither of these studies determined if these sex-specific cardiovascular characteristics varied seasonally or with reproductive status.

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The objective of this study was to test the hypothesis that sex-specific differences exist in the cardiovascular performance of a freshwater teleost fish. Because cardiovascular performance can be altered experimentally through stimulation of the endocrine system (Davie & Thorarensen 1997), there was also merit in evaluating the prediction that sex-specific differences may be apparent only during the reproductive period. To test this hypothesis the cardiovascular performance of adult Largemouth Bass *Micropterus salmoides* was evaluated. Largemouth Bass reproduce in the spring with males providing sole parental care including aeration and defence of offspring in a nest for up to 4 weeks (Cooke, Philipp & Weatherhead 2002). This energetically costly activity requires frequent burst swimming and sustained high-level activity (Cooke *et al.* 2002) and thus relies heavily on the cardiovascular system to deliver oxygen to working tissue. As females do not assist with care, and because only some males in a given year will reproduce, this species serves as an excellent model to assess sex-specific variation in cardiovascular performance. Experiments were conducted at 21 °C in both the spring when bass would typically be engaged in reproductive activity, and in the autumn when fish are not engaged in reproductive activities. These periods were also contrasted with the postreproductive summer period when water temperatures were 24·5 °C. Assessments focused on resting cardiovascular values (cardiac output, Q , and its two components, heart rate, f_H , and stroke volume, SV_H) of field-acclimated individuals as they are ecologically relevant (Priede 1985) and easily measured indicators of overall animal metabolism (Satchell 1991; Webber, Boutilier & Kerr 1998).

Materials and methods

STUDY ANIMALS

All fish used for this study were captured from Lake Opinicon, near Kingston, Ontario. In the spring, females and non-nesting male fish were captured by rod and reel from regions identified by snorkellers as being unsuitable for nesting. Nesting male fish were individually identified by snorkellers and then targeted by anglers. Nesting male fish were restricted to those that had offspring that were not free-swimming, and were usually in the egg or wriggler stage (Cooke *et al.* 2002). Nesting and non-nesting fish were identified with different binary spine clips. The fish captured in the summer and autumn were not reproductively active and thus collections occurred throughout the lake. All fish were landed by the anglers within 20 s to minimize stress (Schreer, Cooke & McKinley 2001) and were then transported to the laboratory in large, aerated coolers (75 l).

In the laboratory, all fish were held in a large common tank (300 l). Flow-through lake water was provided for the fish so that they remained acclimated to field conditions including slight diel variations in temperature. Natural light through windows provided

seasonally appropriate photoperiods. While in captivity, food was withheld. All fish used in this experiment were handled under the following identical schedule: surgery was conducted 24 h after capture and resting cardiovascular rates were monitored 24 h after surgery. Post-mortem calibrations (described below) were conducted immediately following experimentation. All surgery was performed by one of three trained individuals and the same individual conducted all calibrations.

SURGERY AND INSTRUMENTATION

Each fish was anaesthetized prior to surgery with 60 p.p.m. clove oil (emulsified with ethanol, 9 : 1 ethanol : clove oil) for approximately 8 min, until the fish had lost equilibrium and was non-responsive. The anaesthetized state was maintained during surgery by continuously irrigating the gills with water containing a maintenance concentration of anesthetic (30 p.p.m. clove oil). Surgical procedure was identical to that described by Cooke *et al.* (2003b). Briefly, the ventral aorta was exposed and 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 several sutures. The cuff wires were 2 m in length and were potted in a silicone case to minimize tangling and to facilitate securing them to the side of the fish. The cuff was attached to the input cables at a position directly above the tank to permit the fish to swim freely within the confines of the tank. The entire procedure took approximately 15 min.

A flowmeter (545C-4 Directional Pulsed Doppler Flowmeter: Bioengineering, The University of Iowa, Iowa City, IA) and a digital strip-chart recorder (LabVIEW, Version 4·0·1, National Instruments Corporation, Austin, TX) were used to monitor cardiac function. Details on the apparatus and Doppler theory, as well as detail regarding the postexperimentation calibration procedure can be found elsewhere (see Schreer *et al.* 2001; Cooke *et al.* 2003b). Here, only fish that had acceptable calibrations that permitted the determination of actual flow rates were utilized. Reference flow rates were analysed with linear least squares regression. The ventricles were patted dry and weighed to the nearest 0·001 g with weights reported as relative ventricular mass (RVM).

EXPERIMENTAL PROTOCOL

Following surgery, individual fish were placed into a 70 l tank (50 cm × 50 cm) and monitored until they had regained equilibrium. Fish were allowed to recover from surgery and to acclimate to the tank for 24 h. Previous research on centrarchid fishes indicates that cardiovascular variables are recovered by 12 h postsurgery (Schreer *et al.* 2001; Cooke *et al.* 2003b). A darkened area covering approximately 30% of the tank provided

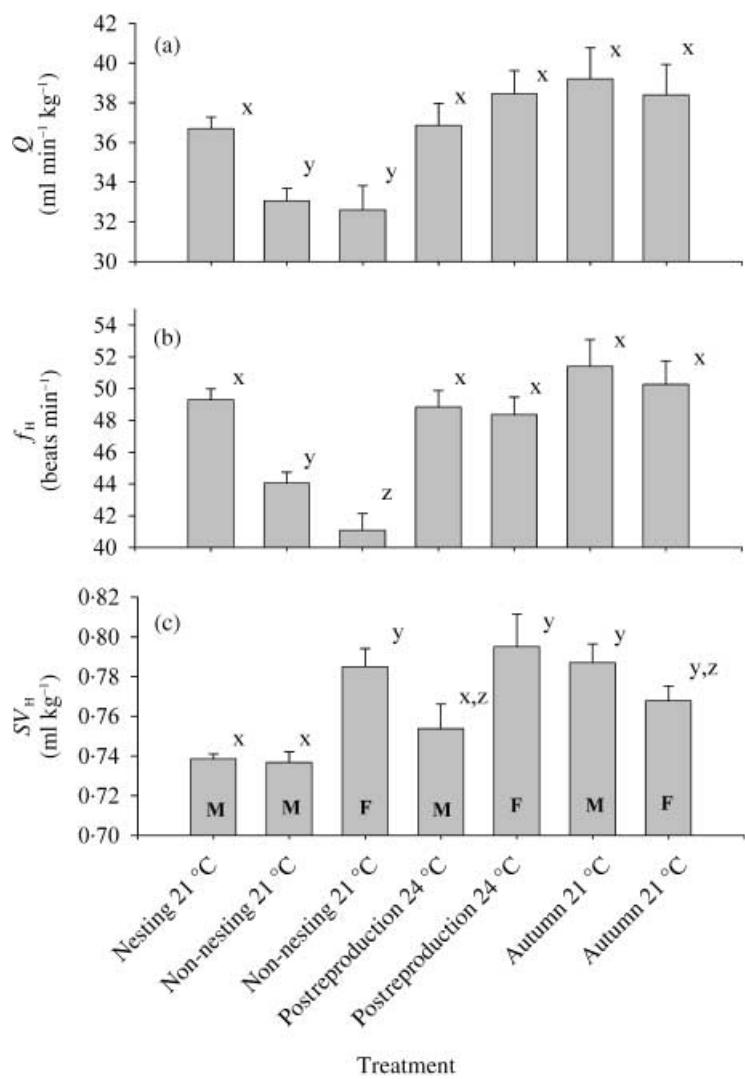


Fig. 1. Resting cardiovascular values for male (M) and female (F) Largemouth Bass of different seasons and reproductive statuses. Resting Q (Fig. 1a), f_H (Fig. 1b), and SV_H (Fig. 1c) varied significantly among treatments (Q , ANOVA, $F = 3.523$, $P = 0.004$; f_H , ANOVA, $F = 6.888$, $P < 0.0001$; SV_H , ANOVA, $F = 2.854$, $P = 0.015$). Statistical differences identified by the Tukey HSD post hoc test ($P < 0.05$) are denoted on the figure by dissimilar letters. Sample sizes and other details are available in Table 1.

cover and ensured that the fish were not disturbed by general laboratory activity. The experimental tanks were continuously supplied with lake water at ambient temperatures. Cardiovascular variables were recorded continuously for at least 2 h to obtain resting values. For the 4 h preceding, and during the recording of experimental data, access to the laboratory was restricted. Resting data used for analyses represented values determined for the lowest stable 10-min period. For instances where there was no variation in resting values, we used the last 10 min of recording. Water temperatures deviated less than 0.2 °C from desired temperatures during recordings.

Results

Despite some apparent differences in sex-specific performance (see below), none of these could be attributed to the size of the fish, and the relative ventricular mass did not vary among any of the different groups that we examined (Table 1).

During the spring at water temperatures of 21 °C, when Largemouth Bass engage in reproduction, clear differences in resting cardiovascular variables were observed. Cardiac output and f_H were 12–15% higher for nesting male Largemouth Bass than for female and non-nesting males (Fig. 1a,b). Conversely, the SV_H of female bass was 5% higher than that of both nesting and non-nesting bass (Fig. 1c). Following the reproductive period and when water temperatures warmed to 24.5 °C, SV_H was 3% lower for male bass than female bass. Despite that difference, Q and f_H were similar between sexes. In the autumn when water temperatures fell to temperatures that were the same as during the spring reproductive period (21 °C), no sex-specific differences in any of the resting cardiac variables were noted (Fig. 1a,b,c).

The patterns of male resting cardiac values varied seasonally. Resting Q and f_H for the nesting male bass at

Table 1. Meristics of Largemouth Bass used for experimentation. Standard errors (SE) in parentheses below mean values. No statistical differences were noted among treatments for total length (ANOVA, $F = 0.57$, $P = 0.682$), mass (ANOVA, $F = 0.45$, $P = 0.701$), or relative ventricular mass (RVM; ANOVA, $F = 1.10$, $P = 0.368$)

Sex and status	Temperature (°C)	Season	N	Mean total length ± SE (mm)	Mean mass ± SE (g)	Mean RVM ± SE
Nesting male	21	Spring	6	319 (17)	427 (21)	0.100 (0.008)
Non-nesting male	21	Spring	10	323 (9)	408 (16)	0.092 (0.009)
Female	21	Spring	8	342 (14)	468 (47)	0.090 (0.013)
Male	24.5	Summer	16	336 (13)	454 (30)	0.088 (0.009)
Female	24.5	Summer	22	350 (11)	477 (22)	0.093 (0.006)
Male	21	Autumn	8	327 (10)	436 (33)	0.090 (0.011)
Female	21	Autumn	8	335 (8)	462 (37)	0.093 (0.013)

21 °C was similar to resting values for males at 24.5 °C in the summer, and 21 °C in the autumn (Fig. 1a,b). However, the non-nesting male bass during the spring reproductive period had the lowest resting values for f_H and Q relative to males at other periods or reproductive states. These patterns were less apparent in SV_H , but there was a general trend towards increased SV_H as the season progressed (Fig. 1c). Females exhibited the lowest Q and f_H during the spring (Fig. 1a,b). These values were similar during the postreproductive period and the autumn. Stroke volume of female fish was stable across all seasons (Fig. 1c).

Discussion

These results clearly illustrate that during the reproductive phase, resting cardiovascular variables of Largemouth Bass do indeed differ between sexes. The most striking pattern was that nesting male bass had elevated Q and f_H relative to both females and non-nesting males. Elevated Q for nesting male bass would be advantageous during a period when fish are engaged in high-intensity locomotory activity associated with defence and aeration (Cooke *et al.* 2002). Elevated Q may enhance the ability of parental male bass to respond rapidly to threats, provide enhanced oxygen delivery and expedite clearance of by-products. This study did not examine the maximum cardiovascular performance to evaluate whether nesting bass were able to maintain cardiac scope (Farrell 1996) or whether it was diminished, potentially increasing risk of mortality (Priede 1977). However, if maximum cardiovascular performance did not increase, it is reasonable that fish with elevated resting f_H and Q would experience reductions in scope. Thus, although nesting males may benefit from increased resting values, there may also be costs associated with that strategy (i.e. reduced scope). High levels of locomotory activity associated with parental care (Cooke *et al.* 2002) may further compress cardiac scope. As such, the cardiovascular system may constrain parental care investment and should be considered in the context of trade-offs between current and future reproduction.

Consistent with the prediction, sex-specific differences in Q and f_H during the reproductive period were observed, but these differences were not maintained postreproduction (summer at 24.5 °C), or in the autumn when water temperatures were identical to that of the reproductive period (21 °C). In other animals, sex-specific differences in performance are apparent throughout the year, not only during the reproductive period as noted in lizards for resting metabolic rate (e.g. Garland & Else 1987; Cullum 1998) and locomotory performance (e.g. Cullum 1998; Lailvaux *et al.* 2003).

The sex-specific differences in cardiac performance observed in this study during the reproductive period probably reflect endocrine alterations associated with preparation for reproduction and in the case of the male, the provision of parental care. A recent assessment

of the reproductive cycle of the Largemouth Bass (Florida subspecies *M. salmoides floridanus*) revealed that several hormones are elevated in male fish during the reproductive period, including 11-ketotestosterone (Gross *et al.* 2002). To date, most sex-specific differences in performance have been attributed to the endocrine system. In fish, for example, Rainbow Trout implanted with 11-ketotestosterone exhibited increased myocardial mass and presumed increases in cardiac performance based upon *in vitro* heart preparations (Franklin & Davie 1992; Davie & Thorarensen 1997). Similar patterns are observed seasonally in wild Rainbow Trout with increased circulating levels of androgens and ventricular hypertrophy (Thorarensen, Knight & Davie 1996). Rainbow Trout do not provide parental care, but the enhanced cardiovascular performance could facilitate migration or enhance the ability of fish to deal with competition for mates or reproductive territories. Similar patterns of endocrine involvement are observed in other animals. For example, John-Alder *et al.* (1996) noted that testosterone implants in male lizards increased exercise endurance and cardiac muscle mass. In some animals with internal fertilization for which females carry developing offspring (i.e. become pregnant), reproductive hormones associated with reproductive state can enhance physiological performance and gas exchange. For example, female Northern Pacific Rattlesnakes, *Crotalus viridis*, exhibit increased oxygen affinity of red blood cells (Ragsdale & Ingemann 1991) and in domesticated cats, *Felis catus*, oestrogen and progesterone alter cardio-respiratory performance during hypoxia challenges (Hannhart, Pickett & Moore 1990). Interestingly, there are also instances where there are no differences in metabolic rates that can be attributed to the endocrine system (e.g. Western Whiptail Lizards, *Cnemidophorus tigris*; Dohm *et al.* 1998).

It is not clear why Q and f_H were higher for females and non-nesting males in the autumn at 21 °C relative to the spring at similar temperatures. In the spring, fish experience increasing water temperatures and acclimate to these higher temperatures. In the autumn, fish were experiencing cooling water temperatures after being acclimated to higher summer temperatures. Based upon a large body of thermal acclimation literature, one would predict that metabolic rates and hence Q would be higher at 21 °C during periods of warming than during periods of cooling (Fry 1971; Lemons & Crawshaw 1985). Since the autumn period is important for food acquisition and accumulation of energy stores to survive the impending winter for Largemouth Bass (Fullerton *et al.* 2000), there may be an overriding need to maintain higher rates of cardiovascular activity during that period to provide additional foraging opportunities until water temperatures fall to levels where activity is known to decrease (i.e. $\sim < 10$ °C; Lemons & Crawshaw 1985; Kolok 1992). The resetting of pacemaker tissue to a lower rate may also require longer periods or lower temperatures (Farrell 1996).

At cool water temperatures, it is presumed that the heart experiences ventricular hypertrophy resulting in increased SV_H as has been observed for Largemouth Bass at 3 °C (Cooke *et al.* 2003a). There was no evidence of such changes in cardiac morphology in the current study and overall, SV_H only varied by 8% between the most extreme treatments. Seasonal effects that are unrelated to temperature have also been documented elsewhere, including variation in the haemodynamics of amphibians (Pelster & Burggren 1991) and variation in swimming performance of Largemouth Bass (Kolok 1991) and respiration of Pumpkinseed *Lepomis gibbosus* (Burns 1975; Evans 1984).

Organisms with parental care provide a unique opportunity to contrast the physiological ecology and energetics of different sexes. Because sex can generally be determined easily in many animals, it is possible to either include it as a factor in analyses or conversely, to focus research activities on a single sex to control for variation associated with that factor. As evidenced by this research, sex-specific differences in physiology may only be apparent during some seasons, probably during the reproductive period as a result of seasonal alterations to the endocrine system.

Acknowledgements

This study was conducted in accordance with the regulations and policies of the University of Illinois Office of Laboratory Animal Research and the Canadian Council for Animal Care guidelines administered by the Queen's University Animal Care Committee. Kate Deters and Emily Grant assisted with surgical procedures and data management and David Philipp and Jason Schreer provided additional support. The staff of the Queen's University Biological Station kindly facilitated this research. Financial assistance was provided by the Illinois Natural History Survey, Illinois Department of Natural Resources, University of Illinois, and the Natural Sciences and Engineering Research Council of Canada.

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Received 29 October 2003; revised 29 January 2004; accepted 5 February 2004