

Why Does Size Matter? A Test of the Benefits of Female Mate Choice in a Teleost Fish Based on Morphological and Physiological Indicators of Male Quality

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Accepted 1/3/2009; Electronically Published 9/21/2009

ABSTRACT

In female mate choice, a female chooses a reproductive partner based on direct or indirect benefits to the female. While sexual selection theory regarding female mate choice is well developed, there are few mechanistic studies of the process by which females evaluate reproductive partners. Using paternal-care-providing smallmouth bass (*Micropterus dolomieu*) as a model, the purpose of this study was to determine the relationship between female mate choice and the morphological and physiological status of chosen males. This was accomplished by locating nests within 1 d of spawning and categorizing brood size (indicator of female mate choice). This was followed by capture of parental males, which were blood sampled (for nutritional analyses), digitally photographed (for morphometric analyses), and released. Principal components analysis (PCA) of morphometric measurements described 72.7% of the variance associated with body morphology and generated three principal components (PCs) indicative of fusiform body shape, increased posterior size, and body stoutness. PCA of nutritional indicators described 75.4% of the variance associated with physiological metrics and generated two PCs indicative of plasma mineral content (Ca^{++} and Mg^+) and energetic condition (total protein, triglyceride, and cholesterol). Male total length and body stoutness were the only significant predictors of female mate choice. Interestingly, no nutritional indicators were predictive of female mate choice, and there were no direct relationships between morphological variables and nutritional physiology indicators. Further research is needed to elucidate the mechanistic relationships between morphology and nutritional physiology (especially in relation to the parental-care

period) of individual fish to determine the basis of female mate preference.

Introduction

The role and consequences of sexual selection have been extensively discussed in the field of evolutionary biology (Darwin 1871; Andersson 1994; Johnstone 1995; Andersson and Iwasa 1996; Lailvaux and Irschick 2006). Biological diversity ranging from the gross scale of speciation (Coyne and Orr 2004) to the fine scale of differences in body ornaments or plumage coloration (Berglund et al. 1996) is thought to be a direct result of sexual selection. Female mate choice, whereby a female selects a mate based on perceived benefits to the female, is a key process within the realm of sexual selection (Andersson 1994). Females may choose a mate based on direct material benefits, such as nuptial gifts or parental care from the male (Kirkpatrick 1982; Reynolds 1996; Vahed 1998; Pizzari 2003), or on secondary sexual characteristics that are indicative of indirect benefits, such as good genes or superior health (Andersson 1994; Andersson and Iwasa 1996; Kirkpatrick 1996; Møller and Alatalo 1999), that should benefit offspring survivability. However, recent syntheses have noted that most studies take an ethological or life-history approach, which leaves many mechanistic questions unanswered (Lailvaux and Irschick 2006; Irschick et al. 2007). In particular, work on female mate choice in a number of species across multiple taxa has repeatedly elucidated traits in males that females choose that are correlated with reproductive success, although rarely is the mechanistic basis of these correlations clear (Irschick et al. 2007).

Smallmouth bass (*Micropterus dolomieu*), a teleost fish species, serve as an interesting model to study female mate choice because of their protracted paternal care period and lack of exaggerated male secondary sexual characteristics. In spring, when the water temperature reaches $\sim 15^\circ\text{C}$, male bass construct nests in the littoral zone that are the site of courtship and egg deposition (Coble 1975; Ridgway 1988). After spawning, females leave the vicinity of the nest, and the male assumes the role of sole parental caregiver (Cooke et al. 2006). Parental care, consisting of brood maintenance and defense, typically lasts 1 mo and is highly energetically demanding because males are extremely active and unable to forage normally (Hinch and Collins 1991; Mackereth et al. 1999; Cooke et al. 2002). During this period, parental-care activities are powered primarily by endogenous energy reserves accrued before the preceding win-

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ter (Mackereth et al. 1999). Parental-care theory suggests that if parental male energy levels decrease to a point that could threaten the potential for future reproduction, the individual should abandon the current brood (Trivers 1972; Sargent and Gross 1986). Previous work has indicated that male body size and body energy reserves are positively related at the onset of parental care and that large males with high energy reserves (assessed using proximate body composition analysis) provide parental care for longer durations when compared with smaller counterparts (Mackereth et al. 1999). Based on this finding, it has been speculated that female preference for large males is due to the ability of large males to use more energy reserves in parental care than smaller conspecifics (Wiegmann and Baylis 1995). Additionally, multiple studies have noted that brood size is positively related to male size (Philipp et al. 1997; Suski and Philipp 2004; Barbosa and Magurran 2006). Because offspring survival is enhanced by parental-care performance (Sargent and Gross 1986), female choice for male characteristics demonstrative of the ability to perform parental care for extended time periods (i.e., larger body size) would increase female reproductive success.

The goal of this study was to determine the relationships between morphological measures, nutritional physiology indicators, and female mate choice (measured as number of eggs in the nest of an individual male) at the onset of parental care in wild smallmouth bass. We predicted that females would choose males in better condition (indicated by increased plasmaborn indicators of energetic and nutritional status) because these males would be most likely to successfully raise a brood and represent the best choice for female investment. We predicted that female choice would be based on male size (larger males with stouter body shapes preferred) because overall body size is an honest signal of energy reserves in parental bass (Mackereth et al. 1999). Consequently, larger, more preferred males should also show increased biochemical indicators of nutritional and energetic status compared with less preferred males.

Material and Methods

Field Techniques

This study was carried out from May 24 to June 5, 2007, on Charleston Lake, eastern Ontario, Canada (44°32'14"N, 75°59'48"W). To eliminate confounding factors associated with a trend in which larger males spawn earlier during the spawning period (typically lasting 3 wk [Wiegmann et al. 1992; Kubacki et al. 2002]), all sampling of males was conducted during the first 3 d of spawning in a lake where we had previously observed a wide range of size among parental males even early in the spawning period. At the beginning of every sampling day (May 24–26), snorkel surveys of the littoral zone (typically less than 1-m water depth) were conducted to locate smallmouth bass that were actively guarding nests with newly deposited eggs (1 or 2 d old). Upon locating an active bass nest, the snorkeler placed a numbered polyvinyl chloride tile near the nest and recorded nest location, nest depth, and number of eggs within the nest (visual, categorical assessment ranging from low of 1

to high of 5; Suski and Philipp 2004). Fish were then captured using heavy-action recreational fishing equipment that could be used to angle fish from the boat or underwater (by the diver). All fish were landed within 20 sec of hooking to minimize nonparental-care-related anaerobic exercise. Upon capture, fish were placed supine in a foam-lined sampling trough filled with fresh lake water and quickly blood sampled by the caudal puncture method using a 1.5-inch, 21-gauge vacutainer syringe (Houston 1990). Approximately 1.5 mL of blood was collected in a 3-mL vacutainer containing lithium heparin to prevent blood coagulation and was then placed into a water-ice slurry. Additionally, total length was measured, and presence or absence of injury was noted. Individuals were transferred to a flat, foam-lined, spatially referenced tray and digitally photographed (Pentax Optio WPI, 6 megapixel, Pentax Imaging, Golden, CO) from 0.60 m directly above. Individuals were then released within 5 m of the nest. During the sampling procedure (191 ± 5 s), a snorkeler remained at the nest site and defended the brood until the male returned (typically in under 5 min). In total, 86 male bass were sampled. Blood samples were centrifuged (after sampling six fish) at 10,000 g for 5 min (Clay Adams Compact II Centrifuge), and plasma samples were stored in liquid nitrogen for subsequent analysis. Snorkel surveys to determine presence or absence of the male were conducted 7 and 10 d after sampling, which roughly corresponded to the end of the larval stage of brood development. Presence of the male on the nest at this time was used as a measure of parental-care success because after the eggs hatch, parental males provide less vigilant parental care and are more prone to abandon the nest as the brood becomes increasingly independent (Sargent and Gross 1986; Ridgway 1988; Cooke et al. 2002).

Lab Analyses

Samples were analyzed for concentrations of various bloodborne biochemical constituents that have been previously identified as indicative of individual energetic and nutritional status (total protein, triglycerides, and cholesterol) as well as dietary minerals (phosphorus, magnesium, and calcium; Wagner and Congleton 2004; Congleton and Wagner 2006; Hanson and Cooke 2009). All biochemical analyses were conducted on a Roche Hitachi 917 analyzer (Basel, Switzerland) and based on the International Federation of Clinical Chemistry and Laboratory Medicine (IFCC) standard reference model. All assays followed procedural guidelines for standardization and quality assurance established by the Veterinary Laboratory Association Quality Assurance Program, College of American Pathologists, and the Canadian Food Inspection Agency External Proficiency Panel.

Digital Image Analysis

Digital images of individuals were measured for a suite of morphological characteristics (Fig. 1) using the program ImageJ (Abramoff et al. 2004). The following metrics, as modified from Hawkins and Quinn (1996) and detailed in Hanson et al.

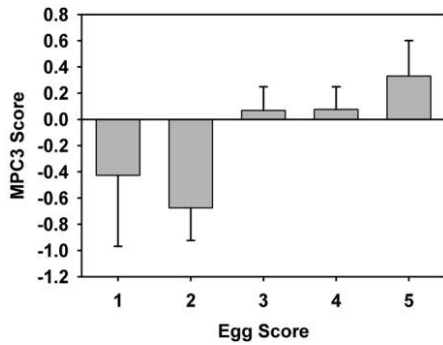


Figure 1. Relationship between morphological principal component 3 (indicative of overall male body stoutness) and female mate preference (as measured by brood size [egg score ranging from a low of 1 to a high of 5]).

(2007), were quantified to the nearest mm: head depth 1 (HD1); head depth 2 (HD2); body depth at posterior aspect of the dorsal fin (PELVDF); origin of the pelvic fin to posterior aspect of the soft dorsal fin (PELVSD); origin of the anal fin to posterior aspect of the soft dorsal fin (ANSDF); origin of the anal fin to the top of caudal flexure (ANC1); insertion of the anal fin to bottom of the caudal flexure (ANC2); posterior aspect of the soft dorsal fin to top of the caudal flexure (SDC1); posterior aspect of the soft dorsal fin to bottom of the caudal flexure (SDC2); and caudal flexure depth (CFD).

Statistical Analyses

To remove the possible effects of allometric growth on morphological measurements (Table 1), the residuals of the least

squares linear regression of log-transformed traits on log-transformed fish lengths were used in subsequent principal components analysis (PCA) with varimax rotation (Kaiser 1960; Tabachnick and Fidell 1989; Hawkins and Quinn 1996; Ojanguren and Brana 2003). The Kaiser-Guttman criteria (or latent root criteria) was used to determine which principal factors would be retained for later analysis (Kaiser 1960). Only principal factors with eigenvalue scores of greater than 1 were used to determine the relationship between morphology and egg scores (Kaiser 1960). Physiological variables (Table 2) were subjected to PCA in the same manner as described above (Kaiser 1960; Tabachnick and Fidell 1989).

To determine which traits female smallmouth bass preferred, a nominal logistic regression of egg score by principal components (PCs) from both morphological and physiological measures as well as total length was performed (Zar 1999). Least squares linear regression was employed to determine whether there was a relationship between morphological and physiological variables (as represented by the above-derived PC scores as well as total length; Zar 1999). To determine whether there were differences in parental-care success between individuals of different sizes, the mean size of successful parental males was compared with the mean size of parental males who abandoned their brood by means of a *t*-test (Zar 1999). To aid in data interpretation, post hoc power analyses were conducted using observed effect size and variance (Thomas 1997). All analyses were performed in the statistical package JMP version 7.0 (SAS Institute, Cary, NC), and the level of significance for all tests (α) was assessed at 0.05. All values presented represent means \pm SE unless otherwise noted.

Table 1: Morphological measurements (mean \pm SD) measured from nest-guarding male smallmouth bass at the commencement of parental care in Charleston Lake, Ontario, separated by brood size

Measurement	ES 1 (N = 5)	ES 2 (N = 10)	ES 3 (N = 22)	ES 4 (N = 33)	ES 5 (N = 17)
HD1	5.1 \pm .8	6.2 \pm .9	6.8 \pm 1.0	6.5 \pm .8	7.2 \pm .6
HD2	8.5 \pm 1.2	10.6 \pm 1.4	11.7 \pm 1.7	11.5 \pm 1.4	12.5 \pm 1.0
PELVDF	9.0 \pm 1.0	11.2 \pm 1.5	12.4 \pm 1.9	12.3 \pm 1.6	13.3 \pm 1.2
PELVSD	14.8 \pm 1.1	18.8 \pm 2.7	19.9 \pm 3.0	19.9 \pm 2.5	21.4 \pm 2.0
ANSDF	7.4 \pm .6	9.4 \pm 1.2	10.0 \pm 1.4	10.2 \pm 1.2	10.9 \pm .9
ANC1	11.3 \pm .6	13.8 \pm 1.2	14.3 \pm 1.7	14.4 \pm 1.5	15.4 \pm 1.2
ANC2	9.5 \pm .2	11.5 \pm 1.2	11.7 \pm 1.4	11.9 \pm 1.3	12.5 \pm 1.4
SDC1	5.4 \pm .8	6.2 \pm .8	6.6 \pm 1.2	6.7 \pm .8	6.9 \pm 1.0
SDC2	6.9 \pm .8	8.2 \pm .9	8.6 \pm 1.2	8.8 \pm 1.0	9.3 \pm 1.1
CFD	4.2 \pm .5	5.2 \pm .5	5.4 \pm .7	5.5 \pm .7	5.8 \pm .6
Total length	328.2 \pm 23.7	398.5 \pm 43.8	423.9 \pm 51.1	418.5 \pm 47.4	446.5 \pm 37.1

Note. Egg score (ES) ranges from a low of 1 to a high of 5. Morphological measurements were modified from Hawkins and Quinn (1996) and are detailed in Hanson et al. (2007). Measurements were quantified to the nearest millimeter and are abbreviated as follows: head depth 1 (HD1); head depth 2 (HD2); body depth at posterior aspect of the dorsal fin (PELVDF); origin of the pelvic fin to posterior aspect of the soft dorsal fin (PELVSD); origin of the anal fin to posterior aspect of the soft dorsal fin (ANSDF); origin of the anal fin to the top of caudal flexure (ANC1); insertion of the anal fin to bottom of the caudal flexure (ANC2); posterior aspect of the soft dorsal fin to top of the caudal flexure (SDC1); posterior aspect of the soft dorsal fin to bottom of the caudal flexure (SDC2); caudal flexure depth (CFD).

Table 2: Physiological measurements (mean \pm SD) measured from nest-guarding male smallmouth bass at the commencement of parental care in Charleston Lake, Ontario, separated by brood size

Measurement	ES 1 (N = 5)	ES 2 (N = 10)	ES 3 (N = 22)	ES 4 (N = 33)	ES 5 (N = 17)
Calcium (mmol/L)	2.60 \pm .35	2.70 \pm .22	2.62 \pm .30	2.66 \pm .30	2.70 \pm .31
Magnesium (mmol/L)	1.07 \pm .07	1.24 \pm .07	1.07 \pm .15	1.17 \pm .13	1.20 \pm .19
Phosphorus (mmol/L)	1.40 \pm .10	1.55 \pm .34	1.41 \pm .25	1.37 \pm .30	1.35 \pm .22
Total protein (g/L)	39.00 \pm 6.92	43.40 \pm 4.14	41.18 \pm 6.10	41.90 \pm 5.62	43.88 \pm 5.86
Triglyceride (mmol/L)	2.79 \pm 1.03	2.90 \pm .84	2.97 \pm .88	3.18 \pm .83	3.07 \pm .95
Cholesterol (mmol/L)	12.00 \pm 4.09	12.8 \pm 1.51	12.38 \pm 2.75	13.51 \pm 2.85	14.83 \pm 3.38

Note. Egg score (ES) ranges from a low of 1 to a high of 5.

Results

Principal Components Analyses

PCA on morphological measurements produced three factors describing 72.7% of the variance in the morphological variables surveyed in this study (Table 3). Morphological PC1 (MPC1) was characterized by high positive-factor loadings for PELVSD, ANSD, ANC1, ANC2 and CFD (Table 3), representing a fusiform body shape and accounting for 26.6% of the variance. SDC1 and SDC2 had high positive-factor loadings for morphological PC2 (MPC2), while PELVSD had a high negative-factor loading (Table 3). This factor accounted for 22.7% of the variance and mainly described the length and depth of the caudal region (potential for propulsion ability). Lastly, morphological PC3 (MPC3) accounted for 23.4% of the variance and described overall body stoutness with high positive-factor loadings for HD1, HD2, PELDVF, and ANSD (Table 3). PCA of physiological variables produced two factors describing 65.5% of the variation in physiological measurements from this study (Table 4). Physiological PC1 (PPC1) was characterized by high factor loadings for Ca⁺⁺, Ma⁺, P, and total protein and represented plasma mineral content (Table 4). Physiological PC2 (PPC2) was characterized by high factor loadings for total protein, triglycerides, and cholesterol and represented plasma lipid content (Table 4).

Correlates of Female Mate Choice

Overall, only 24% of the variance associated with female mate choice was described by the variables included in this study (nominal logistic regression: $df = 24$, $\chi^2 = 57.65$, $P < 0.001$, observed power = 0.98). MPC3 (body stoutness; nominal logistic regression: $df = 4$, $\chi^2 = 9.60$, $P = 0.048$) was positively correlated with female mate choice (Table 5; Fig. 1). Total length was also positively correlated with female mate choice (nominal logistic regression: $df = 4$, $\chi^2 = 32.79$, $P < 0.001$; Table 5; Fig. 2). Interestingly, no physiological variables were significantly predictive of egg score (Table 5), and statistical power for the nominal logistic regression was high (observed power = 0.98). Because there was no direct relationship between female mate choice and biochemical indicators of nutritional status, we investigated the possibility that physiological variables were directly influencing morphological PC scores. However, there

were no significant relationships between either PPC1 or PPC2 and any of the morphological variables included in this study, though the observed power of these analyses was generally low (Table 6). There were no differences in size between fish that abandoned the brood prematurely (410 ± 20 mm) and fish that successfully raised the brood (418 ± 6 mm; t -test: $df = 85$, t value = 0.49, $P = 0.63$; Table 7). Additionally, there were no relationships between any of the morphological or physiological metrics and brood abandonment, though the observed power of these analyses was generally low (Table 7).

Discussion

Mate choice is a complex behavior that requires a female to be able to reliably evaluate the direct or indirect benefits of mating with a particular male (Andersson 1994; Lailvaux and

Table 3: Loading of the morphological measurements into three principal factors by principal components analysis (MPC1, MPC2, MPC3)

Measurement	MPC1	MPC2	MPC3
Eigenvalue	2.660	2.269	2.342
HD1	-.308	.113	.665
HD2	.051	.098	.895
PELDVF	.133	.028	.850
PELVSD	.592	-.527	.200
ANSD	.633	-.292	.537
ANC1	.849	.177	.009
ANC2	.751	-.062	-.099
SDC1	.026	.932	.085
SDC2	.157	.911	.166
CFD	.695	.382	-.054
Variance explained (%)	26.6	22.7	23.4

Note. Variables that contribute maximally to each factor are in bold. Morphological measurements were modified from Hawkins and Quinn (1996) and are detailed in Hanson et al. (2007). Measurements were quantified to the nearest millimeter and are abbreviated as follows: head depth 1 (HD1); head depth 2 (HD2); body depth at posterior aspect of the dorsal fin (PELDVF); origin of the pelvic fin to posterior aspect of the soft dorsal fin (PELVSD); origin of the anal fin to posterior aspect of the soft dorsal fin (ANSD); origin of the anal fin to the top of caudal flexure (ANC1); insertion of the anal fin to bottom of the caudal flexure (ANC2); posterior aspect of the soft dorsal fin to top of the caudal flexure (SDC1); posterior aspect of the soft dorsal fin to bottom of the caudal flexure (SDC2); caudal flexure depth (CFD).

Table 4: Loading of the physiological measurements into three principal factors by principal components analysis (PPC1, PPC2)

Measurements	PPC1	PPC2
Eigenvalue	2.726	1.478
Calcium (mmol/L)	.896	.183
Magnesium (mmol/L)	.777	.188
Phosphorus (mmol/L)	.582	-.253
Total protein (g/L)	.700	.593
Triglyceride (mmol/L)	-.065	.732
Cholesterol (mmol/L)	.202	.796
Variance explained (%)	45.4	20.1

Note. Variables that contribute maximally to each factor are in bold.

Irschick 2006; Irschick et al. 2007). For this to occur, there needs to be some cue that the female favors that relates to the status of the male (Wiegmann and Baylis 1995; Maynard Smith and Harper 2003). In this study, females preferred larger males as evidenced by the positive relationship between brood size and multiple metrics of body shape (total length, body stoutness, size of the posterior end of the body). These findings are consistent with previous studies that have linked brood size to male size in smallmouth bass (Ridgway 1988; Wiegmann and Baylis 1995; Mackereth et al. 1999; Suski and Philipp 2004). Although the relationship between male body size and brood size was noted in these studies, the mechanistic rationale behind the preference for larger males was not tested. In our study, we predicted that larger males would be preferred because they would be in better energetic and nutritional condition at spawning and therefore would be able to withstand the nutritional declines associated with parental care and would not abandon the brood.

Preference for larger males could be related to the energetic dilemma encountered by a parental male bass. The parental-care period is characterized by intense activity, such as brood defense and maintenance (Hinch and Collins 1991; Cooke et al. 2002), that is powered through endogenous energy reserves (Mackereth et al. 1999) because foraging is limited to a small area around the nest and prey intake is greatly curtailed (Hinch and Collins 1991; Cooke et al. 2002). As a result, premature exhaustion of endogenous energy reserves renders the male unable to continue parental care, and the male will abandon the current brood (which will be consumed by brood predators) as an act of self preservation to maintain the possibility for future reproductive activity (Trivers 1972; Sargent and Gross 1986; Philipp et al. 1997). Previous work has noted that larger males (as measured by total length) typically have increased energy stores when compared with smaller males at the onset of spawning, although the relationship to female preference was not investigated (Ridgway and Friesen 1992; Mackereth et al. 1999). Additionally, it has been theorized that large males would be preferred because the loss of energy reserves associated with parental care would be a lower proportion of overall endogenous energy reserves than that of small conspecifics par-

taking in the same behavior (Shuter et al. 1980; Wiegmann and Baylis 1995). In previous studies, circulating levels of triglycerides and cholesterol have been shown to decline in response to starvation in Pacific salmonids (Wagner and Congleton 2004; Congleton and Wagner 2006) and during parental care in black bass (Hanson and Cooke 2009). Additionally, fluctuations in dissolved minerals due to starvation have been noted in parental black bass because minerals acquired from forage were no longer available and the body depleted internal resources (Hanson and Cooke 2009). In this study, no biochemical measures of nutritional or energetic status as measured at the beginning of parental care were directly reflective of female preference (Table 5). Additionally, there were no correlations between morphometric measures and biochemical measures of nutrition or energetic status (Table 6). The lack of a relationship between female preference and circulating indicators of energetic and nutritional status may be the result of two situations. First, morphology may actually not be an honest signal of male energetic status as predicted, and female preference for larger males in this system would not be indicative of energetic or nutritional differences between males at the commencement of parental care. Second, all spawning males may initiate spawning with similar levels of mobilized lipids and minerals (as measured in this study), but only larger males with increased endogenous energy reserves (Mackereth et al. 1999) may be able to maintain these levels across the entirety of parental care. Currently, the exact relationship between plasmaborne nutritional indicators and total endogenous energy reserves as well as differences in rates of change of circulating indicators of nutrition between different sizes of fish is not clearly understood, largely because of the challenges of obtaining estimates of gross somatic energy without lethally sampling fish. However, for the female, there are also other potential direct or indirect benefits of choosing a large male.

The quality of parental care that offspring receive may be a possible indirect benefit gained by the female for choosing a larger male mate. Parental-care activities increase offspring survival at the cost of adult condition (Gross and Sargent 1985; Sargent and Gross 1986; Clutton-Brock 1991). Larger males

Table 5: Results of simple nominal regression of both morphological principal components (MPC) and physiological principal components (PPC) versus female mate choice (as measured by brood size of individual parental male smallmouth bass)

Source	χ^2	<i>P</i>
MPC1 (large posterior)	9.40	.051
MPC2 (fusiform)	2.22	.696
MPC3 (stoutness)	9.60	.048
PPC1 (minerals)	3.45	.486
PPC2 (lipids)	5.12	.277
Total length	28.08	<.001

Note. For each source, *df* = 4. Bold type indicates significant differences at α = 0.05.

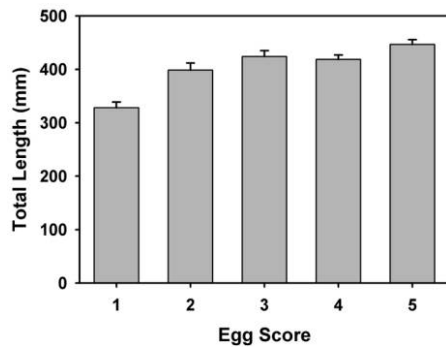


Figure 2. Relationship between parental male smallmouth bass total length and female mate preference (as measured by brood size [egg score ranging from a low of 1 to a high of 5]).

have been shown to provide more rigorous parental care for longer durations of time than small males because larger fish are in better condition at the commencement of spawning (Wiegmann and Baylis 1995; Mackereth et al. 1999). Additional work has shown that large male bass are more aggressive nest defenders, though this finding is confounded by the fact that larger males typically have a larger parental investment due to increased brood sizes (Suski and Philipp 2004). Although we had no direct measure of quality of parental care, we did monitor premature nest abandonment by all males in this study, and there were no relationships between the size of the parental male and premature nest abandonment rates. It is possible that large males are at an advantage when defending the brood against possible predation because large male bass could potentially consume small brood predators themselves. Additionally, as large males typically spawn first, these individuals may monopolize optimal spawning and rearing territories (Ridgway et al. 1991; Wiegmann et al. 1992), although currently, no studies have documented differences in female preference based on male spawning location and habitat.

Table 6: Relationships between morphological principal components (MPC) and physiological principal components (PPC) in parental smallmouth bass

Relationship	<i>F</i>	<i>P</i>	Observed Power
PPC1 (minerals):			
MPC1 (large posterior)	.95	.33	.16
MPC2 (fusiform)	.16	.69	.07
MPC3 (stoutness)	<.001	.99	.05
Total length	.22	.64	.07
PPC2 (lipids):			
MPC1 (large posterior)	.13	.72	.07
MPC2 (fusiform)	.75	.39	.14
MPC3 (stoutness)	1.59	.23	.24
Total length	1.29	.26	.22

Note. For each relationship, *df* = 1, 84.

Table 7: Relationships between morphological principal components (MPC) and physiological principal components (PPC) and the presence of the parental male smallmouth bass on the nest 10 d after sampling

Source	<i>df</i>	<i>t</i>	<i>P</i>	Observed Power
MPC1 (large posterior)	85	1.66	.10	.38
MPC2 (fusiform)	85	1.19	.24	.22
MPC3 (stoutness)	85	-.67	.50	.10
PPC1 (minerals)	84	-.27	.79	.06
PPC2 (lipids)	84	.10	.92	.05
Total length	85	.49	.63	.08

Although not tested in our study, two final mechanisms may account for the correlation between body size and female preference. First, larger body size may be indicative of superior genetic quality of the male, and females that successfully mate with large males then indirectly benefit from having offspring that inherit the favored genotype of the father (Andersson 1994; Møller and Alatalo 1999; Hunt et al. 2004; Neff and Pitcher 2005). Second, because fish exhibit indeterminate growth, size is typically an indication of age of the individual. A female preference for increased male body size may be a result of a preference for males that would have previous parental-care experience and could possibly be dominant in their mating system (Wiegmann et al. 1992; Jacob et al. 2007). The advantages of mating with an older male, however, are not clearly understood.

Mate choice represents a complex interplay of signaling on the part of the chosen sex and evaluation on the part of the choosy sex. The ultimate result that female smallmouth bass preferred larger males with distinctive body shapes is consistent with a wide body of literature on both fish and other taxa (Wiegmann et al. 1992; Husak and Fox 2006; Lailvaux and Irschick 2006; Jacob et al. 2007). Probably the preference for larger males is a result of body size being an honest signal of male quality (Maynard-Smith and Harper 2003). However, the proximate mechanisms behind this choice remain unknown and are probably a result of a complex interplay between direct (e.g., male parental-care performance) and indirect (e.g., good genes) benefits to the female (Barbosa and Magurran 2006). Future studies that include measures of physiological and nutritional status across a range of animal models will help to reveal the extent to which the pattern that we observed in this study (i.e., the apparent lack of relationship between parental male physiology and eggs received as a proxy for female selection) may be a general rule. Furthermore, it would be interesting to replicate such a study in a year or in a study system where resources are extremely limited (e.g., drought, long winter) and where there is a wide range in organismal condition.

Acknowledgments

We thank Rana Sunder, Mike Donaldson, Amanda O'Toole, Michelle Caputo, and Constance O'Connor for assistance in

the collection of data. Scientific collection permits were provided by the Ontario Ministry of Natural Resources (Scott Smithers), and animal care approval was provided by the Carleton University Animal Care Committee. Cory Suski and several anonymous reviewers kindly provided comments on an earlier draft of this manuscript. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (in the form of a Discovery Grant to S.J.C. and a Research Tools and Infrastructure Grant), the Canada Foundation for Innovation, and the Ontario Research Fund.

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