FACTORS IMPACTING SURVIVAL FOLLOWING PARENTAL CARE IN MALE SMALLMOUTH BASS (MICROPTERUS DOLOMIEU)

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ABSTRACT

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Parental care in animals is associated with a high cost of reproduction and hence is linked to high mortality among parents between reproduction episodes. Post-care mortality risk is linked to a variety of causes, including depleted energy reserves and diminished condition, both of which increase the risk of mortality by starvation. However, the magnitude of this risk is expected to vary based on the size of the individual due to metabolic allometry. Further, parents may adjust the care levels based on their current status and the body size-metabolic allometry as a trade-off between current and future reproduction. Here, I leverage a decade-long dataset on the paternal behavior and survival of male smallmouth bass, *Micropterus dolomieu*, a temperate freshwater fish, to explore how body size and parental behavior at first reproduction by 3-year-old males influenced their future survival. The results logistic regression suggest that future survival was influenced by both body size and parental behavior. Two of three equally parsimonious models included a direct influence of male body size on survival, with higher survival of larger individuals, and one of these two models also included a term associated with male parental behavior, where—consistent with a trade-off between current and future reproduction—lower site tenaciousness was associated with higher survival. The third of the three models included these terms and their interaction, where more site tenacious smaller males had higher survival. The mediation of parental behavior by body size implied by the latter model suggests that small, site tenacious males may be more likely to survive post-reproduction because they expend less energy in response to disturbances while on the nest or may, through bold behavior in other contexts, better recover energy lost in the parental care period. The model also highlights the potential complexity of interactions between behavior and individual physical attributes on survival.

I dedicate this work to my mother and brothers who have been incredibly supportive and encouraging during this journey.

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INTRODUCTION

Parental care is a period when organisms are vulnerable and highly susceptible to mortality (Sabat, 1994; Thomas et al., 2015; Oteyza et al., 2021). While parental investment benefits the offspring, this is often at the expense of parents, who incur an increased risk of mortality between reproduction episodes and reduced future reproductive opportunities (Williams, 1966; Trivers, 1972; Mainwaring, 2016). Indeed, many organisms, like birds (Owens and Bennett, 1994; Liker and Székely, 2005; Santos and Nakagawa, 2012), fishes (Dufresne et al., 1990; Sabat, 1994; Bertschy and Fox, 1999), reptiles (Miles et al., 2000; Weatherhead et al., 2012), and mammals (Fisher and Blomberg, 2011) experience high mortality between reproduction episodes and mortality especially high in species that provide parental care (Chr, 1984; Liker and Székely, 2005). Hence, understanding the impact of parental care on adult survival between the reproduction events of iteroparous species is important to understanding population dynamics and recruitment patterns.

Parental care may increase post-care mortality risk for a variety of reasons. For example, parental care may deplete energy reserves and diminish the condition of parents (Milner et al., 2013; Monteith et al., 2013; Abecia et al., 2022). The loss of energy reserves as a result of parental care increases the risk of starvation (Forseth et al. 1999; Neffa and Cargnellib, 2004). The magnitude of this risk, however, may vary based on the size of an individual because of metabolic allometry (Cargnelli and Gross, 1997; Mackereth et al., 1999; Steinhart et al., 2005). Smaller individuals are expected to be at a higher risk of starvation due to energetic expenditures associated with parental care than larger individuals because smaller individuals have proportionately higher metabolic demands, and fewer energy reserves compared to larger individuals (Speakman, 2005). For instance, a small (210 - 250 mm) male smallmouth bass

(*Micropterus dolomieu*) loses approximately 3.0 percent muscle tissue (as a percentage of total muscle dry weight) as compared to about 2.5 percent for a large (280 - 320 mm) male over the period of parental care (Mackereth et al., 1999). Smaller individuals may also be at higher risk of predation both during the parental care and between reproduction episodes (Steinhart et al. 2004a; Berger et al., 2006; Preisser and Orrock, 2012; Rodgers et al., 2015; Taylor and Cox, 2019; Oteyza et al., 2021; but see e.g., Nakazawa et al., 2007).

The body size-metabolic allometry should cause parents to adjust their level of care based on their current status (Stanley, 1983; Townshend and Wootton, 1985; Clutton-Brock, 1991). For instance, larger male smallmouth bass (*Micropterus dolomieu*) are more nest site tenacious, and tenacity is related to the survival of progeny (Wiegmann et al., 1992; Wiegmann and Baylis, 1995; but see Iguchi et al., 2004). The level of care provided by parents has also been linked to the value and physiological of progeny. For instance, the male *M. dolomieu* increase (decrease) their level of nest defense in response to an experimental increase (decrease) in the number of progeny in their nests (Ridgway et al. 1989). Male *M. dolomieu* are also more site tenacious before eggs hatch, presumably because immobile eggs, which are susceptible to fungus infections, have higher ventilation needs than hatched larvae (Wiegmann and Baylis, 1995; see Knotek and Orth, 1998). Larger individuals can presumably provide a higher level of care because males rarely forage while on a nest and larger individuals have larger energy reserves (Calow, 1985; Gillooly and Baylis, 1999; Cooke et al., 2006). Progeny survival is similarly related to nest site tenacity in birds (Cuthbert et al., 1988; Eldegard and Sonerud, 2009; but see Stenhouse and Robertson, 2005) and birds in better condition provide more care (Blums et al., 2005).

The care provided by parents is also expected to be influenced by the inherent trade-off between current and future reproduction, potentially independent of body size (Williams, 1966; see Gross, 2005). For example, more active parents of a given size may deplete more energy while caring for offspring (Cooke et al., 2002; Suski et al., 2003). The depletion of energy by more active parents may necessitate aggressive or risky activities to replenish lost reserves after care has ended. Thomas et al. (2015) found, for instance, that increased parental incubation effort led to increased post-parental mortality among songbirds. Bold parents may also be more likely to be detected and consumed by a predator as they care for their progeny. In birds, for example, adult survival probabilities are higher for cautious individuals that, when disturbed, wait longer to return to the nest in environments where predation events are high (Oteyza et al., 2021). Behavioral responses of parents to predators may also depend on body size, where larger individuals can afford to be bolder (Oteyza et al., 2021). Parental investment is also expected to depend on age, where older individuals may invest more heavily in current progeny due to reduced future breeding opportunities (Roff, 1992; Stearns, 1992). Despite the inroads made by studies of body size and behavior on survival of parents, we still do not fully understand how these factors and their interaction influence mortality risk in the context of parental care.

Fishes offer an ideal opportunity to study the relationship between parental behavior, body size, and survival. Indeterminate growth results in large differences in adult size within a population and individuals exhibit considerable variation in parental behavior (Trivers, 1972; Sargent and Gross, 1986; Gross, 2005; Alonso-Alvarez and Velando, 2012). Many temperate fishes are also found in closed lakes where no migration occurs, which makes it easier to monitor both individual reproduction and survival. Moreover, the ability to non-destructively age fish allows for the control of age-dependent experiences that may influence either parental behavior or survival (Schneider et al., 2000; Hecht et al., 2021; Torres et al., 2011).

Here, we leverage a decade-long dataset on the paternal behavior and survival of male smallmouth bass, *Micropterus dolomieu*, a temperate freshwater fish, to explore how body size and parental behavior of same-aged males when they first reproduced influenced their risk of future mortality. We hypothesized that larger males in better condition would be more likely to survive post-parental care because they are less likely to exhaust their energy reserves and may be less susceptible to predators. Further, we hypothesized that more aggressive parental males may be more aggressive in other contexts, which might make them more susceptible to predators and less likely to survive between reproduction episodes, where body size may mediate the impact of their behavior.

MATERIALS AND METHODS

Natural history

For smallmouth bass, *Micropterus dolomieu*, like all centrarchids, it is the males that provide parental care (Ridgway 1988; Philipp et al. 1997). Parental males fan eggs and guard progeny from potential nest predators and rely largely on energy reserves in the parental care period (Gillooly and Baylis, 1999; Mackereth et al., 1999). The stress of this period is compounded by the fact that smallmouth bass reproduction starts soon after winter, when energy reserves have already been utilized (Ridgway and Shuter, 1994; Mackereth et al., 1999). Because winter is a period of torpor, and small males lose proportionately more of their energy reserves, larger individuals typically spawn earlier in the spring than smaller males (Ridgway et al., 1991; Lukas and Orth, 1995; LaRoche et al., 2023).

Smallmouth bass initiate breeding in the spring as water temperatures approach 15℃ (Hubbs and Bailey 1938; Shuter et al. 1980). Typically, male smallmouth bass first spawn between the ages of two and four years (Latta, 1963; Turner and MacCrimmon, 1970; Pflieger 1975; Fletcher, 1982; Welsh et al., 2017). Males construct nests in the littoral zone, where females release their eggs for the male to fertilize. While most populations appear to be monogamous (Ridgway 1989; Raffetto et al. 1990; Wiegmann et al. 1992), some populations have been found where the largest males are polygynous (Franckowiak et al., 2017).

After spawning, males remain close to their nests and guard the fertilized eggs until they hatch and fry swim up and disperse. Untended eggs and fry may be consumed by small fish such as rock bass (*Ambloplites rupestris*), bullheads (*Ameriurus nebulosus*), bluegill (*Lepomis macrochirus*), sculpins (*Cottus cognatus*), bass fingerlings, white suckers (*Catostomus commersonii*), yellow perch (*Perca flavescens*), minnows (*Phoxinus phoxinus*), as well as crayfish (*Orconectes rusticus*) or large insects (Coble, 1975; Carlender, 1977; Hinch and Collins, 1991; Friesen, 1998). Typically, adult smallmouth bass are preyed on by large predators, such as birds, turtles, goby (*Neogobius melanostomus*), muskellunge (*Esox masquinongy*) and northern pike (*Esox lucius*) (Steinhart et al., 2004).

The spawning period, which is energetically costly, may last a few weeks and during that time males do not actively feed (Hinch and Collins 1991; Gillooly and Baylis 1999). After the period of parental care, males spend their time feeding and replenishing the energy reserves lost as a result of parental care in preparation for winter, when feeding ceases (Hubbs and Bailey 1938; Munther 1970). After the age at first reproduction males that survive generally spawn in each season that they are alive (Ridgway, 1991).

Study site

This study was conducted on Pallette Lake (46.067°/89.604° W), an oligotrophic seepage lake with a surface area of 73 ha and a maximum depth of 18 m that is located in the Northern Highlands Fishery Research Area of north-central Wisconsin (Sass et al., 2022). A detailed description of the benthic and limnological characteristics of the lake is provided in Saunders et al. (2002). The Wisconsin Department of Natural Resources (WDNR) manages the lake and enforces a compulsory creel census that runs all year round (Sass et al., 2022). For the years included in our analyses the legal harvest length-limit was 41cm. The potential predators of eggs and adult smallmouth bass present in Pallette Lake include muskellunge, northern pike, yellow perch, rock bass, and white sucker (Sass et al., 2022).

Field methods

The study was conducted by the same core team of researchers across multiple years, including 1999 and 2001-2009 (Welsh et al., 2017; LaRoche et al., 2023). The nest census every year began in mid-May or early June when the water temperature reached about 15°C and was conducive for males to initiate the construction of nests (Hubbs and Bailey 1938; Shuter et al. 1980). Snorkelers swam along the shoreline in transects in search of nests up to a depth of about 4 m, which is deeper than the majority of *M. dolomieu* nests (Bozek et al., 2002). The census continued until mid to late June or early July when reproduction ended.

Parental males were captured from their nest with a hand net as described in an earlier study (Wiegmann and Baylis, 1995). The body length (total length, mm) and weight (g) of each captured male was recorded, as was the capture time (s) and the development stage (eggs or hatched larvae) of progeny in a nest. In addition, scales were collected from just below the pectoral fin of each male captured. Uniquely numbered Floy FD-67C anchor tags were used to identify the males and track them across years. The males were returned to the water near their nests.

Age and mortality of parental males

The sampled scales were used to age parental males (Ridgway, 1991, Welsh et al., 2017). The males included in our analyses were captured in 2003, 2004 and 2005, when all individuals were identified as age 3 years and first-time breeders from the 2000, 2001, and 2002 cohorts (Welsh et al., 2017). We used a cross sectional method – by including multiple cohorts – to assess uncontrolled cohort effects on predicting survival outcome for individual smallmouth bass males. The body length of the largest male in the dataset was ~30 cm, more than 10 cm shorter than the imposed minimum size limit (Sass et al., 2022). Hence, the natural mortality of males in our sample was determined based on whether they were ever observed on a nest in any year after they were first observed, 2004-2009.

Parental behavior, adjusted for the developmental stage of progeny

Wiegmann and Baylis (1995) found that male *M. dolomieu* guarding eggs were more site tenacious—that is, had shorter capture times—than males guarding fry, likely because of the increased ventilation demands of eggs. Here, we adjusted logged ($\log_{10}$) capture time, our measure of parental behavior, so that capture times of males within and between cohorts could be directly compared irrespective of the developmental stage of their progeny. Males in the sample were grouped into those defending eggs and those defending fry, and the average ($\log_{10}$-transformed) capture time for the two groups determined. We then subtracted the average capture time from the capture times of individual in the two groups and used these residual, log10-transformed capture times in our analyses.

Statistical analysis

Logistic regression was used to predict parental male survival, with cohort, male body length, individual condition and adjusted log10-transformed capture time as predictors (Aldrich and Nelson, 1984; Helveston, 2022). Individual condition (*K*) was computed (based on the Fulton condition factor) as

$$K = W(TL^{-3})100{,}000,$$

where *W* is male weight (g) and body length (mm) is *TL* (Froese, 2006).

The regression analysis included an evaluation of the set of possible linear models—36 in total—with individual predictors, combinations of the predictors, and combinations of predictors with their pair-wise interactions. The 36 models were evaluated using Akaike's Information Criterion with correction (AICc) to identify the model with the best fit and fewest predictor variables (Burnham et al., 2011). Models with a delta AICc < 2 were considered most plausible among the hypothesized alternatives (Burnham and Anderson, 2003). All statistical analyses were conducted in R (R Core Team, 2021). The DHARMA package was used to evaluate residuals of the models (Hartig, 2020).

We calculated pseudo-R^2 values of the top models to estimate and compare their explanatory power (Nakagawa and Schielzeth, 2013). Further, we determined the correctly predicted outcomes – if the model predicted survival for a male that actually survived and if the model predicted mortality for a male that actually died – and calculated survival and mortality accuracy for each model. In particular, if a model predicted a survival probability greater than or equal to 0.5 and it survived or predicted a survival probability less than 0.5 and it died, then the model was deemed to have correctly predicted what was observed. Otherwise, the model failed to predict individual survival.

RESULTS

The numbers of males of the 2000, 2001 and 2002 cohorts that bred for the first time at age 3 years were 21, 77 and 25, respectively, and no males were observed to skip a year between reproduction episodes. Their overall survival rates were 67%, 57%, and 56%, respectively. All the capture time used in the analysis was log transformed ($\log_{10}$) and then adjusted as described in the materials and methods. The shortest adjusted ($\log_{10}$-transformed) capture time was -1.19 (0.78 for the uncorrected logged transformed capture time or 6 s) and the longest was 1.30 (3.08 for the uncorrected logged transformed capture time or 1215 s).

The body length of males in the sample ranged from 201 mm to 305 mm and differed across cohorts ($F_{3,120} = 32.91$, $P < 0.0001$). Post hoc Tukey tests showed that the 2000 cohort differed from both the 2001 ($q_{120} = 8.86$, $P < 0.0001$) and 2002 cohorts ($q_{120} = 15.47$, $P < 0.0001$) and that the lengths of males of the 2001 and 2002 also differed ($q_{120} = 4.94$, $P = 0.0011$). The condition K of males ranged from 0.77 to 1.64 also varied across cohorts ($F_{3,120} = 10.37$, $P < 0.0001$). Post hoc Tukey tests revealed that condition differed only between males of the 2000 and 2001 cohorts ($q_{120} = 6.36$, $P < 0.0001$).

A total of 36 logit models were competed to predict male survival and were compared with AIC. Three models had ΔAICc < 2 (Table 2). Body length and capture time were predictors included in the top models. None of the top models included cohort or condition as a predictor (Table 3). There was, however, no univariate, statistically detectable difference in body length, adjusted capture time, or individual condition between males that survived or died after their first reproduction episode (Table 1).

The top-ranked model included only male body length and indicated that bigger males tended to have better odds of survival (coefficient: 8.13, P = 0.0596). Predicted survival, *p*, from this model was:

$$\boldsymbol{p = \frac{1}{1 + e^{-(-19.1 + (8.1 \times log_{10}(TL))}}}$$

Based on the model, a 300 mm male in the top 10% of the males in our dataset was about 33% more likely to survive post reproduction than a male 200 mm in length in the lowest 10% of the males in our dataset (Figure 1a).

The second top-ranked model included male body length, capture time and the interaction between these variables (Table1). The predicted survival from this model was:

$$\boldsymbol{p = \frac{1}{1 + e^{-(-21.877 + 9.313 * \mathrm{log10(TL)} - 37.828 * \mathrm{CT} + 19.037 * \mathrm{log10(TL)} * \mathrm{CT}\ )}}}$$

In this second model, male body length was a significant predictor of survival, where larger males were again predicted to have a higher chance of survival (coefficient: 9.31, $P = 0.0408$). The main effect of capture time (coefficient: -37.83, $P = 0.0927$) and its interaction effect with male body length (coefficient: 15.91, p = 0.0902) were marginal. If corrected $\log_{10}$-transferred capture time is held constant at the overall average the model predicts that larger males tend to exhibit higher survival (Figure 1b).

To further explore the interaction between body length and capture time for this model, we generated interaction plots of survival over the range of observed values for male body size and capture time. Individuals less than about 240 mm in length, roughly the average body size of males in our sample (Table 1), were more likely to survive if they had shorter capture times, while individuals longer than 240 mm had a higher chance of survival if they had longer capture times (Figure 2a).

The third best model included male length and the capture time, with no interaction between these variables (Table 2). The predicted survival from this model was:

$$\boldsymbol{p} = \frac{\mathbf{1}}{\mathbf{1} + \boldsymbol{e}^{-(-\mathbf{20.3133} + \mathbf{8.6335} * \mathbf{log10(TL)} + \mathbf{0.3042} * \mathbf{CT})}}$$

This model also suggests that larger males were more likely to survive (Figure 1c; coefficient: 8.63, P = 0.0488) and that males with longer capture times tended to have higher survival (Figure 2b; coefficient: 0.30, P = 0.4705). A plot of predicted survival for males of different lengths over the average capture time reveals that a large, 300 mm male had a 36% higher chance of survival compared to a small, 200 mm male (Figure 1c). The survival probability of average body length male (250 mm) plotted over the range of observed capture times reveals a 19% increase in survival between the shortest and longest observed capture times (Figure 2b).

Each of the top models generally correctly predicted which males survived, with the best match between predicted and observed survival from the second of the top models that included an interaction between male body size and capture time (Table 4). The models poorly predicted mortality, where no model correctly predicted more than 30% of males that died. The values of pseudo-R^2 (used to assess the explanatory power of the models) imply that the second-ranked, interaction model had the highest (0.06) explanatory power with the other two models having a pseudo-R^2 value of 0.03 (Table 4). Most of the variability in survival was, however, left unexplained by any model.

DISCUSSION

In this study, we followed three cohorts of 3-year-old smallmouth bass males breeding for the first time to investigate how male physical attributes and paternal care behavior influenced their future survival. The results of our analyses produced three top models (ΔAICc < 2) (Table 2). All three of the models that best predicted male survival included a term for male total length, and two of the models included terms for capture time, a measure of nest site tenacity (Table 2).

Two of the three top-ranked models included a direct influence of male body size on survival, with higher survival of larger individuals (Figure 1). In some fishes, including smallmouth bass, a negative allometric relationship between mass and basal metabolism has been observed (Danylchuk and Fox, 1994; Descamps et al., 2011). For instance, the specific daily metabolic demand for a 202 g smallmouth bass ranges from about 1 to 1.6 percent body weight while for a 71 g smallmouth bass the specific daily metabolic demands ranges from 2.1 to 3.6 percent of the body weight (Whitledge et al., 2002). Nest guarding and overwintering are two periods when foraging by male smallmouth bass is limited, and survival depends on stored energy reserves (Hinch and Collins 1991; Mackereth et al., 1999; Gillooly et al. 2001; Garvey et al., 2004; Steinhart et al., 2005). Thus, our finding that body size is a critical predictor for survival from one reproductive season to the next may reflect increased starvation risk for small males across either of these events. Indeed, previous studies revealed positive relationships between body size and starvation resistance in a variety of animals (Lehmann et al., 2006; Cleasby et al., 2010; Bauchinger and McWilliams, 2012; Gergs and Jager, 2014; but see Couvillon and Dornhaus, 2010).

Terms for male parental behavior were also included in two of the three top-ranked models. The results of one of these models indicated that the survival of more site tenacious males (i.e., males providing more parental care) of any given body size was lower than the survival for individuals that were less site tenacious (Figure 2b). This result is consistent with both theory and empirical work finding trade-offs between current investment in progeny and adult survival (Williams, 1966; Baylis, 1981; Blomquist, 2009; Lynch, 2016). Increased parental care investment could have increased mortality risk through a variety of routes. For example, guarding progeny from nest predators is energetically expensive (Magnhagen, 1992; Steinhart et al. 2004a; Steinhart et al. 2005; Gravel and Cooke, 2009; Baldridge and Lodge, 2013; Gravel and Cooke. 2013; Slagle et al., 2017), potentially putting more site-tenacious males at higher risk of starvation. Additionally, in Pallette Lake there are few boulders and down trees behind which nests can be built, making nest-guarding males potentially easy to find by their predators (see Saunders et al., 2002). Thus, more site tenacious males may expose themselves to a greater risk for predation, as has been observed in smallmouth bass (Gravel and Cooke, 2009; Gravel and Cooke. 2013; Slagle et al., 2017).

The third equally parsimonious model that best predicted male survival included an interaction term between male body length and parental behavior (Figure 2a). Based on the model, small-sized males were more likely to survive if they had shorter capture times while large-sized males had a higher chance of survival if they had longer capture times (Figure 2a). This was an unexpected result because, for reasons already mentioned, parental care is expected to be more energetically costly for smaller individuals. Additionally, smaller individuals would likely be at a greater risk for predation simply because they are smaller (Magnhagen, 1992; Fuiman and Magurran, 1994). So, why are attentive small smallmouth bass males more likely to survive than small, less attentive parents? This result may hint at a behavioral syndrome in this population, as has been observed in many fish species (Conrad et al. 2011) and has been observed in juvenile smallmouth bass in Nebish Lake, a nearby population in the Wisconsin's Northern Highland Fishery Research Area (Smith et al. 2009). In Nebish Lake, juvenile smallmouth bass that flee shorter distances and are less likely to hide in a refuge following a simulated predator attack are also more likely to resume foraging following the attack (Smith et al. 2009). While no studies have looked for the presence of behavioral syndromes in adult smallmouth bass from Pallette Lake, it is possible that males that are more site tenacious are also, for example, fiercer competitors for resources in the lead-up to winter. Males, especially small males, that are more site tenacious may also be more likely to recoup energy lost during parental care and more likely to survive the period of winter torpor. The benefits of this behavioral syndrome could be size-dependent, as larger and more metabolically efficient individuals likely experience a lower overall risk of starvation relative to smaller individuals.

Cohort effect

None of the top models included a predictor for cohort. This result suggests that the relationship between body size and survival for male *M. dolomieu* is consistent across cohorts, even when, as in our study, the average size of individuals differed across cohorts (Table 1). Potential cohort effects may also have been reduced due to the consistent core team of researchers over the multi-year study. Cohort effects reflect all unmeasured formative experiences that may influence the expression of phenotypes, such as body size, and behavior. These effects tend to be more evident early in life presumably because individual experiences diversify as individuals age (Grande et al., 2009; Payo-Payo et al., 2023). For instance, Le Galliard et al. (2010) found a larger effect of cohort on the growth of juvenile and sub-adult common lizard, *Zootoca vivipara*, as compared to adults. The diminished influence of cohort effects as individuals age is also evident in birds and mammals (Jones et al., 2005; Payo-Payo et al., 2023). The cohorts in our study were from three consecutive years, so another possibility is that environmental conditions in this time window may have been similar enough to result in few differences of unmeasured physical or behavioral attributes that contribute to differences of survival.

Individual condition

We hypothesized that, because mortality is influenced by reproductive investment, differences in the condition of individuals would be related to survival rates among parental smallmouth bass males, as has been observed in other organisms. For example, van den Berge (1992) found that *Symphodus tinca*, a Mediterranean fish, in the best condition were more likely to survive between reproduction events (see also Naulleau and Bonnet, 1996; Blums et al., 2005; Kouba et al., 2021; Ross et al., 2021). Contrary to our hypothesis, the male condition was not an informative predictor of survival. There are at least two explanations. First, perhaps only individuals in good condition breed (van den Berge, 1992). On average, all breeding males in our study, including those that were predicted to not survive, were in good condition with the average condition factor of K = 1.19 (range, K = 0.77 to K = 1.64) as observed in other smallmouth bass populations in previous studies (see Orth, 1983 and Eckelbecker, 2023). Second, larger males nest earlier than small males and the development of their progeny may take longer than for small males who nest later (Baylis et al., 1993; Wiegmann et al., 2004). Therefore, large and small males may end up at the same condition at the end of the parental care period.

CONCLUSION

Here, we controlled for both age and prior experience by following three cohorts of first-time 3-year-old breeding male smallmouth bass and found that large size and low parental investment were associated with increased survival across reproductive seasons. The results of the logistic regression models suggested that body size and parental behavior influenced survival of parental males between reproduction episodes with larger males having higher survival rates and lower site tenacity also associated with higher survival rates. The other model included an interaction between body size and parental care where smaller males that were site tenacious being more likely to survive. This model suggests that smaller males that are site tenacious may improve their post reproduction through adoption of bolder behavior in other contexts that allow them to recoup the energy lost during parental care period. This suggests that behavioral syndromes may introduce complex relationships between the physical attributes of individuals and their survival propensity.

REFERENCES

Abecia, J. E., Luiz, O. J., Crook, D. A., Banks, S. C., Wedd, D. J., & King, A. J. (2022). Morphological changes and reproductive costs in brooders of two mouthbrooding freshwater fishes. *Ecology of Freshwater Fish*, 31, 369– 378. https://doi.org/10.1111/eff.12636

Aldrich, J. H. and Nelson, F. D. (1984). *Linear Probability, Logit and Probit Model: Quantitative Application in the Social Science*-Sera Miller McCun. Sage pub. Inc, University of Minnesota and Iola, London.

Alonso-Alvarez, C., and Velando, A., (2012). 'Benefits and costs of parental care', in Nick J. Royle, and Per T. Smiseth (eds), *The Evolution of Parental Care* (Oxford, 2012; online edn, Oxford Academic, 17 Dec. 2013), https://doi.org/10.1093/acprof:oso/9780199692576.003.0003.

Baldridge, A.K. and Lodge, D. M., (2013). Intraguild predation between spawning smallmouth bass (*Micropterus dolomieu)* and nest-raiding crayfish (*Orconectes rusticus)*: implications for bass nesting success. *Freshwater Biology*, 58, 2355-2365. https://doi.org/10.1111/fwb.12215

Bauchinger, U., McWilliams, S. R., (2012). Tissue-Specific Mass Changes During Fasting: The Protein Turnover Hypothesis. In: McCue, M. (eds) *Comparative Physiology of Fasting, Starvation, and Food Limitation*. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-29056-5_12.

Baylis, J. R., Wiegmann, D. D. and Hoff, M. H., (1993). Alternating Life Histories of Smallmouth Bass. *Transactions of the American Fisheries Society,* 122, 500-510. https://doi.org/10.1577/1548-8659(1993)122<0500:ALHOSB>2.3.CO;2

Berger, D., Walters, R. & Gotthard, K., (2006). What keeps insects small? - Size dependent predation on two species of butterfly larvae. *Evolutionary Ecology*, 20, 575–589. https://doi.org/10.1007/s10682-006-9118-8

Bertschy, K.A. and Fox, M.G., (1999). The influence of age-specific survivorship on pumpkinseed sunfish life histories. *Ecology*, 80, 2299-2313. https://doi.org/10.1890/0012-9658(1999)080[2299:TIOASS]2.0.CO;2

Blomquist G. E. (2009). Trade-off between age of first reproduction and survival in a female primate. *Biology letters*, *5*(3), 339–342. https://doi.org/10.1098/rsbl.2009.0009.

Blums, P., Nichols, J. D., Hines, J. E., Lindberg, M. S., & Mednis, A. (2005). Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia*, *143*(3), 365–376. https://doi.org/10.1007/s00442-004-1794-x.

Bozek, M. A., Short, P. H., Edwards, C. J., Jennings, M. J., and Newman, S. P. (2002). Habitat selection of nesting smallmouth bass *Micropterus dolomieu* in two north temperate lakes. *American Fisheries Society Symposium*, 2002(31), 135–148.

Burnham and Anderson (2003). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media.

Burnham KP, Anderson DR. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Edition. New York: Springer-Verlag.

Burnham, K. P., Anderson, D. R. & Huyvaert, K. P., (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6.

Calow, P., (1985) Resource utilization and reproduction. In: Townsend CR, Calow P (eds) *Physiological ecology: an evolutionary approach to resource use*. Sinauer, Sutherland, pp 245–271.

Cargnelli, L. M. and Gross, M. R., (1997). Fish energetics: larger individuals emerge from winter in better condition. *Transactions of the American Fisheries Society*, 126, 153–156.

Carlander, K.D., (1977). *Handbook of Freshwater Fishery Biology*, Vol. 2. pp. 1 52-1 91. The lowa State University Press, Ames, lowa.

Chr., N. S., (1984). Optimal Reproductive Success in Animals with Parental Care. *Oikos*, *43*(2), 251–253. https://doi.org/10.2307/3544777

Cleasby, I. R., Nakagawa, S., Gillespie, D. O. S., & Burke, T., (2010). The influence of sex and body size on nestling survival and recruitment in the house sparrow. *Biological Journal of the Linnean Society*, 101, 680–688.

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton.

Coble, D. W., (1975). Smallmouth bass. Pages 21-33 In H. E. Clepper and R. H. Stroud, editors. *Black Bass Biology and Management*. Sport Fishing Institute, Washington, D.C.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltx, J. B., and Sih, A., (2011). Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology*, 78, 395–435. doi:10.1111/j.1095-8649.2010.02874.x

Cooke, S. J., Philipp, D. P., and Weatherhead, P. J., (2002). Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Canadian Journal of Zoology*, 80, 756-770.

Cooke, S. J., Philipp, D. P., Wahl, D. H., and Weatherhead, P. J., (2006). Energetics of parental care in six syntopic centrarchid fishes. *Oecologia*, 148, 235–249. DOI 10.1007/s00442-006-0375-6.

Couvillon, M. J., & Dornhaus, A. (2010). Small worker bumble bees (*Bombus impatiens*) are hardier against starvation than their larger sisters. *Insectes sociaux*, *57*(2), 193–197. https://doi.org/10.1007/s00040-010-0064-7.

Cuthbert, F. J., (1988). Reproductive success and colony-site tenacity in Caspian terns. *The Auk*, 105: 339-344.

Danylchuk, A. J. and Fox, M. G., (1994). Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*. *Environmental Biology of Fishes*, 39, 119–127.

Descamps, S., Bêty, J., Love, O. P. and Gilchrist, H. G., (2011). Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. *Functional Ecology*, 25, 671–681.

Dufresne, F., FitzGerald, G. J., and Lachance, S., (1990). Age and size-related differences in reproductive success and reproductive costs in threespine sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology*, 1(2), 140–147. https://doi.org/10.1093/beheco/1.2.140.

Eckelbecker, R. W., Heili, N. M., Guy, C. S., & Schmetterling, D. A. (2022). Relative Condition Parameters for Fishes of Montana, USA. *Fishes*, *8*(1), 28. MDPI AG. Retrieved from http://dx.doi.org/10.3390/fishes8010028.

Eldegard, K., & Sonerud, G. A. (2009). Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proceedings. Biological sciences*, *276*(1662), 1713–1721. https://doi.org/10.1098/rspb.2008.1775.

Fisher, D. O. and Blomberg, S.P., (2011). Costs of Reproduction and Terminal Investment by Females in a Semelparous Marsupial. *PLoS ONE*, 6(1): e15226. https://doi.org/10.1371/journal.pone.0015226

Fletcher, D., (1982). *Warmwater fish investigations in Washington State. Annual Report submitted to US Fish and Wildlife Service*. DJ Progress Report No. F-71-R. Washington Department of Wildlife, Olympia, Washington.

Forseth, T., Naesje, T.F., Jonsson, B. & Harsaker, K., (1999). Juvenile migration in brown trout: A consequence of energetic state. *Journal of Animal Ecology*, 68, 783–793.

Franckowiak, RP, Ridgway, MS, Wilson, CC., (2017). Genetic mating system and mate selection in smallmouth bass. *Ecology Evolution*, 7, 8864– 8875. https://doi.org/10.1002/ece3.3423

Friesen, T. G., (1998). *Effects of food abundance and temperature on growth, survival, development and abundance of larval and juvenile smallmouth bass*. Ph. D. Dissertation. University of Guelph, Guelph, Ontario.

Froese R., (2006). Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22:241–253. doi: 10.1111/j.1439-0426.2006.00805.x.

Fuiman, L. A. and Magurran, A. E., (1994). Development of predator defences in fishes. *Review in Fish Biology and Fisheries*, 4, 145–183. https://doi.org/10.1007/BF00044127

Garvey, J. E., Ostrand, K. G. and Wahl, D. H. (2004). Energetics, Predation, and Ration Affect Size-Dependent Growth and Mortality of Fish during Winter. *Ecology*, 85(10), 2860–2871.

Gergs, A. and Jager, T. (2014), Body size-mediated starvation resistance in an insect predator. J Animal Ecology, 83, 758-768. https://doi.org/10.1111/1365-2656.12195

Gillooly J. F. and Baylis, J. R., (1999). Reproductive success and the energetic cost of parental care in male smallmouth bass. *Journal of Fish Biology*. doi:10.1006/jfbi.1998.0888.

Gillooly J. F., Brown, J. H., West, G. B., Savage, V. M. and Charnov, E. L., (2001) Effects of size and temperature on metabolic rate. Science 293:2248–2251

Grande, J. M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Díaz-Delgado, R., Tella, J. L. and Donázar, J. A., (2009). Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos*, 118, 580–590.

Gravel, M. A., and Cooke. S. J., (2013). Does nest predation pressure influence the energetic cost of nest guarding in a teleost fish? *Environmental Biology of Fishes*, 96(1), 93–107.

Gravel, M.-A. and Cooke, S.J., (2009). Influence of Inter-Lake Variation in Natural Nest Predation Pressure on the Parental Care Behaviour of Smallmouth Bass (*Micropterus dolomieu*). *Ethology*, 115, 608-616. https://doi.org/10.1111/j.1439-0310.2009.01641.x

Gross, M. R., (2005). The Evolution of Parental Care. *The Quarterly Review of Biology*, 80(1), 37-45.

Hartig, F., (2020). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. *R package version 0.3*, *3*.

Hecht, L., (2021). The importance of considering age when quantifying wild animals' welfare. *Biological reviews of the Cambridge Philosophical Society*, 96(6), 2602-2616. doi: 10.1111/brv.12769.

Helveston, J. P., (2022). *logitr: Fast Estimation of Multinomial and Mixed Logit Models with Preference Space and Willingness to Pay Space Utility Parameterizations*. R package, https://jhelvy.github.io/logitr/.

Hinch, S.G. and Collins, N.C., (1991). Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations. *Transactions of the American Fisheries Society*, 120, 657–663.

Hubbs C. L. and Bailey, R. M., (1938). The small-mouthed bass. *Cranbrook Institute of Science Bulletin*, 10. 92 pp.

Iguchi, K., Yodo, T. & Matsubara, N., (2004). Spawning and Brood Defense of Smallmouth Bass Under the Process of Invasion into a Novel Habitat. *Environmental Biology of Fishes*, 70, 219–225. https://doi.org/10.1023/B:EBFI.0000033337.44116.e8

Jones O. R., Crawley, M. J., Pilkington, J. G. and Pemberton, J. M., (2005). Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2619-25. doi: 10.1098/rspb.2005.3267.

Knotek, W.L. and Orth, D.J., (1998). Survival for specific life intervals of smallmouth bass, *Micropterus dolomieu*, during parental care. *Environmental Biology of Fishes*, 51, 285–296. https://doi.org/10.1023/A:1007497401717

Kouba, M., Bartoš, L., Bartošová, J., Hongisto, K., & Korpimäki, E., (2021). Long-term trends in the body condition of parents and offspring of Tengmalm's owls under fluctuating food conditions and climate change. *Scientific reports*, *11*(1), 18893. https://doi.org/10.1038/s41598-021-98447-1.

Laroche, R. A. S., Weinersmith, K. L., Davis, M. L., Angeloni, L., Baylis, J. R., Newman, S .P., Egan, S .P. and Wiegmann, D .D. (2023), Size-associated energetic constraints on the seasonal onset of reproduction in a species with indeterminate growth. *Oikos*, 1-12. e09739. https://doi.org/10.1111/oik.09739

Latta, W. C., (1963). *The life history of the smallmouth bass, Micropterus d. dolomieui, at Waugoshance Point, Lake Michigan*. Michigan Department of Conservation. Institute of. Fisheries Research Bulletin, 5. 56 pp.

Le Galliard, J. F., Marquis, O., and Massot, M., (2010). Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology*, 79(6), 1296–1307.

Lehmann, T., Dalton, R., Kim, E. H., Dahl, E., Diabate, A., Dabire, R., & Dujardin, J. P., (2006). Genetic contribution to variation in larval development time, adult size, and longevity of starved adults of Anopheles gambiae. *Infection, genetics and evolution: journal of molecular epidemiology and evolutionary genetics in infectious diseases*, *6*(5), 410–416. https://doi.org/10.1016/j.meegid.2006.01.007.

Liker, A. and Székely, T., (2005). Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*, 59: 890-897. https://doi.org/10.1111/j.0014-3820.2005.tb01762.x

Lynch, R. F., (2016). Parents face quantity-quality trade-offs between reproduction and investment in offspring in Iceland. *Royal Society open science*, 3(5), 160087. https://doi.org/10.1098/rsos.160087.

Mackereth, R.W., Noakes D.L.G. & Ridgway M.S., (1999). Size-based variation in somatic energy reserves and parental care expenditure by male smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes*, 56, 263–275.

Magnhagen, C., (1992). Parental care and predation risk in fish. *Annales Zoologici Fennici*, 29(4), 227–232.

Mainwaring, M. C., (2016). The transition from dependence to independence in birds. *Behavioural Ecology and Sociobiology*, 70:1419–1431.

Miles, D. B., Sinervo, B., & Frankino, W. A., (2000). Reproductive Burden, Locomotor Performance, and the Cost of Reproduction in Free Ranging Lizards. *Evolution*, 54(4), 1386–1395.

Milner, J.M., van Beest, F.M., Solberg, E.J., Storaas, T., (2013). Reproductive success and failure: The role of winter body mass in reproductive allocation in Norwegian moose. Oecologia, 172, pp. 995-1005.

Monteith, K.L., Stephenson, T.R., Bleich, V.C., Conner, M.M., Pierce, B.M., Bowyer, R.T., (2013). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. J. Animal Ecol., 82, pp. 377-388

Munther G. L., (1970). Movement and distribution of smallmouth bass in the Middle SnakeRiver. *Transactions of the American Fisheries Society*. doi:10.1577/1548554 8659(1970)99<44:madosb>2.0.co;2.

Nakagawa, S. and Schielzeth, H., (2013). A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effect Models. *Methods in Ecology and Evolution*, 4, 122-42. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Nakazawa, T., Ishida, N., Kato, M., and Yamamura, N., (2007). Larger body size with higher predation rate. *Ecology of Freshwater Fish*, 16, 362–372.

Naulleau, G., Bonnet, X. Body condition threshold for breeding in a viviparous snake. *Oecologia*, 107, 301–306 (1996). https://doi.org/10.1007/BF00328446

Neffa, B. D. & Cargnellib, L. M., (2004). Relationships between condition factors, parasite load and paternity in bluegill sunfish, Lepomis macrochirus. *Environmental Biology of Fishes*, 71: 297–304.

Oteyza, J. C., Mouton, J. C., & Martin, T. E., (2021). Adult survival probability and body size affect parental risk-taking across latitudes. *Ecology letters*, 24(1), 20–26. https://doi.org/10.1111/ele.13615.

Owens, I. P. F. and Bennett, P. M., (1994). Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society B*, 2571–8. http://doi.org/10.1098/rspb.1994.0086

Payo-Payo, A., Sanz-Aguilar, A. and Oro, D., (2023). Long-lasting effects of harsh early-life conditions on adult survival of a long-lived vertebrate. *Oikos*, 2023: e09371. https://doi.org/10.1111/oik.09371

Pflieger, W. L., (1975). Reproduction and survival of the smallmouth bass in Courtois Creek. Pages 231-239 in H. Clepper, ed. *Black bass biology and management*. Sport Fish. Inst., Washington, DC.

Philipp, D. P., Toline, C. A., Kubacki, M. F., Philipp, D. B. F. and Phelan, F. J. S., (1997). The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. *North American Journal of Fisheries Management*, 17, 557–567.

Preisser, E. L., and Orrock., J. L., (2012). The allometry of fear: interspecific relationships between body size and response to predation risk. *Ecosphere*, 3(9):77. http://dx.doi.org/10.1890/ES12-00084.1

R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.URL https://www.R-project.org/.

Raffetto, N., Baylis, J. R. and Serns, S., (1990). Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieui*). *Ecology*, 71, 1523-1535.

Ridgway M.S., (1989). The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieui*). *Ethology*, 80, 47–54.

Ridgway, M. S. and Shuter, B. J., (1994). The effects of supplemental food on reproduction in parental male smallmouth bass. *Environmental Biology of Fishes*, 39, 201–207.

Ridgway, M. S., Shuter, B. J. & Post, E. E., (1991). The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieui*, Lacepede (Pisces, Centrarchidae). *Journal of Animal Ecology*, 60, 665-681.

Ridgway, M.S., (1988). Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieui*). Canadian Journal of Zoology, 66, 1722–1728.

Ridgway, M.S., and Friesen, T.G., (1992). Annual variation in parental care in smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes*, 35, 243–255. https://doi.org/10.1007/BF00001890

Rodgers, G. M., Downing, B., and Morrell, L. J., (2015). Prey body size mediates the predation risk associated with being “odd”. *Behavioral Ecology*, 26(1), pp. 242–246, https://doi.org/10.1093/beheco/aru185

Roff, D. A., (1992). *The evolution of life histories: theory and analysis*. Chapman and Hall, NY.

Ross, J. G. B., Newman, C., Buesching, C. D., Connolly, E., Nakagawa, S., Macdonald, D. W., (2021). A fat chance of survival: Body condition provides life-history dependent buffering of environmental change in a wild mammal population. *Climate Change Ecology*, 2, 1-13. https://doi.org/10.1016/j.ecochg.2021.100022.

Sabat, M A., (1994). Costs and benefits of parental effort in a brood-guarding fish (*Ambloplites rupestris,* Centrarchidae). *Behavioral Ecology*, 5(2), 195–201. https://doi.org/10.1093/beheco/5.2.195

Santos, E.S.A. and Nakagawa, S., (2012). The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. Journal of Evolutionary Biology, 25, 1911-1917. https://doi.org/10.1111/j.1420-9101.2012.02569.x

Sargent, R.C. and Gross, M.R. (1986). Williams' Principle: An Explanation of Parental Care in Teleost Fishes. In: Pitcher, T.J. (eds) *The Behaviour of Teleost Fishes*. Springer, Boston, MA. https://doi.org/10.1007/978-1-4684-8261-4_11

Sass, G.G., Shaw, S.L. and Renik, K.M. (2022). Celebrating 75 Years of Wisconsin's Northern Highland Fishery Research Area: The Past, Present, and Future. *Fisheries*, 47: 55-67. https://doi.org/10.1002/fsh.10687

Saunders, R., Bozek, M. A., Edwards, C. J., Jennings, M. J. and Newman, S. P., (2002). Habitat features affecting smallmouth bass *Micropterus dolomieu* nesting success in four northern Wisconsin lakes. *American Fisheries Society Symposium*, 31, 123–134.

Schneider, J. C., Laarman, P. W. and Gowing, H., (2000). Age and growth methods and state averages. Chapter 9 in Schneider, James C. (ed.) 2000. *Manual of fisheries survey methods II: with periodic updates*. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.

Shuter, B. J. and Post, J. R., (1990). Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society*, 119, 314–336.

Shuter, B. J., Maclean, J. A., Fry, F. E. J., Regier, H. A., (1980). Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society*. doi:10.1577/15488659(1980)109<1:ssoteo>2.0.co;2.

Slagle, Z., Allen, M. S., and Shaw, S.L., (2017). Factors Influencing Nest Survival in Florida Bass. *Transactions of the American Fisheries Society*, 146, 696-702. https://doi.org/10.1080/00028487.2017.1301996

Smith, K. L., Miner, J. G., Wiegmann D. D. and Newman, S. P., (2009). Individual differences in exploratory and antipredator behaviour in juvenile smallmouth bass (*Micropterus dolomieu*). *Behaviour*, 146, 283-294. DOI:10.1163/156853909X410784

Speakman, J. R., (2005). Body size, energy metabolism and lifespan. Journal of Experimental Biology, 208(9), 1717-30. doi: 10.1242/jeb.01556. PMID: 15855403.

Stanley, B.V. (1983). Effect of food supply on reproductive behaviour of male *Gasterosteus aculeatus.* PhD thesis, Univ. Wales. 155 pp.

Stearns, S. C., (1992). *The evolution of life histories*. Oxford University Press, NY.

Steinhart, G. B. and Lunn, B. D., (2011). When and why do smallmouth bass abandon their broods? The effects of brood and parental characteristics. *Fisheries Management and Ecology*, 18, 1–11.

Steinhart, G. B., Marschall, E. A. & Stein, R. A., (2004b). Round Goby Predation on Smallmouth Bass Offspring in Nests during Simulated Catch-and-Release Angling. *Transactions of the American Fisheries Society*, 133(1), 121-131, DOI: 10.1577/T03-020

Steinhart, G. B., Sandrene, M. E., Weaver, S., Stein, R. A., and Marschall, E. A., (2005). Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators, *Behavioral Ecology*, 16(2), 427–34. https://doi.org/10.1093/beheco/ari006

Steinhart, G.B., Stein, R.A. & Marschall, E.A., (2004a). High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? *Journal of Great Lakes Research*, 30, 381–389.

Stenhouse, I. J. and Robertson, G. J., (2005). Philopatry, Site Tenacity, Mate Fidelity, and Adult Survival in Sabine's Gulls, *The Condor*, 107(2), 416-423. https://doi.org/10.1093/condor/107.2.416

Suski, C. D., Svec, J. H., Ludden, J. B., Phelan, F. J. S. & Philipp, D. P., (2003). The Effect of Catch-and-Release Angling on the Parental Care Behavior of Male Smallmouth Bass. *Transactions of the American Fisheries Society*, 132(2), 210-218. DOI: 10.1577/1548-8659(2003)132<0210:TEOCAR>2.0.CO;2

Taylor, Q. and Cox, C.L., (2019), Evidence of predation risk increases with body size in a diminutive snake. *Journal of Zoology*, 307, 141-148. https://doi.org/10.1111/jzo.12627

Thomas E. M., Juan C. O., Andy J. B., Penn L., and Riccardo T., (2015). Adult Mortality Probability and Nest Predation Rates Explain Parental Effort in Warming Eggs with Consequences for Embryonic Development Time. *The American Naturalist*, 186(2), 223-236.

Torres, R., Drummond, H., & Velando, A. (2011). Parental age and lifespan influence offspring recruitment: a long-term study in a seabird. *PloS one*, *6*(11), e27245. https://doi.org/10.1371/journal.pone.0027245.

Townshend, T.J. and Wootton, R.J. (1985). Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum. Animal Behavior*, 33, 494-501.

Trivers, R. L., (1972). Parental Investment and Sexual Selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man*, 1871-1971 (pp. 136-179). Chicago, IL: Aldine.

Turner, G. E. and H. R. MacCrimmon. 1970. Reproduction and growth of smallmouth bass, *Micropterus dolomieui*, in a Precambrian Lake. *Journal of the Fisheries Research Board of Canada*, 27, 395-400.

van den Berghe, E.P., (1992). Parental care and the cost of reproduction in a Mediterranean fish. *Behavioral Ecology and Sociobiology*, 30, 373–378. https://doi.org/10.1007/BF00176171

Weatherhead, P. J., Blouin-Demers, G., & Sperry, J. H., (2012). Mortality Patterns and the Cost of Reproduction in a Northern Population of Ratsnakes, *Elaphe obsoleta*. *Journal of Herpetology*, 46(1), 100–103.

Welsh, D. P., Wiegmann, D. D., Angeloni, L. M., Newman, S. P., Miner, J. G. and Baylis, J. R., (2017). Condition-dependent reproductive tactics in male smallmouth bass: evidence of an inconsistent birthdate effect on early growth and age at first reproduction. *Journal of Zoology*, 302, 244-251. https://doi.org/10.1111/jzo.12454.

Whitledge, G. W., Hayward, R. S. & Rabeni, C. F., (2002). Effects of Temperature on Specific Daily Metabolic Demand and Growth Scope of Sub-Adult and Adult Smallmouth Bass. *Journal of Freshwater Ecology*, 17(3), 353-361, DOI: 10.1080/02705060.2002.9663908

Wiegmann D.D., J.R. Baylis, and M. Hoff., (1997). Male fitness, body size and timing of reproduction in smallmouth bass, *Micropterus dolomieui*. *Ecology*, 78, 111–128.

Wiegmann, D. D., Baylis, J. R., & Hoff, M. H. (1992). Sexual selection and fitness variation in a population of smallmouth bass, *Micropterus dolomieui* (Pisces:

Centrarchidae). *Evolution; international journal of organic evolution*, *46*(6), 1740–1753. https://doi.org/10.1111/j.1558-5646.1992.tb01166.x.

Wiegmann, D.D. & Baylis, J.R., (1995). Male body size and paternal behavior in smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). *Animal Behavior*, 50, 1543–1555.

Wiegmann, D.D., Angeloni, L.M., Baylis, J.R. & Newman, S.P., (2004). Negative maternal or paternal effects on tactic inheritance under a conditional strategy. *Evolution*, 58, 1530–1535.

Williams, G. C., (1966). "Natural selection, the costs of reproduction, and a refinement of Lack's principle". *The American Naturalist, 100(916): 687–690.*

APPENDIX A. TABLES

Table 1. Summary statistics (mean ± standard error) for 3-year-old first-time breeding male smallmouth bass (*Micropterus dolomieu*) test for within cohort differences and predicting survival. The average body length (mm), $\log_{10}$-transformed capture time (corrected for embryo stage) and logged condition factor of breeding males that survived and those that did not survive to breed the next year are included for each of the three cohorts included in the analysis.

		Survive to Breed Next Season			
Cohort	**Variable**	**Yes**	**No**	**Total**	**ANOVA**
2000	Sample Size	14	7	21	
	Body length (mm)	281.43 + 14.15	274.43 + 12.73	279.1 + 13.79	F = 1.12 P = 0.30
	Condition Factor	1.30 + 0.08	1.28 + 0.14	1.30 + 0.10	F = 0.46 P = 0.50
	Capture Time	0.00 + 0.50	-0.02 + 0.39	-0.08 + 0.50	F = 1.00 P = 0.33
2001	Sample Size	44	33	77	
	Body length (mm)	250.18 + 22.43	242.76 + 21.54	247 + 22.22	F = 2.08 P = 0.15
	Condition Factor	1.16 + 0.15	1.15 + 0.09	1.16 + 0.13	F = 0.00 P = 0.96
	Capture Time	0.00 + 0.47	-0.05 + 0.38	-0.02 + 0.43	F = 0.23 P = 0.63
2002	Sample Size	14	11	25	
	Body length (mm)	231.79 + 14.47	228.09 + 18.42	230.2 + 16.07	F = 0.36 P = 0.56
	Condition Factor	1.23 + 0.18	1.21 + 0.08	1.22 + 0.14	F = 0.01 P = 0.90
	Capture Time	0.07 + 0.57	0.19 + 0.37	0.12 + 0.49	F = 0.40 P = 0.53

Table 2. Delta values and model weights for models predicting male smallmouth bass survival (TL: $\log_{10}$-transformed male body length; CT: corrected $\log_{10}$-transformed capture time).

Model:	Delta	Model weight
TL	0.00	0.22
TL + CT + TL*CT	0.71	0.16
TL + CT	1.58	0.10

Table 3. Parameter estimates and 95% confidence intervals for the top general linear models predicting survival of 3-year-old male smallmouth bass (*Micropterus dolomieu*) that bred for the first time in 2003, 2004 and 2005. The models (in the rows) included predictors (in the columns) such as body length (TL), capture time corrected for embryo stage (CT), and their interaction (TL*CT). Included in the table are the estimates, standard error, and 95% confidence intervals (95%CI) for the estimates.

Model	**Predictors**															
	TL				**CT**				**TL*CT**				**Intercept**			
	Est.	**SE**	**95%CI**		**Est.**	**SE**	**95%CI**		**Est.**	**SE**	**95%CI**		**Est.**	**SE**	**95%CI**	
TL	8.1	4.31	-0.20	16.81									-19.1	10.31	-39.87	0.82
TL*CT	9.3	4.55	0.58	18.55	-37.8		-84.57	4.71	15.9		-1.83	35.43	-21.9	10.88	-43.94	-0.98
TL + CT	8.6	4.38	0.19	17.46	0.3		-0.51	1.15					-20.3	10.48	-41.42	-0.09

Table 4. Correctly predicted fates against the observed survival outcomes for smallmouth bass males based on the top models and the pseudo-R^2 values. The models are listed in the rows.

	Survived	**Did not survive**	**Pseudo-R^2 values**
Body length model	83.33%	27.45%	0.03
Body length*Capture time	87.50%	25.49%	0.06
Body length, Capture time	84.72%	25.49%	0.03

APPENDIX B. FIGURES

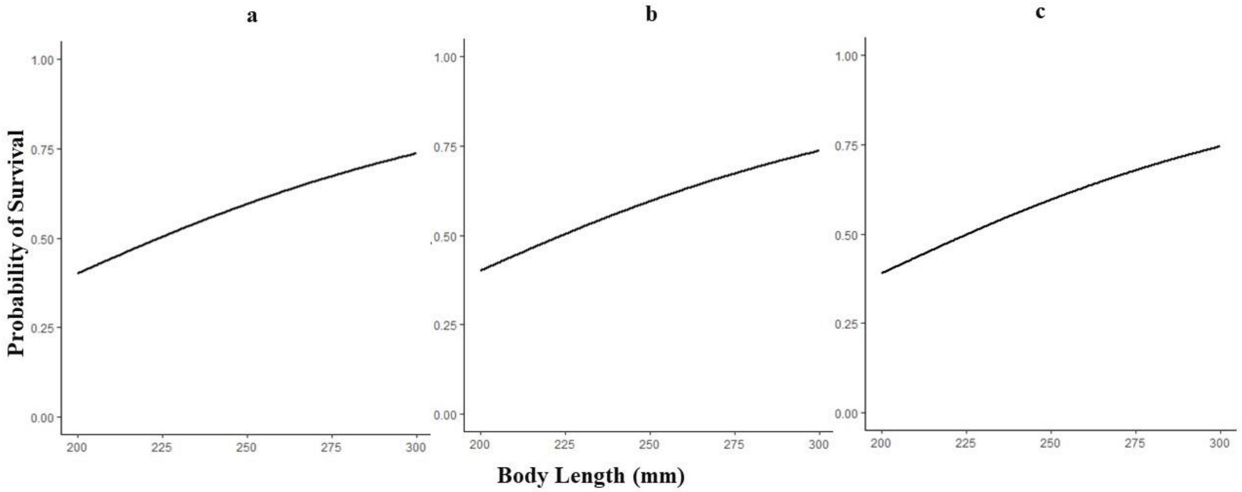

Figure 1. Predicted probability of survival for males of different body lengths (TL, mm) based on general linear models. Predicted probability of survival of males of different sizes from top models: (a) TL, (b) TL + Capture Time (CT) + CT*TL, and (c) TL + CT. Predicted probabilities of survival for males of different lengths in (b) and (c) are based on the average overall capture time for the cohort.

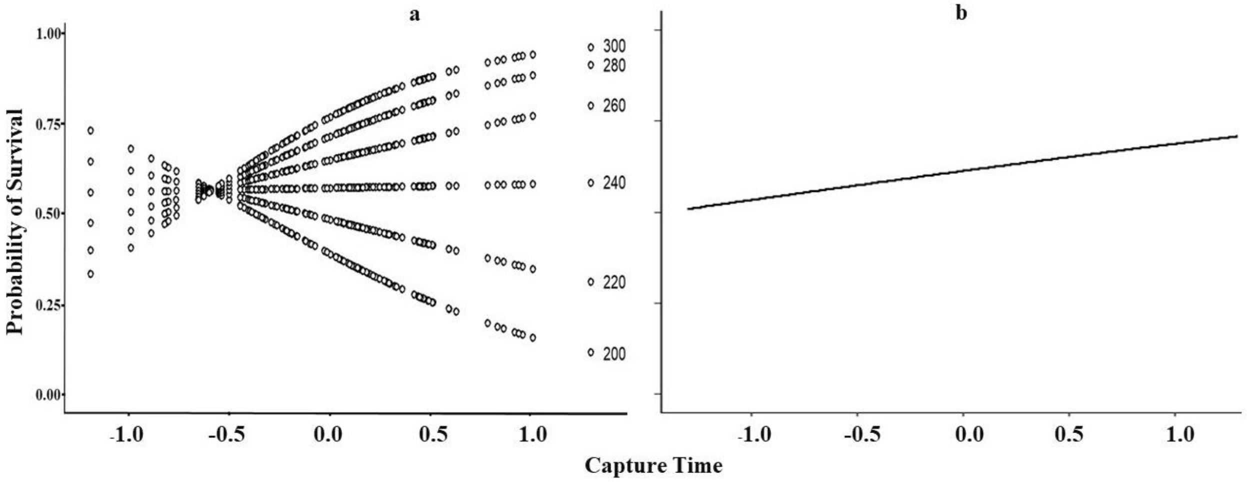

Figure 2. Predicted probability of survival for males of different body lengths (TL, mm) and capture times (CT, corrected for embryo stage) based on general linear models. Predicted probability of survival of males of different CT based models containing these additional predictors: (a) TL + Capture Time (CT) + CT*TL, and (b) TL + CT, holding TL at 250 mm (the average size for a male in this study).