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Brianne D. Lunn a & Geoffrey B. Steinhart a
Department of Biological Sciences, Lake Superior State University, 650 West Easterday Avenue, Sault Sainte Marie, Michigan, 49783, USA

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Effect of Brood Reduction on Nest Abandonment of Smallmouth Bass

BRIANNE D. LUNN*1 AND GEOFFREY B. STEINHART
Department of Biological Sciences, Lake Superior State University, 650 West Easterday Avenue, Sault Sainte Marie, Michigan 49783, USA

Abstract.—Smallmouth bass Micropterus dolomieu are well known for vigilantly guarding their nests, which is done solely by the males. Because parental care is costly, smallmouth bass are faced with a trade-off between current and future reproduction. If the male foregoes current reproductive efforts and abandons his nest, he may be better able to prepare for future efforts. In this article, we present field data on the effect of brood reduction on nest abandonment and explore the role of male age, brood size, and brood age on nest abandonment. We removed 0, 25, 50, or 75% of the brood from males’ nests in Lake Opeongo, Ontario, during the summers of 2007 and 2008 and observed the response (nest success or failure). Across all treatments, 22 of 105 nests (21%) failed and were abandoned, but there was no significant difference among treatments. However, fish that abandoned their nests were significantly younger and had fewer offspring at the time of abandonment than did those that did not. In addition, younger nests were more likely to be abandoned than older nests. Our results differ from those of previous brood reduction experiments, although they match parental care theory overall.

Many fishes in the family Centrarchidae provide parental care for their young, making them a popular species for parental investment research. Male smallmouth bass Micropterus dolomieu guard their nests against potential predators for up to 6 weeks (Ridgway 1988). Nest-guarding males continuously fan their offspring in the nests, which increases oxygen for the embryos and keep them free of silt and waste products (Ridgway 1988). During the nesting period eggs and fry are vulnerable to predation by crayfish (Orconectes and Cambarus spp; Hinch and Collins 1991) and various fishes (Kieffer et al. 1995; Philipp et al. 1997; Steinhart et al. 2004). Providing parental care can become energetically costly to smallmouth bass (Mackereth et al. 1999; Steinhart et al. 2005b); however, it is required or the offspring will be lost to predators (Goff 1986; Hinch and Collins 1991; Steinhart et al. 2004).

The cost of care is associated with several energetic expenses, including the energy spent to defend and fan the nest and cover the duration of care (Cooke et al. 2006). As the number of nest predators increases, the amount of time spent defending the nest also increases, as do the energetic demands on the male (Gillooly and Baylis 1999). Smallmouth bass in Lake Erie, which now contains abundant levels of egg-eating round gobies Neogobius melanostomus, made aggressive chases nine times more frequently than did smallmouth bass in Lake Opeongo, Ontario, a lake that has few nest predators (Steinhart et al. 2005b). Fanning the brood increases brood survival but also requires smallmouth bass to use energy that cannot be replenished because foraging while providing parental care is drastically reduced (Gillooly and Baylis 1999). Overall, the metabolic rate of nesting males may increase by 50% or more (Hinch and Collins 1991; Steinhart et al. 2005b). This can result in reduced body mass and loss of stored energy (Mackereth et al. 1999). Reductions in body mass and energy can lead to an increase in postbreeding mortality (Sabat 1994), especially after the first reproduction (Gillooly and Baylis 1999). Therefore, smallmouth bass are faced with a trade-off between present and future reproductive efforts. If a male chooses to forego current reproductive efforts and abandon a nest, that male may be better able to prepare for potential future reproductive efforts by avoiding the metabolic demands of parental care and increasing consumption, thereby increasing somatic growth (Ochi 2005). However, predators inevitably consume offspring from abandoned nests, resulting in reduced individual fitness and recruitment potential for the current reproductive effort (Goff 1986; Iguchi and Yodo 2004; Steinhart et al. 2004).

Smallmouth bass will abandon their nests when the majority of the brood has been lost to predators (Suski et al. 2003; Hanson et al. 2007). Even during a temporary absence, for example, when a male is removed from the nest by anglers, many predators can swarm the nests until the parent returns or the brood is entirely consumed. The round goby, when found in high densities, has the ability to consume an entire brood within 15 min when a smallmouth bass has been taken from the nest by anglers (Steinhart et al. 2004). Because nesting smallmouth bass are often concentrat-
ed and highly aggressive they often are targeted by anglers, which can lead to many males being removed from their nests. Even these temporary removals may result in significant offspring losses (Steinhart et al. 2004). In lakes where smallmouth bass are subject to high brood-predation rates, angling and nest predation could combine to have a substantial negative effect by increasing nest abandonment and subsequently eliminating future offspring production from the abandoned brood. Although smallmouth bass have been studied extensively, previous research on brood reduction is contradictory. It is still unclear exactly how many offspring can be lost before a male will abandon his nest, especially across a range of lakes where males have different expected future fitness.

Nest abandonment is probably related to expected future fitness, which is a function of growth, fecundity, and survival (Steinhart et al. 2008). For example, fish that experience low mortality rates also can expect a high chance of surviving to reproduce again and, therefore, may be less vigilant or more prone to abandoning a brood and preparing for a future reproductive attempt. Conversely, a male should be more willing to guard a brood if adult mortality rates are high because he may not live until the next spawning season. Nest depredation did not lead to nest abandonment in Lake Erie, a lake with numerous brood predators, frequent storms, and high angling pressure (Steinhart et al. 2005a). It is possible that the conditions in Lake Erie (i.e., low probability of nest success and high adult mortality) led males to guard even very small brood sizes. Similarly, older males have fewer future spawning opportunities than younger males and should not easily abandon their nests (Steinhart et al. 2008). Larger males also may be encouraged to provide a higher quality of parental care due to their tendency to mate with large females that are more fecund than the females that typically spawn with small males (Wiegmann and Baylis 1995). Young males, on the other hand, may gain an increased future fecundity if they used their energy for growth rather than parental care. Finally, as a brood becomes older the likelihood of abandonment should decrease due to the increased value of the brood with age. The increase in the value of older broods results from their higher probability of success (i.e., fewer days are needed to survive to independence; Steinhart et al. 2005a, 2008).

The objectives of this study were to quantify the threshold of brood loss that leads to nest abandonment by smallmouth bass in a north temperate lake. In addition, we hypothesized that nest success (i.e., a nest containing free-swimming offspring was considered successful) would be negatively related to percentage of the brood removed. In addition, we predicted that younger and smaller males would be more likely to abandon, and that smaller and younger broods would be more likely to be abandoned. The results of this study, combined with similar data from other systems, will improve our understanding of the factors regulating smallmouth bass reproductive success and, therefore, improve our ability to conserve and manage this important species.

**Methods**

Snorkel surveys were conducted to find smallmouth bass nests in known spawning areas in Lake Opeongo, Algonquin Provincial Park, Ontario. Lake Opeongo is a 5,780-ha lake containing an introduced and self-sustaining smallmouth bass population. Surveys were conducted over 2 years: May 31 to June 12, 2007, and June 3 to June 29, 2008. Different reaches of shoreline were sampled each year to avoid any resampling or cumulative effects of our treatments (Figure 1). Forty-one nests were marked with numbered rocks to ensure proper identification in 2007 and 64 nests in 2008. Survey areas were revisited an average of every 1–3 d (typically every 2 d), and the presence of the male and developmental stage of the offspring were recorded. Developmental stages were divided into unhatched embryos (“eggs”), hatched embryos (“clear fry” or “pigmented fry”), larvae, or juveniles and were assigned visually. Nests containing offspring that reached the free-swimming larval stage were deemed successful.
Treatments were assigned to nests starting with 0% brood removal and continuing to 25, 50, or 75% brood removal as they were found. However, treatment assignment was essentially random in both space and time because snorkeling starting points varied by day and not all nests were discovered after the first snorkeling pass. In addition, some randomly selected nests were reserved for treatment at later dates to allow for brood reductions of older broods after they were assigned to a treatment group. For all treatments, nest-guarding smallmouth bass were removed from their nests by means of angling with a single-hook jig. Total length (TL) and wet weight were measured. At this time, scale samples were collected from the fish to assess age and then the fish was released. This procedure was performed as quickly as possible (less than 30 s) to reduce stress and air exposure to the fish. All males returned to their nest within 10 min after treatment, even if only temporarily.

Brood removals and information on the brood characteristics were collected immediately after angling the male. A 0.5-m² frame made of polyvinyl chloride piping, divided into eight wedge-shaped sections with string, was placed over the center of the nest. Visual estimation was used to place the frame such that each one-eighth section contained approximately the same percentage of the brood. A turkey baster (pointed plastic tube with a squeeze bulb attached) was used to remove offspring from the appropriate number of sections corresponding to treatment level (e.g., offspring from two of the eight sections were removed to achieve 25% brood removal). Although brood removal estimates were certainly not perfect estimations, the range of treatments (0–75%) were assumed to be far enough apart to still reflect large differences in the percentage removed. All collected offspring were then placed into a mesh bag and transferred to an individually labeled jar filled with 70% ethanol for preservation.

Brood age was defined as the number of days since the nest first received eggs and was determined when spawning was observed or when a nest was empty on one day and had eggs on the following day. If the exact spawning date was unknown, brood age was determined by comparing the developmental stage (unhatched embryos, hatched embryos, larvae, and juveniles) with nests of known ages. Male age was determined by making impressions of the scales on acetate slides. Age estimates were determined by two readers and when age estimates were not in agreement, the slides were viewed again until there was consensus on the age. Offspring removed from broods were later enumerated to allow for estimation of the total brood size for the removal treatments (e.g., if 75% of the brood was removed, the number removed was divided by 0.75 to estimate the total brood size). For broods from which no offspring were removed (0% treatment), we estimated the brood size based on a multiple linear regression on male age and spawning date, that is,

\[
\text{brood size} = 18.16 \times \text{TL}(\text{mm}) - 22.48 \times \text{spawning date};
\]

\[r^2 = 0.66.\]

Data used to create this equation were from the 2007 and 2008 brood removals in Lake Opeongo. The fates (success or failure) of 105 nests in Lake Opeongo were determined by the end of our study (0%: \( n = 25 \) nests; 25%: \( n = 27 \) nests; 50%: \( n = 26 \) nests; 75%: \( n = 27 \) nests).

We compared male age, male length, brood age, and brood size across treatments with one-way analysis of variance to ensure that the brood removal treatment groups had males that were similar in age and broods that were similar in age and size. We used binary logistic regression to test whether the percentage of brood removed and year were related to nest fate using data from individual males and their nests. In addition, a chi-square test was conducted to determine whether treatment affected the number of failed and successful nests. Because we had specific directional hypotheses, one-tailed t-tests were used to determine whether brood size after treatment, age of brood at treatment, or male size (weight and length) or age varied for successful and failed nests (\( \alpha = 0.05 \) for all tests).

### Results

The average age of all nests at the time of brood reduction was 4.1 ± 0.3 d (mean ± SE; range, 1–12 d; Table 1). Males averaged 7.8 ± 0.2 years old and ranged from 4 to 15 years old. Males averaged 367 ± 6.3 mm and had an average of 3,182 ± 269 offspring in their nests (Table 1). There was no significant difference among treatment groups in male age, male length, brood age, or brood size before treatment (Table 1).

Across all treatments, 22 of 105 nests (21%) were abandoned. Although when both years were pooled there was a slight trend for increased nest failure with increasing percent of brood removed. The results were variable in each individual year (Figure 2) and logistic regression suggested that there was no effect of year (\( \chi^2 = -1.64, P = 0.10 \)) or brood removal treatment (\( \chi^2 = 0.93, P = 0.35 \)) on nest failure. When data across years were pooled, there was no effect of the percent of brood removed on nest failure (\( \chi^2 = 0.58, \text{df} = 3, P = 0.92 \)). While treatment level had no effect on abandonment, the size of the brood remaining after treatment was significantly lower in abandoned nests.
There was an average of 600 fewer offspring in failed nests than in successful nests ($t = 1.71$, $df = 57$, $P = 0.046$; Figure 3A). In addition, the fate of nests varied with age of the nest at treatment: abandoned nests were 2 d younger, on average, than nests that remained guarded ($t = 4.37$, $df = 73$, $P < 0.0001$; Figure 3B). Also, young males were more likely to abandon their nests than were old males ($t = 3.66$, $df = 66$, $P = 0.0003$; Figure 3C). Males that abandoned their nests were 1.3 years younger, on average, than males that produced successful broods. Males that had successful broods were larger in both wet weight ($t = 3.02$, $df = 48$, $P = 0.002$) and TL ($t = 2.76$, $df = 48$, $P = 0.004$; Figure 3D), which was expected because successful males were older than abandoning males.

**Discussion**

When male smallmouth bass abandon their nests, it is presumed that all offspring within that nest are lost (Goff 1986; Lukas and Orth 1995; Steinhart et al. 2004); therefore, understanding why and when males abandon their nests would be valuable to ecologists and fisheries managers. In Lake Opeongo, nest failure rates did not vary by brood-reduction treatment making it impossible to identify a brood-size threshold at which males were likely to abandon. However, the nest failure rate did vary with the age of the male as well as the age and size of the brood. These findings indicate that brood reduction was not as important as characteristics of the male and brood. The failure to find a specific brood reduction at which males abandoned is probably a consequence of trade-offs between variables that affect current and future fitness. It is also possible that abandonment becomes more frequent if more than 75% of the brood are removed (see Hanson et al. 2007).

Males that abandoned their nests were younger than those that continued to guard and therefore may have abandoned their broods to prepare for future reproductive attempts. On the other hand, old males that continued to guard their nests might have remained because they had fewer expected future reproductive opportunities than a young male. Natural selection may operate such that males are predisposed to abandoning broods under certain conditions. Also, larger males tend to guard their nests more tenaciously than small males (Wiegmann and Baylis 1995) and are, on average, more successful in doing so (Suski and Ridgway 2007). Males that abandoned young nests might be able to nest again within the same spawning season or begin foraging earlier than guarding males. Early abandonment may result in increased growth and survival of the male because he no longer needs to provide care.

Other research on the effects of brood reduction has found varied results. In Lake Erie, a brood reduction of about 25% by natural predation resulted in no effect on abandonment rates (Steinhart et al. 2005a). Suski et al. (2003) found that angling, coupled with a 50% reduction in the brood, increased abandonment by approximately 60% in Charleston Lake, Ontario.

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**Table 1.** Mean ± SE male age, total length, brood size, and nest age at treatment of all smallmouth bass nests in Lake Opeongo from which portions of the brood were removed in 2007 and 2008.

<table>
<thead>
<tr>
<th>Treatment (percent removal) and statistic</th>
<th>Male age (years)</th>
<th>Total length (mm)</th>
<th>Brood size</th>
<th>Nest age (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>7.6 ± 0.4</td>
<td>362 ± 12</td>
<td>3,229 ± 218</td>
<td>3.7 ± 0.4</td>
</tr>
<tr>
<td>25</td>
<td>7.6 ± 0.4</td>
<td>363 ± 13</td>
<td>3,554 ± 693</td>
<td>4.1 ± 0.6</td>
</tr>
<tr>
<td>50</td>
<td>8.2 ± 0.5</td>
<td>375 ± 13</td>
<td>3,379 ± 650</td>
<td>4.3 ± 0.6</td>
</tr>
<tr>
<td>75</td>
<td>7.7 ± 0.4</td>
<td>368 ± 13</td>
<td>2,579 ± 443</td>
<td>4.4 ± 0.6</td>
</tr>
<tr>
<td>All</td>
<td>7.8 ± 0.2</td>
<td>367.2 ± 6.3</td>
<td>3,182 ± 269</td>
<td>4.1 ± 0.3</td>
</tr>
<tr>
<td>ANOVA</td>
<td>$F_{3, 101}$ = 0.42</td>
<td>$0.22$</td>
<td>1.03</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>$P = 0.74$</td>
<td>0.89</td>
<td>0.38</td>
<td>0.82</td>
</tr>
</tbody>
</table>

---

**Figure 2.—** Percent nest failure for smallmouth bass nests across all brood removal treatment groups in Lake Opeongo in 2007 (filled circles) and 2008 (open circles). The number near each symbol is the number of nests in that treatment.
Hanson et al. (2007) reported that a treatment of 90% brood reduction coupled with catch-and-release angling increased nest abandonment by nearly 70% in Wolfe and Devil lakes, Ontario. Clearly, the effect of brood reduction on smallmouth bass nest abandonment rates has varied widely in the experiments conducted thus far.

What might explain the highly variable results in brood reduction experiments? In our results, brood size played a small role (there was no direct effect of brood removal treatment, but failed broods were smaller after treatment than were successful broods), while male age and brood age were important factors determining nest failure. Our results suggest that individuals may value broods differently, regardless of reductions in brood size. If so, then populations may develop different abandonment thresholds based on environmental conditions. For example, populations with high mortality rates may be predisposed to guarding broods in otherwise suboptimal situations because they are less likely to have another spawning opportunity (Steinhart et al. 2008). Other environmental and demographic factors may also lead to variation in the willingness to guard reduced broods (e.g., risk of storms, cost of care, growth rates, predation risk; Steinhart et al. 2008). Surprisingly, we expected that brood abandonment should have been relatively common in Lake Opeongo because angling mortality is relatively low and, because it is a northern population in the species’ range, fish growth is comparatively slow. A general lack of predation risk in Lake Opeongo, however, theoretically favors guarding reduced broods because of a low cost of care (Steinhart et al. 2005b).

It is generally believed that angling magnifies the frequency of nest abandonment by increasing the mortality of adults via harvest or that of offspring via nest predation in unguarded nests. But clearly the effects of brood reduction are variable and nest success depends on more than these variables. If we understood how different factors affect abandonment rates, a useful tool could be created to help determine appropriate smallmouth bass angling regulations or to simulate the effects of different regulations. For example, lakes that do not experience high frequencies of nest abandonment (or that do not have many factors that increase abandonment rates) could be assigned more liberal angling regulations without incurring the detrimental effects of males abandoning their broods.

**Figure 3.**—Box plots of (A) the number of individuals in a brood after treatment, (B) brood age on the day of treatment, (C) the age of the male guarding the nest, and (D) the total length of the male for all unsuccessful and successful smallmouth bass nests treated in Lake Opeongo in 2007 and 2008. Whiskers indicate the 90th and 10th percentiles; the box indicates the 75th and 25th percentiles; the horizontal line (sometimes obscured by the box) is the median; the filled circle denotes the mean.
where smallmouth bass are prone to nest abandonment, strict protection of at least a portion of the spawning population may increase fish abundance and could improve recruitment and angling success. Implementing the use of no-fishing sanctuaries to protect smallmouth bass while they are nesting is one example of a viable option to protect populations that are prone to abandonment (Suski et al. 2002).

Our research indicates that many factors, including male age and brood age and size, contribute to smallmouth bass nest abandonment. The amount and intensity of parental care given by an organism is a balance between current and future reproductive efforts. Clearly, the results of various brood removal experiments have differed dramatically, presumably because of different selective pressures across the study systems. Therefore, it would be beneficial if future studies incorporated a variety of lakes in several different regions to account for the variability in such factors as predation risk, predator abundance, male mortality, average nest success, and environmental stochasticity. Assessing the strength of the various factors that contribute to abandonment rates, such as the environment and population demographics, would allow managers and ecologists to better understand and predict abandonment rates.

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Suski, C. D., J. H. Svec, J. B. Ludden, F. J. S. Phelan, and...