2017. Proceedings of the Indiana Academy of Science 126(2):158–165

SPOTTAIL DARTER (*ETHEOSTOMA SQUAMICEPS*) SPAWNING ECOLOGY IN SOUTHWESTERN INDIANA: A LONG-TERM STUDY

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ABSTRACT. From 1994 to 2015, the spawning biology of two populations of spottail darters (*Etheostoma squamiceps*) was monitored using artificial nest sites in two first-order streams that are part of the Bayou Creek drainage in southwestern Indiana. During the mid-March to May breeding season, size (standard length) of breeding individuals of both sexes captured under nest sites was measured, and the presence of eggs was noted. In addition, laboratory experiments examined the relationship between female size and both the number of mature ova and the number of eggs spawned. Larger males spawned earlier and were more likely to be defending eggs throughout the breeding season; larger females also spawned earlier. Both the number of mature ova and the number of eggs spawned varied positively with female size; however, for females of the same size the number of ova was consistently greater than the number of eggs spawned, suggesting that spottail darters are fractional spawners. While female size and spawning statistics were similar to those of an Illinois population, males in the current study were much larger than their counterparts in Illinois, which may be due to either more rapid growth or a longer lifespan.

Keywords: Spottail darter, *Etheostoma squamiceps*, resource defense polygyny, nest site competition, standard length, fractional spawning

INTRODUCTION

The spottail darter (*Etheostoma squamiceps*) is found in drainages in western and central Kentucky, southern Illinois, and southwestern Indiana (Page et al. 1992). In a survey of sites in southwest Indiana where spottail darters were found historically, Page et al. (1976) found them at only two sites, both in Posey County. As a result, the species received a designation of Special Concern by the Indiana Department of Natural Resources (Whitaker & Gammon 1988). Subsequent surveys expanded the range to include Gibson, Vanderburgh, Warrick, and Spencer Counties, where they are typically found in small streams draining watersheds of < 260 km^2 (Fisher 2008), and the Special Concern status was removed. However, this species has a patchy distribution within this range, probably due to the limited availability of nesting habitat. As with other members of the subgenus *Catonotus*, *E. squamiceps* females attach eggs in clusters to the ceilings of benthic structures such as slab-rocks where they are guarded by males (Page 1974). Many streams in southwestern Indiana lack these structures due to siltation associated with agricultural activities. Streams with populations of spottail darters often are located in suburban areas with reduced siltation compared to agricultural lands.

For over two decades, sections of ceramic field tile have been added to streams containing spottail darters to serve as artificial nest sites. Males, which practice resource-defense polygyny, readily guard them, and the broods deposited by females on the ceilings of the tiles do not differ in number of eggs from those under rocks at the same sites (Bandoli et al. 1991). Males guarding tiles are easily captured, facilitating studies of male reproductive strategies (Bandoli 1997, 2002; Bandoli et al. 2004). Additionally, attaching lightly sanded acetate sheets to the undersides of the tiles allowed the manipulation of broods to address questions related to filial cannibalism (Bandoli 2006, 2016).

All of the studies cited above were conducted partially or wholly in the field. During these investigations, records of tile guarding by males and the presence of spawning females and eggs were maintained to aid in establishing the timing of concurrent studies of male reproductive strategies. These data, extraordinary for their quantity and time span, allow questions regarding the role of male size in nest defense and attraction of females, associations between males and

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females at the nest site, and temporal patterns in spawning to be addressed.

Female spottail darters do not participate in egg defense, but leave the nest site immediately after spawning. It is not known whether females spawn multiple times during a breeding season (fractional spawning) or just once. Page (1974) found that in an Illinois population, ovary weight peaked just prior to the spawning season and declined during, with no regrowth until the following spring, suggesting that the number of ova is fixed at the start of the spawning season. He also reported that the number of mature ova was linearly related to female size. However, data on the number of eggs spawned was limited to four females, and apparently no other study has addressed this. In an attempt to better understand female reproductive ecology, gravid females were allowed to spawn with mature nest-guarding males in laboratory conditions; additional gravid females were dissected and the number of eggs in their ovaries counted to examine the relationship between female size and both the number of mature eggs in the ovaries and the number of eggs spawned per breeding.

METHODS

Study sites.—All observations reported herein are from two sites – Carpentier Creek at Bohene Camp Road (latitude 37° 59.362′N; longitude 87° 38.595′W) and an unnamed stream paralleling Nurrenbern Road (hereafter Nurrenbern Creek; 37° 56.710′N; 87° 39.417′W). Both streams are first-order tributaries of Bayou Creek, which drains approximately 80 km^2 in southwest Vanderburgh County, Indiana, before joining the Ohio River.

Field methods.—Nest sites are 15 cm long half-cylinders cut from 10 cm diameter ceramic field tile. Except for 2002 and 2006 when no tiles were placed, a mean of 17.5 tiles (range 9–23) was added to a 100 m reach of Carpentier Creek each March from 1994 through 2015. During 13 of those years (1998–2001; 2003–2004; 2007–2011; 2013; 2015), a mean of 8.3 tiles (range 4–18) was also added to a 50 m reach of Nurrenbern Creek, also in March. Frequency of checking the tiles varied from once per week to twice per month during the spawning season (mid-March through late May) depending on the nature of the concurrent studies. Occasional flooding washed some tiles downstream, interrupting or abbreviating some field seasons.

Tiles were checked by placing a hand net over one opening and sweeping it toward the other opening while the tile was lifted, which captured all fish under the tile most of the time. Males that were seen but not captured were often captured later if the tile was re-checked after 10 min. Captured breeding males (signified by the enlarged, darkened head; Page 1974) were usually measured (standard length (SL)) on first capture. Male spottail darters have high nest site fidelity (Bandoli 1997); therefore, the SL of males captured on subsequent surveys during the same spawning season that appeared to be repeat captures based on capture location and size was not usually recorded. Gravid females captured with males were considered to be spawning. They were usually measured (SL); females captured alone, which were often under empty tiles, were viewed as using the tile as a shelter rather than a spawning site and therefore not measured. The presence of eggs under a tile was noted; the number of eggs in a brood is dynamic over time due to new females adding eggs and egg loss due to hatching and filial cannibalism (Bandoli 2016). Therefore, the presence or absence of eggs, not brood size, is the only reproductive variable included in this analysis. Unless the nest site was taken to the lab, the tile and any fish captured were replaced at their original locations (spottail darters released under a tile tend to stay there; Bandoli 1997). These observations allowed the evaluation of the role of size in male reproductive success by comparing SL in males (1) with and without eggs, and (2) defending nest sites in the first and second halves of the spawning season. Additionally, observations of females captured with males permitted an assessment of temporal patterns in spawning, the role of male size in attracting females, and whether larger females spawn earlier.

Female fecundity.—During the spawning seasons of 1989–1992, laboratory aquaria with gravel substrate collected from Carpentier Creek were maintained. Water temperature was not controlled, ranging from 19–22° C. Each aquarium contained a breeding male spottail darter and a tile to defend. Gravid females collected during the spawning season from Carpentier Creek were added individually to aquaria. Thirty spawned, and clutch size (number of eggs) and SL of each female were determined before they were released into their streams of capture.

In 1990 and 1991, an additional 37 gravid females collected in Carpentier and Nurrenbern creeks were measured (SL) and sacrificed to count the number of mature ova, which are translucent orange as opposed to the opaque or yellow appearance of immature eggs (Page 1974). This quantified the number of mature ova that a female could spawn immediately and related it to female size. These data, along with size-based clutch data, were used to assess whether females spawn all mature eggs during a spawning bout. To test whether fecundity varies geographically, the relationship between female size and the number of mature ova of this population was compared to the same metric in a population in Big Creek, Illinois studied by Page (1974).

Statistical analyses.—To determine whether the size of spawning males changed over the 22 years of the study, mean SL of males captured between 1994 and 2003 was compared to that of males captured between 2004 and 2015 using a 2-sample *t*-test (two tails) assuming equal variance. The same test was used to compare the SL of males in Carpentier Creek to those in Nurrenbern Creek. To determine whether larger males were more likely to be guarding eggs than smaller males and whether larger males spawn earlier in the breeding season, the measured males were divided into four groups based on the presence or absence of eggs and on the date of capture (15 March through 15 April and 16 April through the end of May). A two-way GLM ANOVA with eggs and time as factors was used to test for differences between SL in these groups. A two-sample *t*-test (one tail) assuming equal variance was used to compare mean SL of measured females captured with males during the first half of the spawning season to those captured during the second half.

To test whether larger males attract more females, a two-sample *t*-test (one tail) assuming unequal variance was used to compare SL of males that were captured with and without one or more females. However, in many fish species the attractiveness of a male to females is confounded by female preference for nests containing eggs (e.g., fathead minnow, *Pimephales promelas*, Unger & Sargent 1988; fantail darter, *E. flabellare*, Knapp & Sargent 1989; and sand goby, *Pomatoschistus minutus*, Forsgren et al. 1996). To avoid this potential bias, only males guarding empty nest sites were used in this analysis.

Linear regression was used to investigate the relationships between female SL and the number of mature ova and between female SL and the number of eggs spawned. If females spawn most or all of their mature eggs at a spawning, the slopes and intercepts of these regressions should not differ. Because the data sets are independent and normally distributed, the slopes were compared using a *t* statistic (one-tailed since females cannot lay more eggs than mature ova) generated by dividing the difference in the coefficients of the slopes for SL by the square root of the combined squares of the standard errors of the coefficients (Wackerly et al. 2008). Linear regression was similarly used to compare SL with the number of mature ova counted in 18 females in a Big Creek, Illinois population (Table 2 in Page (1974)). The *t* statistic described above (two tails) was used to compare size-dependent fecundity between the Indiana and Illinois populations. Statistical analyses were conducted using SigmaPlot 12 (Systat Software, Inc.) and EXCEL ver. 14 (Microsoft, Inc.). All means are reported $\pm$ 1 standard error.

RESULTS

Of the 504 males captured while defending tiles, 302 were first captures (based on location and size); the remaining 202 were considered recaptures and were not included in subsequent SL analyses. Males captured from 1994–2003 (n = 142) had the same mean SL (69.5 $\pm$ 0.5 mm) as the 160 males captured during 2004–2015 (69.8 $\pm$ 0.5 mm; $t = 0.30$, $p = 0.77$). Mean SL did not differ between males from Carpentier Creek (69.8 $\pm$ 0.4 mm; $n = 277$) and males from Nurrenbern Creek (67.7 $\pm$ 1.4 mm; $n = 25$; $t_{300} = 1.59$, $p = 0.11$); therefore data from all years and both streams were combined for all analyses.

The mean SL of all males measured was 69.7 $\pm$ 0.4 mm (range 53–88 mm with a near-normal distribution; Fig 1). The mean SL of the 153 males captured while defending eggs was 71.2 $\pm$ 0.5 mm, significantly larger than the 149 males defending empty tiles (68.3 $\pm$ 0.5 mm; $F_{1,301} = 14.98$, $p < 0.001$). Males defending tiles between 15 March and 15 April ($n = 135$) were significantly larger (mean SL = 71.0 $\pm$ 0.5 mm) than 167 males defending tiles after that period (68.5 mm; $F_{1,301} = 12.27$, $p < 0.001$). The interaction between date and the presence of eggs was not significant.

The mean SL of 68 measured females captured with males was 44.4 $\pm$ 1.2 mm (range 30–65 mm

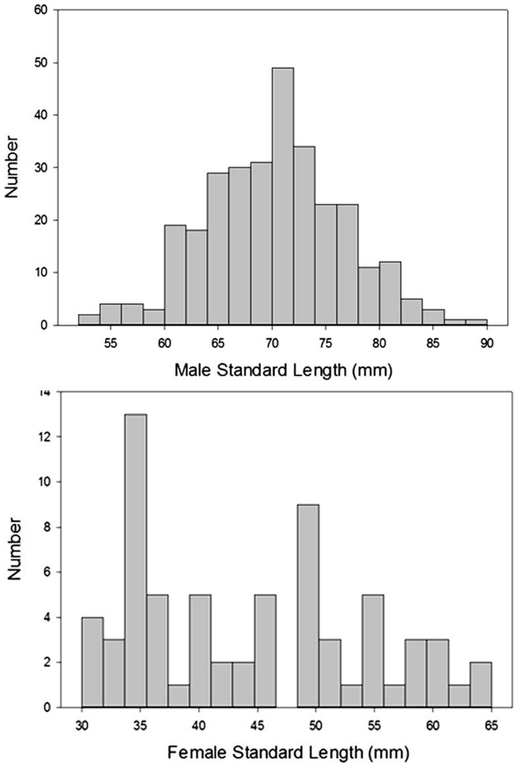

Figure 1.—Standard length distributions for breeding male and female spottail darters (*Etheostoma squamiceps*) in Carpentier and Nurrenbern Creeks between 1994 and 2015.

with a relatively flat distribution; Fig 1). The 22 females captured with males during the first half of the spawning season were significantly larger than the 46 females captured during the second half (47.7 ± 2.0 mm and 42.8 ± 1.4 mm, respectively; $t_{66} = 1.9$, $p = 0.03$).

Seventeen percent of the 504 males captured had females under their tile. Most of these (68.6%) had a single female; 22.1% had two females, 8.1% had three females, and one male had six females. Instances of males captured with two or more females were twice as common during the second half of the spawning season. Mean SL of females alone with a male (46.0 ± 1.6 mm) was not different from that of the largest female in cases of multiple females captured with a male (47.3 ± 3.1 mm; $t_{20} = 0.39$, $p = 0.71$); in captures of multiple females the smaller females averaged 17.4% smaller than the largest female. For males not defending eggs, the mean SL of males captured with least one female (69.7 ± 0.9 mm) was not significantly larger than males captured alone (68.2 ± 0.6 mm; $t_{57} = 1.34$, $p = 0.09$).

There was a significant relationship between female SL and the number of mature ova (O) in the ovaries ($F_{1,36} = 12.3$, $p < 0.001$), with $O = -141.4 + 5.48*SL$; Fig. 2. The number of eggs laid (L) also varied significantly with SL ($F_{1,29} = 7.47$, $p = 0.011$), with $L = -87.8 + 3.24*SL$. The intercepts were similar, but the slopes were significantly different ($t_{63} = 1.77$, $p < 0.05$). The SL vs. mature ova regression for the Illinois population was also significant ($F_{1,17} = 17.0$, $p < 0.001$), with $O = -262.3 + 8.03*SL$. The slope of this regression was not different from that of the mature ova regression for the Indiana population ($t_{51} = 1.28$, $p < 0.20$).

DISCUSSION

The importance of size in reproductive success of male spottail darters was confirmed in this study. Males guarding eggs were larger than those guarding empty tiles, and larger males spawned earlier in the breeding season. These factors did not interact; males guarding eggs were larger than those guarding empty tiles throughout the spawning season. Larger females also spawned earlier in the season. These results confirm earlier observations (Bandoli 1997), and given the positive relationship between female SL and the number of eggs spawned, suggest that earlier-spawning males also benefit by receiving more eggs per female.

A previous laboratory study found that females given a choice between two males defending equal-sized empty nest sites spawned with the larger male (Bandoli 1997), yet male spottail darters with empty nest sites captured with one or more females in the current study were not significantly larger than males captured without a female. Timing of spawning suggests a possible resolution. Larger males spawn earlier in the season, at which time larger females are also spawning. Females in an Illinois population of spottail darters are generally similar in size (weighted mean SL = 42.6 mm, range 32–59 mm, $n = 58$; Page 1974 (Table 4)) to Indiana females. Assuming this size similarity implies similar ages, early-spawning females in Indiana are likely to be two- and three-year-olds. Later-spawning females would also include one-year-olds, which are more numerous than older females, increasing their likelihood of capture with nest-guarding males, which are also smaller than earlier-breeding males. Additionally, cap-

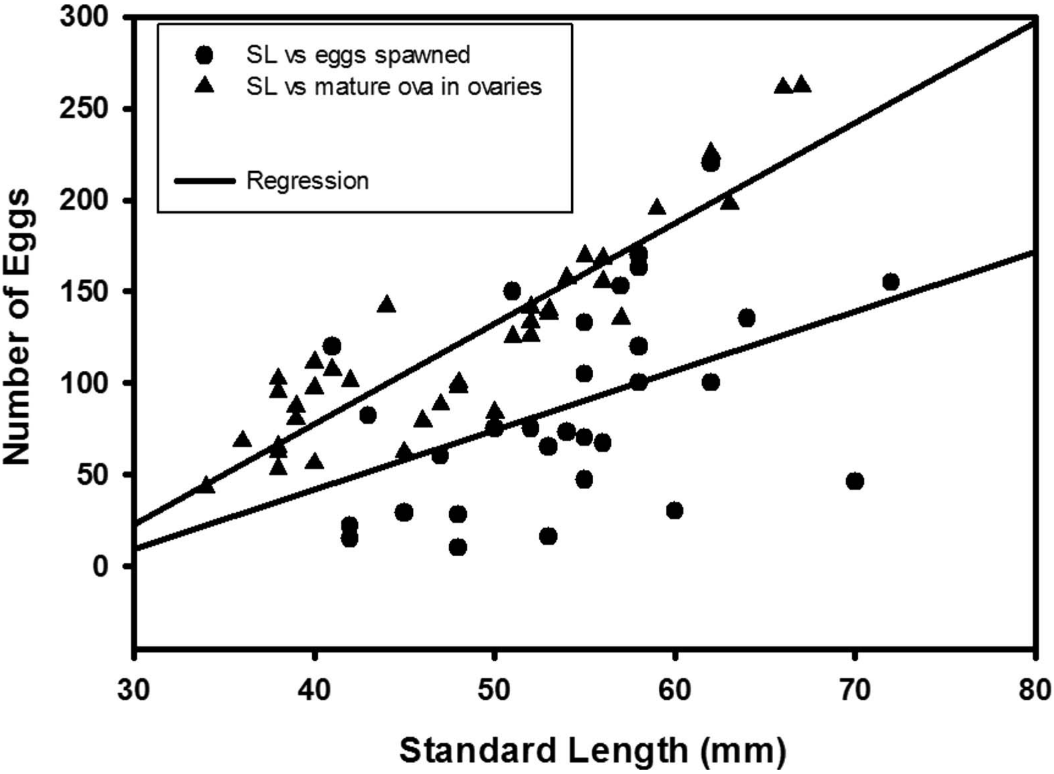

Figure 2.—Linear regressions of the number of mature ova in ovaries ($n = 37$; upper line) and eggs spawned ($n = 30$; lower line) on standard length for female spottail darters (*Etheostoma squamiceps*). The slopes are significantly different.

tures of a male with multiple females were twice as common during the second half of the breeding season and typically included one or two smaller (= younger) females along with a larger female. Many of these smaller females may have been naïve yearling females that may copy the mating choices of older females (Witte & Noltemeier 2002).

During the breeding season, association between males and females is limited to courtship and spawning (Page 1974). Since 17% of males captured had one or more females under their tiles, this may approximate the proportion of time males spend spawning during the breeding season. However, spottail darters occasionally spawn at night (Page 1974; Bandoli, personal observation (laboratory)), so this may be a minimum estimate since all observations in the current study were made during daytime hours.

As is typical for ectotherms in general and fishes in particular, female spottail darters in both Indiana and Illinois have a positive linear relationship between size (age) and egg production. Page (1974) counted scale annuli and found that females first spawned at 11–13 months (28–43 mm in SL), and contained $\leq$ 80 mature ova, whereas those at 35–36 months (56–59 mm in SL) contained 200–400 mature ova. Indiana females also are likely to start spawning at age one and continue through age three given the similarities between the ranges of spawning female SL in the two populations, and the similar slopes relating size and number of mature ova in the two populations suggest that same-sized females spawn similar numbers of eggs.

Despite numerous attempts, I have never witnessed a female spottail darter spawning more than once in the laboratory even when placed with a new male for several hours; however, this may have been a function of the artificial environment and generally short duration of these casual experiments. In this study the number of eggs spawned was consistently less than the number of mature ova for females of a given size, and larger females in particular spawned fewer eggs than expected; limited data for the Illinois population show a similar pattern (Page 1974). This supports the hypothesis that females may not spawn all mature ova during a single spawning event. Fractional spawning is typical for small fishes with prolonged breeding seasons (Burt et al. 1988), and has been observed in tessellated darters (*E. olmstedi*; Gale & Deutsch 1985) and Kentucky darters (*E. rafinesquei*; Weddle & Burr 1991), and inferred for others (Hubbs 1985). Fractional spawning, especially with different males, may be an adaptive form of bet-hedging. Egg development time varies inversely with water temperature (Gillooly et al. 2002); in spottail darters, development to hatching takes approximately 15 days at 15° C (Bandoli, pers. observation) to 11 days at 22° C (Page 1974), a temperature range typical for Carpentier and Nurrenbern streams in April and May. Males may vary in their ability to defend eggs for this long, and lacking reliable cues, a female may hedge her bets by spreading eggs among two or more males. Additionally, the fate of spottail darter eggs is influenced by (1) egg infection by water molds such as *Saprolegnia* (Bruno et al. 2011), and (2) filial cannibalism by the defending male, either to control infection directly (Bandoli 2016) or indirectly through a reduction in egg density (Lehtonen & Kvarnemo 2015), or as an energetic strategy to reduce foraging time away from the nest (Rohwer 1978). The potential for egg loss due to each variable is in turn influenced by the number and density of eggs present when a female spawns; more eggs may increase the potential for infection from adjacent eggs (Bruno et al. 2011) while decreasing the possibility of consumption via the dilution effect (Wrona & Dixon 1991). A female that spawns with a male that is not defending eggs (possibly lower infection risk but increased probability of loss to filial cannibalism) and another already defending eggs (higher infection probability but reduced loss to cannibalism) may have higher reproductive success compared to one that spawns all eggs with only one male.

Page (1974; Table 4) determined that breeding males captured in Big Creek were all 2-year-olds ranging from 38–59 mm in SL and 3-year-olds (the maximum age) ranging from 53–66 mm. The smallest measured male captured guarding a tile in the current study had an SL of 53 mm, and over 95% ranged from 60–88 mm, suggesting that males in Indiana either grow more quickly or live longer than three years. I have attempted to use scale annuli to age male spottail darters collected from Carpentier and Nurrenbern streams, but patterns were too inconsistent for confidence; a more accurate and precise technique may be needed to test the different-lifespan hypothesis (Zymonas & McMahon 2009).

The hypothesis that same-age males are larger in Indiana due to more rapid growth gains support from three differences between the streams. First, at the time of Page's work, Big Creek was a forested spring-fed stream with little to no anthropogenic influences (Lewis 1957); the food base of *E. squamiceps* was primarily chironomid and mayfly larvae, copepods, amphipods, and isopods (Page 1974). Conversely, Carpentier and Nurrenbern creeks flow through suburban and agricultural areas and are subject to fertilizer and field bed runoff. These factors may increase the densities of some of these macroinvertebrates, especially isopods and chironomids (Polls et al. 1980; Lenat & Crawford 1994), both of which were found to be important food items for spottail darters in Sanders Creek, another tributary of Bayou Creek in southwest Indiana (Strange 1992). Second, Big Creek includes three species of *Etheostoma* in addition to *E. squamiceps*; one, the rainbow darter (*E. caeruleum*) is among the more abundant fishes in that stream (Lewis 1957). All these darters would be competing for the same food items. No other darter species occurs consistently in either Carpentier or Nurrenbern streams; while there are other species in these streams with food habits similar to spottail darters (e.g., bluntnose minnows (*Pimephales notatus*) and creek chubs (*Semotilus atromaculatus*)), the lack of other darters may reduce competition for food compared to that of the Big Creek population. Third, the limited number of nest sites in Carpentier and Nurrenbern streams promotes competition, which larger males usually win (Bandoli 1997). In Big Creek, 1-year-old males do not attempt to breed, possibly due to competition for nest sites. Growth curves show that males do not start becoming larger than females until the start of their second year (Page 1974, Fig. 9A), and the increased growth rate may be due to young males not investing energy into reproduction. Low nest site density in Carpentier and Nurrenbern creeks may enhance competition, driving both 1-year-old and smaller 2-year-old males to defer reproduction another year, with the energy savings potentially producing the larger 3-year-old males.

Since a bigger food base and less competition should also promote growth in females, the apparent similarity in size of females in the

Indiana and Illinois populations seems to argue against the hypothesis of more rapid growth in the Indiana population. However, this similarity may be misleading. Page's size data were based on females collected in April, the height of the spawning season. I captured spawning females from late March through late May, but most were taken in the second half of the season when smaller females are spawning; therefore the apparent similarity in mean spawning female SL may be due to sampling differences. Additionally, while more food and less competition should promote growth in both sexes, the energy required for egg production starting at age 1 may moderate this in females (Folkvord et al. 2014), while growth continues in males for an additional year or two to allow them to compete for nest sites. Regardless of whether spottail darters are larger in southwest Indiana due to longer survival or better food resources, size is clearly an important factor in spawning success in both sexes.

ACKNOWLEDGMENTS

Long-term natural history studies are increasing rare in the changing academic environment that favors shorter-term studies and sexier areas of biology. I have been fortunate to have long-term access to a population and the freedom to pursue investigations that interested me. My sincere thanks to all of these USI students who have helped on the various studies of spottail darter reproductive biology over the years: T. Bacon, L. Betancourt, G. Bryant, M. Deen, S. Hampton, T. Hayes, S. Hicks, A. Jackson, A. Johnson, A. Keeping, S. Leatherland, S. Loveless, K. Lutterbach, J. Meuth, A. Niemeier, C. Norrick, D. Phipps, C. Piestrup, R. Stefanich, M. Walls, A. White, and especially R. Strange, who began as a student and became a colleague. I also thank B. Wilding for statistical advice and the University of Southern Indiana for logistical support. Much of this research was supported by grants from the Indiana Department of Natural Resources, the University of Southern Indiana, and the Indiana Academy of Science.

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Manuscript received 6 November 2017, revised 9 January 2018.