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SMALLMOUTH BASS NESTING BEHAVIOR AND NEST SITE SELECTION IN A SMALL OHIO STREAM[1]

KIRK O. WINEMILLER[2] and DOUGLAS H. TAYLOR, Department of Zoology, Miami University, Oxford, OH 45056

ABSTRACT. Individual smallmouth bass, *Micropterus dolomieui*, were observed in a 500-m stretch of Indian Creek, Ohio, during May and June of 1980 and 1981. Nineteen nests were found in 1980; 8 of which received eggs. Spawned nests were more often guarded by larger males than unspawned nests and were located at sites which were protected from increases in water current velocity during moderate flood stages. Unspawned nests were abandoned within 2 days of the peak spawning activity at Indian Creek, and prior to damage by moderate flooding on 11 and 12 May. Extensive flooding on 17, 18 and 19 May terminated smallmouth bass nesting behavior and appeared to destroy all nests under study in 1980.

In 1981, 49 nests were found; 7 of which received eggs. Many of the unspawned nests appeared to be repeated constructions by males that were unsuccessful in attracting mates. Spawned nests were significantly more uniform than abandoned nests in diameter and water depth in 1981. Two aggregations of black fry were located in the study area on 13 and 17 June 1981. The fry were displaced approximately 250 m downstream from their original nest sites by moderate flooding on 12 June. Smallmouth bass nest site selection and breeding success are discussed in relation to the problem of reproducing in a variable environment.

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INTRODUCTION

The life history of the smallmouth bass, *Micropterus dolomieui*, has been extensively investigated due to the ecological and economic importance of the species (Coble 1975). The smallmouth bass is widely distributed in North America and occurs in both lotic and lentic environments, although Trautman (1959) reported in Ohio the species is generally found in streams with a gradient of 0.75–4.73 m/km. Recent ecological studies have focused on the species' habitat (Hubert and Lackey 1980), trophic relationships (Hubert 1977, Stein 1977, George and Hadley 1979), and population dynamics (DeAngelis and Coutant 1979). Investigations of smallmouth bass reproduction have been primarily concerned with the influence of environmental factors on egg/fry production, survivorship, and growth (Carlander 1977). Few behavioral observations have been reported since the early findings of Beeman (1924), Tester (1930), and Hubbs and Bailey (1938).

Smallmouth bass nesting seasons, nest characteristics, and egg/fry production have been quantified in both lentic (Watt 1959, Turner and MacCrimmon 1970) and lotic systems (Cleary 1956, Brown 1960, Pflieger 1966). The effects of environmental variables have traditionally been quantified in terms of the collective responses of local populations. In order to fully understand the evolution of the smallmouth bass mating system, studies are required which focus on the behavioral responses of individual fish to their biotic and abiotic environments. A greater understanding of the

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[2]Present address: Department of Zoology, University of Texas at Austin, Austin, Texas 78712.

adaptive elements of fish behavior should facilitate more effective management practices for fish species as natural resources.

The adaptive value of smallmouth bass nesting behavior is more apparent when viewed within the context of evolution in a stream environment. The stochastic nature of stream flooding should exert a major selective influence on the nest site selection, timing of reproduction, mating system, and/or parental care patterns of stream fishes. The present study was conducted in Indian Creek, a small, relatively undisturbed stream. The conditions within the stream not only permitted the direct observation of fishes, but closely approach those described by Trautman (1959) for Ohio streams upon discovery by early European explorers.

STUDY SITE

Indian Creek flows southeast through deciduous forests and farmlands of Butler County, Ohio. The stream is a tributary of the Great Miami River which continues south to juncture with the Ohio River. The region contains glacial drift soils of the Miami-Bellfontaine series and Miami silt and clay loam soils (Kotila 1963). At low discharge levels, the stream is 1–8 m wide and highly transparent. The stream margins are bordered by gravel bars, boulders, bedrock walls, fallen logs, and tree roots. Diatoms and *Cladophora* species of algae were present in the riffle regions of the stream.

A 500-m stretch of the stream north of Indian Creek Park at Reily, Ohio, was selected as the study area (figs. 1, 2). The pool-to-riffle length ratio was approximately 2 : 1 within the study area.

METHODS AND MATERIALS

Smallmouth bass nesting was observed at Indian Creek during May and June, 1980 and 1981. Behavioral observations were made from shore using binoculars, a stopwatch, and a Braun Super 8 motion picture camera (film speed = 24 frames/s). Near zero turbidity, high observer vantage points, and cover permitted observation without disturbing fish. Focal samples were made in which all behaviors and interspecific interactions of individual bass were recorded.

Unoccupied nests were located by walking the stream upon the completion of behavioral observations. We recorded the following data for each nest discovered: (1) nest diameter, (2) water depth, (3) description of nest site, (4) location, (5) size rank of nesting male (if present), (6) presence of eggs, silt, etc. Size ranks were assigned to nesting males in relation to other males observed on the same day. Water temperature was recorded at each nest site, pool, and riffle. Water current velocity was recorded for each nest site and adjacent pool at low, moderate, and high discharge levels using a Teledyne-Gurley No. 625 Pygmy current meter. A Sargent-Welch pH meter was used to determine pH at 9 sites. A Lafayette film analyzer was used to view behavioral sequences on a frame-by-frame basis. Two statistical procedures were employed to evaluate differences between spawned and abandoned nests. The F_{max} test was used to evaluate variability in nest dimensions and water depth. The 2-tailed t-test was used to test for significance in size rank of males from the 2 types of nests.

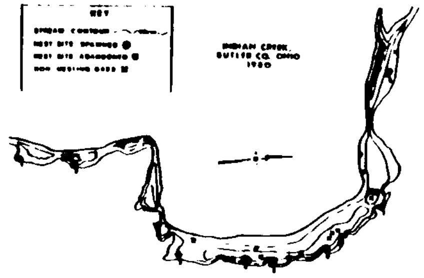

FIGURE 1. Map of the study region at Indian Creek, Ohio, in 1980, showing location of nests and smallmouth bass sitings.

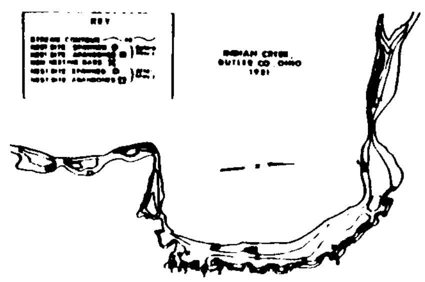

FIGURE 2. Map of the study region at Indian Creek, Ohio, in 1981, showing location of nests and smallmouth bass sitings.

RESULTS

1980. Nineteen smallmouth bass nests were located within the study region during May 1980. The first occurrence of nesting was noted at site 1 on 3 May (noon water temperature: 18.5 C). All nests were constructed of pea-sized gravel with a perimeter of larger flat rocks. The location of nests was always associated with the presence of overhead cover. Tree roots comprised 47.4% of the cover used by nesting bass, followed by boulders (21%), branches (21%), and logs (10.5%). Ninety percent of the nests were in regions of the stream with no measurable water current at normal discharge levels.

Fertilized eggs were first noted at sites 1, 2 and 8 on 6 May (noon water temperature: 18.5 C). The number of nests containing eggs was at a peak on 8 May with 7 nests containing fertilized eggs. Fry were present in 6 nests on 11 May (noon water temperature: 17 C). On 11 May a new clutch of fertilized eggs was found in nest 2 (succeeding the clutch which had been destroyed by predators). Eleven nests had not received eggs and were abandoned by 11 May.

Small males (mean size rank: 2.0) were observed nesting at 3 nest sites which were subsequently abandoned. Males, which remained on their nests following egg depositions tended to be larger (mean size rank: 7.2) in relation to other bass observed within the study area. "Spawned" nests were significantly less variable than abandoned nests in comparisons of nest diameter and water depth (table 1). Spawned nests appeared to be less clumped in their distribution along the stream (mean nearest neighbor distance: 77.9 m) than the abandoned nests, 78% of which occurred in one large pool (fig. 1).

"Moderate" flooding occurred at Indian Creek following evening thundershowers on 11 and 12 May (rainfall: 1.3 cm and 2.0 cm). Mean water current velocities (±1 SE) for the pool main channels at normal discharge and moderate flood discharge levels were 0.19 (±.03) and 0.53 (±.03) m/s at the surface and 0.11 (±.03) and 0.32 (±.05) m/s at the bottom. During the 12 May flooding, 66.7% of the abandoned nests were exposed to measurable currents (mean = 0.15 m/s). Except for nest site 5, all spawned nests remained in regions protected from current during moderate flooding (fig. 3). The mean pH at spawned nests sites changed from 7.76 to 7.48 during flooding. The water became very turbid during flooding on 16 May, and nesting males were detected only at sites 3, 7 and 8. Fry were observed at sites 2, 5, 6 and 7 on 16 May. A newly constructed nest was discovered adjacent to the old one at site 8 (no male or eggs present).

TABLE 1

Comparative statistics for spawned and abandoned nests.

	1980		1981	
	Spawned	Abandoned	Spawned	Abandoned
Total Number	8	10	8	42
$\bar{X}$ Nest Diameter (cm)	45.6 (±1.7)	41.5 (±5.2) $F(9,7) = 11.10^{**}$	52.9 (±6.2)	60.8 (±9.7) $F(41,7) = 14.96^{**}$
$\bar{X}$ Water Depth (cm)	37.5 (±2.7)	46.0 (±5.4) $F(9,7) = 5.04^{*}$	37.6 (±3.4)	71.3 (±17.4) $F(41,7) = 155.63^{***}$
$\bar{X}$ Male Size Rank	7.3 (±.7)	2.0 (±.5) $t(9) = 4.48^{**}$	11.6 (±1.8)	8.1 (±1.6) $t = (16) = 1.42$

± values represent standard errors; $^{*}p < .025$; $^{**}p < .005$; $^{***}p < .001$.
F = F-Distribution (Sokal and Rohlf 1969).

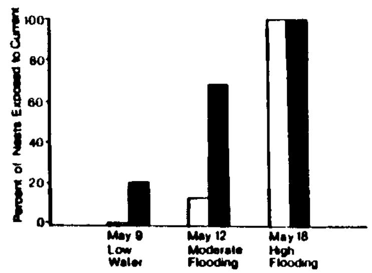

FIGURE 3. The percentages of spawned (open bars) and abandoned nests (dark bars) exposed to water current velocities above .02 m/s at Indian Creek.

Thunderstorms of 17, 18 and 19 May (rainfall: 2.3, 3.0, 2.8 cm) resulted in extreme flooding which destroyed all of the smallmouth bass nests under study. Logs and boulders were swept away, the stream substrate scoured, and turbidity increased. Two smallmouth bass fry were detected within the study area during searches conducted from 23 May to 5 June 1980.

1981. Forty-nine smallmouth bass nests were discovered in the study region during May and June 1981. Eighteen nests were discovered on 3 May after stream turbidity had subsided (noon water temperature: 17 C). Fertilized eggs were present in nests at sites 1, 2, 3, 4 and 5 (fig. 2). Nests were constructed over bedrock or gravel and were surrounded by large flat rocks or boulders. Most nests were associated with overhead cover (tree roots–44.9%; boulders–26.5%; branches-6.1%; logs–2.0%). Except for 3 unattended nests, all sites were protected from water currents above .02 m/s.

Moderate flooding occurred at Indian Creek on 6 May following 2.1 cm of rainfall (noon water temperature: 12 C). The water current pattern at each nest site was unaffected by the 6 May flooding. Several nests were positioned in coves where slow eddies swirled around the nest's perimeter, yet the area above the nest remained calm. Rainfall on 7 May (.58 cm) and 10 May (1.0 cm) kept the stream turbid until 12 May when 26 nests were located, several of which appeared to be newly constructed over the previous sites. Only nest 6 contained eggs on 12 May (noon water temperature: 15 C). The male at site 1 remained near its nest despite the absence of eggs or fry. One smallmouth bass fry (with yolk sac) was discovered in a cut-off pool, approximately 20 m downstream from site 1. On 18 May (noon water temperature: 14.8 C), the male at site 6 abandoned its nest following egg predation.

Rainfall (3.4 cm) from 18 to 20 May resulted in moderate flooding on 20 May. The stream returned to normal discharge levels by 5 May when 7 new nests were discovered. Males were present at sites 1, 2, and at 4 "unspawned" sites.

Moderate to high flooding occurred at Indian Creek from 28 May to 1 June after 3.6 cm of rain from 25 to 31 May. The stream returned to normal discharge levels by 4 June and many previously constructed nests appeared heavily silted. Male bass and newly hatched fry were present at sites 1 and 2 (noon water temperature: 20.6 C).

Moderate flooding on 12 June resulted from 1.1 cm of rainfall from 6 to 10 June. By 13 June, all smallmouth bass nesting activity had ceased within the study region. On 13 and 17 June, 2 large aggregations of smallmouth bass fry were located near the upstream edge of the southernmost pool. These fry were probably the broods from sites 1 and 2, displaced downstream during flooding.

Spawned nests demonstrated greater uniformity in diameter and water depth than abandoned nests in 1981 (table 1). The relative size of males on spawned nests was greater than that of males observed over abandoned nests, however the difference in mean ranks was not significantly different during the second year of the study although the same trend was observed (table 1).

NESTING MALES-PRESPAWNING PERIOD. Nesting males budgeted the majority of their time in rapid fanning and rotating behaviors (table 2). Fanning behavior was characterized by an alternate beating of the

TABLE 2

Percentages of sampled time male smallmouth bass engaged in various behaviors while guarding nests prior to egg deposition.

Site	Total Time Sampled (minutes)	Behavior	% Time Engaged In
1 (1980)	83.4	Fanning with Rotation	88.5
		Fanning, Oriented to Pool	8.8
		Attack Intruders	1.6
		Trips Away from Nest	0.4
		Yawning, Gaping, or Threat Display	0.1
		Nest Inspection	0.6
7 (1980)	15.0	Fanning with Rotation	100.0
8 (1980)	18.5	Fanning with Rotation	77.6
		Fanning Oriented to Pool	10.8
		Trips Away from Nest	6.4
		Threat Display	5.2
A (1981)	23.6	Fanning with Rotation	56.6
		Trips Away from Nest	42.9
		Threat Display	0.6

pectoral fins with a slight "wrist action" (Keast and Webb 1966) and a lateral waving of the soft dorsal and caudal fins. Caudal fin movements were most pronounced in the dorsal portion. Rotation behavior was characterized by periodic changes in the fish's directional orientation while positioned directly above the nest. Fish generally reoriented their longitudinal axes 45–90 ° per turn. Rotation was in either direction and involved 0.5–1.2 turns per second. Males were positioned above their nests 98.9% of the time sampled. Aquatic organisms approaching within approximately 5 m of a male's nest were aggressively pursued. Organisms which were attacked by nesting bass included: crayfish (*Orconetes rusticus*), garter snakes (*Thamnophis sirtalis*), redhorse suckers (*Moxostoma species*), hogsuckers (*Hypentelium nigricans*), common shiners (*Notropis cornutus*), stonerollers (*Campostoma anomalum*), and smallmouth bass.

NESTING MALES–POST-SPAWNING PERIOD. The fanning behavior of males was much slower when fertilized eggs were present in the nest. The stereotyped rotation behavior ceased, allowing the bass to appear more cryptic. The males frequently lowered their snouts toward the center of the nest and visually and/or olfactorally inspected their broods. The guarding males remained above their nests 96.5% of the time sampled and were usually oriented to deeper water. Aggression was most frequently directed toward smaller conspecifics during this period.

NON-NESTING SMALLMOUTH BASS. Adult smallmouth bass were observed swimming in pools no less than 1.2 m deep near the substrate where water current velocities did not exceed 0.23 m/s. Bass were frequently seen swimming within large schools of redhorse suckers. Yearling bass were frequently observed in the shoreline and pool-riffle interface regions of the stream.

DISCUSSION

The nest rotation behavior exhibited by male bass prior to egg deposition by females may be adaptive in allowing the bass to visually scan the area beyond the nest in all directions. This facilitates an early detection of predators, competing males, and reproductive females. Pre-spawning nest rotation behavior makes the male bass

more vulnerable to visual detection and may serve as an epigamic display for potential mates as well as a threat display to other males in search of nest sites.

No non-nesting bass were observed in the pool or adjacent riffles near nest site 1 in 1980. The fact that the male at site 1 spawned on the first day of observed spawnings suggests some female bass migrate from pool to pool in search of suitable mates.

Eddy and Underhill (1974) reported smallmouth bass nests invariably occurred in stream regions with a decided current. The absence of current and the presence of cover appeared to be the primary factors associated with smallmouth bass nest site selection in Indian Creek. These findings are in general agreement with those of Cleary (1956) and Pflieger (1966) for smallmouth bass nesting in streams.

At Indian Creek (1980), 57.9% of the nests were abandoned prior to flooding, compared to 18% and 11% recorded by Pflieger (1966) in a small Ozark stream. The Indian Creek value probably includes several nests which were constructed by the same individual (Cleary 1956). Brown (1960) reported that 14 of 30 nests being guarded by male bass in 1953 at Massie Creek, Ohio, were damaged by floodwaters. Nests which had remained undamaged were built earlier in better protected sites. These findings closely parallel the Indian Creek flood stage and nest exposure data presented in figure 3. Yet female bass at Indian Creek were selective in depositing eggs at protected sites. Furthermore, 85.7% of the nests exposed to current at moderate flood levels were abandoned prior to damage by high water current velocities. This strongly suggests females spawn in the optimally protected sites during a peak initial period of reproduction. Males which do not receive eggs on their nests during this period (duration approximately 2 days in 1980) may have abandoned their nests due to the lack of stimulus (eggs/fry) for parental care behavior. It should be noted that low temperatures in April may have contributed to the synchronized "burst" of smallmouth bass reproductive activity at Indian Creek in early May 1980. The initiation of nesting could not be precisely determined in 1981 due to turbid stream conditions. Brown (1960) reported the initiation of spawning at Massie Creek, Ohio, varied by as much as 3 weeks over a 5-year period, this being dependent upon water temperatures. Subsequent periods of increased nesting activity were not observed at Indian Creek in 1980 due to the disruptive action of high flooding in May and early June. In 1981 periods of moderate flooding were followed by renewed nesting activity until 13 June.

It may be suggested that the unsuccessful males were young, subordinate individuals, since most of the successful males tended to be relatively large (table 1). Winemiller (1981) observed that smallmouth bass developed social hierarchies in laboratory tanks, and that larger fish tended to dominate small ones. The reason for nest abandonments prior to flooding was not apparent since nearly all were constructed at sites with suitable nesting habitat, i.e., cover, lack of current, gravel substrate, escape routes, etc. With the onset of moderate flooding, an important difference between spawned and abandoned nests became perceivable. Apparently, larger "dominant" males were able to secure nest sites which provided the greatest protection against unpredictable flooding events (fig. 3). Smaller "subordinate" males may have exploited the remaining suitable nest sites.

It is unknown how optimal sites might be recognized by male bass prior to flooding. It is possible that bass innately select sites which are recognized on the basis of stream structure and current patterns. An alternative hypothesis is that older dominant males recognize optimal sites based on experience from previous periods of flooding. Support for the "experience hypothesis" is provided by table 1, in which successful males exhibited significantly greater uniformity in parameters of nest site selection and construction than did unspawned individuals.

The social structure of reproductive smallmouth bass in stream communities appears to be adaptive for maximizing the production of fry in an unpredictable environment. The oldest and most experienced individuals, via territorial behavior, acquire the sites with the highest probability of allowing brood success in the event of a flood. If no flooding occurs, production may be augmented by the reproductive activity of small subordinate fishes provided that females breed with them. Our data suggest female bass at Indian Creek did not breed with subordinate males at suboptimal sites. It is unknown whether this negative selection was based on some characteristic of the males, i. e., size, behavior, or the nest site held by the male. Theoretically, it would be most adaptive for females of all ages to spawn at optimal nest sites. At Indian Creek, these sites were often occupied by large aggressive males. The greater propensity of young males to abandon nests is consistent with recent discussions of reproductive strategies. Pianka (1976) proposed that younger individuals with a higher potential for future reproductive success (by virtue of a greater future life expectancy) should be less likely to risk their soma in a current act of reproduction than older individuals. For a nesting smallmouth bass, risk is manifested in increased vulnerability to predators, reliance on stored energy, chance of injury from aggressive encounters with conspecifics and heterospecifics, and exposure to extreme environmental conditions. The detrimental effects of these risk factors are buffered to a degree in larger individuals by virtue of their mass and its role in defense, energy storage, dominance relationships, etc.

The iteroparous nature of this species is one form of adaptation for reproductive success in unpredictable stream environments. Territoriality and a dominance heirarchy insure that the individuals most capable of protecting young are afforded optimal nest sites. The factors driving the evolution of this system are not complex. These individuals which seek out optimal (within the context of an unpredictable stream environment) nest sites are reproductively more successful. The trait of selecting these nesting habitats would increase in frequency among subsequent generations (whether by innate or learned recognition) due to selection against broods located in unfavorable sites. The result would be increased competition among males for limited optimal nest sites. In time, only the most dominant individuals would hold optimal sites.

In smallmouth bass, the most dominant individuals are also the largest (Winemiller 1981) and presumably the most capable of successfully rearing a large brood. Subordinate males remain to exploit sub-optimal sites. It follows that females would maximize their fitness by recognizing and spawning at optimal nest sites with dominant males. The paternal brood care system of *Micropterus domieui* appears to conform to the sex roles-brood care theory of Perrone and Zaret (1979). Intense territorial defense of the nest site insures paternity for each brood. Repeated spawnings by females permits egg deposition at several protected nest sites and following brood destruction by unpredictable flooding. A promiscuous mating system allows many females to spawn at optimal nest sites with large males. Inslee (1975) reported some female smallmouth bass may spawn 9 times in a single season in pond cultures, however this value is probably high for natural populations.

If stream structure is rapidly and adversely altered, as in channelization, the result will certainly be a decrease in smallmouth bass reproductive activity due to the negative effects of flood waters on brood survival. Conversely, there should be a potential to increase smallmouth bass fry production in disturbed environments by increasing the availability of critical parameters of nest site selection such as cover and protection from water current during flooding.

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