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**THE LIFE HISTORY OF THE SPOTTAIL DARTER,
ETHEOSTOMA SQUAMICEPS,
IN BIG CREEK, ILLINOIS, AND FERGUSON CREEK, KENTUCKY**

Lawrence M. Page

**ILLINOIS NATURAL HISTORY SURVEY
Biological Notes No. 89**

Urbana, Illinois • May, 1974

State of Illinois

Department of Registration and Education

NATURAL HISTORY SURVEY DIVISION

Fig. 1.—The total range (left) of *Etheostoma squamiceps* and the distribution of the species in Illinois and adjacent Kentucky and Indiana (right). The two study areas are shaded.

THE LIFE HISTORY OF THE SPOTTAIL DARTER, *ETHEOSTOMA SQUAMICEPS*, IN BIG CREEK, ILLINOIS, AND FERGUSON CREEK, KENTUCKY

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WITH THE DESCRIPTION of *Etheostoma barbouri* Kuehne and Small (1971) the number of described species of the subgenus *Catonotus* was raised to six. Other species are known but undescribed. All *Catonotus* species except the wide-ranging *E. flabellare* have relatively small ranges, and published ecological information on *Catonotus* species is limited to brief notes in state ichthyofaunal reports and species descriptions and to studies on the reproduction and diet of *E. flabellare* (Lake 1936; Daiber 1956; Winn 1958a and 1958b; Karr 1964).

The paucity of ecological information on *Catonotus* and the occurrence of four species of the subgenus in a small area encompassing southeastern Illinois and adjacent Kentucky prompted life-history studies of *E. squamiceps*, *E. kennicottii*, and *E. obeyeense*. This report on *E. squamiceps* will be followed by similar accounts on *E. kennicottii* and *E. obeyeense*.

Etheostoma squamiceps was described by Jordan (1877:11) from specimens collected at Russellville, Logan County, Kentucky. The range of the species (Fig. 1) includes southern Illinois, southwestern Indiana, western Kentucky, west-central Tennessee, and the Tennessee River drainage of Alabama (Smith-Vaniz 1968:106) and Mississippi (Cook 1959:207). Morphological descriptions of *E. squamiceps* are given by Jordan (1877:11-12), Jordan & Evermann (1896:1096), Forbes & Richardson (1908:312-313), Fowler (1922:26), Cook (1959:207), Moore (1968:150), and Collette & Knapp (1966:39).

I am indebted to Brooks M. Burr, Ernest L. List, George W. Lewis, William Raino, Douglas W. Schemske, Philip W. Smith, Richard L. Smith, Lewis J. Stannard, Jr., John A. Tranquilli, and John D. Unzicker for aid in collecting specimens; to Dr. Smith, Mr. Burr, and Mr. Schemske for counsel on numerous matters; to Mr. Schemske for identifying most of the stomach contents; to Drs. David A. Etnier and Vincent H. Resh for information on the distribution of *E. squamiceps*; and to Dr. Francis J. Kruidenier for identification of the acanthocephalan parasite.

The cover illustration was done by Mrs. Alice

Ann Prickett, University of Illinois School of Life Sciences Artist. Assistance in preparing the other illustrations was provided by Illinois Natural History Survey Illustrator Lloyd LeMere and Survey Photographer Wilmer D. Zehr. The manuscript was edited for publication by Robert M. Zewadski, Associate Technical Editor of the Survey, and Dr. Howard E. Winn, University of Rhode Island, served as guest reviewer.

THE STUDY AREAS

Big Creek in Hardin County, Illinois, supports large populations of both *E. squamiceps* and *E. kennicottii*, and for this reason was selected as one of two streams to be used as study areas. Big Creek is a spring-fed, direct tributary of the Ohio River and lies in limestone formations of the Shawnee Hills. The upstream substrate is predominantly a mixture of slab rocks and gravel, the middle stream bed is mostly coarse gravel, and the downstream substrate is mostly sand. The stream system is forested throughout, and the water is usually quite clear.

General characteristics and fish populations of Big Creek were discussed by Lewis (1957), who found the most abundant fishes to be *Campostoma anomalum*, *Pimephales notatus*, *Notropis chrysocephalus*, and *Etheostoma caeruleum*. Other darters present in his collections were *Etheostoma kennicottii*, *E. squamiceps*, *E. nigrum*, and *Percina caprodes*; old records (Forbes & Richardson 1908) exist for *E. chlorosomum* and *E. asprigene*.

The second study area, Ferguson Creek in Livingston County, Kentucky, is a short, direct tributary of the lower Cumberland River and supports large populations of *E. squamiceps* and *E. obeyeense*. The stream extends only about 3 miles, under normal conditions consists almost entirely of shallow slab-rock pools and slab riffles, and has a few deeper sand-bottomed pools. The most abundant fishes are *Pimephales notatus*, *Notropis umbratilis*, *Etheostoma obeyeense*, *E. squamiceps*, and *Erimyzon oblongus*. Other species of darters in Ferguson Creek are *Etheostoma gracile*, *E. chlorosomum*, *E. asprigene*, *Percina maculata*, and *P. caprodes*, all of which are uncommon. Most observations and collections, in

This paper is published by authority of the State of Illinois, IRS Ch. 127, Par. 58.12, and is a contribution from the Section of Faunistic Surveys and Insect Identification of the Illinois Natural History Survey, where Dr. Page is an Assistant Taxonomist.

COVER ILLUSTRATION: *Etheostoma squamiceps* collected in Gibbons Creek in Pope County, Illinois. From a drawing by Mrs. Alice Ann Prickett.

Ferguson Creek were made near the Route 70 bridge 2 miles east of Smithland, a locality approximately 30 miles (48 km) from the Big Creek study area (Fig. 1).

Both study streams have three predominant habitats: riffles, slab pools, and non-slab pools. Riffles in Big Creek are mostly of coarse gravel, non-slab pools are only moderately deep (seldom over 1 m) and usually have a sand and gravel bottom, and slab pools are shallow with a substrate of gravel laden with slab rocks ranging from 100 to 400 mm across. In Ferguson Creek, slab pools have essentially the same physical characteristics as those of Big Creek, non-slab pools are generally deeper and almost exclusively sandbottomed, and riffles are of larger stones, mainly small slab rocks up to 150 mm across.

METHODS

Observations and minnow-seine collections were made at approximately monthly intervals except during spawning periods, when more frequent observations were made. Studies were begun in Big Creek on 6 October 1970 and in Ferguson Creek on 22 April 1971 and were terminated in both streams on 19 June 1973. Specimens collected for laboratory examination were preserved and stored in 10-percent formalin. From Big Creek 601 *E. squamiceps* and

from Ferguson Creek 430 *E. squamiceps* were preserved and examined.

Beginning in August 1971, collections were made by habitat in the two streams, and numbers of specimens were recorded by month as having been taken from riffles, slab pools, or non-slab pools. What was considered to be approximately the same sampling effort was expended on each of the three habitats. Potential predators captured during seining operations were preserved in formalin for later examination of stomach contents. Field notes on ambient conditions and darter behavior were routinely taken.

By repeatedly seining a measured area until no more darters were collected, quantitative samples were taken in each of the three habitats in July 1972, October 1972, January 1973, and April 1973.

In the laboratory, all darters were sexed, measured and aged. Large specimens were sexed by examining the genital papillae; small ones were sexed by examining the gonads. In addition to the standard lengths (SL) of all specimens, the lengths of the anal, pectoral, pelvic, and soft-dorsal fins and the depths of the caudal peduncles of 40 males and 40 females of more than 30 mm SL from Ferguson Creek were measured as potential expressions of sexual dimorphism. Unless stated otherwise, measurements in the text are standard lengths.

Aging to year class was done by counting the annuli on scales removed from the dorsum near the

TABLE 1.—Habitat distribution by percentages of *Etheostoma squamiceps* collected in Big and Ferguson Creeks between 25 August 1971 and 19 June 1973.

Month	Number Collected	Big Creek Sample			Number Collected	Ferguson Creek Sample		
		Percentage of <i>E. squamiceps</i> in				Percentage of <i>E. squamiceps</i> in		
		Slab Pools	Gravel Riffles	Non-slab Pools		Slab Pools	Slab Riffles	Non-slab Pools
Adults								
January	3	100	0	0	15	7	93	0
February	9	100	0	0	9	33	67	0
March	4	100	0	0	5	0	100	0
April	4	100	0	0	3	100	0	0
May	37	57	0	43	16	19	81	0
June	8	100	0	0	8	0	100	0
July	6	100	0	0	3	0	100	0
August	22	100	0	0	8	0	100	0
September	30	100	0	0	13	30	70	0
October	21	86	9	5	1	0	100	0
November	11	100	0	0	9	11	89	0
December	5	80	20	0	4	0	75	25
Young								
January	8	100	0	0	27	26	41	33
February	14	93	0	7	28	57	43	0
March	19	100	0	0	4	0	100	0
April	11	100	0	0	19	63	37	0
June	0	...	..	..	1	0	0	100
July	10	30	70	0	64	11	73	16
August	21	100	0	0	15	0	100	0
September	25	56	44	0	43	2	96	2
October	19	32	68	0	30	0	100	0
November	47	94	4	2	38	21	76	3
December	13	92	8	0	9	0	100	0

junction of the spinous and soft-dorsal fins. Aging to month was done by using April, the month of the greatest breeding activity in the study areas, as month zero. Thus, a darter collected in September and having two scale annuli was estimated to have lived 2 years and 5 months. For certain comparisons

darters were divided into young (through 12 months) and adult (over 12 months) age groups.

A representative sample of each collection was dissected to identify stomach contents and endoparasites and to note the conditions of the gonads. Weights of the ovaries of 87 females were obtained and recorded as a proportion of the adjusted body weight (the specimen minus the ovaries, stomach, intestine, and liver) of the female; the weight after the removal of the digestive system was used to eliminate variations resulting from the weight of recently ingested food. Mature ova from 18 preserved breeding females were counted.

In addition to specimens collected from the study areas during the study period, all *E. squamiceps* in the Illinois Natural History Survey collection were examined to ascertain probable spawning periods in other localities and other years. Indicators used were that males were in extreme breeding coloration and that females were heavy with mature ova.

The relative survival of each year class of the two populations was calculated by expressing the number of individuals in that year class as a proportion of the number of individuals in a younger year class.

The breeding behavior and territoriality of darters in laboratory aquaria were observed. Stream observations had indicated that territories centered naturally about large slab stones, and one or more slab stones (elevated slightly on small stones) were placed in each aquarium.

HABITAT

Adults of the Big Creek *E. squamiceps* population showed a distinct difference in their preference in habitat (as defined) from the preference of the Ferguson Creek adult population (Table 1). In Big Creek

Fig. 2.—(Upper Photo) Slab pool in the headwaters of Big Creek, Hardin County, Illinois. (Lower Photo) Slab riffles in Ferguson Creek, Livingston County, Kentucky.

they strongly preferred slab pools (Fig. 2) during all seasons and were seldom taken in riffles or in non-slab pools. In contrast, in Ferguson Creek adults were almost exclusively taken in slab riffles (Fig. 2) during the nonspawning seasons. During the height of the spawning season (April), adults of both populations were most common in the slab pools.

Comparative collections made at localities other than the study streams revealed that *E. squamiceps* adults are most commonly found in slab riffles, i.e., among and under small slab rocks (100–200 mm) characteristically forming the substrate of riffles in upper elevation streams. The seemingly dichotomous habitat preference found in the two study areas results from the strong association of the species with slab rocks. In Ferguson Creek both the riffles and the shallow pools have substrates composed of slab rocks, and *E. squamiceps* prefers the riffles. However, in Big Creek the riffles are of coarse gravel, or if of slab are very shallow, and *E. squamiceps* is forced to occupy the slab pools.

The occupation of slab pools in Big Creek indicates that slab rocks are more important to the species than other physical factors such as temperature and current. The slab pools of Big Creek are shallow and often become hot and stagnant in late summer, contrasting strongly with the cool, swift-flowing riffles of Ferguson Creek. The importance of slab rocks is further demonstrated by the absence of the species in Coastal Plain streams in extreme southern Illinois and elsewhere (Fig. 1), which typically lack a slab substrate.

Young *E. squamiceps* were somewhat more scattered throughout the stream systems than were the adults but still showed a rather strong preference for slab riffles in Ferguson Creek and for slab pools in Big Creek (Table 1). In Big Creek the young moved downstream from the spawning areas and were found generally distributed in slab pools and riffles throughout the stream system. The occupation of gravel riffles in Big Creek by a greater proportion of young than adults may reflect the capacity of young darters, in contrast to the larger adults, to hide among the coarse gravel. Winn (1958b:161) observed a similar lack of restriction of young *E. flabellare* to the large-rock riffles occupied by adults.

REPRODUCTION

Reproductive Cycle of the Male

The testes of the male *E. squamiceps* enlarged, as did the genital papilla (Fig. 3), as the spawning season approached. In breeding males testes were large, white, and spongy; following the spawning season the testes diminished in size and returned to the translucency characteristic of nonbreeding males. Breeding tubercles did not develop on *E. squamiceps* and are not thought to develop on any species of *Catnotus* (Collette 1965:603).

Fig. 3.—Genital papillae of *Etheostoma squamiceps*. A, nonbreeding male; B, breeding male; C, nonbreeding female; and D, breeding female. The nonbreeding specimens were 1+-year-old darters collected on 21 July; the breeding specimens were 2+-year-olds collected on 24 March. All papillae are shown 12 times actual size.

In early spring large males became very dark and could be sexed on sight. The darkening of the male prior to spawning is a phenomenon observed in several other species of darters, including the closely related *E. flabellare* (Lake 1936:818; Winn 1958b:172), *E. nigrum* (Winn 1958b:172), and several species of *Percina* (Winn 1958b:172; Page & Smith 1970:6 and 1971:6).

The most extreme breeding pigmentation was observed on males in aquaria spawning (Fig. 7) and nestguarding. In contrast to the female and the nonbreeding male, the breeding male was without the typical mottled pattern. The entire head to the posterior margin of the opercle was black and swollen. From the head to below the junction of the dorsal fins the body was nearly white. The posterior half of the body was boldly marked with 7 or 8 vertical bars. The three caudal spots were coalesced into a vertical bar. The flesh over the anal spines was thickened. All fins except the pectorals blackened, but the caudal and soft-dorsal fins retained their characteristic clear banding. The membranes of the spinous-dorsal fin were black except for a proximal zone without pigment. The spines of the spinous-dorsal fin were tipped with small, white knobs, each knob being preceded by a small but prominent black spot. The rays of the soft-dorsal fin were tipped with small knobs, white in some individuals and black in others.

Males of *E. squamiceps* selected cavities under slab rocks as future nesting sites (Fig. 4) a few

Fig. 4.—A typical nesting site of *Etheostoma squamiceps* photographed in Big Creek on 22 April 1971. The male was guarding his nest beneath a slab rock.

days or weeks before spawning and vigorously defended them against intruders. Such a cavity was always cleaned of silt and debris; in contrast, lifting a stone which did not harbor a *Catnotus* male beneath it always released a flurry of small debris. The requirement noted for *E. flabellare* (Winn 1958a:208), that to be used as a nest site a stone must be between 1.5 and 2.5 cm above the substrate, was not found for *E. squamiceps*.

Aquarium-held males were observed to shake their tails repeatedly and vigorously under stones selected as nest sites, forcing out silt and small gravel and enlarging the cavity. One male was observed to shake the posterior half of his body with the soft-dorsal fin against the bottom of the nest stone, apparently cleaning the area to be used for egg deposition.

In both Ferguson and Big creeks the largest concentrations of nests were found in the shallow (to 300 mm) slab pools in the uppermost portions of the stream systems, where the stream beds were typically 1–3 m wide and the current slight but observable. A few nests were found in slab riffles in Ferguson Creek and in spring runs in Big Creek. Deep water (over 400 mm) was usually avoided; however, during the prolonged 1973 spring floods *E. squamiceps* was found spawning in water as deep as 600 mm.

Only large males developed the breeding pattern, underwent gross enlargement of the testes, and were found guarding nests. These large males probably did most or all of the spawning. Young males that had not reached a standard length of 40 mm by the end of the spawning season did not have enlarged testes and presumably were not sexually mature. All males of 40 mm or more appeared to be sexually mature;

however, there was no evidence that 1-year-old males actually spawned.

Reproductive Cycle of the Female

Generally, the largest *E. squamiceps* females of all age-classes spawned the earliest in the season although a few 1-year-old females as small as 40 mm spawned as early as 24 March. A few females as small as 35 mm spawned in late April and early May.

TABLE 2.—Relationship between size, age, and ovary weight of *Etheostoma squamiceps* females and the number of mature ova produced. An age of 1 year = 11–13 months, 2 years = 23–25 months, 3 years = 35–36 months.

Standard Length in mm	Adjusted Body Weight in Grams ^a	Age in Years	Ovary Weight in Grams	Number of Mature (Orange or Translucent) Ova
32	0.57	1	0.07	54
35	0.59	1	0.06	44
37	0.74	1	0.21	80
40	0.93	1	0.17	40
41	0.85	2	0.15	56
42	1.11	2	0.25	70
43	1.05	1	0.23	50
44	1.18	2	0.20	64
48	1.27	2	0.12	28
48	1.79	2	0.37	140
48	1.64	2	0.32	110
49	1.71	2	0.33	132
51	2.27	2	0.60	91
51	2.16	2	0.33	116
55	2.56	2	0.21	80
55	2.77	3	0.72	234
57	3.32	3	0.78	227
58	3.22	3	0.79	357

^a Adjusted body weight is the specimen's weight after the removal of the ovaries, stomach, intestine, and liver.

In contrast to males, females did not undergo a color and pattern change with the approach of the spawning season. The most evident morphological changes associated with spring were a marked distention of the belly, accompanying the presence of maturing ova, and an enlargement of the genital papilla (Fig. 3). Enlargement of the papilla in most females was evident by February; gross distention of the belly preceded spawning by only a few days or weeks.

Small white ova were present in most females by October, but in very small females ova did not appear until December. Larger yellow ova began appearing in December and were present in most females by February. Large, maturing orange ova appeared in March and April. Just prior to spawning the mature ova lost their orange opacity and became translucent. The oldest and largest females produced the largest numbers of mature ova; the youngest and smallest generally produced the fewest. The number of mature ova counted in 18 females ranged from 28 to 357 (Table 2). For these females the relationship between the number of mature ova (F) and the adjusted body weight (W) was $F = -27.12 + 83.88W$, with $r = 0.845$, and between the number of mature ova and the standard length (L) was $\log F = -2.589 + 2.729 \log L$, with $r = 0.691$.

Estimates of the number of eggs laid in aquaria by individual females were 50 (by a 57-mm, 3-year-old), 50 (by a 62-mm, 3-year-old), 20 (by a 41-mm, 1-year-old), and 120 (by a 54-mm, 2-year-old). Ma-

ture ova averaged 1.6 mm in diameter, were translucent, and contained a single oil droplet.

Spawning and the subsequent absorption of remaining immature ova resulted in a rapid decrease in the size of the ovaries. Ovaries of postspawning females collected in April and May contained only small, white ova and were very small in comparison to ovaries of prespawning females collected in March and April (Fig. 5). Ovaries increased markedly in size between the recovery period and the spawning period in the following spring (Fig. 5). The proportionally largest ovaries (equalling 26.4 percent and 28.7 percent, respectively, of the adjusted body weights of the females) were found in a 2-year-old, 51-mm female collected in Big Creek on 9 April 1971 and in a 1-year-old, 37-mm female collected in Big Creek on 31 March 1973. Ovary-weight-to-adjusted-weight ratios ranged from 0.091 to 0.287 and averaged 0.189 in the 18 females represented in Table 2.

Spawning

E. squamiceps spawned at the study areas from late March through May on the undersides of the slab rocks (Fig. 6) selected as nesting sites by the males. Temperatures at which spottail darters were found spawning ranged from 14° to 19° C. These temperatures usually prevailed from late March to late May, warming from temperatures ranging from 3° to 10° C in January, February, and early March.

Nests of *E. squamiceps* were found in Trousdale County, Tennessee, on 21 April 1973 and in Todd County, Kentucky, on 22 April 1973. Late March was the most probable time of spawning for *E. squamiceps* collected at other localities (Table 3).

Eight spawnings occurred in the laboratory, five of which were observed. Four of the spawnings occurred in the morning hours, one in the afternoon, and three during the night or early morning. Aquarium temperatures ranged from 19° to 25° C.

Fig. 5.—Monthly variations in ovarian weight relative to adjusted body weight of *Etheostoma squamiceps*. The vertical axis is a logarithmic scale. The number beside each dot is the age of the female. The lower five dots for May represent postspawning females.

Fig. 6.—Eggs of *Etheostoma squamiceps* on the underside of a stone removed from a slab pool in the headwaters of Big Creek on 22 April 1971.

TABLE 3.—Collections of breeding *Etheostoma squamiceps*.

Locality	Collection Date	Remarks
Ferguson Creek, Livingston Co., Ky.	24 March 1972	Spawning when collected.
Ferguson Creek, Livingston Co., Ky.	23 March–20 May 1973	Spawning when collected.
Big Creek, Hardin Co., Ill.	15 April–3 May 1971	Spawning when collected.
Big Creek, Hardin Co., Ill.	31 March–20 May 1973	Spawning when collected.
Hickory Creek, Livingston Co., Ky.	27 March 1964	Female in extreme breeding condition.
Duck River, Coffee Co., Tenn.	28 March 1965	Male in extreme breeding coloration.
Rush Creek, Posey Co., Ind.	29 March 1963	Males and females in extreme breeding condition.

Preceding spawning, males periodically left the nest stone to court females. When attempting to lure a female back to the stone, a male would swim near a female, display his bold pattern and spread fins, and wag his tail at or against the female.

After joining a male under his nest stone, a female usually remained passive while the male courted her. The male was extremely active at this time, constantly darting about, nudging the female with his snout, and occasionally bobbing his spinous dorsal fin up and down, the contrasting dark and clear areas of which created a blinking effect.

Eventually the female began moving about, arching her head upward, and holding her snout near the underside of the stone, apparently selecting a site for egg deposition.

Both male and female assumed an inverted position when laying and fertilizing eggs. After nosing about the rock for a time, the female rolled to one side and simultaneously rose to press her venter against the underside of the nest stone. Usually almost immediately after the female had inverted, the male rolled to one side and positioned himself tightly alongside and slightly overlapping the female, with a pelvic fin across her nape, in an inverted head-to-head position (Fig. 7). Pressed against the stone, the female began quivering slightly, barely moving forward as she did so, and laying a series of two to five eggs on the stone. As she laid the eggs, the male trembled and released sperm. Then both fish immediately returned to a right-side-up position beneath the stone for a short time before courting by the male began the sequence again.

Fifteen seconds to several minutes elapsed between inversions. Each inversion lasted less than 5 seconds. The eggs were concentrated in a constricted area but never were laid on top of other eggs. Eggs were deposited as high as 35 mm above the substrate.

The presence of a second female with a spawning pair was tolerated, and in fact, both females were courted by the male. No instances of more than one of the females spawning at a time were observed, however.

At least three females spawned with one male in an aquarium, two with another. In one instance the spawnings with different females occurred within 2

hours of one another; in another instance the spawnings were 5 days apart. Eggs laid by a second or third female were added to those already in the nest, enlarging the concentrated egg mass.

Counts and estimates of the numbers of eggs in 20 nests of *E. squamiceps* found in Big and Ferguson creeks were 8, 90, 125, 125, 160, 200, 200, 200, 200, 250, 275, 300, 450, 475, 475, 500, 850, 1100, 1500, and 1500, the mean being 449. Several nests contained many more eggs than the largest number of mature ova (357) found in preserved females and, as in aquarium nests, contained eggs from more than one female. Eggs in nests averaged 1.8 mm in diameter.

Males vigorously guarded the eggs. Whenever a nest stone in a stream was lifted for observation, a male was found underneath and usually swam away only when provoked. When a male did dart away, he usually returned soon after the rock was replaced. In all nests which were re-examined on a later date, the male had returned and was again guarding the nest.

Aquarium-held males were constantly active while guarding eggs, darting back and forth and continuously brushing the eggs with their dorsal fins. The knobs on the tips of the dorsal spines of *E. squamiceps* males may be an adaptation to reduce the sharpness of the spines, thereby reducing the probability of rupturing eggs, during the nest-guarding time. Periodic nipping at the eggs presumably removed invading organisms. The breeding pattern of the male was retained during the egg-guarding period.

Nests were guarded against potential egg predators, including crayfishes. Large crayfishes introduced into aquaria were driven from the nest stone by the male *E. squamiceps* as he repeatedly charged the crayfishes and bit them or hit them on the abdomen. A 63-mm male *E. squamiceps* succeeded in driving from his nest a 75-mm total length *Orconectes kentuckiensis* but not a 90-mm *Cambarus laevis*, both common crayfishes in Big Creek.

Nests were never tended by females. Lake (1936: 823) believed that only *E. flabellare* males provide parental care to their eggs.

Some areas used as breeding grounds contained large numbers of nests. Separate nest stones of *E. squamiceps* were found as close as 200 mm from one another. Two large stones with two *Catnotus* nests

Fig. 7.—*Etheostoma squamiceps* spawning in aquaria. A nest of eggs is on the underside of the stone above each pair of darters.

under each were located; one had two nests of *E. squamiceps* (approximately 200 mm apart); the other had one nest of *E. squamiceps* and one of *E. kennicotti*. In both instances of double occupancy of a nest stone, the two nests were completely separated from one another by substrate material when the rock was in place in the stream. Similar sharing of one nest stone was described by Lake (1936:823) for *E. flabellare*.

The spawning behavior of *E. squamiceps* is similar to that of *E. flabellare*, described by Lake (1936) and Winn (1958a and 1958b). Differences in the spawning behavior of *E. flabellare* from that of *E. squamiceps* are the head-to-tail egg-laying position, the fact that females may remain inverted for as long as 2 hours, the habit of the female of usually laying only one egg at a time, and the intolerance by the male of the presence of a right-side-up female under the nest stone.

Sexual Dimorphism

Winn (1958b:172) listed among the sexually dimorphic characters of *E. flabellare* the larger anal, pectoral, and pelvic fins of the male. In addition to behavioral (territorial) and morphological (coloration and size) differences between the sexes of *E. squamiceps*, the anal, soft-dorsal, pelvic ($P < 0.01$), and pectoral fins ($P < 0.10$) were significantly longer in males. The depth of the caudal peduncle was also greater in males ($P < 0.01$).

DEVELOPMENT AND GROWTH

Eggs incubated in aquaria at temperatures varying from 18° to 22°C (64°–72°F) hatched in 270–275 hours (11.3–11.5 days), and eggs incubated at 22°–26°C (72°–79°F) hatched in 125–130 hours (5.2–5.4 days).

Three nests of *E. squamiceps* eggs were found to be hatching in Big Creek on 3 May 1971, including one nest first discovered and marked on 17 April. This nest had been observed periodically between 17 April and 3 May, during which time water temperatures varied from 14° to 18°C (57°–64°F). No eggs were added during this time; thus, a minimum of 16 days of incubation is required at this temperature range. Lake (1936:826) found eggs of *E. flabellare* to have much longer incubation periods: 14–16 days at an average temperature of 74°F, 21 days at 70°–71°F, and 30–35 days at 63°–68°F.

E. squamiceps hatchlings (Fig. 8) were 6.5 mm in

Fig. 8.—*Etheostoma squamiceps* hatchling.

total length and mostly translucent, but they had red blood, black melanophores over most of the body, and metallic gold eyes. Melanophores were especially prominent on top of the head and on the lower one-third of the yolk sac. Pectoral fins and the lower jaw were well developed, as they are in *E. flabellare* hatchlings (Lake 1936:826–827), making these two species more precocious at hatching than are *Etheostoma gracile* (Braasch & Smith 1967:9) and *Percina sciera* (Page & Smith 1970:9).

In aquaria, fry left the nest stone soon after hatching and sought refuge among the gravel substrate. Propulsion was accomplished by rapid movements of the caudal fin.

The smallest specimens examined from the study areas were two 12-mm females collected 20 July 1971 in Big Creek. Several specimens from 13 to 20 mm were collected in a number of habitats in both study areas between 23 June and 25 August of 1971 and 1972.

At 12 mm juveniles had essentially the morphology of adults but were without scales on the nape, breast, and belly, and were without a lateral-line canal. In

Fig. 9.—Size distribution by age of *Etheostoma squamiceps* collected in A, Big Creek, and B, Ferguson Creek. Black circles represent sample means for males; white circles represent sample means for females. From Big Creek 601 specimens were collected, and from Ferguson Creek 430.

TABLE 4.—Standard lengths of *Etheostoma squamiceps* at 1, 2, and 3 years (12, 24, and 36 months) of age. These specimens were collected in April 1971 and 1973.

Study Area and Sex	Age	Number	Standard Length		
			Mean	Range	Standard Deviation
Big Creek males	1	15	34.8	27.1–43.2	4.1
Big Creek females	1	22	36.2	28.0–43.1	4.1
Ferguson Creek males	1	3	37.7	27.4–46.7	9.7
Ferguson Creek females	1	21	37.2	31.9–44.6	4.0
Big Creek males	2	17	51.3	43.3–59.8	4.4
Big Creek females	2	33	45.5	37.9–55.3	4.4
Ferguson Creek males	2	2	57.5	51.4–63.5	8.6
Ferguson Creek females	2	4	54.7	48.0–55.6	4.9
Big Creek males	3	5	61.2	53.5–65.9	5.4
Big Creek females	3	3	57.4	56.2–58.7	1.3
Ferguson Creek males ^a	3	2	64.6	62.3–66.9	3.3

^a No 3-year-old females were found in Ferguson Creek.

contrast to the mottled pattern of adults, they had a pattern consisting of large spots over all areas of the body except the belly. At 16 mm the lateral-line canal had begun to form. At 19 mm the mottled pattern characteristic of the adult was present; scales were present on the nape, breast, and belly; and the lateral line extended to the soft-dorsal fin.

Both populations studied grew at nearly the same decreasing rate (Fig. 9). The equation expressing the relationship between standard length (Y) and age in months (X) of Big Creek males is $Y = -7.00 + 42.83 \log X$, $r = 0.958$; of Big Creek females is $Y = -0.35 + 34.21 \log X$, $r = 0.962$; of Ferguson Creek males is $Y = -3.08 + 41.99 \log X$, $r = 0.921$; and of Ferguson Creek females is $Y = 3.19 + 34.92 \log X$, $r = 0.947$.

During the first year of growth sex had little influence on the growth rate. During subsequent years, however, males grew more rapidly than did females (Fig. 9), and by the third year males were significantly larger than females ($t = 3.78$, $df = 53$ for the Big Creek population; $t = 2.79$, $df = 27$ for the Ferguson Creek population). Males in younger year classes were not significantly larger than females. The largest specimen examined was a 72-mm male from Ferguson Creek. Table 4 presents the standard lengths of 1-, 2-, and 3-year-old *E. squamiceps* collected in April.

E. squamiceps reached one-half of the first year's mean growth in approximately 12 weeks; this period is much longer than that required for *E. gracile* (1 week, Braasch & Smith 1967:9) and *Percina phoxocephala* (2 weeks, Page & Smith 1971:9).

Although captive *E. squamiceps* individuals occasionally swam up and down the side of an aquarium seeking to escape, the species in general has almost totally benthic habits. Both field and aquarium observations indicated that the fry, juveniles, and adults mainly rest on the substrate or dart about in short,

jerky movements. The only rapid swimming observed in the field were escape maneuvers, which usually involved distances of less than 2 m.

DEMOGRAPHY

Density

On four separate dates at approximately 3-month intervals, quantitative samples of *E. squamiceps* were taken in both Big and Ferguson creeks by repeatedly seining a measured area of stream until no more darters were collected. The number of specimens collected was transposed into the number per square meter (Table 5).

In Big Creek the highest density of adults was consistently found in the slab pools. In Ferguson Creek the highest densities of adults during the nonspawning season were in the slab riffles and in April were in slab pools, where they had moved to spawn.

Young darters in Big Creek were common in both slab pools and riffles in summer and autumn, but common only in the slab pools in winter and spring. Young in Ferguson Creek were consistently most common in the slab riffles although at 1 year of age many had moved to the slab pools where the spawning activity was greatest.

Including both young and adults, the greatest density of *E. squamiceps* in Ferguson Creek (9.6 per m^2) was in the slab riffles in July, and in Big Creek the greatest density (2.0 per m^2) was in the slab pools in April.

Composition

Of the 601 *E. squamiceps* collected in Big Creek, 55.7 percent were up to 1 year of age, 34.6 percent were over 1 and up to 2 years of age, 9.2 percent were over 2 and up to 3 years, and 0.5 percent were over 3 years. Of the 430 specimens collected in Ferguson

TABLE 5.—Number of *Etheostoma squamiceps* individuals per square meter collected at approximately 3-month intervals, by habitat. Young were up to 1 year of age, adults over 1 year.

Big Creek Sample					Ferguson Creek Sample				
Collection Date	Number Collected	Number of <i>E. squamiceps</i> Per Square Meter in			Collection Date	Number Collected	Number of <i>E. squamiceps</i> Per Square Meter in		
		Slab Pools	Gravel Riffles	Non-Slab Pools			Slab Pools	Slab Riffles	Non-Slab Pools
Adults									
8 July 1972	6	0.81	0.0	0.0	8 July 1972	3	0.0	0.58	0.0
19 October 1972	9	0.73	0.63	0.05	20 October 1972	1	0.0	0.27	0.0
17 January 1973	2	0.22	0.0	0.0	16 January 1973	5	0.04	0.63	0.0
16 April 1973	4	0.54	0.0	0.0	30 April 1973	3	0.25	0.0	0.0
	MEAN	0.58	0.16	0.01		MEAN	0.07	0.37	0
	SD	0.26	0.32	0.03		SD	0.12	0.29	
Young									
8 July 1972	10	0.40	0.60	0.0	8 July 1972	64	0.25	9.03	1.08
19 October 1972	4	0.24	0.63	0.0	20 October 1972	30	0.0	8.07	0.0
17 January 1973	7	0.77	0.0	0.0	16 January 1973	21	0.27	1.11	0.39
16 April 1973	11	1.48	0.0	0.0	30 April 1973	19	0.99	1.26	0.0
	MEAN	0.72	0.31	0		MEAN	0.38	4.87	0.37
	SD	0.55	0.36			SD	0.43	4.27	0.51

Creek, 72.1 percent were up to 1 year of age, 20.5 percent were over 1 year and up to 2 years, 6.7 percent were over 2 and up to 3 years, and 0.7 percent were over 3 years. The very small number of these darters over 3 years of age effectively demonstrates that 3+ is the maximum age of *E. squamiceps* (Table 6).

A skewed sex ratio was found in each study population, both among the young [1.3 females to 1 male in Big Creek ($\chi^2 = 5.52$; $P < 0.025$), 1.7 to 1 in Ferguson Creek ($\chi^2 = 20.64$; $P < 0.005$)] and among the total samples [1.3 to 1 in Big Creek ($\chi^2 = 12.02$; $P < 0.005$), 1.9 to 1 in Ferguson Creek ($\chi^2 = 43.01$; $P < 0.005$)]. The only year class in which males predominated was 3+, indicating a greater longevity for males.

The skewed sex ratios among young-of-the-year spottail darters suggest a genetic rather than a direct environmental cause for the predominance of females. The absence of spawning activities by all but the

large males (a small proportion of the population) and the fact that several females may contribute to the nest of one male may have resulted in selection against a 50-50 sex ratio.

Survival

Relative survival values (Table 7) for each year of life were calculated for males, females, and total samples of *E. squamiceps*, using the data in Table 6. It was assumed that each age class was collected in proportion to its relative number in the population, that the population was neither increasing nor decreasing, and that the number of fry entering the population each year was constant.

Because approximately one-third of the sampling effort each month was expended in the slab pools, which constitute less than one-third of the habitat of Big Creek but in which adults tended to be concentrated (Tables 1 and 4), the number of adults in Table 6 probably exaggerates their actual proportion in the population. Survival was therefore computed on the 1+ year class as well as the -1 year class (Table 7).

The general shapes of survival curves for males, females, and total samples (Fig. 10) were similar to one another except for the Ferguson Creek male 1x' curve. The increasing steepness of the slope with age reflects the lower rate of survival for each age class. The unusual shape of the Ferguson Creek male 1x' curve is a result of the very low number of 1+ males and is probably due to sampling error.

The decrease in survival of *E. squamiceps* with each year of life demonstrates a tendency toward a life-span characteristic of the species (Deevey 1947: 286). Very few individuals of either sex live longer than 3 years. The oldest *E. squamiceps* examined

TABLE 6.—Distribution of sexes and year classes in samples of *Etheostoma squamiceps* collected between 6 October 1970 and 19 June 1973.

Sex	Number by Year Class				Total
	-1	1+	2+	3+	
Big Creek					
Male	146	83	26	3	258
Female	189	125	29	0	343
<i>Total</i>	335	208	55	3	601
Ferguson Creek					
Male	115	18	12	2	147
Female	195	70	17	1	283
<i>Total</i>	310	88	29	3	430

was (assuming an April hatching) a 3-year, 5-month-old female from Ferguson Creek.

TABLE 7. — Relative survival of year classes of *Etheostoma squamiceps* expressed as proportions of the —1 year class ($1x^1$) and the $1+$ year class ($1x^2$).

Sample	Year Class	Number of Specimens	Survival	
			1x ¹	1x ²
Big Creek				
Males	—1	146	1.000	...
	1+	83	0.568	1.000
	2+	26	0.178	0.313
	3+	3	0.021	0.036
Females	—1	189	1.000	...
	1+	125	0.661	1.000
	2+	29	0.153	0.232
	3+	0	0.000	0.000
Total sample	—1	335	1.000	...
	1+	208	0.620	1.000
	2+	55	0.164	0.264
	3+	3	0.008	0.014
Ferguson Creek				
Males	—1	115	1.000	...
	1+	18	0.156	1.000
	2+	12	0.104	0.666
	3+	2	0.017	0.111
Females	—1	195	1.000	...
	1+	70	0.359	1.000
	2+	17	0.087	0.242
	3+	1	0.005	0.014
Total sample	—1	310	1.000	...
	1+	88	0.284	1.000
	2+	29	0.093	0.329
	3+	3	0.010	0.034

FIG. 10.—Survival curves for *Etheostoma squamiceps*. Points on the curves were obtained by multiplying the data in the survival columns of Table 6 by 1000. The vertical axis is a logarithmic scale.

Migration

After hatching in the upstream slab pools, young *E. squamiceps* dispersed throughout the Big Creek system, mostly moving downstream. As they approached 1 year of age, the darters returned to upstream concentrations of slab rocks, where they generally remained the rest of their lives (Table 1). For the majority of the Big Creek population the dispersal as young from the spawning grounds and the upstream return to slab pools by 1 year of age were the only major migratory movements.

An indication of the magnitude of the upstream spring migration of 1-year-old *E. squamiceps* was the large number of individuals collected at a bridge dam on a headwater tributary of Big Creek on 30 March 1973. Darters moving upstream were unable to get around the bridge and were concentrated in large numbers. One seine haul covering approximately 4 square meters yielded over 50 *E. squamiceps*; all were 1-year-old (11 months) fish.

For the majority of the Ferguson Creek population, migratory movements consisted of an annual exodus each spring from the slab riffles into the slab pools, where most of the spawning activity occurred, and then a return to the riffles.

Territoriality

Aquarium and field observations indicated that *E. squamiceps* breeding males are strongly territorial; females and nonbreeding males are only weakly territorial.

When actively defending a territory, males were boldly patterned with vertical banding and a darkened head and fins; breeding and nest-guarding males had especially bold patterning. The threat posture of a male was a lateral display of his pattern and erect median fins. Persistent intruders were chased from the territory.

Occasionally when two or more breeding males were introduced into an aquarium, they briefly battled to determine the ownership of a nest stone. Such combat consisted of repeated threat displays: nipping, and tail wagging against one another.

The selective advantage for an aquarium-held male in establishing and holding a nest territory was evident: all females after the first to spawn laid eggs only in an already existing nest, and therefore, the first male to spawn was the only male to spawn.

In a large aquarium in which the males established territories centered about slab stones and several females were forced to share the remaining limited area, one female became highly belligerent toward the other females and seemed to be guarding a nonstationary territory. She was easily recognized, having a darkened head and vertical bands similar to those of a territorial male.

DIET

Stomach contents of 173 *E. squamiceps* from Big Creek and of 67 from Ferguson Creek were ex-

TABLE 8.—Stomach contents of *Etheostoma squamiceps* from Big and Ferguson creeks, by month of collection. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred																							
	Big Creek												Ferguson Creek											
	Jan. (13)	Feb. (12)	Mar. (9)	Apr. (11)	May (12)	June (7)	July (28)	Aug. (18)	Sept. (16)	Oct. (17)	Nov. (14)	Dec. (14)	Jan. (3)	Feb. (7)	Mar. (3)	Apr. (6)	May (6)	June (5)	July (13)	Aug. (6)	Sept. (6)	Oct. (3)	Nov. (6)	Dec. (3)
Nematoda	..	8.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Oligochaeta	..	25.0	..	..	..	..	..	..	..	..	7.1	..	..	..	..	..	..	..	..	..	..	..	..	..
Gastropoda	..	8.3	11.1	..	8.3	14.3	7.1	..	12.5	5.9	6.3	14.3	..	28.6	..	..	..	..	..	..	..	..	..	..
Arachnida	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Araneae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20.0	7.7	..	16.7	..	..	..
Acarina	..	..	..	..	..	14.3	3.6	11.1	..	..	..	..	..	..	..	..	..	..	7.7	..	..	..	..	..
Crustacea	..	..	..	..	..	..	7.1	16.7	18.8	41.2	..	..	..	..	..	..	..	..	30.8	..	..	..	..	..
Cladocera	..	..	..	..	..	..	42.9	25.0	22.2	6.3	11.8	..	..	..	..	..	..	20.0	7.7	..	..	..	..	..
Ostracoda	..	..	..	..	..	..	28.6	10.7	5.6	25.0	35.3	56.3	28.6	..	..	..	..	..	46.2	..	..	..	..	..
Copepoda	15.4	50.0	..	9.1	8.3	28.6	10.7	5.6	25.0	35.3	56.3	28.6	..	..	..	..	..	..	..	..	..	..	..	..
Isopoda	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Asellidae	7.7	16.7	..	27.3	8.3	..	..	5.6	..	..	25.0	50.0	..	14.3	33.3	16.7	16.7	..	7.7	16.7	..	..	100.0	..
Amphipoda	7.7	75.0	..	90.9	..	14.3	7.1	5.6	..	35.3	..	14.3	..	..	33.3	..	33.3	..	7.7	16.7	16.7	..	66.7	33.3
Decapoda	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Astacidae	..	..	..	9.1	25.0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Insecta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Plecoptera	46.2	8.3	..	9.1	..	..	..	..	..	..	..	28.6	..	14.3	..	..	..	..	..	..	..	..	..	..
Ephemeroptera	23.1	33.3	11.1	..	41.7	42.9	39.3	50.0	56.3	58.8	25.0	21.4	..	33.3	..	..	16.7	20.0	7.7	33.3	..	66.7	50.0	33.3
Odonata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Zygoptera	..	8.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trichoptera	7.7	16.7	..	9.1	8.3	..	..	..	6.3	5.9	..	14.3	..	..	..	..	..	..	23.1	33.3	33.3	66.7	66.7	66.7
Coleoptera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dytiscidae	..	8.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Hydrophilidae	..	8.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Psephenidae	..	16.7	..	..	..	3.6	5.6	12.5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Elmidae	..	8.3	..	..	..	..	5.6	6.3	..	..	..	..	..	..	..	..	..	..	7.7	..	..	..	..	..
Diptera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tipulidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16.7	..
Simuliidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	7.7	..	..	66.7	..	..
Chironomidae	30.8	75.0	88.9	90.9	83.3	57.1	35.7	38.9	37.5	23.5	75.0	64.3	..	66.7	71.4	100.0	33.3	66.7	80.0	84.6	66.7	50.0	100.0	66.7
Ceratopogonidae	..	8.3	..	..	..	..	3.6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Others	7.7	16.7	..	..	..	..	10.7	..	6.3	5.9	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Miscellaneous	..	8.3	..	27.3	..	..	..	..	..	..	..	7.1	..	..	..	16.7	..	7.7	..	..	..	..	..	33.3

TABLE 8.—Continued

Food Organism	Mean Number of Food Organisms Per Stomach																							
	Big Creek												Ferguson Creek											
	Jan. (13)	Feb. (12)	Mar. (9)	Apr. (11)	May (12)	June (7)	July (28)	Aug. (18)	Sept. (16)	Oct. (17)	Nov. (16)	Dec. (14)	Jan. (3)	Feb. (7)	Mar. (3)	Apr. (6)	May (6)	June (5)	July (13)	Aug. (13)	Sept. (6)	Oct. (3)	Nov. (6)	Dec. (3)
Nematoda	..	0.08	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Oligochaeta	..	0.33	..	..	..	..	..	..	..	..	..	0.07	..	..	..	..	..	..	..	..	..	..	..	..
Gastropoda	..	0.25	0.11	..	0.17	0.29	0.07	..	0.13	0.06	0.06	0.14	..	0.29	..	..	..	..	..	..	..	..	..	..
Arachnida	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Araneae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.20	0.15	..	0.17	..	..	..
Acarina	..	..	..	..	..	0.14	0.04	0.11	..	..	..	..	..	..	..	..	..	..	0.08	..	..	..	..	..
Crustacea	..	..	..	..	..	..	..	0.46	1.50	0.25	2.76	..	..	..	..	..	..	..	3.08	..	..	..	..	..
Cladocera	..	..	..	..	..	0.57	1.46	1.11	0.19	0.12	..	..	..	..	..	..	..	0.20	0.08	..	..	..	..	..
Ostracoda	0.23	0.83	..	0.09	0.25	0.29	0.29	0.11	0.75	1.18	2.25	0.86	..	..	..	..	..	..	2.85	..	..	..	..	..
Isopoda	0.15	0.17	..	0.91	0.83	..	..	0.11	..	..	0.25	0.86	..	..	0.14	0.33	1.00	0.17	..	0.08	0.17	..	..	1.00
Asellidae	0.54	1.50	..	2.27	..	0.29	0.07	0.06	..	0.35	..	0.14	..	..	0.67	..	2.33	..	0.08	0.17	0.17	..	0.67	0.33
Amphipoda	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Decapoda	..	..	..	0.09	0.42	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Astariidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Insecta	0.54	0.08	..	0.09	..	..	..	..	..	..	..	0.36	..	0.14	..	..	..	..	..	..	..	..	..	..
Plecoptera	0.31	0.33	0.22	..	0.67	0.71	0.46	0.56	0.69	1.18	0.25	0.21	0.33	..	..	..	0.17	0.20	0.08	0.33	..	1.33	0.67	0.67
Ephemeroptera	..	0.08	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Odonata	0.08	0.17	..	0.27	0.83	..	..	..	0.06	0.24	..	0.21	..	0.67	0.14	0.33	..	..	0.69	1.33	0.50	1.67	5.17	1.67
Trichoptera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Coleoptera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dytiscidae	..	0.08	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Hydrophilidae	..	0.08	..	..	0.08	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Psephenidae	..	0.17	..	..	..	..	0.04	0.06	0.75	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Elmidae	..	0.08	..	..	0.08	..	..	0.06	0.06	..	..	..	..	..	..	..	..	..	0.08	..	..	..	..	..
Eimidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Diptera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tipulidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Simuliidae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.62	..	..	2.00	..	..
Chironomidae	1.23	7.83	8.33	6.00	1.92	1.00	0.64	1.44	0.56	0.24	1.31	1.71	1.33	8.86	7.33	1.67	6.17	5.40	4.77	1.00	5.83	17.00	4.50	3.33
Ceratopogonidae	..	0.08	..	..	..	..	0.07	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Others	0.08	0.17	..	..	..	..	0.11	..	0.06	0.06	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Miscellaneous	..	0.08	..	2.23	..	..	..	..	..	..	..	0.07	..	..	..	0.17	..	..	0.08	..	..	..	..	0.33

TABLE 9.—Stomach contents of *Etheostoma squamiceps* from Big and Ferguson creeks, by size class of darter. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred											
	Big Creek						Ferguson Creek					
	< 21 mm (10)	21-30 mm (41)	31-40 mm (43)	41-50 mm (57)	51-60 mm (16)	> 60 mm (6)	< 21 mm (7)	21-30 mm (10)	31-40 mm (17)	41-50 mm (14)	51-60 mm (14)	> 60 mm (5)
Nematoda	..	2.4	..	..	..	..	..	..	..	..	..	..
Oligochaeta	..	2.4	4.7	1.8	..	..	..	..	..	..	..	..
Gastropoda	..	2.4	7.3	8.8	12.5	..	..	..	..	..	7.1	20.0
Arachnida												
Araneae	..	..	..	..	..	..	..	20.0	..	7.1	..	..
Acarina	10.0	4.8	2.3	..	..	..	..	10.0	..	..	..	..
Crustacea												
Cladocera	30.0	22.0	4.7	1.8	..	..	42.9	..	..	..	..	..
Ostracoda	50.0	17.1	2.3	3.5	12.5	..	28.6	..	..	..	..	..
Copepoda	30.0	43.9	20.9	7.0	12.5	..	71.4	..	..	..	..	..
Isopoda												
Asellidae	..	7.3	9.8	8.8	37.5	16.7	14.3	..	17.6	14.3	14.3	20.0
Amphipoda	10.0	7.3	20.9	17.5	37.5	50.0	14.3	10.0	23.5	..	35.7	..
Decapoda												
Astacidae	..	..	..	1.8	12.5	16.7	..	..	..	..	..	..
Insecta												
Plecoptera	..	17.1	7.3	1.8	..	..	..	..	..	..	7.1	..
Ephemeroptera	30.0	29.3	27.9	45.6	31.3	16.7	28.6	10.0	11.8	28.6	28.6	..
Odonata												
Zygoptera	..	2.4	..	..	..	..	..	..	..	..	..	..
Trichoptera	..	12.2	2.3	5.3	6.3	..	..	10.0	58.8	14.3	42.9	..
Coleoptera												
Dytiscidae	..	..	..	1.8	..	..	..	..	..	..	..	..
Hydrophilidae	..	..	2.3	..	6.3	..	..	..	..	..	..	..
Psephenidae	..	7.3	2.3	1.8	6.3	..	..	..	..	..	..	..
Elmidae	..	4.8	..	1.8	..	..	14.3	..	..	..	..	..
Diptera												
Tipulidae	..	..	..	..	..	..	..	..	..	..	7.1	..
Simuliidae	..	..	..	..	..	..	..	20.0	11.8	..	..	..
Chironomidae	70.0	56.1	72.1	36.8	43.8	50.0	100.0	90.0	82.4	64.3	50.0	40.0
Ceratopogonidae	..	..	4.7	..	..	..	..	..	..	..	..	..
Others	10.0	7.3	4.7	3.5	..	..	..	..	..	..	..	..
Miscellaneous	..	2.4	4.7	..	..	16.7	..	..	5.9	7.1	7.1	..

amined. A large variety of food organisms was found (Tables 8 and 9). The predominant components of the diet of the Big Creek population were chironomid larvae, mayfly naiads, copepods, amphipods, isopods, ostracods, and cladocerans, and of the Ferguson Creek population were chironomids, caddisflies, mayflies, amphipods, and isopods.

Little seasonal variation in the diet was found (Table 8). The use of cladocera, ostracods, and acarina by juvenile *E. squamiceps* accounts for their presence in the diet during summer and early autumn and their absence in the rest of the year. The large populations of small crayfishes in spring correlates with their appearance in stomachs of May- and April-collected darters. The most commonly eaten organisms, chironomids, were eaten in the largest

numbers in the months immediately preceding spawning, presumably reflecting an increase in consumption associated with spawning preparedness.

The smallest darters examined fed predominantly on copepods, cladocera, ostracods, and chironomids; the largest darters fed mainly on amphipods, isopods, and chironomids in Big Creek, and on amphipods, chironomids, and caddisflies in Ferguson Creek (Table 9).

Aquarium-held *E. squamiceps* searched for food by moving over the gravel bottom in short, jerky movements. When a benthic organism was located, the darter approached closely, directed his snout toward it, and then quickly sucked it into his mouth. Nest-guarding males fed as readily as other individuals. Fry were successfully raised on brine shrimp.

TABLE 9.—Continued

Food Organism	Mean Number of Food Organisms Per Stomach													
	Big Creek							Ferguson Creek						
	< 21 mm (10)	21-30 mm (41)	31-40 mm (43)	41-50 mm (57)	51-60 mm (16)	> 60 mm (6)		< 21 mm (7)	21-30 mm (10)	31-40 mm (17)	41-50 mm (14)	51-60 mm (14)	> 60 mm (5)	
Nematoda	..	0.02	..	..	..	..		..	..	..	..	..	..	
Oligochaeta	..	0.02	0.07	0.02	..	..		..	..	..	..	..	..	
Gastropoda	..	0.02	0.07	0.12	0.25	..		..	..	..	..	0.07	0.20	
Arachnida														
Araneae	..	..	..	..	..	..		..	0.30	..	0.07	..	..	
Acarina	0.10	0.05	0.02	..	..	..		..	0.10	..	..	..	..	
Crustacea														
Cladocera	1.70	1.39	0.14	0.02	..	..		5.43	..	..	..	..	..	
Ostracoda	2.70	0.63	0.02	0.25	0.13	..		0.29	..	..	..	..	..	
Copepoda	0.50	1.68	0.51	0.11	0.13	..		5.14	..	..	..	..	..	
Isopoda														
Asellidae	..	0.07	0.09	0.16	0.94	0.33		0.14	..	0.18	0.50	0.14	0.26	
Amphipoda	0.10	0.10	0.37	0.28	1.00	1.83		0.14	0.10	0.65	..	0.79	..	
Decapoda														
Astacidae	..	..	..	0.04	0.19	0.17		..	..	..	..	..	..	
Insecta														
Plecoptera	..	0.22	0.07	0.02	..	..		..	..	..	..	0.07	..	
Ephemeroptera	0.30	0.37	0.30	0.68	0.44	0.33		0.71	0.30	0.12	0.29	0.43	..	
Odonata														
Zygoptera	..	0.02	..	..	..	..		..	..	..	..	..	..	
Trichoptera	..	0.15	0.02	0.11	0.19	..		..	0.20	1.53	0.14	2.29	..	
Coleoptera														
Dytiscidae	..	..	..	0.02	..	..		..	..	..	..	..	..	
Hydrophilidae	..	..	0.02	..	0.06	..		..	..	..	..	..	..	
Psephenidae	..	0.32	0.02	0.02	0.06	..		..	..	..	..	..	..	
Elmidae	..	0.05	..	0.02	..	..		0.14	..	..	..	..	..	
Diptera														
Tipulidae	..	..	..	..	..	..		..	..	..	..	0.07	..	
Simuliidae	..	..	..	..	..	..		..	1.20	0.18	..	..	..	
Chironomidae	1.10	2.29	4.07	1.44	0.75	0.83		8.14	12.00	5.82	4.64	1.21	1.00	
Ceratopogonidae	..	..	0.07	..	..	..		..	..	..	..	..	..	
Others	0.10	0.07	0.05	0.04	..	..		..	..	..	..	..	..	
Miscellaneous	..	0.02	0.05	..	..	3.83		..	..	0.06	0.07	0.07	..	

INTERACTIONS WITH OTHER ORGANISMS

Competition

E. squamiceps occurs syntopically with all other described species of *Catonotus*, demonstrating a lack of total competitive exclusion between *E. squamiceps* and any closely related (and described) species.

At the study areas, interspecific competition for habitat space seemed unlikely except possibly between *E. squamiceps* and *E. kennicotti* in the slab pools of Big Creek. In Ferguson Creek no other riffle-inhabiting darters occurred. In both Ferguson and Big creeks the slab pools generally had a small variety of fishes, and the species of *Catonotus* were almost always the most commonly occurring fishes.

The number of nesting sites of *E. squamiceps* and other slab-rock users in a given area was often great

and seemed nearly to account for all available sites. Competition for these sites was somewhat reduced by the partial staggering of spawning periods. The sequence of spawning by the species known to spawn on the undersides of slab rocks in the study areas was, from earliest to latest: *Eumeca bislineata* (Amphibia), *Etheostoma squamiceps*, *Etheostoma kennicotti*, *Etheostoma oblique*, and *Pimephales notatus*. No nests of *Etheostoma nigrum* were found although the species is known to spawn on the undersides of stones (Winn 1958a:205, 206 and 1958b:176, 180).

Predation

As potential predators nine *Esox americanus* and 12 *Lepomis cyanellus* collected with *E. squamiceps* from Big and Ferguson creeks were preserved and

later examined for ingested *Catnotus*. One 121-mm *E. americanus* contained a recently ingested 44-mm *E. squamiceps*. No other evidence of predation was found.

Parasitism

Both study populations of *E. squamiceps* were heavily parasitized by a spiny-headed worm, *Acantho-*

cephalus jacksoni. A total of 194 of these worms was removed from the intestines of 240 darters. The infestation was more severe in Big Creek (0.91 worms per darter) than in Ferguson Creek (0.53), and more severe in large darters (as many as 19 worms in a 69-mm male) than in small. In Ferguson Creek these worms were found only in darters collected from February through May and in August, but in

TABLE 10.—Characteristics of *Etheostoma squamiceps* (24 specimens), *E. kennicotti* (24 specimens) and a hybrid *E. squamiceps* x *E. kennicotti*, all from southern Illinois.

Characteristic	<i>E. squamiceps</i>				Hybrid	<i>E. kennicotti</i>			
	Range	Mean	Standard Deviation			Range	Mean	Standard Deviation	
Number of lateral-line scales	48–54	50.5	2.0		46	39–46	42.6	1.8	
Number of pored lateral-line scales	25–40	33.8	3.4		30	14–25	19.7	3.0	
Number of scales around caudal peduncle	17–21	19.6	1.2		20	17–20	18.3	0.8	
Number of vertical bands on caudal fin	6–9	7.6	0.8		7	8–11	9.3	0.8	
Number of dorsal spines	7–9	8.3	0.6		8	6–8	7.2	0.5	
Number of dorsal rays	12–14	13.0	0.4		13	11–13	12.1	0.5	
Number of pectoral rays	10–12	11.1	0.4		12	11–13	12.0	0.2	
Pectoral fin length/standard length	0.21–0.25	0.23	0.01		0.26	0.23–0.28	0.25	0.01	
Spinous dorsal fin base length/standard length	0.21–0.24	0.23	0.01		0.23	0.23–0.28	0.26	0.01	
Spinous dorsal fin base length/soft dorsal fin base length	0.87–1.04	0.94	0.06		1.00	0.73–0.91	0.81	0.06	
Spinous dorsal fin height/soft dorsal fin height	0.50–0.86	0.62	0.08		0.54	0.44–0.55	0.47	0.03	
Spinous dorsal fin height/body depth	0.35–0.52	0.46	0.05		0.39	0.35–0.43	0.39	0.02	
Nape squamation	Fully scaled				Partially scaled	Naked			
Belly squamation	Fully scaled				Fully scaled	Variable naked strip			
Dorsal fin pigmentation	Without marginal band				Light marginal band	Distinct marginal band			
Caudal spots	Three black spots				Three black spots	No black spots			

TABLE 11.—Summary of life-history information on Big Creek and Ferguson Creek populations of *Etheostoma squamiceps*.

Characteristic	Life-History Data
Principal habitat of adults	Slab riffles in Ferguson Creek; slab pools in Big Creek
Principal habitat of young	Slab riffles in Ferguson Creek; slab pools in Big Creek
Age at reaching sexual maturity	1 year
Age at first spawning	Females 1 year; males 2 years
Size at reaching sexual maturity	Females about 35 mm; males about 40 mm
Sexual dimorphism	Males are larger, have longer fins and a deeper caudal peduncle, and in spring are much more boldly patterned
Breeding tubercles	Absent
Number of mature ova counted	28–357
Description of egg in nest	1.8 mm in diameter, translucent, adhesive
Spawning period	From late March to May or early June
Spawning habitat	Slab pools
Spawning position	Both male and female briefly inverted, head to head
Nesting site	Underside of a slab stone
Number of eggs counted in nests	8–1500
Egg guarding	Only by the male
Incubation periods	270–275 hours at 18°–22° C, 125–130 hours at 22°–26° C
Influence of sex on growth rate	By the third year males are significantly larger than females
Density	Up to 9.6 darters/m ² in slab riffles in Ferguson Creek; up to 2.0 darters/m ² in slab pools in Big Creek
Sex ratio among young	1.7 females: 1 male in Ferguson Creek; 1.3 females: 1 male in Big Creek
Longevity	3+ years
Maximum size	72 mm standard length
Migrations	To and from spawning grounds
Territoriality	Extreme in breeding males; weak in females and nonbreeding males
Principal diet	Aquatic insect immatures and crustaceans

Big Creek worms were found in darters collected in every month except June, July, and August. *A. jacksoni* has previously not been known to parasitize *Etheostoma* (Hoffman 1967:283).

The only ectoparasites found were two piscicolid leeches attached to the caudal fins of two young *E. squamiceps* collected in Big Creek in October.

Hybridization

No accounts of hybridization involving *E. squamiceps* were listed by Schwartz (1972). One *E. squamiceps* x *E. kennicottii* hybrid male was collected in Big Creek on 1 October 1971. The specimen measured 40 mm, was 1+ years old, and shared morphological characteristics with both parent species (Table 10).

SUMMARY

The life-history information on *E. squamiceps* collected in Big and Ferguson creeks between 6 October 1970 and 19 June 1973 is summarized in Table 11.

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