ABSTRACT.—The social behavior of the tessellated darter (Etheostoma olmstedi) is apparently unique among fishes in that males regularly clean and defend eggs which they did not fertilize. Large, behaviorally dominant males defend the few rocks in the stream which are suitable for spawning. After fertilizing eggs deposited by the female at one rock, dominant males often move to other rocks which appear to offer more uncovered spawning surface, apparently because these rocks are preferred by spawning females. Subordinate males occupy newly-vacated rocks and clean the remaining uncovered surface, incidentally cleaning the dominant male’s eggs. I hypothesize that dominant males maximize their reproductive success by exploiting the smaller males’ limited access to spawning rocks. This assures incidental cleaning of dominant males’ eggs by subordinates, freeing dominant males from parental care and allowing them to pursue additional spawning opportunities elsewhere. [breeding patterns, darters, Etheostoma, parental care, Percidae, Pisces, reproductive strategies, sexual selection, social hierarchy, territoriality]

Natural selection has presumably favored individuals whose behavior maximizes the survivorship of their own offspring or of close relatives. Among fishes exhibiting parental care, one or both parents may feed and defend their own offspring or, in a few cases, mimics of their young (Ribbink 1977), while harming (Keenleyside 1972) or behaving neutrally to other conspecific juveniles. Male tessellated darters (Etheostoma olmstedi) defend an area about a rock from conspecific males and maintain its flat underside and any attached eggs free of silt for courtship and further oviposition. A unique feature of this species is that males regularly clean eggs which have been fertilized by unrelated conspecific males. This paper presents an initial qualitative description of the social behavior of the tessellated darter, an understanding of which leads to a tentative hypothesis on the adaptive significance of this form of parental care.

MATERIAL AND METHODS

During the spring of 1977, I studied a natural population of the tessellated darter in the East Branch of White Clay Creek (75°47'04"W, 39°51'23"N), Chester Co., Pennsylvania. In the clear, shallow stream, the movements of individuals fitted with color-coded tags were observed from the shore through binoculars. The color-coded tags consisted of line (0.3 mm diam. monofilament) through the muscles below the second dorsal fin at 45° with the caudal peduncle; the anterior end was fitted with a plastic washer and knotted proximally, the other end was threaded through colored beads (colorfast polypropylene insulation from electric wire, 0.8 mm O.D.) and knotted distally. Within minutes after their release, tagged fish resumed normal feeding and courtship. Social interactions were studied for a total of 97 hours. Clutches on natural nest rocks were photographed to evaluate the proportions of living and dead eggs—white, opaque eggs were scored as dead, in contrast to the translucent yellow appearance of living eggs. Field observations were primarily made from 0800 to 1600 hrs.

During the spring of 1978, I observed de-
tails of fertilization and egg-tending in a plexiglas tank (2.4 m long and 1.2 m wide) which was located in a greenhouse near the study creek. Water from the creek flowed through the tank. I made artificial nest rocks by using cement blocks as the base and pieces of rectangular slate as the ceiling. The slate was supported on one side by a stone two cm high and rested on the block along its opposite side.

RESULTS

This section is composed of three parts. First, I explicitly define certain motor patterns and social interactions. Second, a qualitative description of mating behavior provides a basis for understanding the social behavior. And third, I describe the interactions among dominant males, floating males, females, and offspring.

DEFINITION OF BEHAVIOR PATTERNS

Adpression. Pressing the urogenital opening against a spawning surface.

Cruising. Movement by a male among a series of nest rocks by aggressively displacing occupant males.

Fin flare. Erecting dorsal and caudal fins.

Floating. Movement by a male among potential spawning surfaces because he is unable to monopolize a suitable nest rock.

Head vibration. Trembling of head and anterior part of body while exhibiting lateral display. Body does not move directionally.

Inverting. Turning upside-down, i.e., ventral surface up.

Lateral display. Presenting lateral surface and flared fins to opponent.

Reverting. Turning rightside-up, i.e., ventral surface down.

Quivering. During courtship, trembling of the whole body with no directional movement.

Wiggling. Exaggerated sinusoidal motion while moving slightly. May be performed in inverted or reverted position.

MATING BEHAVIOR. The following description represents a summary of detailed observations of six spawning sequences. In response to nearby movement, a territorial male would often emerge from his nest rock. If the movement had been produced by a female with depressed fins, the male would flare his fins and swim to his rock with exaggerated swimming motions. Often, the female followed. Females with erect fins and males were driven away. Immediately after returning to his nest rock, the male inverted, and wiggled and quivered over the ceiling.

After entering the nest rock, the female either inverted for a few seconds and adpressed weakly, or remained reverted. The male usually remained inverted continuously for 5–10 minutes and quivered frequently. Gradually, the female would invert more frequently and for longer duration, while increasing the firmness of her adpression. After one to two hours, the female's inverted wiggling began to be followed by a sharp quiver. During each quiver, she deposited a single egg directly on the bare surface of the ceiling. At the end of each quiver by the female, the male pushed the female laterally and quivered while firmly adpressed, placing his urogenital opening directly on the newly-deposited egg. I interpret this as the instant of sperm emission. During peak spawning activity, several (≤6) eggs were laid in a quick series of quivers before resting. The rate of egg laying gradually slowed and the female would be driven off by the male. The eggs of a clutch were usually arrayed as a loose cluster on the underside of the nest rock. Complete courtship and spawning required several hours.

During courtship and spawning, the male would occasionally leave the female to drive off other nearby fish. Although visiting males and females with erect fins were repelled, visiting females with depressed fins were allowed to remain under the nest rock. This infrequently led to a single male simultaneously courting several females. Large courting males quickly drove off most visitors and returned promptly to the female. Small spawning males were usually
displaced by larger visiting males and the victor would proceed to fertilize the remainder of the clutch at that nest rock. Because the largest male was able to monopolize the nest rocks within a given area (see below), all eggs of most clutches and some eggs in other clutches were probably fertilized by the largest male.

In the tank with 12 males, I knew the paternity of six clutches. Four were fertilized by the largest male, and the two remaining clutches were each fertilized by smaller, territorial males. No other males achieved any fertilizations. The two fertilizations by subordinate males occurred within one day after the dominant male had fertilized a clutch, during which he was presumably defending soft, newly-laid eggs. As discussed later, dominant males do not cruise during this period, allowing subordinate males to complete courtship without being interrupted by a larger, cruising male.

SOCIAL DYNAMICS. Social interactions in the creek changed predictably during the course of a day. Several males (2-4) often spent the night under a single rock and as the water warmed to 14-15°C by mid-morning, the largest male at each rock became darker in body color, became aggressive, and drove off smaller males. The lone occupant then began defending the area immediately about the entrance of the nest and frequently inverted and wiggled over the ceiling and attached eggs. Displaced males immediately became pale and after a variable period (5-30 mins.), began floating. Females began to visit nest rocks about one hour after males began agonism.

Later in the day, usually late morning, dominant males would begin cruising. The movement of such a male among rocks was quick and direct, indicating that he was experienced with the locations of nearby nest rocks. The larger the male, the larger was the area he covered: males 70 mm total length visited most or all of the suitable rocks (4-5) within an average pool (3-4 m long), males 60 mm long cruised among several (2-3) nearby rocks, and 55 mm males only visited other rocks near (5 cm) their own. I rarely observed 50 mm males control a rock for more than a few minutes; instead, they floated almost continuously.

When large males cruised, they usually displaced smaller males from their rocks by displaying the following behaviors, in order of increasing aggression: fin flare, lateral display, head vibration, and biting fins. This series reflects increasing levels of aggression because: (1) the patterns were usually displayed in this order; (2) the latter entailed more gross movement; and (3) the latter displays include the former, e.g., head vibration includes the lateral display. After displacing the occupant, the cruising male usually entered the nest rock and immediately inverted and wiggled over the ceiling and any attached eggs. These eggs were not necessarily fertilized by him. The occupant typically went through several sequences of inverted wiggling and reverting, and if there were no interactions with conspecifics of either sex after several minutes, he would swim to another nest rock and repeat the sequence.

After being displaced from a rock, small males usually became pale and remained motionless for several minutes near the rock from which they had been displaced. For a variable period (5-30 mins.), the small male would periodically return to the rock. Often, the dominant male did not remain long (2-5 mins.) and would move to another rock, whereupon the small male would then reoccupy the rock. If the dominant male remained for longer periods (10 mins.-1 hr.), the small male would be repelled repeatedly and would begin to exhibit the behavior of a floater.

If the original occupant male had been courting a female, the female would usually resume courtship with the dominant victor; thus, large cruising males usurped fertilizations from smaller courting males. I ob-
served this kind of sexual interference (in the sense of Arnold 1976) several times in both the creek and tank. I have twice observed such a displaced male assume the appearance and behavior of a female that is ready to spawn (pale body color, depressed fins, approaching the nest by short movements of the pectoral fins) and return to the nest. Males in this condition were usually not repelled immediately, and were often allowed to enter the nest and to invert alongside the spawning pair. This suggests that subordinate males may mimic females in order to achieve sneak fertilizations (in the sense of Van den Assem 1967 and Constantz 1975).

Typically, a dominant male spent more time at one specific rock than at any other; I term this the primary rock. In the manner described above, cruising males occupied a series of nest rocks, cleaned any attached eggs, and did not return to their primary rock for periods that ranged from one minute to the remainder of the breeding season. As discussed later, one reason why a dominant male may not return to his primary rock is that he may encounter a receptive female elsewhere and remains to guard fresh, soft eggs which are vulnerable to cannibalism.

Usually within minutes after the dominant males had left their primary rocks to cruise, floating males would enter the vacant rock, darken their body color, become aggressive, and invert and wiggle over the ceiling and any attached eggs. When the cruising male returned to his primary rock, the smaller occupant was usually the more aggressive and darker of the two, and often swam out to challenge the larger male. Although such encounters infrequently developed into protracted and energetic clashes, the smaller male would usually yield after a brief lateral display. This sequence—cruising by the dominant male, temporary occupancy of most nest rocks by both floating and cruising males, and return of the dominant male to his primary rock—resulted in the eggs at most nests being tended by several different males during the day. When large males did not cruise, most smaller males remained at specific nest rocks.

Although the breeding behavior of several rock-spawning darters has been studied (Lake 1936; Winn 1958a, 1958b; Page 1974, 1975; Page and Burr 1976), movement among nests by individual males has not been previously reported. In fact, to the best of my knowledge, it has not been described for any other egg-tending fish.

In the plexiglas tank I observed three males fertilize a total of six clutches. When these fathers began cruising, smaller males invariably and promptly occupied their nest rocks, and immediately inverted and wiggled over the ceiling and the attached eggs. This occurred with every clutch deposited in the tank and strongly suggests that in nature, males clean unrelated eggs.

**DISCUSSION**

The social system of the tessellated darter appears to be a complex blend of territoriality, sexual interference, female choice, and tradeoffs between the costs and benefits of cruising vs. remaining in place. An interesting outcome of these behaviors is that males regularly defend and clean unrelated eggs. I will develop six specific points, which then allow the construction of an hypothesis on the adaptive significance of this social system.

(1) Improved egg survivorship is a result of inverted wiggling by males. In the plexiglas tank, I clearly saw that a male which is inverted and wiggling rubs his ventral surface, and his pelvic and pectoral fins over the rock surface and any attached eggs. In a preliminary experiment, I isolated two clutches in the tank and monitored egg survivorship—after two days without male attention, all eggs appeared to be alive even though their surface was cov-
ered with silt; by four days, about three percent were dead; and after seven days, about 33% were dead. In the creek, egg mortality was about one percent. In two related species, *E. nigrum* and *E. flabellare*, eggs became infected with fungus if they went untended by a male (Lake 1936; Winn 1958a).

(2) The adaptive significance of inverted wiggling by a male appears to be the maintenance of a clean spawning surface. A clean, hard surface appeared to be critical for the firm adhesion of eggs; thus, females should be perceptive to cues which indicate the cleanliness of the ceiling. Several additional observations suggest that the function of inverted wiggling is to clean the spawning surface. First, males wiggled over ceilings that had no attached eggs, apparently maintaining the ceiling for initial oviposition. Second, preliminary data from the tank indicated that males inverted at rates of 0.38 and 0.31 times/min. under rocks with and without attached eggs, respectively, suggesting that the presence of attached eggs made no difference in the rate at which males wiggled over the ceiling. Third, males wiggled over attached eggs and adjacent bare rock without obvious preference.

(3) Eggs are partially immune from cannibalism. I infrequently observed males that had just arrived at a nest rock invert and peck at the attached eggs. Eggs were seldom consumed because they were normally hard and firmly adhered. However, eggs were soft for about two-thirds of a day after their oviposition and for about one and one-half days prior to hatching. After fertilization, fathers guarded their eggs for about one and one-half days, presumably until they hardened. Parental males did not cruise during this period. Cannibalism occurred when nest rocks with hatching eggs were occupied by males which had not fertilized the clutch. In one such case, I observed a male cannibalize the entire clutch of soft eggs. Unfortunately, I have no estimates of the frequency of cannibalism in nature. Time from egg laying to hatching ranged from 12 to 21 days, depending upon temperature. Assuming that fathers protect their eggs during the period from their fertilization to the onset of rigidity, eggs were vulnerable to cannibalism for about the latter nine percent of their embryonic life.

(4) There are fewer nest rocks than mature males. In a thorough search of the study area (470 m of creek) during the height of the spawning season, I found only 37 rocks with attached eggs. Virtually all rocks that appeared suitable to me (smooth underside and a 2–3 cm gap between ceiling and substrate) contained attached eggs. A cursory mark-recapture estimate indicated 5,000 adult darters in this stretch. Thus, the low number of suitable rocks appears to have limited the reproductive success of most males.

When artificial nest rocks (sheets of slate) were added to the creek, many males were defending and inverting under them within 15 minutes. The earliest occupants of new nests appeared to be former floaters because they were small to medium-sized males and because larger males that had been occupying natural nest rocks maintained their positions. After several hours, large males occupied some of the artificial nest rocks, presumably after having displaced the smaller original occupants.

(5) Cruising results in more fertilizations by dominant males. In both creek and tank, I observed cruising dominant males displace smaller males from courtships, and then the larger male proceeding to spawn with the female at that rock. When cruising males encountered females in areas between nest rocks, they usually attempted to lure them to the nearest rock.

Cruising may also increase the rate of fertilization by large males through another, complementary pathway. If egg survivorship depends on male attendance, females
should select for oviposition those rocks which signal the greatest probability of male occupancy. Males should spend little time at nest rocks with little or no surface that is uncovered by eggs. Therefore, individuals of both sexes should select nest rocks with sufficient or with the most uncovered surface area. Preliminary observations in the tank are consistent with this idea. On three artificial nest rocks, the first three clutches were laid one per rock; after the second set of three, each rock contained two clutches. Assuming that the location of each clutch is independent and random, the probability of the observed pattern is \((1)(\frac{2}{3})(\frac{3}{5})^2 = 0.049\). This suggests that females oviposited preferentially on rocks with the fewest clutches. If females choose nest rocks with sufficient or the most available spawning area, which varies with further egg laying and hatching, males should occasionally visit a variety of nest rocks to assess their amount of available surface. In this manner cruising males may be attempting to predict and occupy the rock most preferred by females, thereby maximizing their rate of clutch production.

(6) Small males achieve more fertilizations while occupying vacated rocks than by floating. As floaters moved through a pool, they would invert for short periods under objects such as tree roots and mud clods. When a floater encountered a female, he would often flare his fins and swim to the nearest potential spawning object. Usually, the female would not follow, but if she did, she would depart promptly after having inverted under the object. I have never observed floating males achieve a single fertilization.

If, however, a floating male occupied a vacant nest rock, two general outcomes were possible. First, if the rock was temporarily vacated by a cruising male, the small male would probably not achieve any fertilizations because the average absence of cruising males was only about eight minutes, yet courtship prior to egg laying normally required at least one hour. Second, the cruising male may have encountered a receptive female elsewhere and may have been defending newly-laid eggs at another rock. In this case, the subordinate occupant would have use of the rock for at least one and one-half days, adequate time for consummating a courtship. In the tank, I observed the latter outcome twice. Subordinate males which occupied a nest rock, regardless of duration, inverted and wiggled over the ceiling, and courted all females. Thus, attached eggs which had been fertilized by a previous male would benefit from the inverted wiggling of a subsequent subordinate occupant.

**Adaptive Significance.** Why should subordinate males tend eggs which were fertilized by a dominant male? One possible mechanism maintaining this behavior could be kin selection (Hamilton 1964)—related males defend and clean each other’s eggs. This explanation requires at least one of the following conditions: (1) relatives are nearby, or (2) individuals can recognize relatives. Preliminary studies of tagged fish in the creek suggest that kin disperse widely: occasional floods displaced many individuals; on other days, some individuals swam 100 m upstream. There is no evidence that adult fish can assess their degree of genetic relatedness. Therefore, I do not invoke kin selection.

I suggest the following hypothesis. The number of mature males far exceeds the number of suitable spawning rocks. Consequently, males compete for nest rocks. Large males win aggressive encounters and occupy nest rocks, and the smaller losers roam the stream searching for suitable spawning surfaces. Within a given area, the largest male has access to all rocks.

Because bare rock is critical for the adhe-
sion of eggs, females invert to evaluate the cleanliness of its ceiling. Males, therefore, invert and wiggle over the ceiling to maintain a clean spawning surface.

The probability of a male remaining at a particular nest rock is a function of its amount of available spawning area. However, the deposition of a clutch onto a spawning surface will necessarily decrease the area available for further oviposition on that rock. Because egg survivorship is a function of male occupancy, females should therefore select for oviposition those rocks with the greatest or at least a sufficient amount of uncovered area. This would help assure male occupancy, and thereby egg-cleaning, once the clutch is in place.

The amount of available spawning area on a rock varies through time as eggs hatch and are deposited. If not guarding fresh, vulnerable eggs, dominant males should visit (cruise) local nest rocks to compare their available spawning area. Like females, males should prefer the rock with the greatest or at least a sufficient amount of uncovered surface. This rock would then become the center of that male’s activity, his primary rock. Dominant males cruise more frequently than that required to monitor ceilings, apparently because this increases the probability of intercepting receptive females at locations other than the primary rock.

The previous two paragraphs suggest that sexual selection in this species involves females choosing specific rocks for oviposition, while male-male competition for nest rocks determines which males fertilize the most eggs. Thus, intersexual selection in the sense of females evaluating the quality of males directly may not be operating in this species. Because there is at least a small probability that rocks vacated by cruising dominant males will be available to a subsequent occupant long enough to complete courtship, small males occupy such rocks, and while there, maintain the spawning surface clean of silt. This results in incidental cleaning of the attached eggs. When the dominant male remains away from his eggs for extended periods, the survivorship of his eggs is dependent on the cleaning movements of subordinate males. Thus, dominant males appear to exploit the certainty that subordinate males are rock-limited.

Lastly, one value of these observations is that they suggest a set of conditions which maintain a social behavior that increases the survivorship of unrelated offspring. For this species, they appear to be: (1) Offspring are somewhat immune from cannibalism; (2) Mating and offspring development occur within the same habitat patch; (3) Males compete for such patches; (4) Behavior which functions to maintain a breeding patch results in improved offspring survivorship; and (5) The quality of patches varies through space and time. Not only do these conditions appear to apply to darters of the subgenera *Boleosoma* (five spp., including the widespread johnny darter) and *Catonotus* (about 10 spp.), but a cursory survey of the teleosts suggests that of 58 families listed as providing parental care (Breder and Rosen 1966), ten meet at least several of these conditions (e.g., loricariid catfishes, blennioids).

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LITERATURE CITED


