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SEXUAL BEHAVIOR OF THE OYSTER DRILLS: EUPLEURA CAUDATA AND UROSALPINX CINEREA[1]

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The observations reported herein are part of an extensive study of the biology of *Urosalpinx cinerea* (Say), the smooth oyster drill, and *Eupleura caudata* (Say), the rough oyster drill, which is in progress at our laboratory. Results of studies of other aspects of the behavior and ecology of these predatory snails will be reported as they become available.

Little is known of the copulatory behavior of dioecious marine gastropods. Though Stauber (1943) reported a partial pairing of *E. caudata,* pairing of *U. cinerea* has never been described. Our studies show that pairing of both species is a complex process involving fairly intricate behavior of both sexes.

Copulation of Eupleura caudata. According to Stauber's (1943) description of a partial mating of *E. caudata* the male mounted the right side of the female and formed the anterior part of his foot into a copulatory groove through which the penis was ex-

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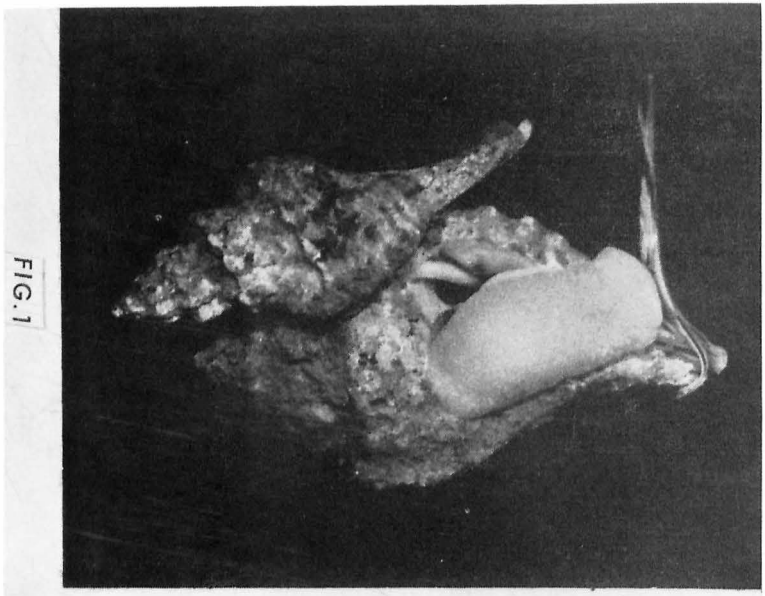

FIG. 1

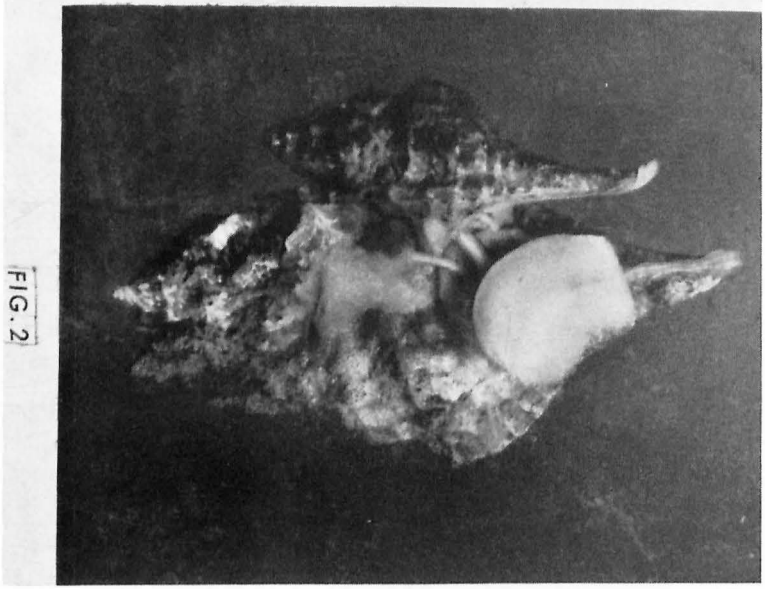

FIG. 2

Eupleura caudata (Say). Fig. 1, male and female in copula. Fig. 2, two males attempting copulation with one female.

tended into her mantle cavity. Even though disturbed repeatedly this pair copulated intermittently for 21 days. Our laboratory observations of pairing of captive *E. caudata* confirm and enlarge upon those of Stauber. Eighty-one separate pairings were observed but because the average time each couple was together was extensive and coitus occurred intermittently, only two copulations were seen from beginning to end.

Prior to coupling, the female usually moved about the aquarium walls and finally assumed a stationary position with her siphonal tip upward. Pairing also occurred in horizontal positions on oysters, or on the aquarium bottom, or rarely, on the walls. The mantle cavity was then exposed by allowing the shell to hang down and away from the posterior part of the foot. Though in most cases a male (or males) had already assumed a position upon the shell of the female, several unpaired females also exposed their mantle cavities in the same fashion prior to copulating and probably this behavior is normal precopulatory activity. Following this the male often moved about on the female's shell for a short time but eventually assumed a stationary position on her right ventral surface slightly posterior to the mantle cavity with his siphonal cavity pointing in the same direction as hers (Fig. 1, p. 6). The foot of the male extended to the rim of the mantle cavity and a copulatory groove formed in its anterior surface through which the penis was protruded into the mantle cavity and presumably the vagina, though that orifice was always hidden from view by the shell. On termination of copulation, the female often twisted from side to side and opened and closed the cavity opening. Similar twisting behavior has been observed in other gastropods apparently attempting to dislodge predatory snails, *Odostomia,* from their shells (Allen, 1958). The male then withdrew and either remained in position or moved about on the shell of the female or to the substrate.

E. caudata usually remained in position and copulated intermittently for extensive periods, often up to 48 hours. Two pairs copulated continuously for 2 hours 45 minutes ± 15 minutes and 3 hour 39 minutes ± 10 minutes, and a third for 5 hours ± 10 minutes, but all were paired longer. Another pair copulated intermittently for a total of at least 8 hours 48 minutes over a period of two days, during which the male maintained his posi-

tion on the female. A marked pair copulated 11 times in five months. During this period the pair often separated and the female paired with other males.

Eupleura caudata showed marked promiscuity. Of 29 marked pairs, 12 females copulated with more than one male and 15 males with more than one female. One male copulated with 6 different females and one female accepted 5 males throughout the season. Although these are observations on drills confined in running-water aquaria and cages, there is little reason to doubt that, depending on density and movement, similar promiscuity occurs in nature.

Usually, males were smaller than their consorts (48 males: mean height 18.7 mm., range 14.9-23.5 mm., standard deviation 2.3; 44 females: mean height 22.6 mm., range 17.5-28.9 mm., standard deviation 3.2).

Seasonal periodicity of copulation was determined in outside cage experiments and running-water aquarium observations. Though the frequency of observation was not always constant throughout the year, the number of pairings seen in aquaria per month roughly corresponded to those in more careful cage experiments. In 1956 pairings were recorded as follows: March-6, April-14, May-15, June-3, July-9, August-1, September-1, October-9, November-1, and December-1. The first occurred on March 7 (12.9°) and the first peak occurred in late April and early May. A second peak came in July, comparatively few pairings occurred from July through September, but an increase took place in the last part of October. Copulation ceased after December 10 (10.3°C). The lowest temperature at which pairings were observed was 10.3°C, the highest 28.4°C. Also in 1956, 30 females and 30 males, caged in a single large compartment, were examined every two days between 1400 and 1700 hours. Onset of the mating period was not observed because the experiment was established too late in the season. Pairing was first seen in late April at 13.7°C, reached a peak on June 7 at 23.7°C, and ceased on July 7 at 26.1°C, (Figure 3). A late wave of 28 pairings, about one-third as intense as the spring wave, began at the end of September (21.7°C) and ended November 11 (16.4°C.) Observations made two or three times a week during the winter of 1956-57 revealed no copulatory activity but this was expected because all other

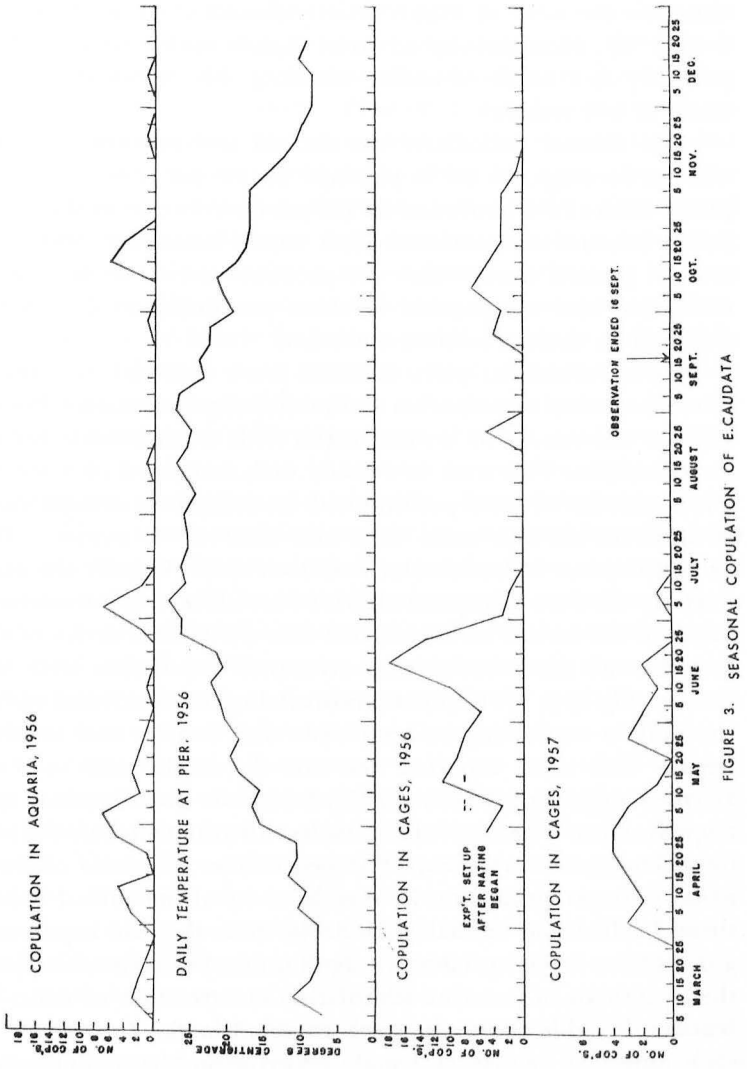

FIGURE 3. SEASONAL COPULATION OF E.CAUDATA

overt activity had ceased. Observations in the first half of the summer of 1957 on two cage compartments containing 45 specimens each (sex ratio of entire sample, 50 females to 40 males) indicated that copulation was less intense than in 1956. Pairing was first observed on April 4 (11.1°C). There was no distinct peak

and after the week of May 6 activity slowed and ceased on July 6 (26.1°C). Most activity occurred slightly earlier than in 1956, probably as a result of earlier warming. No observations were made in late summer.

Little diurnal periodicity was noticed and nocturnal activity was not investigated. Of 56 pairings, 23 (48 per cent) were completed before 1200 hours and 29 (52 per cent) occurred after 1200 hours. Because observational effort varied somewhat these data are not precise, though they are probably indicative of general conditions and comparable to those pertaining to *U. cinerea* gathered in similar fashion, see below.

On two occasions, pairs of males were observed *in copula*. Careful external examination and studies of gonad smears showed all four animals to be normal males with no detectable female characteristics. Five trios *in copula,* each composed of a female and a male in the usual position with an extra male in copulatory position on the first male, were also observed in aquaria. The extended penes of both males were seen twice. Usually the male next to the female copulated with her while the intromittent organ of the second male extended into the mantle cavity of the first, but at times both males attempted copulation with the female (Fig. 2, p. 6). Copulations involving two functional males, the middle one acting as both male and female, and another female has been reported for the hermaphroditic species, *Lymnea stagnalis,* (Crabbe, 1927) but never for dioecious gastropods. Once a quartet with 3 males, all situated chain-fashion on a female, was observed. The penes of at least two of these males were extended into the mantle cavity of the animal before them. In dioecious animals, like drills, these aberrant copulatory groups have little reproductive significance, but seem to support the hypothesis of exocrine stimulation or attraction of males to females. Possibly the males were attracted to the females, or to each other, by release of female exocrine in the vicinity and, without being able to discriminate further, established and maintained contact with each other.

Copulation of Urosalpinx cinerea. Observations of 76 pairs of *U. cinerea* showed their copulatory behavior to be generally the same as that of *E. caudata,* but with several distinct differences. The female usually assumed a stationary position with her

siphonal tip upwards, allowed the shell to fall away from the substrate, thus exposing the right rear corner of the mantle cavity and twisted the shell from side to side several times in a sort of "precopulatory dance." Most often a male was already on the female's back when this precopulatory play was observed, but several times males appeared to be attracted from afar to the demonstrating female. Sometimes unattached males, often several at a time, were attached to a demonstrating female or copulating pair, possibly drawn to the receptive female or the pair by some stimulus, probably an exocrine. Following the precopulatory demonstration by the female the male assumed a position on her right ventral side, formed a copulatory groove of the anterior portion of his foot and inserted his penis through the groove into the female's mantle cavity. On completion of coitus, the intromittent organ was withdrawn, and in contrast to the slow separation or intermittent resumption of *E. caudata,* the male moved quickly away. The shortest complete copulation observed lasted 4 minutes, the longest 32 min. Including preplay time, one complete pairing occupied one hour and 25 minutes, but actual copulatory contact required only 11 minutes. Usually *U. cinerea* copulation occupied only 3 to 4 minutes. This characteristic short contact, seldom more than 4 or 5 minutes, probably explains why *U. cinerea* mating has not been previously reported.

According to our observations, only one pair of 20 marked pairs recopulated and the pairings were 1½ months apart. Of the marked pairs 7 males and 2 females coupled with different mates. Thus, *E. caudata* seemed more promiscuous than *U. cinerea.* However, the incidence of promiscuity in *U. cinerea* may be actually greater than these data indicate because of the unlikelihood of observing its brief sexual contacts as readily as the much longer ones of *E. caudata.*

The male is usually the smaller of the pair: 41 pairing Seaside (from the ocean coast of the Eastern Shore of Virginia) males averaged 29.8 mm. in height, range 19.5-38.7, standard deviation 5.1; 46 females averaged 34.4 mm. in height, range 21.9-44.6 mm., standard deviation 4.7; six York River males averaged 19.3 mm. in height, range 16.5-24.6 mm. and five females averaged 19.5 mm. (17.3-21.2 mm.).

Pairing was seen in late October and early November, 1955,

until the temperature dropped to 13.7°C. In 1956, it began on February 29 (8.2°C., increased in March with 10 pairings, reached a peak in April with 17 pairings, and diminished in May to three pairings (20.3°C). Pairing was not observed again until October, (20.8°C), none in November and 2 on December 7 (11.5°C). Of 59 pairings, nine (15 per cent) were observed before 1200 hours and 50 (85 per cent) after 1200 hours. In contrast to *E. caudata, U. cinerea* seems to exhibit marked preference for the afternoon.

Two pairs of structurally normal males were observed *in copula* and, on another occasion, two males were observed copulating with one female.

Sperm viability and storage. One *U. cinerea* male, forcibly separated from a female, exuded sperm in a continuous, viscous stream, thus indicating that discrete spermatophores are probably not employed. Examination of seminal receptacles of at least 50 females of both species support this conclusion. Seminal receptacle smears of two females taken immediately after copulation contained immotile sperm while those in another were motile; therefore, it is not clear whether the sperm are immotile when passed. Microscopic examinations of seminal receptacles of several hundred individuals of both species revealed that many mature females contained fully or partially motile sperm at all times of the year though the sperm in some were entirely immotile. Whether they are stored in the motile condition is not clear because the mechanical action of smearing may have stimulated the sperm to activity. Apparently spermatozoal energy is sustained in some way, either through conservation of energy by immotility or special nourishment because both species can store viable sperm for considerable periods of time.

Stauber (1943) reported that a *U. cinerea* female isolated from April to October of the same year deposited egg cases containing viable embryos through the period. In our experiments 4 females isolated in November and December of 1955 produced viable eggs the following spring and summer. Of these, one deposited in May after 5 months, two spawned in August, after somewhat less than 9 months, and one in September after 9 months. Two post copula *E. caudata* females isolated in 1955 produced egg cases through 1956 and into 1957, but the embryos produced in 1957

did not develop. Unless parthenogenesis occurred—which is most unlikely—or the so-called "embryos" included in these 1957 egg cases were merely unfertilized ova and not really embryos at all, the sperm must have been vigorous enough to affect fertilization even after a storage period of over 14 months. In any case, however, the embryos (or unfertilized ova) produced in 1957 failed to develop even though handled in the same fashion as others which survived. Eight other females, isolated in late fall or early winter of 1956 produced viable cases for periods of at least six months after isolation.

Discussion. Several points of biological interest have arisen during the present study. Because of the nature of the photo receptive organs it is doubtful, but not certainly so, that the precopulatory "dance" or movements of the female attracts the male. More feasible is the chemical stimulation of the male by the female. If female oyster drills actually attract males during their "premating ritual" by release of an exocrine, such a chemical might be useful as an experimental or control tool because it is probably highly specific and powerful enough to be effective in extreme dilution.

It has been shown that females of both species are able to store sperm in their seminal receptacles for extensive periods. The mechanisms by which they are sustained should be of interest in studies of cell culture and nutrition.

Oyster drills are promiscuous and have the facility for sperm storage; therefore, unless sperm from previous pairings are discarded or resorbed completely before another mating occurs, a female contains viable sperm from several different males in her seminal receptacle. Under these circumstances, embryos produced therefrom might have different paternal hereditary materials. Thus, differences in rate of embryonic development, time of hatching, appearance, etc. may be due to varied paternity and not the usual genetic difference found among siblings. Until the precise nature of sperm storage, syngamy and egg case formation is understood, experimenters working with drill embryos cannot safely assume that all embryos in a unimaternal cluster or even a single egg case are of the same parentage.

Summary

1. *Eupleura caudata* and *U. cinerea* exhibited fairly complex

mating behavior involving definite precopulatory movement patterns by the female, stimulation of nearby males, possibly by exocrine activity, assumption of relatively constant copulatory positions by both sexes and copulatory groove formation by males. Females often twisted violently immediately prior to cessation of copulation.

2. *Urosalpinx cinerea* completed copulation in a matter of minutes, but *E. caudata* often persisted intermittently for days, remaining in position all the while.

3. *Eupleura caudata* was apparently more promiscuous than *U. cinerea* but possibly this disparity may have been a function of a species different in frequency of a pairing, *i.e.*, if *E. caudata* normally pairs more often, its comparative incidence of promiscuity would naturally be greater. Or, it may also have been a function of the length of time that pairing consumes. For example, *E. caudata* pairing takes much longer than *U. cinerea* (12 to 20 hours vs. 3 to 4 minutes or up to 200 times longer); therefore, *U. cinerea* copulation would more easily be overlooked, resulting in a numerical bias in favor of *E. caudata* in any comparison of frequency of pairing.

4. Though *U. cinerea* paired at lower temperatures than *E. caudata* (8.2°C vs. 10.2°C), mating activities of both increased during April. *U. cinerea* ceased copulatory activity in June while *E. caudata* persisted through the first week in July before stopping temporarily. Both resumed mating activities in September which increased in October, diminished in November and ceased altogether in early December.

5. In our laboratory aquaria, *U. cinerea* copulated more frequently in the afternoon and evening while mating activities of *E. caudata* were more evenly distributed throughout the day.

6. Females of both species stored viable sperm in their seminal receptacles for periods of at least 6 to 9 months.

7. Several items of general biological interest, sperm nutrition and multiple paternity of embryos within a single egg case, etc., have been discussed.

Literature cited

Allen, J. Frances. 1958. Nautilus *72*:11-15.

Bushland, R. C., A. W. Lindquist and E. F. Knipling, 1955. Science *122*:287-288.

Crabbe, E. D. 1927. Biol. Bull. *53*:67-109.

Stauber, L. A. 1943. Ecological studies on the Oyster Drill, *Urosalpinx cinerea* in Delaware Bay, with notes on the associated drill, *Eupleura* and with special consideration of control methods, Unpubl. Typescript, Oyster Res. Lab., Rutgers Univ. New Brunswick, N. J.: 1-180.