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The Natural History of Necturus, IV. Reproduction

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Information on the life cycle of Necturus has accumulated slowly. Naturalists long were uncertain as to whether they had adult animals, since Mitchill's (1822) mistaken idea that they get to be two feet long was widely current. Lacépède (1807) believed that mudpuppies might be larval, and their adults unknown; Say (1818) that the mudpuppy was the larva of the hellbender. Barton (1807) confused the mudpuppy and the hellbender. Gray (1857) was ". . . inclined for the present to consider the Proteus of the Lakes as a distinct kind of Batrachian, which is arrested in its development, and never reaches the perfect state." Cope (1866) said, "The relation then between *Necturus* and *Spelerpes* is probably the same as that between *Siredon* and *Amblystoma* . . ."; and Kollman (1885) that the relation between Necturus and *Batrachosops* was the same as that between Axolotl and Amblystoma. Cox (1907) believed that members of the Proteidae undergo metamorphosis, ". . . the young being more or less unlike the adults." Necturus was described as ". . . a form arrested in development". Netting (1933) called Necturus the "Peter Pan" of salamanders, for it "never grows up".

The mudpuppies are so obviously larval in many of their features that they escaped notice as reproductive forms. Since it was not known whether the animals came on land, one did not know where

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to look for materials elucidating the life cycle. The secretive nature of the mudpuppies also retarded, understandably, accumulation of data on the animal's life-history.

Holbrook (1842) published the first note on the breeding habits of Necturus; April and May he found the time for spawning, and that a female could produce as many as 120 pea-sized eggs. Eycleshymer (1906) credited Professor O. Whitman with the first discovery of the nests and eggs *c.* 1888, in Lake Oconomowoc, Wisconsin.

The usual breeding season is in the fall. In September and October the animals begin to appear in shallow water (Kneeland 1857). The males may search out the females in a nest favored by her; or both males and females may congregate in numbers in suitable spots as the breeding season approaches. The males are ready to mate when they join the females; the cloaca appears inflamed, and the cloacal glands are swollen. Sometimes the females are not ready to mate as soon as the males; the length of time the animals stay together in the same retreat may thus, in part, be determined by the condition of the female.

A form of courtship may precede insemination. Bishop (1926) records the only observation of courtship as follows:

> . . . In the fall of 1922 or 1923, Paul A. Webb placed a pair of mudpuppies in a large aquarium. The male manifested considerable interest in the female and behaved somewhat after the manner of the male newt, *Triturus viridescens.* The female received the attentions, held herself erect by supporting the body on the hind legs and tail and made no attempt to escape. The male swam and crawled around the female and frequently passed over the tail and between the legs. This performance was continued for a considerable period. An actual venter to venter copulation was not observed nor were spermatophores noticed in the aquarium. Unfortunately no record was kept of the exact date of the occurrence. These observations indicate that courtship may be a mating procedure as in *Triturus* and others . . .

Fertilization is internal. Von Siebold (1858) recognized and described a receptaculum seminis in female *Salamandra atra* and *Triton taeniatus.* Robin (1874) showed that internal fertilization is usual for many urodeles, and that the male axolotl produces a spermatophore. Spermatozoa were discovered in the reproductive tracts of female mudpuppies by Kingsbury (1895), Pearse (1921), Dawson (1922), Dunn (1923), before it was known that spermatophores are produced.

As early as 1857 Kneeland observed the occasional deposition of clear gelatinous masses by his mudpuppies, but did not recognize them as spermatophores, which they undoubtedly were. Kingsbury (1895) suggested by homology with other urodeles that the male Necturus probably produces a spermatophore. Dawson (1822) studied the histology of the cloacal glands of male Necturus, and suggested a method by which its various glandular components might enter into spermatophore formation.

In October, 1930, Bishop found sperm masses in the vents of some females. A year later (October 12, 1931) he obtained several more specimens, and separated the sexes. The males were given daily injections of 2 cc. alkaline aqueous extract of whole pituitary (Parke-Davis). The first spermatophore was deposited on the third day; several additional spermatophores were obtained on following days.

Bishop's (1932) description follows: "The spermatophore consists of a gelatinous basal part supporting an apical milky-white mass. These parts are enclosed within a thin tube of clear jelly which becomes more tenuous where it passes over the sperm mass and continues from either end as a slender string. The continuation of the tube at the apical end of the spermatophore is at one side. The gelatinous basal part may be oval in outline or distinctly vase-shaped and there is no suggestion of a broad base for attachment as in the spermatophores of *Amblystoma maculatun, Triturus viridescens* and others. The terminal portion containing the spermatozoa is frequently whorled in two or more turns. A characteristic feature is the presence, in the basal part, of many hexagonal crystals, apparently carbonate of lime.

"The tube-like envelope which surrounds the spermatophores and which with a small amount of enclosed jelly forms the connection between spermatophores deposited in strings, suggests the sperm strings of *Cryptobranchus*. It may also indicate that the spermatophores of *Necturus* are normally produced in strings and that when dropped singly they have simply been pinched off by the vent. The lack of a broad base for attachment also suggests the possibility of direct transfer of the sperm mass to the female in a venter to venter copulation. The discovery of spermatophores of *Necturus*, deposited under natural conditions and without stimulation, will determine whether or not those described above are typical of the species.

"Single spermatophores vary in length from 10 to 12 mm. and in diameter, across the widest part of the apical portion, from 6 to 8 mm."

The spermatophores lack any sort of attachment base. It is possible, but not likely, that they are transferred directly to the female (Bishop 1932, 1941). Though the exact method by which the spermatophore gets into the female cloaca is unknown, it is probable that it is deposited in the water by the male, and is picked up by the female.

It is obvious that the success of the spermatophore method of insemination requires proximity of the female. In some urodeles specialized skin glands produce secretions that either serve to keep the attention of the female, or make it possible for the male to recognize the female (Noble 1931). Dawson (1920) failed to find such specialized integumentary glands in Necturus, and suggested (1922) that the male abdominal glands (a component of the large cloacal glands) may produce a chemical substance attractive to female Necturus.

The usual time for insemination is in the fall. Evidence supporting this is gained from many sources. Males taken in the fall often have a clear gelatinous mass filling the vent (Bishop 1926). Both sexes in the fall have the cloaca developed as for reproduction; the cloaca of the male is swollen by the enlarged cloacal glands. At this season males and females are together in shallow water. Sperm have been found in the reproductive tracts of the females in the fall (Kingsbury 1895, Bishop 1941). In the spring male and female cloacas do not show evidence of reproductive readiness (Pearse 1921; Bishop 1926). Males are seldom seen in the spring when the female is on the spawning ground (Pearse 1921; Bishop 1926, 1941). Sperm received by the female in the fall are held in recesses of the cloacal gland ("spermatheca", Kingsbury 1895), and impregnate eggs as they are laid in the spring (Pearse 1921).

In spite of the evidence presented above, the breeding season may not be limited to the fall. Pearse (1921) reported that male Necturus caught in Wisconsin before the lakes froze over, had swollen white testes, but no sperm could be stripped from them, nor did they show white "milt" when cut. Also, the swollen condition of the male cloaca may be retained for several months. Bishop (1941) reported that on April 28, 1932, he caught 3 females and 1 male beneath a single flat stone; the male cloaca and cloacal glands were as developed as they normally are during the fall breeding season—an observation that he repeated on February 4, 1933.

Ovulation occurs in the spring in April, May, and June (Maximilian 1865, Milner 1874, Garnier 1888, Hurter 1893, Virchow 1894, and many others). The time varies in different lakes and streams, depending on when the water temperature becomes warm enough (Eycleshymer 1906). Larger, deeper lakes therefore have a later season than smaller, shallower lakes with much shoal. Ovulation takes place earliest in the southern part of the mudpuppies' range, and in waters that warm faster (Bishop 1926). He also observed ovulation when the water temperature reached 74-78° F., near the surface in shallow streams in Pennsylvania; the temperature in the nests proper was probably a few degrees lower.

Before egg-laying the Necturus (females only, Pearse, 1921) seek the sandy shoals of lakes or streams. They prefer areas strewn with logs, boards, or flat stones, beneath which they can build nests. They probably move to these nesting grounds at night, since they are seldom seen moving about during the day. It is not yet reported when the Necturus of sluggish streams (such as *N. punctatus and N. lewisi*) spawn.

The nests are always well concealed, and consist of a slight excavation beneath some object, with a narrow opening through which the head of the animal may protrude. Clean logs or boards which lie partially imbedded in the sand are given preference as nesting sites according to Eycleshymer (1906); large flat stones, 1½ to 2 feet in diameter are preferred, according to Pearse (1921) and Smith (1911); almost any convenient cover-object may be used. Eycleshymer found nests under pieces of tin cans, canvas, an old hat. Nests may be closely spaced, not more than a foot apart; in one instance, 10 nests were found beneath a 12-foot board (Eycleshymer 1906).

The nests are usually placed in shoal waters. While Eycleshymer (1906) found nests in lakes in water only four inches deep, and others in water 10 feet deep, most of the nests lay at a depth of

2 to 4 feet. Smith (1911) found nests in water 3 to 5 feet deep, and 50 to 100 feet from the shore.

Nests of stream-dwelling Necturus are much like those of lake-dwelling forms. A flat object is preferred as cover; there is usually some evidence of excavation beneath it. The nests are not found in the fastest water, nor are they found beneath stones that the current sweeps under. The nest-site usually has the up-stream side of the cover imbedded in the bottom with its opening on the down-stream side; this prevents debris from filling the nest. The nests are in water varying from a few inches in depth to two feet or more (Bishop 1941). Bishop (1941) never found nests in very small streams, but preferably in rather broad, shallow streams that had stretches of bed rock alternating with deeper pools and riffles.

The female ordinarily stays in the nest; she is usually alone during the egg-laying and incubation period (Pearse 1921; Bishop 1941). Males are seldom seen during the nesting season; indeed, Eycleshymer (1906) never found males on the nest with the female. This "brooding" action of the female has been interpreted as guarding the eggs (Eycleshymer 1906) or as brooding the eggs (Bishop 1926); but it may be nothing more than evidence of her unwillingness to leave a favorite retreat (Noble 1931). The female has been described as a faithful, jealous guard, fighting off any intruder that tries to enter the nest, but the weight of evidence indicates that she is not much concerned with nidamental security. *Crypotobranchus* may be in the nest also, eating *Necturus* eggs; on occasion, Necturus returns the favor and is found in *Cryptobranchus* nests, eating *Cryptobranchus* eggs. Female Necturus are often found gorged with eggs, perhaps their own, perhaps robbed from other mudpuppy nests (Fulleborn 1894). Any brooding activity on the part of Necturus is probably incidental; her back may occasionally brush the eggs as they hang from the protecting object, but there is no evidence of special care. Dunn (1923), on the other hand, believed that the eggs are laid and then abandoned.

OVIPOSITION

The eggs are found attached to the under surface of the sheltering object which covers the nest. Palmer (1949) is apparently in error when he says the eggs may be deposited in a "sunlit sandy nest". The female turns her body upsidedown so that the eggs can be deposited. How this is accomplished was reported by Bishop (1926). A female ". . . discovered in the act of laying her eggs, was transported to the laboratory where the process was continued. A large flat stone supported on smaller stones provided a suitable 'nest'. The female turned herself upside down and supported her body with the toes of the front feet resting against the edge of the stone. This position she maintained for hours and deposited about a dozen eggs in the course of a day. The position assumed by this female is exactly that which might be expected in view of the disposition of the eggs; and it is no doubt the position taken by *Eurycea bislineata, Pseudotriton ruber, Gyrinophilus danielsi* and others which attach the eggs to the lower surface of a support in water." Noble (1931) suggests that the habit of laying eggs on the under surface of rocks etc., may indicate that the Proteidae arose in mountain brooks.

The eggs are attached by the outermost of the three membranes which cover them. They are attached singly, and may be scattered over an area six to twelve inches in diameter (Eycleshymer 1906; Bishop 1926, 1941).

The period of egg-laying may be brief. Virchow (1894) suggested that all the animals in an area spawn nearly simultaneously. Smith (1911) found all the eggs in a nest and all the nests in a restricted area to be in about the same stage of development—a view which Bishop (1926) also adopted. Bishop found that eggs are deposited in shallow stream habitats over a very brief period of time. (Cautiously, Bishop notes that Paul A. Webb transferred an ovipositing female from warm stream water to tap-water at 62 - 66° F. In this colder water the female Necturus took an entire day to deposit about a dozen eggs. This indicates a longer ovulation period for colder, deeper waters.) Eycleshymer (1906) found that in lake-forms the ovulation period covers many hours, or even days. In several cases he removed all the eggs from a nest, and next day found freshly deposited eggs. Both early and late cleavage stages may be found in the oviducts of females several days after the onset of oviposition. If the nest is disturbed, the female may eat her own eggs; Eycleshymer (1906) in several instances found females whose stomachs were gorged with eggs and assumed they had eaten their own spawn because of such disturbance. There is some evidence that more than one female may spawn in a single nest (Lagler and Goellner 1941).

The numbers of eggs reported found in nests have ranged from as few as 18 to as many as 180. Lake-located nests generally show fewer eggs than stream-located nests (Bishop 1941). Sixty-two eggs were found in a lake-nest in Wisconsin (Eycleshymer 1906). In 5 lake nests Smith (1911) found 18, 61, 80, 84, and 87 eggs—an average of 66 eggs per nest. Eggs numbering 87, 96, 140—an average of 107—were found in stream-nests in Pennsylvania; one such in New York had 125 eggs (Bishop 1941). Bishop (1941) also reports egg counts ranging from 90 to 180, and suggests that the higher number probably represents the egg production of two females.

Holbrook (1842) found on dissection 120 eggs in the ovaries of one female. Lagler and Goellner (1941) made a count of the numbers of eggs in the ovaries of 25 females just prior to the spawning season; they ranged in numbers from 75 to 193, with an average number of 122. Possibly this average figure represents the fecundity of lake Necturus better than does a count of the eggs in nests, since guardian females are known to eat some of the eggs; it is also possible that more than one female may spawn in a nest.

The egg proper is white, pale cream or yellow in color. Smith (1912) believes lack of color is due to the fact that the eggs are laid in dark places. On occasion the eggs may have a green tinge (Eycleshymer 1906). Immediately surrounding the egg is a thin, tough and elastic membrane that encloses a jelly-like substance that is sometimes milky in appearance. A second coat is also thin, but clear. The third membrane is thicker, jelly-like, and very elastic (B. G. Smith, 1912; Bishop 1926, 1941); the egg is attached by this outer membrane, which forms a sort of attachment disc. The weight of the egg suspended in water pulls the outer membrane into a short stalk, producing a slight constriction below the attachment disc; and when the object to which the eggs are attached is taken out of water, this membrane stretches into a longer, more slender stalk (Bishop 1926). Many lamellae were observed in the inner and middle membranes by Smith (1912).

The ova are 5-6 mm. in diameter. The diameter of the inner membrane is 7 mm.; of the middle membrane, 8 mm. The short diameter of the outer membrane is 11 mm., and the long diameter, as the egg hangs naturally in water, is 14 mm. (Bishop 1926). There may be variations in the thickness of the membranes*; the middle membrane reported by Smith (1912) is thicker and denser than in Bishop's specimens. The dense inner layer is often very thin, and fits so closely as to be difficult to distinguish; thus Fulleborn (1894) apparently missed this inner layer entirely, for he described only two membrane layers.

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* Hypochlorite of sodium is an excellent solvent for the jelly around the egg of Necturus. Eggs are first hardened by heating or preservation; then placed in hypochlorite of sodium (10% solution diluted with 5 or 6 times its volume of water) until the jelly membranes are so far dissolved that they can be shaken free. About five minutes' treatment suffices to dissolve the membranes (Whitman, 1888).

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Note to Librarians:

The Journal, *Field & Laboratory* (vols. I—XXVII, 1932-59), changed its title to that of the present Journal in April, 1960, and was numbered "XXVIII,,' with the double-title. This volume was completed with the single issue, No. 1. It is our hope to continue the journal with four issues to the volume, to appear in January, April, July, and October.

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