The Natural History of Necturus: III. Food and Feeding

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Necturus normally forage at night, when they leave their favored hiding places and move slowly over the bottom seeking food. Slow, undulating movements of the tail propel them; the legs seem scarcely used.

Movements of other "denizens of the deep" produce vibrations which are received by the lateral line organs; this "radar" orients the mudpuppy toward possible food. Their approach to possible food is cautious.* If lateral line stimulation is reinforced by proper olfactory or optic stimulus, a snapping response is finally produced (Whitman 1899).† Of course, if the lateral line stimulation is too strong, or if the stimulus received from (by) nares and eyes is "out of order," the Necturus beats a retreat, or does not bite. Because Necturus instinctively makes a deliberate approach before the final attack, it is very successful in capturing food. Its chain of responses serve it as well as intelligence might.

Although the eyes of Necturus are poorly developed, and at night are probably useless in the search for food, lack of keen vision is no handicap.

Large nasal passages are present, and are fitted out with an internal choanal valve which makes it possible for Necturus to "sniff" water. Intaken water passes out through the gill slits; the choanal valve prevents water leaving the mouth through the narial passages (Bruner 1914). The entire skin is plentifully studded with sensory endings (Sayle 1916) which bring to these animals a marvellous array of sensation. A general cutaneous sense is difficult to appreciate—but just imagine the kaleidoscopic sensations a mudpuppy must receive as it thrusts about in the water, directed by the common chemical sense of the entire body surface!

Internal stimulus may also affect the food-seeking habits. Stomach contractions possibly are continuous in Necturus as

* Copeland (1913) using *Diemyctalus viridescens* (Rafinesque) and Kunz & Zozaya (1923) using *Ambystoma tigrinum* (Green) described an approach to food involving an "approaching", a "nosing" and a "seizing" reaction. The "approaching" reaction is usually a response to sight stimulus; it may be followed by the "seizing" reaction. The "nosing" and "seizing" reactions are usually produced by olfactory stimulus. Moving objects are detected more readily than non-moving. By its sense of smell the animal can detect foods not seen; and edible and inedible are discriminated by it.

† The complete bibliography will be printed following the last paper of this series.

they are in the frog (Patterson 1921). Hunger-contractions of the frog stomach are inhibited at temperatures below 13° and above 35°C. (Patterson 1921; Noble 1931). What effect temperature changes have upon the stomach contractions of Necturus, I cannot say; this is an interesting problem in view of the indication that Necturus estivates but does not hibernate.

The act of feeding was described by Kneeland (1858) as follows:

> They seize living worms eagerly, and suck them down, if small, with a single swallow; if the worm is large, it is swallowed by repeated suctions, the teeth preventing its escape; the act of the suction may be seen by the movement of impurities in the water as it is drawn in and afterward expelled. They often miss the worm; sometimes it may be too far off, but at others so close to them that it seems as if their vision must be imperfect. They will not eat a dead worm unless they have been kept without food for a considerable time.

The mudpuppies are essentially carnivorous and rapacious; almost any kind of animal matter which they can find will serve as food. They probably feed consistently on the bottom, though they have been reported caught on shallow-set hooks. Plant remains are sometimes found in stomachs in such quantity that it is obvious they were intentionally ingested. Hamilton (1932) tells of finding one group of Necturus in which stones were so abundant in the stomachs that they must been intentionally swallowed.

The size-range of foodstuff swallowed is great. *Daphnia* ephippia are on occasion so plentiful as to preclude the possibility they were accidentally included (Pearse 1921). Small forms may be pursued separately (Hamilton 1932). Or, the object swallowed may be two-thirds as large as the swallower (Hurter 1893; Willey 1918). Cannibalism is probably common; the instances just cited involved the swallowing of another Necturus over a period of more than 24 hours. Adults eagerly eat larvae of their own and other species of salamanders (Bennett 1937; Hamilton 1932), as well as eggs of its own species, sometimes even their own spawn! (Eycleshymer 1906).

An accusing finger has been pointed at Necturus, charging them with eating the eggs of various fish. They were first so charged by Milner in 1874:

> The lizards (*sic*) were so gorged with white-fish spawn that when they were thrown on the shore, hundreds of eggs would fly out of their mouths. . . . Some of the larger lizards would devour the whole

spawning of a white-fish in a day or two; and when we consider that these reptiles are feeding upon eggs from November till April, some idea may be formed of their vast capacity for destruction.

Evermann & Clark (1920) cited the removal of 288 whitefish eggs and four cisco eggs from the stomach of a mudpuppy captured at Put-in-Bay in 1897, and said that many other specimens contained fish eggs. Pearse (1921) accused mudpuppies of following whitefish and perch to their spawning grounds to get their eggs. But in his tabulation of data Pearse shows perch eggs making up only 1% of the food found in one animal. Bishop (1926) states that ". . . its habit of eating eggs marks it as an enemy of certain fishes." Over (1923), Abbott (1934), Palmer (1947) all include fish eggs as part of the diet of the mudpuppy. However, Bennett (1937) could not induce his five Necturus to eat the eggs of whitefish or perch, no matter how hungry they were! Somewhat charitably, Abbott (1934) suggests its destruction of the eggs of the hellbender compensates for the eating of fish eggs. Lagler & Goellner (1939) neither convict nor exonerate Necturus in the matter of eating fish eggs. They thought the mudpuppies are more important indirectly as competitors for food than as predators of small fish. Bishop (1941) said Necturus takes the same type of food used by some game fishes, and must reduce the available supply. The abundance of food present, as well as the extent to which the larvae of Necturus are eaten by fish, need to be known before the significance of the competition for food can be judged.

A wide variety of food-stuffs have been found in the stomachs. There is little evidence of selectivity in the diet. Crustaceans, larvae of insects, and annelida, make up the bulk of the diet. As many as 10 nymphs of Odonata, or more than 200 mayfly nymphs, or 49 annelids have been reported found in single stomachs. These animals that are eaten are secretive in habit, as are the Necturus. Probably similar habitat preference accounts for their abundant inclusion in the diet, rather than any selectivity on the part of the mudpuppy. Evermann & Clark (1920) reported finding in one stomach, 7 large and 1 small *Labidesthes sicculus* (skipjack), 2 bluegills (1 and 2 inches long, respectively), one small fish not identifiable, one worm and a small quantity of vegetation. What an appetite for a 12½ inch mudpuppy! Percentage frequency of occurrence of various items in the diet as shown in Table I.

The list of food-stuffs found in the stomachs (Table II) fur-

TABLE I. FOOD OF NECTURUS

	Percentage Composition of Food, by Volume			*Percentage Frequency of Occurrence*
Fishes	12.5	13.2	13.2	22.0
Amphibians	---- --	4.1	0.2	1.0 (frog)
Turtles	---- --	---- --	0.5	1.9
Insects	17.2	30.1	49.3	92.4
Crustaceans	39.1	32.7	13.9	30.5
Annelids	2.0	11.0	20.0	34.3
Gastropods	7.1	5.2	3.3	22.0
Sticks & debris	5.0	---- --	---- --	---- --
Water plants	17.9	trace	---- --	---- --
Inorganic material	---- --	3.3	---- --	---- --
Specimens examined	33	500	107	107
Specimens with food	24	340	105	105
Place of collection	Madison, Wisconsin	Eastern U.S.	Lenawee Co., Michigan	Lenawee Co., Michigan
Source of data	Pearse 1921	Hamilton 1932	Lagler & Goellner 1941	Lagler & Goellner 1941

ther illustrates the absence of selectivity in the diet, other than that imposed by habitat restrictions. It is a little surprising to find honey bees and adult hemiptera, and perhaps just as surprising to find no clams. Howard (1951) suggested that the mudpuppies become infected with the glochidia of *Simpsoniconcha ambigua* when they eat the adult gravid clam.

Captured animals readily regurgitate quantities of ingested matter, such as bones of frogs, larger fish scales, and other indigestible materials.

Though the Necturus are rapacious feeders, they can live for months without food. Survival of Necturus for 16 months without food was reported by Smallwood & Rogers (1911); their animals decreased both in weight and size. Three of my specimens lived 20 months, and a fourth lived 24½ months, without food. Long as this time seems, there is a record of a *Proteus anguinus* Laur. surviving 8 years without food (de Kerrville 1926). Hunger may produce cannibalism (Willey 1918).

Feces are discharged as granular deposits (Gibbes 1853) encased in slimy capsules. Dawson (1930) aptly described them as pellets of meconium-like material, light brown in color, which soon disintegrate in the water. Such granular deposits are often noted in the water after uncommon activity; Kneeland (1858) suggested that the body contortions facilitate discharge of the excrement.

A number of species of salamanders are a source of colon-bacillus contamination in spring water (Hassler 1932; Kline & Fuller 1932). Laboratory tests on such waters would suggest

TABLE II. FOOD-STUFFS FOUND IN STOMACH OF NECTURUS

[Numbers in parentheses after each organism named refer to sources of data, as follows: (1) Lagler & Goellner 1941; (2) Pearse 1921; (3) Hamilton 1932; (4) Evermann & Clark 1920; (5) Abbott 1934; (6) Allyn & Shockley 1939; (7) Barton 1807; (8) Bennett 1937; (9) Bishop 1926; (10) Eycleshymer 1906; (11) Fowler 1900; (12) Harlan 1835; (13) Hay 1891; (14) Hurter 1893; (15) Hurter 1911; (16) James 1823; (17) Kneeland 1857; (18) Lagler and Goellner; (19) Maximilian 1865; (20) Milner 1874; (21) Surface 1913; (22) Willey 1918.]

Annelida
  Oligochaeta
    Aquatic oligochaetes (3)
    Oligochaete earthworms (1)
    "Earthworms" (1, 3, 10, 12, 16, 17, 18, 21)
  Hirudinea
    Herpobdella punctata (2)
    Nephelopsis obscura (2)
    Leeches, unidentified (1, 4)
Mollusca
  Gastropoda
    Physa heterostropha (2)
    Lymnaea (1, 3)
    Physa (1, 4)
    Planorbula (1)
    Zonitoides (1)
    Gyraulus (1)
    Valvata (1)
    Succinea (1)
    Snails, unidentified (19)
    Mollusks, unidentified (6, 13)
    Planorbis (3)
Arthropoda
  Crustacea
    Subclass Branchiopoda
      Order Cladocera
        Chydorus (2)
        Daphnia ephippia (2)
    Subclass Ostracoda
        Unidentified ostracods (2)
    Subclass Malacostraca
      Order Isopoda
        Porcellionidae (1)
        Asellus (4)
        "Sowbugs" (21)
      Order Amphipoda
        Gammarus (3)
        Hyallela sp. (3)
        Hyallela knickerbockeri (1)
        Dikerogammarus (2)
        Gammarus (4)
      Order Decapoda
        Cambarus propinquus (1, 2)
        Cambarus sp. (3)
        Crayfishes, unidentified (2, 4, 21)
  Insecta
    Sialidae (3)
    Ephemerida
      Stenonema tripunctatum (Banks) (1)
      Blasturus nebulosus (Walker) (1)
      Ephemera sp. (1)
      Ephemerella sp. (1)
      Hexagenia (3)
      Unidentified nymphs (2)
    Odonata
      Dragonflies
        Gomphus (1)
        Enallagma (1)
        Celithemis (1)
        Sympetrum (1)
        Tetragoneuria (1)
        Unidentified nymphs (2, 3, 4)
      Damselflies
        Amphiagrion (1)
        Ischnura (1)
        Unidentified nymphs (2)
    Hemiptera
      Benacus (1)
      Pelocoris (1)
      Belostoma (3)
    Coleoptera
      Adult Dytiscid (1)
      Adult Berosus sp. (1)
      Larval Dytiscus (3)
      Larval Haliplus (3)
      Unidentified larvae (1)
    Trichoptera
      Leptoceridae (1)
      Limnephilidae (1)
      Limnophilus (3)
      Phryganea larvae (2)
      Leptocella (Leptocerus?). uvarowii larv. (2)
      Leptocerus dilutus larvae (2)
      Unidentified nymphs (2)
    Lepidoptera
      1 larva, in case (1)
    Diptera
      Tipula (1)
      Stratiomyia (1)
      Chironominae (1)
      Chironomid larvae (2, 3)
      Tipulid larvae (3)
    Hymenoptera
      Apis mellifica (1)
    Unidentified insects (21)
    Unidentified insect larvae (2, 4, 15)
  Arachnida
    Spiders (21)
Chordata
  Pisces
    Lepomis incisor (2)
    Lepomis macrochirus (Ref.) (1)
    Lepomis gibbosus (Linn.) (1)

Unidentified Centrarchidae (1, 11)
Poecilichthys exilis Girard (1)
Notropis heterodon (Cope) (1)
Umbra pygmaea (11)
Sculpins (3)
Hybopsis (3)
Hyborhynchus (3)
Black-nosed dace (3)
Labidesthes sicculus (4)
Notropis blennius (4)
Fundulus diaphanus (4)
"2 or 3 spp. of bait minnows" (4)
Blue gills (4)
Unidentified minnows (17)
Unidentified small fish (19)
Unidentified fish remains (2)
Whitefish eggs (4, 20)
Cisco eggs (4)
Perch eggs (2)
Amphibia
Larvae of Ambystoma (8)
Larvae of Necturus (8)
Smaller salamanders (6, 14, 22)
Newt (3)
Desmognathus (3)
Eurycea b. bislineata (3)
Eggs of Hellbender (3, 9)
Cast skins of Necturus (3)
Small frogs (1, 2)
Tadpoles (11)
Reptilia
Sternotherus odoratus (Lat.) (1)
Plants
Water plants (2, 4)
Plant detritus (1)
Sticks (2)
Sand (1)
Sedimentary debris (2)
Stones (3)
Rotten wood (4)
Algae (3)
"Offal of various kinds" (7)

condemnation, even though the supply was otherwise unpolluted. To date, Necturus has not been implicated in these studies.

Poison glands in the skin are said to produce a bitter secretion that makes Necturus distasteful to many animals that might feed on them (Pearse 1917; Hegner 1935). The poison is not injurious to man, and probably serves as a protection because it is distasteful to animals which normally eat salamanders (Hegner 1935). Whether this is true or not, there are only a few records of Necturus being eaten by other animals. Kneeland (1858) found a Necturus that had been partially swallowed by a water snake and disgorged. Bishop (1926) suggested that herons and crows which frequent the shallow water "may be expected to take the smaller individuals when opportunity offers". The Great Blue Heron eats some Necturus on occasion (Karl F. Lagler—personal communication), as does the common watersnake *Natrix s. sipedon* (Lagler & Salyer 1947), and the otter *Lutra c. canadensis* (Lagler & Ostenson 1945). Necturus eggs are sometimes eaten by *Cryptobranchus* (Noble 1926); and it is suggested (Alexander 1927) that the hellbender may on occasion eat mudpuppies.

The secretive habits of Necturus may explain their rare incidence in the diet of other animals; indeed, these habits may allow them to survive when other amphibia disappear. (For example, at Wintergreen Lake, which is a part of a waterfowl sanctuary in Kalamazoo County, Michigan, there is a large population of waterfowl most of the year. Necturus seems to be the only salamander present in the lake, and is abundant; there are no *Rana palustris,* and very few bullfrogs (Allen 1937).

Cannibalism may account for the loss of more Necturus than predation by other animals. Older Necturus sometimes become addicted to the habit of egg-eating (Bishop 1926, and others). Hurter (1893) reported the attempt of a 14-inch Necturus to swallow a 10-inch one; both died in the process. As shown above, Willey (1918) reported a case in which a "larger" Necturus succeeded in swallowing a "smaller" one; but the swallowing required more than 24 hours.

Men of Science in Texas, 1820-1880: IV

S. W. Geiser

(Continued from page 96)

KER, Henry (*c.* 1785-?) I have included Henry Ker's name among naturalists and explorers of early Texas, although profoundly dubious of the veracity of his account of the ascent of the Red River. *Appleton's Cyclopaedia of American Biography* (not the best authority in biographical matters as Dr. J. H. Barnhart has beautifully shown in *Jour. N.Y. Botan. Garden, 20,* 1919, 171-81), says that Ker was a traveller, born in Boston, Mass., about 1785; had schooling in London; that he travelled throughout the Southern United States after 1808; and about 1810 went up the Red River. Here he found a tribe of Indians whose language and customs caused him to believe them of Welsh ancestry. His book, *Travels throughout the United States and Mexico* (Elizabethton, N.J., 1816, several times reprinted) seems to me to be a colossal aggregation of pure hokum; and Sabin and *LCC* hold the same opinion. ... Dr. William Baldwin, the botanist, in a letter to Aylmer B. Lambert, F.L.S., F.R.S. [patron of Frederick Pursh], dated September 2, 1817, mentions having seen Ker in Savannah, in June, 1817; and that Ker "delivered your message [on botanical matters], expressed the pleasure he had in your company, and requested me to inform you that I had seen him, and to present his best respects. ..." *Biographical materials: ACAB.*

KERBER, Charles (*d. post* 1921) The *Special Report no. 36,* 1881, of the U.S. Department of Agriculture includes observations by Kerber on grape-growing and wine-making in El Paso County. Here he was sheriff during the years ...1874-78..., and was mayor of Isleta, in that county, in 1889. His last recorded deed in the El Paso County courthouse is dated Sept. 13, 1921. Nothing further is at hand regarding him.

KERN, Edward M. (........-........) Naturalist; he accompanied Capt. J. C. Frémont (1845-6) in his explorations of the Far West. In 1849 he made natural-history collections while with Lieut. J. H.