AMERICAN MUSEUM NOVITATES

Published by
Number 1224 THE AMERICAN MUSEUM OF NATURAL HISTORY April 8, 1943
New York City

THE SEXUAL BEHAVIOR OF ANURA

5. OVIPOSITION IN THE GREEN FROG, *RANA CLAMITANS*, AND THE BULL FROG, *RANA CATESBEIANA*[1, 2]

BY LESTER R. ARONSON

The mechanism whereby certain species of frogs of the genus *Rana* deposit their eggs as a surface film has not been adequately described. Only brief accounts of the oviposition of *Rana clamitans* have been published by Wright (1914) and Noble and Aronson (1942). No description of the oviposition of *Rana catesbeiana* is available in the literature.

The green frogs used for this investigation were collected in the vicinity of Middle Village, Long Island, and Liberty, New York. The bull frogs were collected at Pine Plains, New York. The description of the oviposition of *Rana clamitans* is based upon over ten spawnings, but only one complete oviposition of *Rana catesbeiana* was seen.

OVIPOSITION OF *RANA CLAMITANS*

Most male green frogs brought into the laboratory just prior to the breeding season readily clasped females. Many clasped spontaneously, while in the use of others it was necessary to place the female underneath the male. Even males kept in the laboratory over the winter from the previous breeding season often clasped when females were placed underneath them. This was in striking contrast to *Rana pipiens* in which about 65 per cent of the males rapidly lost their sexual activity when kept in captivity only a short time (Noble and Aronson, 1942).

It is of special interest to note that amplexus was induced most readily in the green frog by holding the female by her hind limbs and guiding her body underneath the forelimbs of a floating male. With *Rana pipiens*, on the other hand, it was more effective to hold the male by his hind limbs, lift him out of the water and lower him gently over the back of the female.

Most of the females required injections of two to four homoplastic pituitaries before they ovulated. The test for ovulation was similar to that described in previous experiments with *Rana pipiens* (Noble and Aronson, 1942).

The egg-layings took place in 15 gallon aquaria, 36 cm. × 45 cm. × 34 cm. containing water from 5 to 25 cm. in depth at 23° C. Regardless of the height of the water, the spawnings always took place just below the surface.

Amplexus (Fig. 1) was axillo-pectoral (halfway between axillary and pectoral). The thumbs of the male were pressed into the lateral body wall of the female. They did not extend to the ventral pectoral region as in *Rana pipiens*. Wright (1914) noted in some of his pairs that the clasp was more axillary or of the *Hyla* type rather than pectoral or of the *Rana* type. Wright's photographs (1914, Pl. IV, figs. 3, 4 and 6) illustrate clearly the difference between the typical pectoral clasp of *Rana pipiens* and the axillo-pectoral clasp of *Rana clamitans*. The mode of amplexus

[1] This study was supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

[2] The author wishes to acknowledge the assistance of Miss Arline Douglis in making the observations and expresses his appreciation to Dr. Frank A. Beach for reading and criticizing the manuscript. Figs. 1–4 were drawn by Miss Margaret Sorensen and Fig. 5 by Mr. Richmond E. Lawlor.

which Wright (1914) labels as "partly pectoral-like" was found to be most typical for the species. The cross-embraces between male green frogs and female leopard frogs (Noble and Aronson, 1942) were axillo-pectoral.

Backward shuffling which was so outstanding in the pre-oviposition activity of *Rana pipiens* and *Rana septentrionalis* (Aronson, 1943) was absent in *Rana clamitans*. A slight increase in activity on the part of the female green frog was the only indication that the spawning was about to start. As in the case of *pipiens* the oviposition posture of the pair was sometimes assumed several times before the egg-laying actually began.

In assuming the spawning posture (Fig. 2), the female lowered her head (often below the surface of the water), arched her back concavely, raised her cloaca just above the surface of the water, and extended her hind limbs caudo-ventrally and laterad. Immediately following this change in posture of the female, the male slid forward on the back of the female until the center of his tympanum was on a vertical line with the tip of the female's mouth. This movement caused the male's forelimbs to become fully extended, and the clasp now appeared to be supra-axillary. At the same time the male rotated his hind limbs upward so that his thighs now extended laterally, forming a 60° angle with the longitudinal body axis. The shanks of his hind limbs were dorsal to his thighs and were directed medially at about the same angle. The ankles pointed caudally and the toes were directed caudo-laterad. The cloacal aperture of the male was situated about 3 mm. anterior to the cloaca of the female.

The female appeared to start the oviposition by an abdominal contraction and an increase in the concave arch of her back. There occurred almost simultaneously an abdominal contraction and upstroke of the male (Fig. 3). This stroke consisted of an anterior movement of the shank of the hind limbs, rotating at the knees, which carried the male's feet anteriorly, first past the female's cloaca and then past the male's. The ankles approached within 2 or 3 mm. of each other, as the heels touched (or almost touched) along the midline. The toes now pointed caudally, slightly laterad and nearly touched the male's cloaca.

Fig. 1. Typical amplexus of *Rana clamitans;* lateral view.

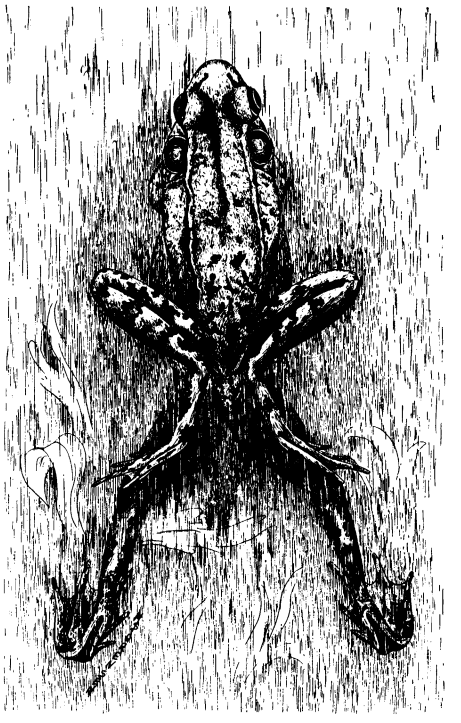

Fig. 2. Egg-laying posture of *Rana clamitans* just prior to the onset of the oviposition; dorsal view.[1]

Almost immediately a batch of from thirty to fifty eggs was extruded from the female's cloaca. They spread out between the ankles and feet of the male, and many came in contact with the male's cloaca. It may be presumed that the sperm were emitted at this time although no seminal fluid was visible.

The male's downstroke which followed at once (Fig. 4) was characterized by a caudal movement of the shanks of the hind limbs of approximately 10 mm. rotating again at the knees. Simultaneously, the toes pushed laterad about 15 mm. rotating mostly at the ankles and heels, and tending to push the egg mass away from the female's cloaca.

The female's abdominal muscles contracted again, the male started the upstroke, and the process was repeated continuously until all the eggs were laid. It was a rhythmical movement, one cycle of activity following immediately after the previous one. Occasionally the process ceased for a few minutes in the midst of the oviposition, and at this time the female often shifted her position.

Pushed from the female's cloaca onto the surface of the water by the action of the male, the eggs floated off, forming the characteristic surface film. Interruptions in the oviposition as described above caused the film to break.

The duration of the oviposition, calculated as the length of time the pair remained in the egg-laying posture, was recorded in four cases. They were 25 min., 10 min., 15 min. and 10 min. In each of these cases, the male released immediately following the female's movement out of the oviposition posture.

As in *pipiens*, the females did not regain

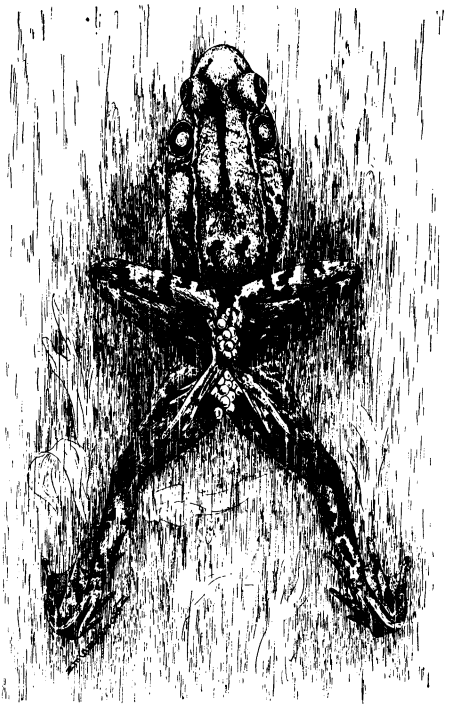

Fig. 3. Upstroke of the male *Rana clamitans* and the appearance of the first batch of eggs; dorsal view.

[1] Figs. 2–4 were drawn from sketches made during the egg-layings. Fig. 5 was copied from a flashlight photograph of the oviposition.

their warning croak until the following day. The males would often reclasp thin silent females for several hours. On the other hand, sexually active males seldom retained a clasp on fat croaking females for more than a few minutes. Males never retained a clasp on other croaking males for more than a few seconds. These observations suggested that the mechanisms of sex recognition and release of the female after oviposition were similar to that previously described for *Rana pipiens* (Noble and Aronson, 1942).

Sex recognition was found in *Rana pipiens* to depend upon the warning croak and girth of the frog being clasped; a loud croak plus a small girth caused the male to release his clasp, while a large girth and no warning croak caused retention of the clasp. Release of the female at the termination of the oviposition was found to depend upon a number of factors including: (1) the ejaculations of the male, (2) reduction in girth of the female, (3) cessation of the female abdominal contractions and (4) movement of the female from the egg-laying posture.

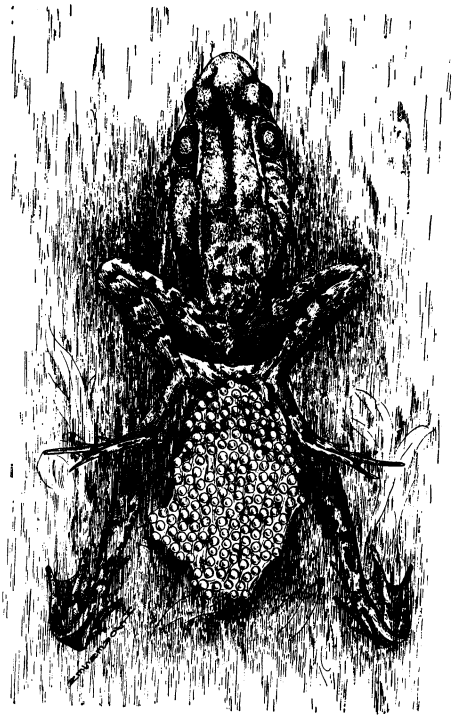

Fig. 4. Downstroke of the male *Rana clamitans* and the formation of the surface film; dorsal view.

OVIPOSITION OF *RANA CATESBEIANA*

Following a series of unsuccessful attempts to study the spawning behavior of the bull frog, an oviposition was witnessed on June 19, 1940. *Rana catesbeiana* responded much less readily to pituitary injections than either *Rana clamitans* or *pipiens*. Some female bull frogs failed to ovulate after as many as ten daily injections of two homoplastic pituitaries. Although the males generally sounded the sex call without any treatment they would not clasp. Pituitary treatment increased their clasping activity, but an overdose seemed to depress this response. Consequently, great difficulty was encountered in obtaining ovulated females and clasping males at the same time.

The male used in the successful oviposition was injected with one homoplastic pituitary on June 17 and with a second on June 18. The female received two pituitaries on June 17 and two on June 18. On the following day it was noticed that the female had ovulated, and she was placed with the male in a tank 110 cm. × 50 cm. × 31 cm. containing 18 cm. of water at 23° C. The room was darkened and the tank illuminated by two 15-watt red colored bulbs.

At 1:45 P.M. the female was placed underneath the male. Amplexus occurred immediately. The clasp was axillo-pectoral, just as in the green frog. Until 2:50 P.M. none of the actions of the pair suggested that the oviposition was approaching. At this time, however, the female became slightly restless and began to move about the tank extending her hind limbs. In five minutes this activity ceased and did not begin again until 3:25 P.M. At 3:37 P.M. the female assumed the oviposition posture. Her hind limbs extended

backward, downward and laterally. Her back was arched concavely, head under the surface of the water and cloacal aperture directed upward and just above the surface of the water. The forelimbs were extended caudoventrally and appeared rigid.

The male slipped forward over the back of the female, and as in *Rana clamitans*, the tip of the female's head was on a vertical level with the middle of the male's tympanum. The male now clasped the female dorsal to her axillae and partly on the lateral surface of her arms. The male's thighs extended laterally. The shanks of the hind limbs were directed medially, the ankles touched along the repeated itself five or six times. This behavior of the male was followed by a contraction of the female's abdominal muscles, and a mass of forty to sixty eggs issued from her cloaca.

The extruded eggs came to rest between the feet and ankles of the male and many touched his cloaca. Almost immediately the male executed an abdominal contraction and instroke of his hind limbs. The outstroke which followed pushed the eggs from the female, and they spread out on the surface of the water. This process (Fig. 5) of male and female abdominal contractions, male instrokes and outstrokes and the extrusion of small groups of eggs

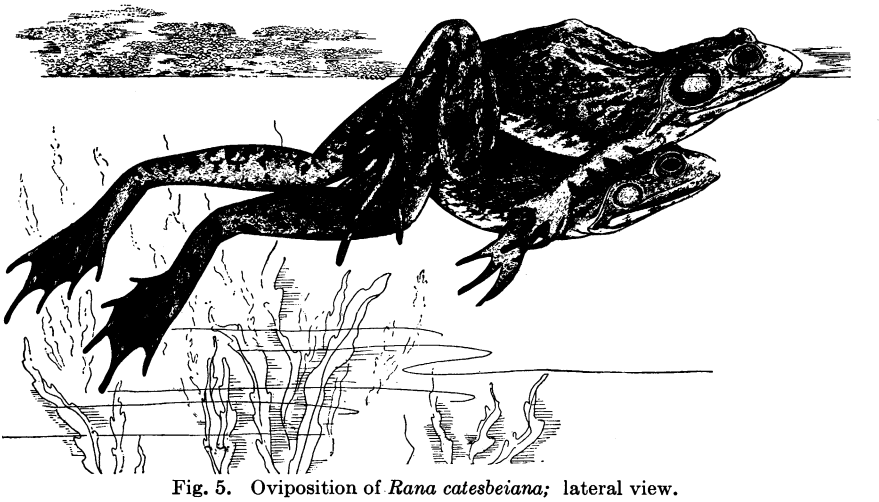

Fig. 5. Oviposition of *Rana catesbeiana;* lateral view.

midline and the heels were 2 to 3 mm. apart. The male's cloaca was about 1 cm. anterior to the female's.

The male's abdominal muscles contracted, and the feet moved outward and only slightly caudad, rotating at the ankles and knees (outstroke). The feet then moved inward (instroke), and the process was repeated rhythmically until 3:45 P.M. when it stopped abruptly as the female shifted her position. The spawning was resumed and continued until 3:49 P.M. when the female moved out of the oviposition posture and the male released. The interruption during the spawning caused the eggs to form two discrete films.

DISCUSSION

From the foregoing description it can be seen that the oviposition patterns of *Rana clamitans* and *Rana catesbeiana* are very much alike, the major difference being the caudal movement of the male's feet in the downstroke of *Rana clamitans* as compared with the outward stroke of *Rana catesbeiana*. Even here it is possible that this was an individual rather than a species variation. Experience with

Rana pipiens demonstrated that there was often considerable variation in the oviposition pattern among different individuals.

In *Rana catesbeiana*, it seemed that the oviposition was initiated by the abdominal contractions of the male rather than by those of the female. It is possible, in the light of our experiments with *Rana pipiens*, that the first contractions of the female preceded those of the male but were too weak to cause any egg extrusion and consequently passed unobserved.

Comparing the ovipositions of *Rana clamitans*, and *catesbeiana* with *Rana pipiens* and *Rana septentrionalis* (Aronson, 1943) and with other plinth-laying *Rana*, which probably spawn in a similar manner, the differences are marked. There are, nevertheless, points of similarity, so that it is possible to speculate as to how the plinth form of oviposition might have evolved into (or from) the surface film type. It is probable that the major departure was the extension of the female's hind limbs. This conceivably raised her pelvic region, pushed her cloaca upward and facilitated the forward slide of the male. This new position of the male forced his hind limbs upward and laterally. The upstroke and downstroke (or outstroke and instroke) of the hind limbs are basically alike in all four species, the superficial differences being due in the most part to the changed relationship of the male and female bodies in the film type of spawning.

SUMMARY

The oviposition behavior of the green frog, *Rana clamitans*, and the bull frog, *Rana catesbeiana*, induced by injections of homoplastic anterior pituitaries and witnessed in a laboratory habitat, is described. A possible course of evolution from the plinth type of spawning to the surface film type is discussed.

LITERATURE CITED

ARONSON, L. R.
1943. The sexual behavior of Anura. IV. Oviposition in the mink frog, *Rana septentrionalis* Baird. Amer. Midl. Nat., XXIX, pp. 242–244.

NOBLE, G. K., AND ARONSON, L. R.
1942. The sexual behavior of Anura. 1. The normal mating pattern of *Rana pipiens*. Bull. Amer. Mus. Nat. Hist., LXXX, pp. 127–142, Pl. I.

WRIGHT, A. H.
1914. North American Anura. Carnegie Inst. Washington, Pub. No. 197.