

7. The Breeding Behaviour of the Common Frog, *Rana temporaria temporaria* Linn., and of the Common Toad, *Bufo bufo bufo* Linn.

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I. THE BREEDING BEHAVIOUR OF THE COMMON FROG,
RANA TEMPORARIA TEMPORARIA LINN.

The life-history of the Common Frog is so well known in outline that the knowledge may almost be said to be traditional. It appears that the earliest detailed description of the behaviour of this animal was given by Jan. Swammerdam (1), 1637-80. No important additions to our knowledge of oviposition and the associated behaviour have apparently been made since that date, a circumstance which is due partly to the excellence of Swammerdam's account, which seemed to leave little for his successors to do, and partly to the difficulties of observation of an event which may occur at any moment, day or night, over a period which has hitherto been generally believed to be many days or even weeks. Roesel von Rosenhof (2), in 1758, recorded arranging his glass vessels in his room and scarcely leaving them by day or night for ten days. He succeeded in witnessing oviposition, and confirmed Swammerdam's account. Spallanzani (3) gave another account, and Nussbaum, in 1895 (4) and 1897 (5), published two papers on oviposition, which, however, are anatomical and deductive, but not the result of direct observation. On the whole, therefore, it may be said that, although one important feature of oviposition was not seen by Swammerdam, his description still stands after nearly three centuries, and the only important error in it, concerning the duration of normal amplexus, is one which only new methods of attack on the problem have now revealed, while the other additions made in this paper are mainly those resulting from attention to points which were not considered in Swammerdam's time.

In the spring of 1932 a field-study was made by the "Frog-tagging" method described by Breder, Breder, and Redmond (6). This consists simply in attaching a small waterproofed label, with a number on it, round the "waist" of the frog by means of string, and is entirely analogous to the ringing process so much used for birds. The method is perfectly adapted for the purpose, and the movements of an individual frog can be followed with ease and certainty night after night. The animals were not apparently inconvenienced by the tags, and some were, in fact, very successful in securing mates in competition with their untagged companions.

The pond selected for the work contained usually about sixty males on each night. This is a convenient number, for more would make the time required for the nightly "roll-call" unduly long. This pond is a horse-pond, through which carts are driven, and is provided with a hard bottom, which

SUMMARY OF RESULTS.

March 1932.												April 1932.		
22.	23.	24.	25.	26.	27.	28.	29.	30.	31.	1.	2.			
Males:														
Frog no.														
A 1	0	0		0	0	0	0	0	+	0	0			
A 2	0	0		0	0	0	0	0	+	0	0			
A 3	0	0		0	0	0	0	0	0	0	0			
A 4	0	0		0	0	0	0	0	0	0	0			
A 5	+	0		0	+	+	+	+	+	0	0			
A 6	0	0		0	+	+	+	+	0	0	0			
A 9	0	0		+	+	0	0	0	+	0	0			
A 11				+	+	0	0	0	0	0	0			
A 12				+	+	0	0	0	0	0	0			
A 15				+	+	0	0	0	0	0	0			
A 18				+	+	0	0	0	0	0	0			
B 1				+	+	+	0	0	0	0	0			
B 3				+	+	+	0	0	0	0	0			
B 4				+	+	+	0	0	0	0	0			
B 6				+	+	+	0	0	0	0	0			
B 10				+	+	+	0	0	0	0	0			
B 16				+	+	+	0	0	0	0	0			
B 18				+	+	+	0	0	0	0	0			
B 20				+	+	+	0	0	0	0	0			
C 4				+	+	+	0	0	0	0	0			
C 5				+	+	+	0	0	0	0	0			
C 7				+	+	+	0	0	0	0	0			
C 8				+	+	+	0	0	0	0	0			
C 9				+	+	+	0	0	0	0	0			

[illegible]

(*) Mated with female without a left hand.

allowed one to move about among the animals without sinking in or stirring up mud which would obscure the tags. The season lasted twelve nights, and I was present on eleven of them. Usually about two hours were spent at the pond, from about 9 P.M. to 11 P.M. The majority of the tags could be read and recorded in a few minutes, and it was unusual for a tagged frog to put in its first appearance on any particular night after the first twenty minutes' watching.

A large number, mostly males, were tagged in the first few days, but subsequently attention was directed mainly to tagging pairs. I am much indebted to my wife for her assistance, which greatly facilitated the work, especially with pairs, because the male possesses an instinct, normally directed to dislodging a competitor, which is remarkably effective for untying partly made knots. Single-handed tagging is quite practicable, but very slow.

In the table on pp. 56 and 57, + signifies presence of the frog on that particular night the first entry being the date of first tagging. Pairs are distinguished by the symbol after the +, this being the reference number of the mate.

Little explanation of this table is required. It will be seen that several of the males secured more than one female in this season; A 18, for example, was mated with a different female on each of three successive nights. Since the numbers of the two sexes of this species are about equal, it follows not only that males which arrive early have a much greater chance of leaving offspring, but that many males do not mate at all in any given season.

With the doubtful exception which is noted (C 6) no female was ever seen a second time. Although recorded six days later, this individual was unpaired, looked like a male, and was swimming freely among the other males. Because the lists made on each night were not compared until later, the anomaly was not noticed at the time, and it is almost certain that this is a mere error in reading.

Clearly, not more than twenty-four hours are spent in amplexus, and the long periods that are usually stated to be spent in this way are abnormal, being induced by the conditions of captivity. Although this has been suspected by Wright (7) and others in species which have been credited with amplexus of long duration, proof has been lacking. Fischer-Sigwart (8) stated that three to thirty days were spent in amplexus in the wild state, but he does not say how this period was determined, and he himself remarks that the observations have not the same certainty as those made in a terrarium ("Die Beobachtungen über die Kopulationsdauer im Freien konnten natürlich nicht so genau gemacht werden, wie im Terrarium, weil man nicht alle Tage nachsehen und daher Anfang und Schluss nicht genau festsetzen konnte"). It is possible that under some conditions of weather amplexus may be extended.

The number of frogs in this pond remained approximately constant until nearly the end of the season; and since a good many tagged males were not seen again, the inference is that there is some coming and going among the males.

Wide differences existed between the behaviour of individual males. One or two were very regular in their attendance, for example, A 5; others absented themselves for long periods, for instance A 4 and A 9. It is very unlikely that these frogs were missed, since, as usual in this species, all the frogs were congregated within a small area of the pond.

The difference between the behaviour of the two sexes is not quite adequately expressed by the usual statement that the males arrive first, followed by the females. Most of the males do arrive before most of the females, but the chief difference is that the females arrive, or enter the spawning areas, a few

on each night, but large numbers of the males arrive on one or two nights at the beginning of the season and a much smaller stream of males continues throughout the season. In 1933 these conclusions were confirmed by direct observation of the migration—males, females, and mated pairs in considerable numbers were seen journeying to the ponds up to a late date in the season.

B 2 and B 13 cast their tags, which were found in the pond on the next night. This was probably due to the great diminution in size following oviposition, which causes the string to become loose. The conclusions are not affected by these occurrences.

Voice.—The normal croak of the male is a harsh sound without much carrying power. A breeding chorus of about a thousand males which was to be found in a neighbouring pond was sometimes inaudible fifty yards from the pond side. The warning note used when one male touches another is a quicker sound, about two to four to the second, sometimes resembling the grunt of a pig. There is a good deal of variation in both notes at different times and in different individuals, and the two voices are not so sharply distinguished from one another as those of *Bombina variegata* or *Bufo bufo*. As in *B. variegata*, the ordinary croak is sometimes used when slight contact with another male occurs.

The term "call-note" for the ordinary croak of this species is not very appropriate. In other Salientia, for example *Bufo bufo*, the male takes up a more or less definite station from which he calls. The note is clearly an individual affair, to guide a female to that particular male. In *R. temporaria* a male does not stay still, even while croaking, but jostles continually in a crowd with his croaking companions. The croak is communal, and while no doubt effective over a short range in guiding females to the spawning site, cannot function for attracting a female to any particular male. Ponds with very few frogs in them may be quite silent, and vigorous croaking is characteristic of a crowd of frogs and not of individuals.

Aquarium Observations.—Formerly, when it was believed that many days were spent in amplexus, it appeared that the witnessing of oviposition was largely a matter of chance, because days might elapse before even continuous observation was rewarded. It now appears that this delay is quite abnormal, and must be due to some inhibiting factor acting under conditions of even temporary captivity. An attempt was therefore made to witness oviposition and sexual behaviour by constructing a tank 3 ft. × 1 ft. × 1 ft., with a glass bottom and a mirror back. By supporting the tank 1 ft. above a table, and laying another mirror on the table, the undersides of the animals could comfortably be observed by looking into the mirror, and a direct view be obtained in the ordinary way with no more than a slight change of direction of view. Illumination was arranged from below. This tank was filled with tap-water, and two females and seven males which had been captured about an hour previously were placed in it. This study yielded much information about sex recognition, but more work was necessary before oviposition was witnessed.

Observations commenced at 10.50 p.m. on the 11th of March, 1933. The pairs had separated during the journey from the pond. For a few minutes the animals dashed excitedly about the tank, but quite suddenly became quiet, and then settled down to what had every appearance of being similar behaviour to that seen in the ponds. When males came into contact with the females, grabs of immense vigour were made, and within five minutes both females had been seized. One male secured his hold in the normal position, but the other seized his mate from the ventral side. She immediately feigned death, and remained in this rigid posture for the next two hours. During the

whole of this time the female did not struggle. When the male became quiet she sometimes made slight attempts to turn or to back out of his embrace, but desisted immediately he made the slightest movement. He croaked frequently. The frogs were finally lifted out of the water and separated forcibly. She was seized by the head in three minutes, released, and in ten minutes was recaptured finally.

Pugnacity.—On another occasion, a male secured a hold of a female from the ventral side when she was already in the normal possession of another male. Her actions in this case were just the same, consisting of instant rigidity. The males, on the other hand, were exceedingly active; each croaked frequently and struck at the other with his feet, reaching far forward as if endeavouring to get a foothold on the anterior part of his opponent. If the foot touched any part of him a vigorous push followed. It is this action which so much hinders the tagging of pairs; the strength of the animals is sufficient to push one's hand aside. There is not the slightest resemblance to swimming movements, but the feet are reached round to the opposite side, where the rival is situated, and the three frogs roll over and over in the water. The objective is obviously the arms of the other male. These contests may frequently be seen in the ponds. In no case has the actual dislodgment of the rightful male been seen, but there can be little doubt that in the initial stages, before either had secured a good hold, this kind of action would be decisive. This seems to be the only period when the nuptial pads are of use. Ripe females do not struggle when seized. If taken by the ventral surface they feign death, but if seized either in the normal position or around the groin they accept their mate, who attains his correct position in the latter case by a series of short swimming and wriggling movements. It is most unlikely that a male should slip either forwards or backwards accidentally because of the shape of the female and the position of her arms, and the intensity of the grip is such that rotation would seem almost impossible, for it is a matter of difficulty to force open the arms of a male sufficiently to extricate the female.

The fact that frogs fight in this way has been recorded before, notably by Fischer-Sigwart (*loc. cit.*), but the special significance of the nuptial pads at such times does not appear to have been indicated. This view was put forward in a previous paper (9) on *Bombina variegata variegata*, but was then based on a single observation. Since then numerous instances of the same behaviour have been seen in this species, and one interesting case where a *Bombina bombina* male was removed from his own female by a *Bombina variegata* male, who hooked his toes under the arms of his rival, and with one mighty thrust forced the animal to part from his mate, who was then promptly appropriated by the successful toad. Whether the much better nuptial pad equipment of *Bombina variegata* was the sole deciding factor must be doubted, since *B. variegata* is also the stronger animal; but the function of the pads is perfectly clear, and it is a fact that *B. bombina* males seem unable to secure their own females so long as *B. variegata* males are present. The further investigation of these points belongs to a study of these two species, but the facts are mentioned here because they show that actions which are exactly similar in appearance to those of *R. temporaria* are actually effective if there is a difference in nuptial pad equipment or strength between the combatants.

During the breeding season the skin of the male *R. temporaria* becomes more slimy than at other times, and this development may be correlated with the fighting, since it would obviously be an advantage to a male if he were so slippery that his rival had difficulty in getting a foothold. In fact, the feet of struggling frogs do often slip violently off their opponents. On the other

hand, this slimy skin may be more important for sex recognition, by increasing the contrast between the skins of the two sexes, on which sex recognition depends.

It is, then, extremely probable that the nuptial pads of frogs and toads are not really copulatory accessories, but structures analogous to the weapons possessed by the males of other animals. They are used during fights with other males for possession of a female, and it is the peculiar nature of these combats, which take the form of a tug-of-war, with a female acting as the rope, which has determined the development of the structures and also perhaps hindered recognition of their true function. Frictional pads on the arms prevent a male being dislodged either by another male or by the reaction of his own thrust, and *B. variegata variegata* and some other species have developed similar pads on the feet which are used during these combats. In view of the fact that these structures have been much used to illustrate zoological theory, it seems of some general interest to determine exactly how they are employed by living animals, since it is clear that different sets of facts must be considered in assessing their survival value if the pads are, on the one hand, copulatory accessories, or, on the other hand, structures used in combat.

Sex Recognition.—During this period of observation and of other occasions, both at the ponds and in the aquarium, only rarely did one male vigorously grab another, and even then the embraces lasted only a few seconds. The males do not invariably give either their sex warning grunt or their ordinary croak when mere contact with another occurs. It is stated above that both females were seized within about five minutes of introduction into the tank, and in the description of the behaviour of spent females, below, it will be shown that these females, which resemble the male in figure, are frequently seized vigorously. It is impossible to reconcile these observations with the scheme of sex recognition which Noble and Farris (10) described in *Rana sylvatica*, and which appears to apply, with modifications, to other species (*Bombina variegata variegata* for example). In these cases a male seizes another frog or toad indiscriminately. If the seized animal is a female she remains silent and possesses a stout figure, but a male has a slender figure and gives out a short rapidly repeated note which acts as an indication of his sex. Cummins (11) and Liu (12) attach importance to the repulsive action of the male which is seized. Release or retention depends on these differences of behaviour and characteristics. In *R. temporaria* it is clear that a female is recognized positively by some character which is peculiar to her and which she still retains after oviposition. The factors which in other species are effective for sex recognition merely determine in this species whether she will be retained or released after she has been recognized as a female and seized. The recognition occurs only on contact. Owing to the angle at which the animals float it is the fingers of one frog which come into contact with the back of another, but below water the nose of the animal often touches first. Now the skin of a breeding female of *R. temporaria* is very noticeably different from that of a male. In the female there appear on the posterior part of the back, thighs, flanks, and the sides of the head a large number of so-called "pearly granulations," which were described and investigated in detail by Huber (13). He found that, although the structures themselves are horny and impart to the skin a roughness like sandpaper, the bases are provided with a special innervation, and, in consequence, he concluded that they have a tactile function. Whatever may be the sensation which the female receives from them, and whatever part they may play as tactile organs in her life, it seems clear that they have a great significance for the male, since they provide him with a means for recognizing his mate,

By placing males and spent females in a bowl of water covered with a cloth it was found possible to seize and remove an animal of either sex, as desired, using touch alone to distinguish them. The rough females could often be felt as they merely brushed by the hand placed in the water, and no mistakes were made in the selection. There seems little doubt that tactile sex recognition plays the principal part in this species, but since these granules are confined to *R. temporaria* and *R. terrestris* among the European members of the genus it is easily realized that corresponding differences in the manner of sex recognition are to be expected.

An interesting sidelight on the part which sight plays is provided by the observation that a frog would occasionally catch sight of himself in the mirror back of the tank, and swim croaking towards his image just as he would to another frog. This confronting of one frog by another is a noticeable feature of the behaviour of the frogs in the ponds.

Oviposition.—The above observations were continued until 4 A.M., but no spawning took place. The animals were left in the tank until the 14th March, but they did not spawn. On that day one pair was removed and placed in another aquarium having sand on the bottom, with no result up to the following day. Both pairs were then removed and placed in an outdoor terrarium, containing a pool that had been established some two years, where they spawned within twenty-four hours. Certain results which had been obtained in a migration study which was in progress suggested that frogs are able to discriminate very well between pond-water and water of other origin, and it seemed that this might be the clue to an explanation of the anomalous behaviour in tap-water. Using this as a working hypothesis, two tests with pond-water in the tank were made, and in both tests the pairs collected afresh spawned within twenty-four hours of collection. These results seemed to justify another attempt to witness oviposition, and on the afternoon of the 18th March some water was obtained from the field-pond together with five pairs and three males. It was thought that success was more likely to attend observation very early in the morning, so a start was made at 4 A.M. At this hour one pair had already spawned. Nothing further of interest occurred until about 5.45 A.M., when one of the females commenced a few ill-defined scrambling movements, and at 5.55 A.M. spawning occurred, clear away from other frogs or egg masses, on the glass bottom of the tank. First a small clump of eggs appeared at the cloaca of the female and remained there for about one second. Then the whole mass of ova was violently and suddenly ejected, the dense black mass streaming over the bottom of the tank like molten pitch pouring over a cold surface. The envelopes were, of course, not swollen. The ejection of the eggs was aided by the hands of the female, who pressed them hard on her abdomen. Possibly the greater part of the propulsive power required was provided in this way, and the initial small clump may be all that were expelled by muscular action or internal pressure. The process was exceedingly rapid, and not more than five seconds elapsed between the first appearance of the eggs and the completion of the expulsion. During this time the male made several emissions of sperm as far as could be judged from his movements. About five more seconds then elapsed, during which both animals remained still, and then the female made a few swimming strokes and gently disengaged herself from the grip of the male, now quite relaxed.

This account resembles that of Swammerdam and Roesel von Rosenhof (*loc. cit.*), but the action of the hands of the female, which clearly plays a great part in the process and explains how it is that this enormous mass of eggs can be ejected in an instant, has apparently not been observed before. There

is evidently much variation in the process of oviposition within the genus *Rana*, and it should not be assumed that this peculiar method is characteristic of the genus. *Rana esculenta* (14) and *Rana nigromaculata* (12) deposit their eggs in a number of separate emissions, and in the latter case the process is preceded by actions in the male resembling those of the toad, while *Rana fuscigula* (15) lays its eggs singly.

During normal amplexus the pair swam about or remained quiet under the water. Both animals helped in the swimming. The eyes of each were sometimes closed and sometimes open. The male readily reacted to touch stimuli by his sex warning grunt or by a muffled croak, and also pushed out with his feet. When under water he continuously made an exceedingly quiet chirp at intervals of about one second. This noise could only be heard when the pair were close to the glass, and was accompanied by a synchronous puffing out of the vocal sacs to a slight degree. This action and voice ceased above water, and the function is quite obscure. No abdominal movements were seen in the female.

No special sperm-emission stimulus was seen, but the eggs themselves appeared to come into contact with the pubic region of the male. No other similar stimulus ever reaches a male frog during his life in the pond, because although the pair may crawl among the egg-masses, which must touch the male occasionally, the stream of eggs emerging from the female are not at all similar to these. Their envelopes are not swollen, and they are sticky and firm, not slippery and soft.

Two more pairs spawned at 6.20 and 7 A.M., and the above observations were confirmed. In one case spawning took place on top of another egg-mass, and the recoil of the eggs, which caused the pair to glide slowly through the water, brought the animals into view, the position of the arms of the female drawing my attention to the fact that she had just spawned.

Behaviour after Oviposition.—The female which has just deposited her eggs is now a different animal both in appearance and behaviour. She is now at least as thin as a male, a fact which ensures her release if she is molested while she is making her way out of the pond, but she is still provided with the badge of her sex, the horny granules, and she is very liable to be seized by any male which touches her. When this occurs (it happened very frequently in the tank) she no longer feigns death or remains silent, but behaves exactly as the males do. Voiceless before, she now grunts vigorously, with a note which is perceptibly but not greatly different in tone from the male grunt. The combination of this warning note and the lack of the stoutness which caused the male to retain her until she had laid her eggs results in a fairly rapid release. There is now no vigour in the grip of the male, but the spent females may often be feebly retained for periods of several minutes. It is improbable that a spent female would experience difficulty in making her way out of a pond through a crowd of males, even though she would frequently be detained.

The female is capable of using her voice before she lays her eggs. The only pair which did not spawn during the observation period was left in the tank, now filled with tap-water, while observations on toads were being made during the next week. After some days the frogs were found separate, and the female, although still full of eggs, grunted and dodged away when touched or seized by the male. Not much significance can be attached to the fact that he did not retain her, since he was by then probably somewhat exhausted, but the observation seems to show that some change had occurred in the female which caused rejection of the male and the use of her voice. Her silence during normal breeding is not the result of mechanical inability to croak, due to the

condition of her body packed with eggs, but is, in fact, another expression of the readiness with which a ripe female accepts the male.

I have to thank Mr. H. W. Parker for his interest and assistance in obtaining references nos. 6 and 10, and Mr. L. A. Lantz for no. 14; and also Dr. W. J. Purdy, whose readiness to accompany me, often at awkward hours, and help with the transport of frogs, pond-water, and accessories enabled more to be done during the very short breeding season than would otherwise have been possible.

SUMMARY.

(1) By tagging individual frogs in a pond it was found that the males, after mating once, remained behind in the pond with the other males, and often mated several times in one season. Other males did not secure mates at all. Pairs remained in amplexus under natural conditions less than twenty-four hours.

(2) The recognition of the female by the male depends primarily on the rough granules of her skin, which are developed during the breeding season, a different method of sex recognition from any hitherto described. She is retained after seizure because she remains silent and has a stout figure. When she lays her eggs she is released by the automatic cessation of the impulse to grip, resulting from her diminished size, aided by the use of her voice.

(3) The female assists the expulsion of her eggs by pressing her hands on her abdomen and forcing them out.

(4) The sperm-emission stimulus is merely the contact of the eggs with the symphysis pubis region of the male.

(5) The males struggle for the possession of the females by using their feet to push away or force off their opponents, especially by hooking their toes under the encircling arms of the other frog. This appears to be the only point at which the nuptial pads perform a useful function.

REFERENCES.

1. SWAMMERDAM, J. [1637-80.] The Book of Nature. A Particular Treatise on the Generation of Frogs. (English Translation, 1758.)
2. ROESEL VON ROSENHOF, A. J. 1758. *Historia Naturalis Ranarum Nostratium*.
3. SPALLANZANI, L. 1786. *Experiences pour servir à l'histoire de la génération des animaux et des plantes*. (French Translation.)
4. NUSSBAUM, M. 1895. Zur Mechanik der Eiablage bei *Rana fusca*. *Arch. f. mikr. Anat.* xlvii. pp. 479-498.
5. NUSSBAUM, M. 1897. *Loc. cit.* xlviii. pp. 545-550.
6. BREDER, C. M. Jr., BREDER, R. B., & REDMOND, A. C. 1927. Frog Tagging; a method of Studying Anuran Life-habits. *Zoologica*, ix. p. 3.
7. WRIGHT, A. H. 1914. North American Anura. *Carnegie Inst. Wash. Pub.* 197, pp. 11-12.
8. FISCHER-SIGWART, H. 1897. Biologische Beobachtungen an unsern Amphibien. *Vierteljahres. Naturforsch. Ges. in Zürich*, xlii. pp. 238-316.
9. SAVAGE, R. M. 1932. The Spawning, Voice, and Sexual Behaviour of *Bombina variegata variegata*. *Proc. Zool. Soc.* iv. pp. 889-898.
10. NOBLE, G. K., & FARRIS, E. J. 1929. The Method of Sex Recognition in the Wood-Frog, *Rana sylvatica*. *Amer. Mus. Novit.* p. 363.
11. CUMMINS, H. 1920. The Rôle of Voice and Coloration in Spring Migration in Frogs. *Journ. Exp. Zool.* xxx. pp. 325-343.
12. LIU, CH'ENG-CHAO. 1931-32. Sexual Behaviour of the Siberian Toad, *Bufo raddei*, and the Pond-Frog, *Rana nigromaculata*. *Pekin Nat. Hist. Bull.* vi. 2, pp. 43-60.

13. HUBER, O. 1887. Zeitschr. f. wiss. Zool. xlv. p. 664.
14. HERON-ROYER. 1885, L. F. Notices sur les Mœurs des Batraciens. Ext. Bull. Soc. Étud. Sci. Angers, i.
15. POWER, J. H. 1927. Notes on the Habits and Life-History of South African Anura, with Descriptions of the Tadpoles. Trans. Roy. Soc. S. Afr. xiv. 3, pp. 237-247.

II. THE BREEDING BEHAVIOUR OF THE COMMON TOAD,

BUFO BUFO BUFO LINN.

As early as 1754 Roesel von Rosenhof made some observations on the breeding habits of the Common Toad, *Bufo bufo bufo*, and published a good general account in 1758 (1). Since then several other descriptions have appeared by Spallanzani (2), Heron-Royer (3), and Boulenger (4). Recently Hinsche (5), has studied sex recognition, and Liu (6), working on the subspecies *Bufo bufo asiaticus*, has published detailed observations on sex recognition and general breeding behaviour. However, there does not appear to be an account in which those actions which are closely connected with oviposition have been described with sufficient accurate detail to show clearly their place in the life-history of the animals. Moreover, the conclusions of Liu on sex recognition do not agree with those of Hinsche. The present paper is a description in which these points have been borne in mind.

Most of the observations were made by capturing toads from their breeding pond, and placing them in the observation tank which was described in Part I. of this paper; but these aquarium observations were checked by watching the animals by night in their natural environment, where they appeared to behave in the same manner, although some of the details cannot readily be seen under these conditions.

Field Observations.—At the beginning of the season the male toads were found round the margins of the ponds. Later they gathered more towards the spawning sites, which were clumps of water-grass near the edge of another part of the pond where the water was deeper; but a few males were usually to be found round the edge throughout the season. The call-note is rather strident and rises to a grating maximum, but is somewhat more musical at the beginning and ending. The toad calls when he is stationary and usually when he is able to raise himself a little out of the water by resting his arms upon a branch or piece of weed. Poised thus, half in and half out of the water, he calls loudly and repeatedly. Each note lasts about one second. These calling stations are more or less isolated, and there is little doubt that the voice of a male could act for guiding a female to the individual performer, which cannot be the case with frogs. Besides this voice the male toad possesses a sex-warning chirp used when one male is touched or seized by another.

Although the female is apparently voiceless, if she is seized after she has laid her eggs she sometimes goes through the motions of the rapid sex-warning chirp of the male without emitting any sound. This peculiar action finds a parallel in *Bombina variegata variegata* (7), where it occurs as an occasional variant of the usual cluck which both sexes employ under somewhat similar circumstances, and the cause may be the same as that suggested in this case, namely, that the instinct and capacity for making the jerky movements which turn an ordinary croak into a cluck have been acquired separately from the ability to produce sound. In *Bombina* the dissociation of the two is temporary, but the female *Bufo bufo* has never acquired the capacity to make a noise at all, although she has inherited the other actions, quite useless as far as can be seen.

Oviposition.—The process of oviposition is preceded by a complicated

13. HUBER, O. 1887. Zeitschr. f. wiss. Zool. xlv. p. 664.
14. HERON-ROYER. 1885, L. F. Notices sur les Mœurs des Batraciens. Ext. Bull. Soc. Étud. Sci. Angers, i.
15. POWER, J. H. 1927. Notes on the Habits and Life-History of South African Anura, with Descriptions of the Tadpoles. Trans. Roy. Soc. S. Afr. xiv. 3, pp. 237-247.

II. THE BREEDING BEHAVIOUR OF THE COMMON TOAD,

BUFO BUFO BUFO LINN.

As early as 1754 Roesel von Rosenhof made some observations on the breeding habits of the Common Toad, *Bufo bufo bufo*, and published a good general account in 1758 (1). Since then several other descriptions have appeared by Spallanzani (2), Heron-Royer (3), and Boulenger (4). Recently Hinsche (5), has studied sex recognition, and Liu (6), working on the subspecies *Bufo bufo asiaticus*, has published detailed observations on sex recognition and general breeding behaviour. However, there does not appear to be an account in which those actions which are closely connected with oviposition have been described with sufficient accurate detail to show clearly their place in the life-history of the animals. Moreover, the conclusions of Liu on sex recognition do not agree with those of Hinsche. The present paper is a description in which these points have been borne in mind.

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Field Observations.—At the beginning of the season the male toads were found round the margins of the ponds. Later they gathered more towards the spawning sites, which were clumps of water-grass near the edge of another part of the pond where the water was deeper; but a few males were usually to be found round the edge throughout the season. The call-note is rather strident and rises to a grating maximum, but is somewhat more musical at the beginning and ending. The toad calls when he is stationary and usually when he is able to raise himself a little out of the water by resting his arms upon a branch or piece of weed. Poised thus, half in and half out of the water, he calls loudly and repeatedly. Each note lasts about one second. These calling stations are more or less isolated, and there is little doubt that the voice of a male could act for guiding a female to the individual performer, which cannot be the case with frogs. Besides this voice the male toad possesses a sex-warning chirp used when one male is touched or seized by another.

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Oviposition.—The process of oviposition is preceded by a complicated

series of movements, and although the outlines of this have been sketched by some of the authors mentioned in the introductory paragraph, the existing descriptions are not entirely correct. It follows naturally that the interpretations which have been made are equally lacking in precision, and the significance of the process has not been indicated.

The animals swim about in amplexus until the female comes into contact with some of the water-weed, when she immediately stops, with her feet or arms upon it. She may leave the weed and repeat the process several times, but after she has once commenced to lay she is more or less anchored by her egg-string, and her excursions are limited to the neighbourhood of the weed.

The commencement of oviposition is marked by a slow stretching movement of the body of the female, who straightens her back and extends her legs behind her. The male immediately responds to this movement, even before its completion, by stretching his legs behind him, heels together, knees somewhat bent, rotated ventrally, and digging into the flanks of the female, toes close to her cloaca. If the male is a large one the toes are hooked round to the ventral side of the female, but if he is small his toes just reach the cloaca. As soon as this movement is complete the egg-string, a pair of double rows, slowly emerges from the cloaca of the female and falls loosely in the water, passing over the toes of the male, often between the web of the foot and the toes. With a large male the egg-string glides over the tarsus of the male. The length of egg-string extruded varies considerably on different occasions. The time taken for each portion to emerge is about ten seconds. While the eggs are emerging the male ejects his sperm, as far as can be judged from his pumping movements. The egg-string then ceases to flow and the pair remain quiet for several minutes. Before any movement of the female has occurred the male often resumes his normal position on the back of his partner. After this pause the female commences to move about, and generally comes up for air. As a result of this and of her subsequent wanderings about the weed-clump the egg-strings are wound round the weeds. It is doubtful if there is any deliberate winding; there is certainly nothing resembling the spinning action of *Bombina variegata variegata*, and haphazard wandering seems adequate to explain the manner in which the eggs are distributed. The description of Héron-Royer and Boulenger (*loc. cit.*) that the eggs are helped out by the male appears to be erroneous, and due to a mistaken interpretation of what is actually a sperm-emission stimulus.

Oviposition occurs at fairly regular intervals of about half an hour and lasts for several hours altogether. There is no difficulty in making the observations or persuading the animals to lay, and although the first observations were made before dawn subsequent experience showed that more comfortable hours could be quite as productive.

In this species there is no action such as Miller (8) described in *Bufo lentiginosus*, where the feet of the male, hooked beneath the cloaca of the female, formed a "basket" for the reception of the eggs. Roesel von Rosenhof (*loc. cit.*) made a somewhat similar remark about *Bufo bufo*, and described the male as gathering the eggs together with his toes. From the illustrations accompanying both these authors' accounts it would seem that the animals were not spawning upon weed. It is clear that when this natural condition is satisfied, and the animals are able to support themselves in the water above the bottom of the tank, the eggs fall freely from the cloaca, and the feet of the male perform no supporting function.

Release Stimulus.—In a previous paper (7) I pointed out that an animal such as *Bombina*, in which the eggs are laid a few at a time at intervals during the

night, must possess some special means of releasing the male from his hold when egg laying is over. The mere diminution of size, which serves *Rana temporaria* for the purpose, will not do in this case, because there is no sudden decrease in size which could form a stimulus receivable by the male. *Bufo bufo* is in this respect a precisely similar case to *Bombina*, and it is interesting to find that *Bufo bufo* also possesses a special release mechanism. The conclusion of oviposition was seen on one occasion, and many subsequent cases of spent females being seized by males gave ample opportunity for studying the details of this phase of behaviour.

A spent female seized by a male does not usually exhibit any immediate reaction. She swims about for a period, which may be several minutes, just as if she were still full of eggs, and the male shows no sign that the amplexus is not quite normal. Sooner or later, however, she comes to rest and commences exactly the same actions as if she were going to lay. The male responds exactly as before. The pair remain in this position for a few seconds, but of course no eggs emerge. After a brief interval, either before or after relaxation by the female, the male suddenly releases and swims away.

Now in the description of oviposition it was seen that the process is a chain of actions: female stretches—male gets ready—female emits eggs—male fertilizes them—female relaxes and resumes swimming—male continues to hold on. It seems that release follows a break in this chain of instinctive actions, and we may now examine where the break occurs. Apparently up to the point where eggs would be emitted everything happens just as in actual oviposition, and the actions of the male confirm this, because his behaviour is identical up to this point. Is it the absence of eggs which causes the male to let go, or does he release because in the absence of eggs he does not emit sperms, and this failure of function on his part puts an end to his gripping instinct? Now on some occasions males apparently emitted sperm without eggs having been laid, but nevertheless released. It is evident, then, that not only can sperm emission follow directly upon the oviposition warning, but that the only factor which certainly produces release is the absence of eggs. It is not unusual in animal behaviour to find that in a sequence of actions some "short-circuiting," or skipping a stage, may occur, and in my opinion the passage of the eggs over the toes of the male is to be regarded as the normal sperm-emission stimulus, but occasionally the excitement of the male is such that premature emission occurs. The function of the peculiar position taken up by the male is therefore twofold: it enables him to receive the sperm-emission stimulus if eggs pass, while if they do not he fails to receive the stimulus which ensures the maintenance of amplexus after this performance, and consequently releases.

The biological importance of prompt release after egg laying is over is probably considerable. A male who continued to hold on would have no chance of securing another mate, and would be likely to leave less progeny than an animal better equipped to receive and act upon the release stimulus. A female who failed to deliver the stimulus to her male would not only be impeded in her departure for food after the exertion of egg laying but might suffer serious mechanical injury from the too prolonged pressure of the arms of the male. Examples of the injuries caused in this way are illustrated by Wright (9).

The release reaction, although entirely different in mechanism to that of *Bombina variegata* or *Rana temporaria*, has one feature in common—it is psychological or nervous and not mechanical. The male is not forced off—he lets go.

It is always a matter of some difficulty in making such observations as these

to be certain that some minute action of great importance has not occurred unnoticed. Fortunately the animals themselves performed an experiment which throws additional light on this question, and also upon sex recognition.

At 6.30 A.M., a female had laid some eggs. At 7.0 A.M. an unattached male approached and succeeded in securing the female on the ventral side. After the usual shrill protests by the rightful male the animals became quiet, and it was noticed that, unlike a female *Rana temporaria* under such circumstances, the female toad was apparently quite unconcerned, and moved about and breathed as if nothing out of the ordinary was happening. Neither male now seemed aware of the presence of the other, possibly because in axillary amplexus the arms of the male do not pass round the female to the other side where the rival is situated, and so there is nothing to tell either toad that he is not alone with the female. It will be seen from the time that the female was due to lay again very shortly: what was going to happen? At 7.6 A.M. she gave the usual oviposition warning by stretching herself, and in this ludicrous situation both males immediately adopted the fertilizing attitude! Eggs then passed, but since only the rightful male had his toes at the cloaca, and his rival did not reach so far, he alone made the movements of emitting sperm. Observations were then discontinued, and on their resumption some hours later the second male had departed. Now in this case there can be no question of the female administering any special contact stimulus to her male beyond the stretching of her body, which would be apparent to both males.

Sex Recognition.—It is now possible to collect from the above observations some data, which, together with facts to be described, provide information on the mechanism of sex recognition. This subject has already been studied by Hinsche (*loc. cit.*), but the conditions employed for many of his observations were so highly artificial that his description of events does not agree very well with the behaviour seen under more natural conditions. Many of his observations were made on animals out of water, and however valuable they may be for the elucidation of land-mating, which does occasionally occur in this and other species, they would not appear to have much bearing on the behaviour of the animals during their aquatic existence. The very lengthy period which Hinsche's toads spent in amplexus (eleven to nineteen days), together with the observation that release occurred before eggs were completely laid and the male slipped into abnormal positions during the deposition of eggs (on land), suggests that the toads were seriously affected by the artificial conditions. All my toads spawned within twenty-four hours of capture, and the subspecies *Bufo bufo asiaticus* has been studied under natural conditions by Liu, whose account, while covering somewhat different ground, agrees well with events which I describe for *Bufo bufo bufo*.

The male toad is an excitable and vociferous little animal. He swims rapidly hither and thither, and seizes either male or female toad as he comes across them. Males thus seized chirp immediately, often on mere contact, and this sensitiveness is increased when in amplexus, mere motion through the water often exciting them to this action. Females have never been heard to make a sound, and are seized and retained whether with or without eggs. In neither case does she resist, but if spent she releases herself by actions described above.

This behaviour is clearly of the trial and error type. The males of this species often breed when very much smaller than the females, and in such cases the ratio between the sizes of a small male and a large male is not different from that of a large male and a small female. This consideration, taken in conjunction with the readiness to seize and retain spent females, show that the

bulkiness of the female, which Noble and Farris (10) found the main factor in the sex recognition of *Rana sylvatica*, is not acting here. It appears that the conclusions of Liu apply to this species, and that the dominant rôle is played by the voice acting as a warning that a male has been seized, and also by the "repulsive" action—a kind of dodging dive—which males alone display when seized.

Hinsche considered that the voice could not be an important factor, because pairs in amplexus were often attacked in spite of the vigorous croaking of the male. At first sight this appears an important objection, but Hinsche's own observations show that a toad is capable of distinguishing between the gait of a female and that of a male. The manner of swimming of a pair differs to an even greater extent from the swimming of a single toad of either sex, so we should credit a toad with the capacity at least for recognizing a pair. Now a toad seized at random by another in a pond may be either a male or a female, but on account of the greater number of the former it is probably a male. No such ambiguity exists with pairs; the lower member is certainly a female. It will be seen in the next section that a male which attacks a pair has some chance of dislodging his rival. Both the capacity for recognizing a pair and the advantage of attacking it seem to exist. It is a commonplace of animal behaviour that one reaction may override another, and toads which in these special circumstances took no notice of croaking would doubtless leave more progeny.

Pugnacity.—The fact that toads fight has been recorded several times. Héron-Royer (3) has a good general account, and Hinsche (5) has some good photographs and points out that fighting is conducted by the attacking male attempting to force his body between the pair like a wedge. This is a different method from that used by *Rana temporaria* or *Bombina variegata*, where the hind feet are employed. In *Bufo bufo* the hind feet are defensive and are actively used to fend off other toads, but do not seem to be used by the attacking animal. The hind feet are capable of reaching far forward and are directed to whichever side the little animal is touched. The small size of the male may be a definite advantage, because the point from which the thrusts take place is central, being about the middle of the back of the female. A larger toad might be unable to protect the vulnerable angle between his body and that of his partner.

On one occasion, the water in the tank was drawn down to about 5 cm. in depth in order to move it. It remained so for some minutes, and during this time one male succeeded in attaching himself to a female already in amplexus, getting a good grip just behind the rightful male. The scuffle, accompanied by much splashing and chirping, attracted two other males, who hurried up and threw themselves on the three struggling toads. One by one all were pushed off, until only the original contestant remained. He was wedging himself forward, and for a time it looked as if he would be successful. Then the rightful male succeeded in getting a good foothold on the chin of his rival, and with a mighty push, which bent the head far back, forced the attacker to let go, and remained in undisputed possession.

SUMMARY.

(1) Oviposition in the toad is preceded by a stretching action of the female, which warns the male that laying is about to commence. He responds by placing his toes so that they feel the eggs emerging. This acts as a sperm-emission stimulus.

(2) The male is discharged by the female at the conclusion of oviposition

by a repetition of the oviposition warning. Since there are no eggs the chain of instinctive reactions in the male is broken, and he leaves go and swims away.

(3) Sex recognition depends on the voice, possessed by the male but not by the female, and on the dodging, repulsive action which males show when seized.

(4) Fighting is vigorous, and is conducted mainly by the attacking toad forcing himself between the pair from behind. Defence is carried out by thrusts of the feet.

REFERENCES.

1. ROESEL VON ROSENHOF, A. J. 1758. *Historia Naturalis Ranarum Nostratum*.
2. SPALLANZANI, L. 1786. *Experiences pour servir a l'histoire de la génération des animaux et des plantes*. (French Translation.)
3. HÉRON-ROYER, L. F. 1887. *Notices sur des Mœurs des Batraciens*. Ext. Bull. Soc. Études Sci Angers, iii. p. 91.
4. BOULENGER, G. A. 1897. The Tailless Batrachians of Europe.
5. HINSCHKE, G. 1926. Ueber Brunst und Kopulationsreaktionen des *Bufo vulgaris*. Zeitschr. vergl. Physiol. iv. pp. 564-606.
6. LIU, CH'ENG-CHAO. 1931-32. Sexual Behaviour of the Siberian Toad, *Bufo raddei*, and the Pond-Frog, *Rana nigromaculata*. Peking Nat. Hist. Bull. vi. 2, pp. 43-60.
7. SAVAGE, R. M. 1932. The Spawning, Voice, and Sexual Behaviour of *Bombina variegata variegata*. Proc. Zool. Soc. iv. pp. 889-898.
8. MILLER, N. 1909. The American Toad. Amer. Nat. xliii. pp. 641-688 & 730-745.
9. WRIGHT, A. H. 1912. North American Anura. Carnegie Inst. Pub. 197, pl. iv.
10. NOBLE, G. K., & FARRIS, E. J. 1928. The Method of Sex Recognition in the Wood-Frog, *Rana sylvatica*. Amer. Mus. Novit. 363.