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Medical College, Turner Street, London, E.1. Articles should be typed in double spacing,
on one side of the paper only. Figures should be drawn in Indian ink on plain white paper.

The development of Hybrids between *Rana esculenta* Linn.
and *Rana ridibunda* Pallas.

by

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Two main forms are recognised among the water frogs of Europe, and a full grown animal can usually be assigned, by measurements or colour differences, to one or other of them. They are believed to be distinct over the areas in which they occur together, while producing fertile hybrids in artificial conditions. The suggested barrier is that of differences in the mating times where they overlap (Boulenger 1897, Schreiber 1912, Angel 1946.) If the above summary is correct the two forms offer interesting material for the investigation of speciation, while providing the nice problem for the taxonomist of whether *ridibunda* should be regarded as a subspecies of *esculenta*.

The opening paragraph, though generally accepted, unfortunately contains several doubtful statements based on the consideration of inadequate numbers of animals and localities, and even misquotation of previous authors. Neither form is believed to be native to Great Britain, but in the Spring of 1947 we had distinct non-overlapping colonies of both in the South of England. Dr. Malcolm A. Smith (1949) is therefore reinvestigating the problem, including the making and rearing of hybrids in captivity.

He has made some parts of this work co-operative, and we wish to make clear both our gratitude to him for including us in his scheme, thus giving us an opportunity to observe this extremely interesting material, and also the incomplete nature of this paper.

EARLY HISTORY OF THE MATERIAL. The adult *ridibunda* belong to the colony made by liberating twelve frogs in a garden at Stone-in-Oxney East Kent, in 1935 (E. P. Smith, 1939). These frogs had been imported by Professor A. V. Hill from the neighbourhood of Debreczen in Hungary. In 1947 they had colonised Romney Marshes in the quadrangle formed by Rye, Tenterden, Hythe and Dungeness (Taylor, 1948). In 1947 and preceding seasons all frogs seen in this new habitat were unstriped, and coloured fawn, grey or green, frequently with large dark blotches. The striped pattern illustrated by Boulenger (1897) plate XVI had not been recorded.* The animals used in these crosses were all captured near Appledore, Kent. The *esculenta* both adult and tadpoles came from the colonies in the Ham Gravel Pits and on Ham Common in Surrey, which have existed at least since 1929 (M. A. Smith in Taylor 1948) though their origin is unknown. All the frogs have the striped pattern. The most conspicuous feature of this is a narrow fawn, yellow or green band down the centre of the back but there are conspicuous pale markings on the flanks, which are often golden or pinkish (Boulenger 1897 Plate XVII).

The unstriped pattern also occurs in *esculenta* but has not been recorded in England. This homogeneity of the two colonies for a different form of a

*One adult female agreeing well with Boulenger's figure, was caught this spring.—Eds.

dimorphism found in both forms, and not a systematic difference between them, gave the crosses an added genetical interest.

The crosses were made in the gardens of the Zoological Society of London in outdoor ponds made for them by Mr. J. W. Lester, the Curator of Reptiles. One basin contained 6 male *esculenta* and 6 female *ridibunda*, and the other 3 male *ridibunda* and 3 female *esculenta* (Smith M. A. 1949). These crosses will be referred to as R ♀ x E ♂ and E ♀ x R ♂. On 11.6.1947 Mr. Lester showed us these basins and collected from them samples of spawn, which we kept in about 2 litres of pond water in jars in the laboratory. R ♀ x E ♂ appeared to have been freshly laid and was almost certainly the unmixed spawn of a single pair. E ♀ x R ♂ was mixed spawn, some was newly laid, but the majority of the eggs were caused to hatch by the disturbance. On analogy with our *ridibunda* control we suggest that they had been laid about six days previously. The spawn in the ponds and in our jars appeared perfectly normal.

Our *ridibunda* control called RR was the offspring of a pair captured in amplexus at Snargate, Kent, on the night 3-4.6.1947. Amplexus, accompanied by quiet croaking, continued while they were brought to Ruislip, Middlesex, and put out of doors in a 90 x 25 x 20 cm. glass tank. They spawned on 4.6.1947, between 9 a.m. and 5 p.m., and the parents separated.

The spawn, left out of doors, hatched on 12.6. On 15.6, when the tadpoles were swimming freely, a few of them were brought into the laboratory and kept in tap water in a similar jar. The rest of this hatch remained out of doors. The first two metamorphosed on 23.9.1947. These will be called the "non-control" RR sample. They may indicate how comparable with the experimental material our *esculenta* material can be considered.

The *esculenta* sample, EE, were tadpoles captured by Miss Joyce Callow of Teddington, Middlesex, on 5.10.1947 in the Ham gravel pits on the south bank of the Thames. On 11.10 she graciously brought 30-35 tadpoles to the laboratory. All had hind legs and 7 had forelegs. From these the following 18 were selected :

- 2 with forelegs and a withered tail
- 5 with forelegs and a perfect tail
- 7 with no forelegs and large hind legs
- 4 with no forelegs and small hind legs.

Thus we owe to her the most advanced animals of a natural sample, which comparison with our non-control RR sample suggests, were of the same age.

EE cannot be considered as a control for the development of the other three cultures during 1947. The animals of EE were smaller at metamorphosis than were the other three during October, which permitted this sample alone to be fed to repletion throughout the winter. Therefore by the time the four groups were measured on 28.4.48 we consider that these two differences in conditions had cancelled out, and the four samples are probably comparable by the spring of 1948.

In addition to these four groups of animals reference will be made to a small group of French *esculenta*. These, which we owe to the hospitality of M. André Pacaud, Directeur du Centre d'Etudes Hydrobiologiques du Centre National de la Recherche Scientifique, who showed one of us the

locality, were captured on 21.4.1947 and 24.4.1947 in the Mare Saint-Leu in the Bois de Verrières to the south of Paris. They were small frogs, almost certainly yearlings, sitting in the herbage and jumping into the water when disturbed. One only was measured, and that only after a year in alcohol. It was 31 mm. long.

These animals were also of the striped form and coloured predominantly with vivid light and dark greens.

CULTURE CONDITIONS. There have been two experimental environments, though the animals have been temporarily placed in less controlled conditions. Balanced aquaria in glass sided and lidded tanks measuring 40 x 23 x 20 cm. stood in the southern window of a laboratory kept at 20° C. except during the summer of 1947 when the temperature rose several times to 30° C. and the night temperature was allowed to drop to 17° C. This room is artificially lit on most evenings until nearly midnight. Water plants and food were transferred from one tank to another to keep the conditions in them as similar as possible. Bricks and stones were provided so that the metamorphosed animals could leave the water.

The second environment was the outdoor vivaria at Ruislip. These were walled enclosures with tight fitting covers of perforated zinc, ultra-violet-permeable "windolite" and glass. Each wall was 1.2 metres long and 0.2 metres high. Half the area inside was occupied by a pond 0.5 metres deep sloping up at one side to the level of the surface of the soil. Each sample shared a vivarium with one or two *Triturus*.

The Verrières *esculenta* both in a laboratory aquarium and in a vivarium were kept in similar conditions, but they always lived with other species of comparable size. In the laboratory they had much less sunlight. Foods will be described later.

On 31.10.1948 an attempt was made to hibernate these animals in what was hoped would be systematised natural conditions. As, when they were examined on 27.2.1949, all the animals were dead, there is little point in describing our apparatus for this.

HISTORY OF THE ANIMALS IN THE LABORATORY. The development of the frogs is summarised in Table 1.

Hatching and the changes preceding it in the three groups of spawn RR, R ♀ x E ♂, and E ♀ x R ♂, were indistinguishable, and not pathological. There then must have been a great mortality in all groups, indicated implicitly in the notes, but only among R ♀ x E ♂ were sick and dead tadpoles observed. The tadpoles fed on dead worms, raw meat and a prepared food for laboratory rodents. They did not eat the plants which filled the tanks densely.

The three groups RR, R ♀ x E ♂, and E ♀ x R ♂, developed with striking parallelism. The bent tail observed in most animals was due to two bends in the vertebral column, just behind the anus, one laterally away from the midline, and the other sagittally so that the tail extended functionally medianly behind the body of the animal. It was hardly displaced in the dorso-ventral plane. This deformity has been observed before among tadpoles reared in captivity (Smallcombe, 1949). As it also occurred in RR and later (27.10) in EE we consider it due to deficiencies in the culture conditions.

At metamorphosis all three groups of animals were indistinguishable.

The young frogs were a darkish olive grey in colour with a few large black blotches. They had thus the pattern of their *ridibunda* parent. There was no trace of green.

The *Enchytracus* were fed in open petri dishes laid on the brick. The worms crawled out fouling the water. It is not thought that the frogs ate them. *Drosophila* of various species were fed in two ways. A jar containing a hatching culture of flies was stood in the tank. The flies flying out produced violent activity, frogs crashing against the cover glass while catching them. Next morning four frogs were found at the bottom of the narrow jars, one of which, in RR culture, was dead, perhaps from exhaustion, concussion, or being trapped in sunlight. The jars were then covered with coarse muslin, on which the frogs sat and caught the flies as they crawled through. Later etherised *Drosophila* were laid on the brick and eaten as they wriggled when recovering from the anæsthetic. The animals remained thin as too much energy was required to catch an individual fly.

14.10. Through the generosity of Mrs. E. M. Stephenson of the University of Auckland and the Department of Zoology of this College, we were able to feed our animals on house flies obtained as pupæ from the department of Entomology at Imperial College.

Recently enclosed etherised animals were laid on the brick and usually eaten before they were able to fly. This food permitted the animals to grow. They were not always fed to repletion which for this size and temperature we would estimate as 10 flies a day on 4 or 5 days a week. Attempts were made to ration food when it was inadequate, but extra food was also given to groups that appeared hungry. A hungry frog sits on land unless disturbed, a full one stays under water. We have not seen a frog eating under water. We observed the phenomenon first described by Honigmann (1944) in *Bufo*, of a frog precisely licking the eye of another frog which has snatched a fly away from it. We were not able to confirm that this can take place when there is no movement of the eye itself, as a frog's eye is very active in swallowing, but it is curious that of all their companions' movements, this alone regularly produced an attack.

The EE tadpoles, metamorphoses took place over a longer period at a lower temperature. Animals with tails hardly regressed, the tadpole shaped head and eyes, frog lips but tadpole-sized mouth, were seen to sit out of water for periods of about 2 hours at a time opening and almost closing their mouths with a frequency of 40 times a minute, the frequency of a tadpole's respiratory movements. Deaths usually occurred when the animals had undergone this much change. The laggard tadpole in both the E ♀ x R ♂ and EE groups was much smaller than the animals that metamorphosed at the normal times. They had the typical shape and did not resemble the giant tadpoles sometimes observed in this species.

During February and March the striped pattern developed in both groups of hybrids and the larger EE animals. Thus the striped pattern is genetically dominant over the spotted. The hybrids alone developed any green coloration, and this was a very dull colour confined to the snout.

The RR and hybrids samples by early spring ate *calliphora* as well as house flies. The RR and R ♀ x E ♂ grew quicker and ate more than E ♀ x R ♂. Probably because of this quicker growth R ♀ x E ♂, and later

RR, developed a clumsiness in jumping and climbing, then a difficulty in righting themselves if placed on their backs, and finally a deformity of the hind legs which might be held in a splayed position away from the body or twisted and dragged in walking. This was clearly the softening of the bones described by Bruce Parkes and Lantz (1947) in *Discoglossus pictus*, though in our animals the hind legs rather than the jaws seemed the most sensitive region, and hindered the capture of food. Mr. Lantz believed these symptoms to be common in frogs of species that habitually sit in the sunshine, when reared under glass. These two deformed cultures still fed and were clearly the most advanced as they were the only animals that produced a voice. Only the EE animals would take flies from forceps, the frogs of the other three groups, however weak, always splashing into the water if approached.

By 23.4 all animals in RR and R ♀ x E ♂ groups were unable to jump, so their tanks were placed out of doors, without lids, in the sunshine every day for a period of about 7 hours. On the 1st of May the animals were liberated in the comparatively natural conditions of the outdoor vivaria, after acclimatising them to lower temperatures for the six previous nights. On 28.4 the snout-vent measurement was made with vernier calipers while the animals were under ether. The larger animals, i.e., RR and R ♀ x E ♂ required surprisingly more ether than the other two groups to become flaccid. While recovering they produced a mucous described as smelling of blackberries, half-cooked beans, or almonds. The smallest RR animals became pale green with a vertebral line wider than that seen in the hybrids and EE. To the RR were added two "non-control" RR. They had metamorphosed on 23.9.47, had spent the winter in a small greenhouse for tropical animals (18°—26° C.) developed bone softening and been partially cured by exposure to sunlight. These had been the first animals of the *ridibunda* spawn, reared out of doors, to leave the water. Only twelve tadpoles were with them. In artificial heat these all metamorphosed completely by 19.11, but then died immediately.

The Verrières *esculenta* throughout the summer of 1947 were fed on worms and slugs. Of the six animals that arrived alive 3 had died by 25.7. The remainder were growing. On 14.10 their diet was changed to house flies. On 16.10 in artificial light during the evening the animals attempted amplexus. Two animals grabbed at each other on land sometimes while facing each other. They produced a low gentle resonant caw, inflating the front of the throat. This terrestrial incomplete sexual activity, extending over many hours, continued through the winter usually at night and under strong electric light. The animal held, which was occasionally a *R. temporaria*, always struggled and succeeded in escaping. Attempts were made to drag it from the land into the water. At least two animals appeared to behave as males.

At the end of January the animals began to croak while under water. The extension of the throat while croaking became more conspicuous, when the animal was looked at dorsally, but no external sacs could be seen. On 8.2 the long gargling or bubbling noise breaking into a croak was first recorded. During February the animals made several unusual noises, and on 26.3 it is possible that external sacs were extended, but the observation is doubtful. On 29.4 on one animal only could the external lips of the ex-

trusable croak sacs be found. During this time though the animals had grown to the region of 60 mm. long they showed no signs of bone softening. These six frogs in all conditions of temperature, light, health and emotional state, were green. The three that developed produced a vivid pattern of green, yellow, pink, black and brown bands. This was strikingly constant, and a marked contrast to our four experimental groups which were always drab in coloration, whatever their pattern. When the frogs were put out of doors, the feeding with house flies and blow flies was continued, pupæ and etherised imagines being put in the vivaria in earthenware dishes. Earthworms may well have been eaten.

The RR animals quickly recovered from the bone softening but the R ♀ x E ♂ remained weak and passive. They seldom left their hiding places which were therefore removed. They found less accessible ones. Though actively given food and not left to find it, fewer were seen and these became weaker. None could be found after 20.6.

As the EE sample grew the striped pattern appeared in all individuals, but unexpectedly the climatic and diurnal changes of natural conditions produced no marked changes in coloration. The RR sample remained olive or slaty with dull brown blotches, the E ♀ x R ♂ and EE showed the complicate striped pattern in dull browns and olives and fawns, and the Verrières *esculenta* showed their invariable brilliance in which a saturated green predominated. These *esculenta*, probably in their third year, ceased any sexual activity now that they were given a suitable environment for it, though there was considerable croaking by *Hyla arborea* in the same vivarium. May and June were cool in 1948. No noises were heard from any of these animals. On 4.10 the RR animals were offered new born mice, and ate them. Immediately after this the weather became cold and all frogs stopped feeding.

On 28.10 an attempt was made to capture all the animals, which were measured, though not etherised, before packing for hibernation. We nevertheless consider the measurements comparable. The four large RR squeaked or grunted while held for measurement, but no traces of external croak sacs were seen. The small RR was the only animal that showed any trace of the bone softening, its hind legs being twisted and trailing. On 14.11 the smallest EE animal was caught, measured and packed with the rest of the sample. No animals were seen on warm days in the vivaria until 1.5.1949, when an RR animal 64 mm. long was seen in his appropriate vivarium. He was greyish fawn with two rows of dark green blotches down his back and dark green bands on his hind legs. He expanded lateral croak sacs when handled.

On 27.2.1949 when the packed animals were examined, the condition of the corpses of EE suggest that this group survived the longest. One corpse each in both the RR and EE groups could not be found. Large calluses were found on the long bones of RR where they had healed.

VIABILITY AND GROWTH. Table 2 shows the numbers of the four groups that survived metamorphosis. Between 26.7 and 7.10 the following animals were killed, 1 R ♀ x E ♂ tadpole, 2 individuals of each kind of hybrid immediately after metamorphosis, and one escaped frog which should have been included in one of the second series of totals, probably of E ♀ x R ♂.

The similar proportion dying in EE, first counted when metamorphosis had begun, to those observed in the other three groups counted early in

TABLE 2.

	RR control	R ♀ x E ♂	E ♀ x R ♂	EE
No. of tadpoles that could metamorphose	19	23	21	18
No. that metamorphosed successfully	7	13	12	8

development, suggests that there is little mortality between the complicated crises of hatching and beginning to feed, and of metamorphosis and leaving the water. There is no evidence of a difference between the hybrids and the wild forms in this experiment (chi squared = 1.53).

Returning to table 1, comparison of the numbers alive on 18.12.47 and 28.4.48 shows that the mortality of the frogs during their first winter was negligible, even though two groups were developing a highly pathological condition. The summer mortalities were high (compare numbers on 1.5 and on 31.10) and *in these data* seem to have been selective, for out of 20 hybrids liberated only 5 survived while of 16 controls 12 were recovered (chi squared = 7.023). The RR animal, missed on 31.10 and recaptured on 1.5.1949, makes the difference between the mortalities observed in the hybrids and the

TABLE 3
Snout—vent measurements in millimetres

	RR	R ♀ x E ♂	E ♀ x R ♂	EE
	control metamorphosed	metamorphosed	metamorphosed	metamorphosed
	8.47	8.47	8.47	10 & 11.47
measurements 4.48	37	35.5	31	27.5
	38	36	33.5	28
	40	41	35.5	29
	41.5	41	37	29
	44.5	41.5	38	31.5
	47	41.5	39	33
	mean 41.3 ± 1.6	42	39	34
	S.D. 3.8 ± 1.1	42.5	41	36.5
		43.5	42.5	
		44.5	43	
	non-control metamorphosed			
	34			
	38			
	mean of total 40.0 ± 1.5	mean 40.9 ± 0.9	mean 38.0 ± 1.2	mean 31.1 ± 1.1
	S.D. 4.2 ± 1.1	S.D. 2.9 ± 0.7	S.D. 3.8 ± 0.9	S.D. 3.2 ± 0.8
measurements 10.48	43		49	37
	58		49	38
	59		50	38
	66		50	40
	66		51	42
				44
				52
	mean 58.4 ± 4.2		mean 48.8 ± 0.4	mean 41.6 ± 2.0
	S.D. 9.4 ± 3.0		S.D. 0.8 ± 0.3	S.D. 5.2 ± 1.4

TABLE 1

	RR	R♀ x E♂	E♀ x R♂	EE
1947				
4.6	Spawned out of doors.			
12.6	Hatched.	11.6	11.6	
		Young spawn probably from one pair brought to laboratory.	Brought to laboratory. Spawns from at least 2 pairs. Older spawn hatched.	
15.6	Tadpoles brought to laboratory.	15.6	15.6	
		Hatched.	Newly hatched tadpoles perhaps from young spawn.	
25.6	6 tadpoles put in 40 x 23 x 20 mm. aquarium.	2.7	2.7	
		24 tadpoles put in 40 x 23 x 20 mm. aquarium.	21 tadpoles put in 40 x 23 x 20 mm. aquarium.	
2.7	3 tadpoles surviving in aquarium. 16 more added.	17.7	26.7	
		Contained largest animals.	Hind leg rudiments in some.	
26.7	Hind leg rudiments in some.	26.7	26.7	
		No animals with hind leg rudiments.	Hind leg rudiments in some.	
	Animals not examined until :	Animals not examined until :	Animals not examined until :	
15.8	All have hind leg rudiments, some with bent tails.	15.8	15.8	
		All have hind leg rudiments, many with bent tails.	All have hind leg rudiments, some with bent tails.	
17.8	Water depth decreased to about 100 mm., its surface level with brick.	17.8	17.8	
		Water depth decreased to about 100 mm., its surface level with brick.	1 with well-developed forelegs and withered tail. Water depth decreased to about 100 mm., its surface level with top of brick.	
18.8	1 metamorphosed.	19.8	18.8	
		2 metamorphosed. <i>Enchytraeus</i> offered.	2 metamorphosed.	
19.8	<i>Enchytraeus</i> offered.	27.8	19.8	
		<i>Drosophila</i> fed.	<i>Enchytraeus</i> offered.	
27.8	<i>Drosophila</i> fed.	29.8	27.8	
		All animals have forelegs.	<i>Drosophila</i> fed.	
29.8	All animals have forelegs. Water level reduced to 50 mm.	29.8	29.8	
		All animals have forelegs. Water level reduced to 50 mm.	One tadpole with only minute hind legs still present. Water level reduced to 50 mm.	
7.10	6 frogs.	7.10	7.10	
		11 frogs.	10 frogs, 1 tadpole.	5.10 Tadpoles caught.
				11.10 18 tadpoles. 2 metamorphosing brought to laboratory. Put in 40 x 23 x 20 mm. aquarium.
14.10	<i>Musca</i> fed.	14.10	14.10	
		<i>Musca</i> fed.	<i>Musca</i> fed.	14.10 <i>Musca</i> fed.
16.11	Yellow on thighs.		24.11	22.10 Some animals eat <i>Musca</i> .
			Tadpole still has minute leg rudiments.	27.10 One tadpole with bent tail.
18.12	6 frogs.	18.12	18.12	8.11 6 frogs. 4 with forelegs and tail. 2 with hind legs only.
		11 frogs.	10 frogs. 1 tadpole.	24.11 8 frogs. 1 with forelegs and tail. 1 hind legs only.
				18.12 8 frogs. 1 tadpole with hind legs only.
			1948 :	
		2.2	9.1	
		Animals becoming clumsy.	Tadpole has forelegs.	
		12.2	14.1	
		Pale green snouts.	Tadpole decayed ; no tail.	
		Vertebral line.		
		27.2	27.2	
		Animals have difficulty in turning over if placed on their backs. Brick lowered in water.	Vertebral line.	
10.3	No sign of vertebral line. Animals blotched.	10.3	10.3	
		Pale green snouts.	Pale green snouts.	10.3 Vertebral line in larger Animals.
26.3	Largest animal dragging its back leg.	23.3		
		Clicking. One dead.		
28.3	Clicking.	23.4		
		Sunlight treatment.		
23.4	All animals have deformed back legs. Sunlight treatment.	28.4	28.4	
		6 animals measured.	10 animals measured.	28.4 8 frogs measured. Tadpole not found.
28.4	6 animals measured.	1.5	1.5	
		Liberated in outdoor vivarium.	Liberated in outdoor vivarium.	1.5 Liberated in outdoor vivarium.
1.5	Liberated in outdoor vivarium with 2 non-control RR.	30.5	30.5	
		5 animals seen.	7 animals seen.	30.5 7 animals seen.
30.5	6 animals seen.	7.6		
		5 animals seen.		
		11.6		
		2 animals seen.		
		20.6		
		1 animal. Last note.		
31.10	5 animals measured and packed.	31.10	31.10	
		5 animals measured and packed.	5 animals measured and packed.	31.10 6 animals measured and packed.
1949 :				14.11 1 animal measured and packed.
1.5	1 additional animal discovered and measured.	*29.5.48	*29.5.48	
		1 additional animal discovered and measured.	1 additional animal discovered and measured.	

cently even more significant. On the other hand its discovery throws doubt on all the numbers on which the comparison is based.

Table 3 shows the growth that took place during this time. It is a difficult table to analyse statistically as the samples are too small to substantiate many of the suggestions which can be made from it.

In April there is no significant difference between the size of the control RR, R♀ x E♂ and E♀ x R♂ but the EE sample are significantly smaller even when the non-control RR frogs are included. In October EE are still significantly smaller than RR and the surviving hybrids, which still do not differ significantly from each other, though it must be emphasised that the large variances of the October RR and EE samples, both depending on single individuals, make the comparison very dubious. Similarly a comparison of the growth rates of the three surviving groups is tentative. RR would appear to have grown 48%, E♀ x R♂ 29% and EE 34%. Thus again there is some suggestion of lower efficiency in the hybrids, but it is doubtful if the last two percentages are significantly different, owing to the small sizes of the samples, and the greater variety of EE.

DISCUSSION. Any complete account of these two forms will contain answers to the following questions:

1. Do the differences in the choruses of *ridibunda* and *esculenta* discourage hybridisation between the two forms? Using what would have seemed convenient forms of Nearctic *Bufo* Blair (1942) was unable to obtain evidence for this expected function of the Anuran voice.
2. In regions where the two forms occur together do they always breed at different times (Boulenger, 1897)? Do these always bear the same relationship to one another, and is any sort of gradient to be observed in this temporal feature between such regions, and regions where one form occurs alone, and the breeding seasons are extremely prolonged? Is any difference in time of mating correlated with any difference in optimal temperature of development such as Moore (1942) found to exist for many Nearctic species of the genus.
3. Are hybrid larvæ equally viable in crosses made from parents from all localities, or even uniform from parents of one form from widely separated geographical regions? This question is prompted by Moore's (1946 a and b) discovery of deformed larvæ in crosses between *R. pipiens* from the extremes of its range, whereas such deformities did not appear in crosses between *R. pipiens* and *R. palustris*. Our ignorance of the origin of the Surrey colony of *esculenta* thus becomes a serious handicap. Also is the discrepancy between the evaluation of the two forms by French and German systematists a reflection of difference between *R. ridibunda perezii* Scoane and *R. ridibunda ridibunda* Pallas, accepted as subspecies by Müller and Mertens (1940)?
4. At what stage or stages of development is the greater size of *ridibunda* achieved? Can these alter in different conditions? Our data suggests that the animals grow quicker, not that they grow for a longer time.

* These are further vitiated by the discovery on 29.5.1948 of an E♀ x R♂ animal, 51 mm. in length, without croak-sacs and showing the usual dark colouring of *esculenta*. It has been noted on the 29th but not elsewhere.

1. Is there a period of immaturity of the hybrid and post-femoral genetic contribution to the zygote are adapted to produce different growth rates? Have we obtained evidence for such a period of weakness by the greater mortality of our hybrids in their second summer?

5. Will larger numbers reveal that the hybrids are significantly smaller than the *ridibunda* controls, as they are significantly larger than the *esculenta*? Or is a dominance of the *ridibunda* size and perhaps form, responsible for the failure of systematists to find intermediate animals in nature.
6. Are there other barriers, perhaps to the sexual maturation and fertility of the hybrids, as in the crosses between *Triturus cristatus* x *T. marmoratus* (Lantz, 1947), or even in the development of the F₂ generation as in that from the hybrids between *Pleurodeles waltli* x *P. hagenmulleri* (Steiner, 1945)?
7. What environmental conditions produce the bright yellow colour on the lumbar and post-femoral regions of our *ridibunda* in their first year? This is so constantly absent in wild *ridibunda* that this colour difference is used as a taxonomic character to distinguish between the forms. Why did this not develop in *esculenta*, where it was expected, or in the hybrids?
8. Our animals reared for their first year after metamorphosis under glass maintained constantly the coloration characteristic of darkness or artificial light. As Seecroov (1914) showed and Boulenger (1921) confirmed that early environment has an influence on pattern development in this group, some potentialities may not be realised if they are not stimulated when the animal is young. Our observation that our Verrières *esculenta*, caught when a year old, seemed incapable of losing their sunlight coloration, is much more difficult to explain. Can the long exposures to artificial light, so that during their first year in captivity the light period lasted 20 hours in summer, produce a weakening of the mechanism of colour response to changes in the environment? Is this constant sunlight phase connected with the absence of bone softening?
9. Will the dominance of the striped pattern over the unstriped prove to be due to a single gene substitution as it is in *Discoglossus pictus* (Bruce Parkes and Lantz, 1947) and as the less certainly comparable unspotted effect of the *burnsi*-gene is over the typical spotting of *Rana pipiens* (Moore, 1942b)? Is the delay in the development of the striped pattern an artifact of unnatural conditions? Even so, is it delayed until the hybrids are significantly larger than the control *esculenta*, as is suggested by our animals, and is this a difference between the effect of the genetic mechanism in heterozygous and homozygous condition? Alternatively, was the development of the pattern delayed in all forms only until the Spring light intensity became great enough to evoke it? We saw our EE control freshly captured at a stage in metamorphosis in which the two patterns in *D. pictus* or *R. pipiens* would have been undulced even when reared under laboratory conditions.

The number and magnitude of these questions are sufficient emphasis on the indefinite and abortive nature of this report.

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The Reptiles and Amphibia of the Channel Isles, and their Distribution.

by

J. F. D. FRAZER.

The distribution of reptiles and amphibians in Gt. Britain has recently been described by Taylor (1948), but his account does not include a detailed survey of the Channel Islands.

The subject of the reptile and amphibian fauna of these Islands is one not easily approached. The latest published information would appear to be two articles by Sinel (1907, 1908), which are over forty years old and that there are inaccuracies in these is shown by his statements that *Rana temporaria* inhabits Jersey, and that *Natrix natrix* "has no local characteristics."

In order to understand the distribution of the various species amongst the islands, it is wise to consider how these lie.

From the map it will be seen that Alderney, although the most northerly, is the nearest to the French coast; while Jersey is the next nearest, the Guernsey group being well separated from each of these two. Jersey and Guernsey are large islands, while Alderney and Sark are much smaller. Herm is surrounded by shallows, and has obviously at one time been joined to the lesser island of Jethou. Sark juts further out of the sea and is mainly well above the sea level, while Brecqhou has only recently become separated from it: despite none being shown on the map, at least three ponds occur on Sark.

The Guernsey group has been separated from the mainland longer than Jersey, so that its fauna is correspondingly less. It is interesting to note that here again in legend St. Patrick is given the credit. The story runs that he came from his residence in Jersey to meet St. George in Guernsey, where their rendezvous is still known as St. George's Hill. St. Patrick is said to have been so annoyed on this occasion by the rudeness shown him by the inhabitants of Jersey during his residence there that he gathered up all the Guernsey reptiles in his cloak and liberated them in Jersey on his return thither.

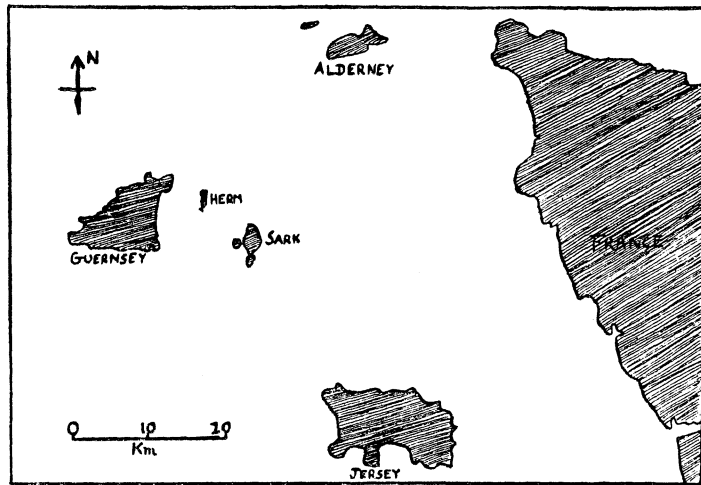
Distribution list.

JERSEY

Kemp's Loggerhead Turtle (*Lepidochelys kempi*)—One stray specimen at Beaumont in December, 1938, now in the Jersey museum.

Slow-worm (*Anguis fragilis*)—Fairly common in waste places throughout the island.

Green Lizard (*Lacerta viridis*)—This is a fairly common species throughout the island, and very common in some parts. Very large specimens are found in Jersey, and the usual adult size is 12 to 14 inches: the species here is very brightly coloured, the difference between specimens from Jersey and the continent of Europe being very marked.



Wall Lizard (*Lacerta muralis*)—Found only along the North-East coast of the island, from Gorey Common to Bouley Bay. It occurs on the cliffs, but never more than 200 yards inland. Its haunts only very rarely coincide with those of *L. viridis*.

Grass Snake (*Natrix natrix*)—Only the var. *astreptophorus*, Seoane is found in this island. This variety occurs also in Cyprus and the Spanish peninsula, and is characterised when adult by the loss of the white or yellow collar (and sometimes also of the black neck markings). No other snakes occur in the island, despite the record of *Coronella austriaca* (Paton, 1949); from the description given, it would appear that this was the present species.

Palmate Newt (*Triturus helveticus*)—The only newt found in Jersey.

Smooth Newt (*Triturus vulgaris*)—Stated by Sinel to be extremely plentiful in Jersey. It does not now occur there.

Common Toad (*Bufo bufo*)—The only toad present, extremely large specimens being not uncommon; this probably accounts for the fact that the Guernsey fisherman's term of opprobrium for a Jerseyman is "a Jersey *crapaud*." It is suggested that the increased size is associated with good feeding, both because insects are plentiful and also on account of the shorter hibernation period: this is about four weeks less than in England.

Nimble Frog (*Rana dalmatina*)—This European type is the only frog occurring in Jersey. It is commoner in the West, getting rarer as one goes East: it is not often seen further East than Mont Mado quarry ponds at St. John's. It is an inhabitant of both North Brittany and Normandy. Sinel has apparently mistaken this species for *R. temporaria* in his Jersey list.

GUERNSEY

Slow-worm (*Anguis fragilis*)—Stated by Sinel to occur in Guernsey. It appears to be still quite common. The patois term for it is "orvée."

Green Lizard (*Lacerta viridis*)—Found in Guernsey by Sinel and others forty years ago and earlier, having apparently been introduced from Jersey. By 1902 it had apparently become very rare, but is still to be found around Fermain Bay. Said to have been fairly plentiful there a few years ago. Also known at Vallette cliffs.

Common Frog (*Rana temporaria*)—The only amphibian occurring in the island.

ALDERNEY

Information about this island is almost non-existent.

Slow-worm (*Anguis fragilis*)—Fairly common (Sinel).

Common Frog (*Rana temporaria*)—Stated by Sinel to occur, presumably in the one well-watered valley. Until specimens are obtained there, it must remain uncertain (in view of his statement about Jersey) whether this species or *R. dalmatina* (formerly *agilis*) is present in the island.

SARK and BRECQHOU

Since these two islands have obviously only recently become separated from one another, they are taken together. Brecqhou is in private ownership, so landing is not possible.

Common Frog (*Rana temporaria*)—The only species found in Sark. The only specimen I have taken there was very large by English standards.

HERM and JETHOU

Another pair of islands which seem to merit being taken together.

Slow-worm (*Anguis fragilis*)—Stated by Sinel to be fairly common in both islands.

My thanks are due to Miss F. Jackson of the Société Guerneseaise for suggesting certain references for this paper: to Nigel Bellairs, Esq., of Ethonpe, Limpsfield, Surrey, and to his correspondents for information about the present status of the two Guernsey lizards; and to H. J. Baal, Esq., of the Société Jerseyaise for information on the distribution and habits of various species in Jersey.

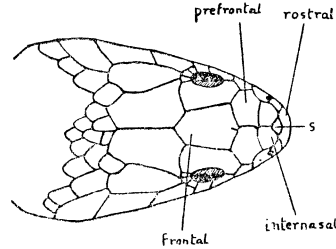
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NOTES

SCALE VARIATION IN *NATRIX NATRIX HELVETICA*.

In 14.7.47 I caught a grass snake in Epping Forest, a male of length about 775 mms. The following unusual variations were noted; a small shield (s, in figure), between the rostral and internasals and a cleft in the anterior border of the frontal;



also the ventral immediately preceding the anal was divided (which variation is not uncommon in snakes). The other scale characters were normal; V 173, C 63; 19 rows of scales as far as V No. 82, 17 rows from V No. 83 to cloaca.—GARTH UNDERWOOD (Dept. of Zoology, University College of the West Indies, Jamaica).

AUTUMN MATING IN YOUNG GRASS SNAKES.

Rollinat in *La Vie des Reptiles de la France Centrale* (1934) has recorded the autumn mating of snakes but this has not been observed in any species in the U.K. It is therefore, of interest to be able to record the following: early in November, 1948, a number of fully grown female *Natrix natrix* were obtained by the Zoological Society from Lancashire. They were all emaciated, having laid eggs. The evening of their arrival they were placed in a cage already containing six young males, one of which started mating immediately. The following day three other pairs were observed copulating. None of the male snakes was more than 450 mm. long and it is assumed that they had become sexually mature during the summer.—J. LESTER.

SEXUAL BEHAVIOUR OF GRASS SNAKE WITH HAMADRYAD.

In October, 1948, two *Natrix natrix* were offered as food for a twelve foot Hamadryad (*Hamadryas hannah*). The larger of the two was taken immediately, but the other, a small male, approximately 300 mm. long, became sexually excited and in spite of the cobra feeding on the other *Natrix*, it endeavoured to mate with the cobra. It was most persistent throughout the day, coiling round various parts of the cobra's body, but at no time was it in a position to copulate. The cobra was obviously worried by this attention and moved round the cage, carrying the small grass snake with it. The latter was eaten on the following day. The sex of the cobra is not known.—J. LESTER (Zoological Society of London).

SLOW-WORM WITH YOUNG IN FEBRUARY.

On February 29th, 1947, some schoolboys when walking along a hedgerow near Deal in Kent, saw an adult Slow-worm lying on a heap of dead leaves. Thinking it was an adder they killed it and were surprised to see young ones emerging from the body. Eight of these were taken back to the school and have since had a more critical examination. The young were fully developed and apparently ready to be born. They measure between 75 and 82 mm. in total length.—MAXWELL KNIGHT (The Homestead, Park Road, Camberley, Hants).

ECTOPIC CALCIFIED EMBRYO IN VIPER.

W. T. Neill (Copeia, 1948, No. 2, p. 139) describes a calcified embryo found in the body cavity in specimens of *Natrix sipedon* and *Thamnophis radix*. While considering the possibility of ectopic fertilisation, Neill suggests that the anomaly was more probably caused by the most anterior embryo being forced out of the front end of the oviduct, either as a result of overcrowding, or by a disturbance of the normal oviduct peristalsis. He notes that the condition has only been described in oviviparous forms, where the number of the young may be very large.

I have observed a similar occurrence in *Vipera berus*. The specimen had been in captivity several weeks and was somewhat emaciated, though above the average in length. On dissection the oviducts were found to contain a total of 14 live embryos at a fairly advanced stage. The calcified embryo was lying in the body cavity near the left ovary, and was embedded in a hard chalky mass, just as described by Neill. This embryo seemed further advanced in development than those in the oviducts: it was presumably the relic of a previous pregnancy. The neighbouring tissues showed no obvious signs of injury. I have heard of an apparently similar case in *Anguis fragilis*.—A. d'A. BELLAIRS (London Hospital Medical College, Turner Street, E.1).

THE MIDWIFE TOAD (*ALYTES OBSTETRICANS*) IN ENGLAND.

In 1919 in an address entitled "British Batrachians" given before the South London Entomological Natural History Society, Mr. G. A. Boulenger recorded that the Midwife Toad "has established itself, no one knows how, in a former nursery garden in Bedford; it has been there for many years, and a friend of mine found it still in plenty last summer. Its presence is revealed by its whistling note, which suggests the sound of a small bell, or a chime when uttered as is usually the case by a number of individuals, and is produced chiefly in the evening and at night. This so-called toad, a member of the very distinct family Discoglossidae, furnishes an interesting example of parental solicitude, the male taking charge of the eggs, which are large and few and strung together like a rosary, immediately after oviposition on land, not in the water as in most other Batrachians. After extraordinary contortions, which it has been my good fortune to witness on several occasions, the male fastens the string of eggs round its hind limbs and carries them for a period of about six weeks, when he betakes himself to the water for the purpose of releasing his progeny, which escapes from the egg-capsules in the tadpole condition."

Eight years later this colony was recorded as still in existence, but since that date nothing has been heard of it and it was believed to be extinct. It is of interest to record, therefore, that the toads still flourish and I am indebted to Mr. W. S. Brocklehurst, J.P., in whose garden they now live, for a more complete history of their introduction.

The nursery garden referred to belonged to Messrs. Horton and Smart and the toads first appeared there about the year 1903. Their origin is not known but they are believed to have been imported in some packing cases of ferns and plants which were brought over from the south of France at that time. They first attracted attention by their bell-like notes. In Messrs. Horton and Smart's garden they remained until 1922 when a part of it was taken over by the Bedford Council to build a new Drill Hall and the pond in which the toads were accustomed to breed filled in. About a dozen of them, however, were taken by Mr. Brocklehurst and released in his garden a quarter of a mile away.

The spot in which the toads now live covers about an acre of ground. It is completely walled in except for the gate by which one enters, and should the toads wish to escape by that route there is nothing to prevent them. In one corner of the garden is a pond 17 by 8 feet in extent and 3 feet deep. It is surrounded on all sides by an extensive rockery where there is plenty of cover. The toads, however, do not remain in the vicinity of the pond but wander all over the garden, and their musical notes can be heard after dark all through the summer months. They are most active during May and June. The size of the colony is not known but it must be fairly large as there is no difficulty in finding specimens at any time when they are looked for. Breeding goes on all through the summer, the female of this species being able

to spawn several times in the year. On September 2nd of last year three males with eggs attached were found under one stone.

No special care has been taken of this colony except that as the garden is enclosed and is within the town limits, the toads are protected against their natural predators such as the smaller mammals, predacious birds and snakes. On one occasion the introduction of a hedgehog into the garden led to the destruction of a certain number of the toads but with the disappearance of the animal the population again increased. The English climate is evidently not hostile to this small creature.

—MALCOLM SMITH (Pyrford, Surrey).

GRASS SNAKE EATEN BY TOAD.

A young grass snake (*Natrix natrix*), measuring 9-10in., was placed in a vivarium with a common toad (*Bufo bufo*) which had been in captivity for about a year. Shortly afterwards the toad was seen with the posterior half of the snake hanging from its mouth. It was not until the third day after this attack was first noted that the toad succeeded in completely engulfing the young snake.—ELLEN HAZELWOOD (54, Somerset Road, Bolton, Lancs.).