The ecology of the common frog (Rana Temporaria Linn) in County Durham

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THE ECOLOGY OF THE COMMON FROG (RANA TEMPORARIA LINN.) IN COUNTY DURHAM

BY

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A dissertation submitted in accordance with the regulations for the Degree of Master of Science (Advanced Course in Ecology)

September 1971

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1.0 SYNOPSIS

The main aim of the project was to carry out a reconnaissance survey of the population ecology of the common frog, Rana temporaria. Both adult and larval stages were studied. The adults of a breeding population were caught, marked by toe clipping, measured and weighed. Information was gathered about breeding behaviour, and movements at the breeeding site. The sex-ratio and growth rates of individuals were estimated for this population.

The mean number of eggs laid per mass was determined. The decline in numbers of tadpoles was followed from the embryonic stage to metamorphosis in two study sites different from the breeding site. Numbers apparently fell by a factor of several hundred, the estimates depending on the method used. The possible influence of predators on the numbers of tadpoles is discussed.

The growth and development of tadpoles to metamorphosis was followed by taking samples of 30 tadpoles at weekly intervals and calculating the mean weight, mean stage of development and mean body length of these individuals.

A production figure was estimated for one of these populations on the basis of the population estimates and these means.

A culture method for Rana temporaria tadpoles was devised using a standard diet of oxoid ltd. SG1 prepared diet. The growth rate of tadpoles in both crowded and uncrowded cultures were studied. The assimilation efficiency of tadpoles fed on this diet was calculated by calorimetric methods.

2.0 Introduction

There are several reasons why the ecosystem containing a population of the tadpoles of Rana temporaria is rewarding to study. One is that the scale of the system can be chosen so that different elements may be added as the size of the pool chosen and its geographic location is altered. A high attitude pool, such as that studied by the author at 7000' in the Pyrenees (Falconer 1969), may contain only a few species besides Rana temporaria, whereas lowland eutrophic lakes may contain many more ~~of~~ species.

Another reason is that the animal ~~itself~~ lends itself to ecological studies of population dynamics. The eggs at any given spawning ground are laid virtually simultaneously and the tadpoles develop as a cohort of similar age. There is no risk of immigration or emigration occurring if small pools where only one population of frogs breeds are selected for study, as in the present work. This removes the need for xomplex sampling procedures or for marking large numbers of the population. The short aquatic life of this species facilitates population studies and production estimates.

The adult frog population may be readily studied by trapping and marking at the breeding site, where the majority of mature individuals in a given population may be trapped and marked in a single week. Age and growth data may be subsequently accumulated by annual visits thereafter.

Other reasons for carrying out this study included the fact that

the animal is still a common species in Britain despite the recent fears for its status as expressed in the popular press in the winter of 1970. Studies on the life history of this species in recent years have been very few, limited to the works of Oldham (1963), Ashby (1969), and Haapenen (1970). However, the observations of Savage (1961) form a stable base of published information for more detailed studies.

Savage (1961) described the larval development of Rana temporaria in many different ponds in the south of England. His data shows that there is much variability in the rate of growth and feeding behaviour of populations of tadpoles. It follows that the results given below are valid only for the populations described and should be used as a basis for generalisation, only with the utmost caution.

3.0 A review of Anuran Literature

3.1 Introduction

The information needed for comprehensive ecological studies on anuran species is not very extensive but has not yet been the subject of a wide-ranging review. No attempt has been made to describe the work of each author in any detail but the subject of the work of each author has been placed under broad headings.

3.2 Population Ecology

Dice (1952) stated that "thorough and long continued quantitative studies on the rates of increase, rates of mortality and fluctuations of populations living under natural conditions are very much needed". Because this type of study is the most difficult task in ecology, the type of study that Dice pleads for are still very few. Pearson (1955) uses Dice's words in the introduction to the first study of anura that extends over more than one year's observations. Previous authors had largely limited their comments to short descriptions of events of interest to natural historians. Work on the population ecology of anurans had, however, been accumulating. Force (1933) had analysed the size-frequency of a large number of Rana pipiens caught by hand on a single day, whilst Raney et al (1943, 1947) had developed the method of tagging large species of ranid with a metal tag and subsequently following growth and movements. However, it was Martof (1953a, 1953b), using toe-clipping as a more successful method of marking Rana clamitans, for behavioural studies, who provided the method used by Pearson (1955) in his comprehensive

study.

Since Pearson's work was published there has been a steady accumulation of data concerning the population ecology of frogs and toads. However, when Turner (1962) wrote a review of the demography of frogs and toads, only Bannikov (1950) had given life-table data for an anuran. The studies of Anderson (1954), Blair (1943), (1953), Breckinridge (and Tester (1961, 1964), Fitch (1956), Green (1957), Heatwole (1961), Jameson (1955, 1956a), Martof (1956b), Thornton (1960) and Turner (1959, 1960), all contribute towards a deeper understanding of anuran population ecology. No-one has yet followed the success of a marked cohort over its entire life cycle.

The population ecology of Rana temporaria is dealt with by Ashby (1969), Bannikov (1948) and Gaizauskiene (1966). The demography of natural populations of this species is not yet well known. Sergieiv and Vassheva (1949) record this species' response to a drought.

3.3 Growth Rates and Life Expectancy

The studies mentioned above contain a large quantity of information also applicable to this section, but reviews specifically on the subject of anuran growth or life expectancy are to be found in Flower (1925, 36), Pearl and Miner (1935) and Turner (1961). Little information on the rate of growth, survival or life expectancy of Rana temporaria has been published, but the work of Flower (1936), Wilson (1950), and March (1937) gives some

details, largely from captive specimens. Smith (1951) provides a good summary of what was known at that time.

Papers concerned in part or fully, with anuran growth rates are Blair (1953), Breckinridge and Tester (1961), Durham and Bennett (1963), Force (1933), Green (1957), Hamilton (1934), Kelleher and Tester (1969), Martof (1956a), Raney and Ingram (1941), Raney and Lachner (1947), and Ryan (1953).

3.4 Breeding Behaviour

Information on the breeding of Rana temporaria is given in Savage (1934, 1935, 1961), Curry-Lindhahl (1958) and the other works on this species previously mentioned. Other papers on the breeding of anurans are Blair (1961), Bragg (1940), Heusser and Ott (1968), Harrison (1922), Licht (1969a, 1969b).

3.5 Distribution and Evolution

The work of Smith (1951) gives the distribution of Rana temporaria, in the British Isles. Gislen and Kauri (1959) describe the distribution of this frog in Sweden and Boulenger (1897) describes the range of the species in Europe and Asia. Balcells (1956) discusses the temperature adaptations of Rana temporaria in relation to its southwards limits in Spain. Work by Moore (1939, 1949, 1950, 1954), has directed the attention of evolutionists to the temperature adaptations of the egg stage of the life-cycle, work that has been followed up on Rana temporaria by Douglas (1948) who confirmed that this species was adapted

to develop in cold waters. Other works on anuran evolution and competitive relations are Aebli (1966) on populations of Rana temporaria living at different altitudes in Switzerland, Dumas (1964), Inger (1969), Inger and Greenwood (1966) Licht (1969b), Martof and Humphries (1959) on American or tropical species.

3.6 The ecology of tadpoles

The ecology of anuran larvae has been neglected except by Savage (1935, 1950, 1952, 1961) working on Rana temporaria. Burgess (1950) followed the development of Scaphiophus hammondi larvae in the laboratory and tried to relate what he saw to events in the field. The absence of published field observations contrasts with the largelquantity of information and discussion in the literature on the subject of what limits growth in crowded cultures of tadpoles in the laboratory. This discussion is historical and began in the mid-nineteenth century. Akin (1966), Devenport (1899), Adolph (1931a, 1931b), Lynn and Edelman (1936), Swingle (1919a, 1919b), Wilder (1924) and Yung (1878) are works containing the bulk of this discussion. Recently Brockelman (1969) has made the important step of extending this work to field conditions.

The diet of anuran tadpoles is discussed in Belova (1965), Brockelman (1969), Costa and Balasubraniam (1965), Jensson (1967) and Savage (1952).

Herreid and Kinney (1966) discuss larval mortality in Rana sylvatica in Alaska.

3.7 Behaviour, Home-range and Movement

Studies of anuran behaviour were largely occupied with the highly developed homing behaviour exhibited by many, perhaps all, species of anura. Bogert's (1947), study is a good example of the earlier work. More recent studies have given insight into the role of navigation in the life of anura. Awbry (1963), Barlow (1964), Brattstrom (1962) Currie and Bellis (1969), Chapman and Chapman (1958), Dole (1965a, 1965b), Ferguson (1960), Heusser and Ott (1968), hage all published information about homing behaviour. These works have been carried out on breeeding migrations or on resident populations, the work of Kelleher and Tester (1969) and Breckinridge and Tester (1961, 1964) on hibernatory migrations provides interesting comparisons. Homing behaviour has been described for Rana temporaria by Savage (1935) and Oldham (1963). Studies on the method of navigation include those of Dole (1968) Heusser (1969) and Tracy and Dole (1969). Oldham (1967) gives a short review and a comprehensive survey of the phenomenon in Rana clamitans in Canada.

The existence of home-range in anura is now well documented and the possibility of territoriality and competitive exclusion of closely related species is not to be discounted. The initial work of Martof (1953a, 1953b), has been followed by Kikuchi (1958), studying a Japanese ranid and Ferguson (1960) studying the toad Bufo fowleri.. Heatwole (1961) carried out his research on Rana sylvatica and Bellis (1965) again worked on Rana sylvatica whilst Dole (1965a 1965b) studied the home-range and spatial relation-

ships of Rana pipiens. Recently Currie and Bellis (1969) have studied the home-range of the bullfrog Rana catesbiana. Work on Rana temporaria in this field is limited to the comments of Asby (1969) and the study of Haapenen (1970). Both authors find that the behaviour of this species resembles that of Rana pipiens and Rana sylvatica. The frogs of all three species have been observed to spend long periods of inactivity in the field, often making a form in which to sit. The protection afforded by this behaviour against dessiccation is discussed by Dole (1967). Heatwole (1961) also describes how strong behavioural responses to dehydration exist in Rana sylvatica.

Observations by Test (1954) confirm the existence of territorial defence in some species of tropical frog. Sexton (1960) studied this phenomenon in a tropical dendrobatid frog Prostherapis sp. No observations of this kind have been made for species of frog dwelling at temperate latitudes.

The work of Inger and Greenwood (1966) and Inger (1969) seem to indicate that inter-specific competion may occur in closely related species of tropical frog. There is no evidence for competitive exclusion in temperate climates.

3.8 Food

The food of Rana temporaria has been noted by Cott (1936) and his report is quoted by both Savage (1961) and Smith (1951) in their respective volumes. Work by the autor (Falconer, 1969) and Houston (unpublished) confirm that this species is an opportunist

feeder devouring any creature that it is able to capture. Mazur (1966) Shows that 95% of an anuran's diet is of insects. Work by Zimka (1968) on the closely related Rana arvalis show that this species feeds in the same manner but takes relatively a higher proportion of predatory invertebrates because these are more exposed to predation, due to their own feeding movements. Linley (1967) with Rana pipiens and Whitaker (1961) on Rana clamitans show that these ranids feed in the same opportunist manner.

Zimka describes the pattern of feeding as having two peaks daily, occurring in mid-morning and lateafternoon. He did not consider that food was ingested during the time of overnight darkness.

3.9 Predation

The frog is quoted by Smith (1951) as being widely preyed upon but Savage (1961) considers that mortality due to predation must be low. There are few references to predation on Rana temporaria in the literature but Grigo'ev and Egorov (1969) found that a major portion of the identifiable remains in scats from both the otter and the mink in an area near Archangel, in the U.S.S.R, were of frogs. Kabisch and Weiss (1967) report what must be a rare cause of winter mortality when they record brook trout (salmo trutta) feeding on hibernating frogs (Rana temporaria in Central Europe. Elsewhere Dole (1965) records a major part of the mortality occurring in Rana pipiens in Northern Michigan, in marked frogs was due to predation by the garter snake (However, he pointed out that losses

due to predation were small and thus lent some weight to Savage's idea. Turner (1960) also found very little mortality due to predation in his study area in the Yellowstone National Park.

3.10 The Bio-energetics of Anura

As yet little work has been published on the bio-energetics of anurans. Hill (1911) has given information on energy consumption of resting frogs. Mazur (1969) has studied the seasonal changes in energy reserves of Rana arvalis and Bufo bufo in Poland and also given important data on the cost of maintenance of Rana arval is. (Mazur, 1968). Chlodny & Mazure (1969) have studied the food requirements and efficiency of utilization of food by Rana arvalis and have found the apparent assimilation efficiency of this animal on a diet of earthworms to be approximately 85%. Avery (1971a) gives comprehensive information on the food consumption and assimilation efficiency of a lizard, Lacerta viridis, and (1971b) on the food consumption growth rates and assimilation efficiency of newt tadpoles, Triturus sp. which may assist studies.

3.11 Conclusion

There are few extensive or long term studies on the population ecology or bio-energetics of anuran amphibia. The field where information is most needed is that of population dynamics. The fluctuating growth rates of many anura Turner (1962) causes the

blurring of size-frequency distributions into normal curves so that even the first age group is often not distinguishable. The best way to obtain the needed information is to mark a cohort in a population and to follow the disappearance from this population of marked individuals. Few workers have had the time to carry out this essentially long term type of study.

In contrast the other large gap in the literature, in the field of anuran energetics, may be quickly filled as results are readily obtained. Rana temporaria has been little-studied and basic information on growth rates, life expectancy, causes of mortality, larval success in natural populations, was lacking prior to this study.

The Study Areas

4.1 Selection of Sites

The sites used for study had to be convenient to Durham and known to contain breeding populations of frogs each year. For studies of the behaviour of adults, and for hand-trapping the area of the pool or pools chosen had to be small, the surrounding ground had to be firm enough to move about on and the vegetation had to be sparce enough to allow good visibility. After several sites had been visited and found to be unsuitable one at Waldridge Fell in Co. Durham, was found to fulfil many of these conditions.

This was then visited at intervals of three to six days until spawning began.

After the spawning season had finished, several sites containing unhatched eggs were visited and two, one at Brasside, one at a Field Station, were found suitable for the study of the population dynamics of the tadpoles. Interference by young children made the site at Waldridge Fell unsuitable for population studies. There was no evidence of interference at the other sites.

Observations were also carried out at the Moorhouse National Nature Reserve where large numbers of frogs form part of a simplified ecosystem. Transport difficulties during the breeding season prevented large amounts of data from being accumulated from this site.

4.2 The Waldridge Fell Study Area

G.R. NZ 254497 Altitude 250 - 300' O.D. (80 - 100m) Sketch Map 1/ Plate 1.

The marsh which was the site for all studies on adult frogs and their breeding behaviour was situated below a disused spoil heap and is a basin in which two springs maintained the moist state of the surface. At the time of breeding the water table was high with much of the marsh flooded by clear water. There were only two areas of open water at the time that the site was s selected for study, although temporary pools on the surface of the vegetation were common. These pools are marked on the sketch map as shaded areas A and B. Spawn was laid either in the pool (Pool A) or adjacent to it (Pool B), The location of spawning sites is marked by S.

The vegetation at the site was a typical marsh assoication with a dense growth of Juncus sp. Other prominent angiosprems were Equisetum sp. and Epilobium sp. The dimensions of the marsh are approximately 24m + 25m, and did not vary throughout the time of the study.

4.3 Brasside Ponds

G.R. NZ 292451. Altitude 150 - 200' O. D. (50 - 70m)
See Sketch Map 2. Plate 2.

At this site a complex of pools has formed in the site of old brickworkings. Several larger areas of water lie to the north but in the shallower diggings to the south eleven small pools have formed. The pond selected for study is that designated A1 by Morphy (1967). Frogs spawned in one other pool besides the one studies approximately 30m. away. The ppol (A1) is not

separated from others in the areas, being linked by a channel through which water drains during the times of high rainfall. The plant association is again dominated by Juncus sp. Since the surrounding land was not marshy, a typical grass sward extends to the edge of the pool. Maximum dimenstions of the pool were 14m. + 6m. and depth was at maximum, 0.8m. Temperature regimes, descriptions of whater chemistry and faunal lists for several of the pools are to be found in Morphy (1967), Clennell (1968) and Lawton (1969). Higgs (1970) analysed the "communities" of all pools in the excavation and found no significant differences between them. There is no reason to suppose that the pools chosen for spawning by the frogs were different in any great degree from the others. It was not known why these pools in particular were chosen.

The water level in this pool varied but showed a consistent fall after May, until at the time of tadpole metamorphosis the area had diminished by about 25%. See sketch map. The growth of emergent vegetation also diminished the area of open water.

4.4 Field Station Pond

G.R. NZ 273405. Altitude 200' - 250' O.D. (70 - 80m)
Sketch Map 3. Plate 3.

This artificial pool is sited in a small valley bottom and is the most sheltered of the sites described in this study. It is shaded in part by mature trees and does not receive the sun until

fairly late in the morning. Another pool constructed at the same time lower down the feeder stream has been completely overgrown. The pool used in this study is also being invaded by vegetation.

The plant association is markedly different to that of other pools studied, and is dominated by grasses and not Juncus sp. The main grass growing on the margins and in the pool is Glyceria fluitans. This plant is an active invader into open water spreading by means of underwater runners. Veronica beccabunga is another major element in the association.

The water level in this pool was highly variable and the area submerged rose and fell according to the rainfall. The level is also partially controlled by an overflow where the feeder stream exits. This overflow was liable to erode and, if not repaired, could drain the pool.

The dimensions of the pool at its maximum size were 7m x 21m. The maximum depth was about 0.4m.

4.5 Moorhouse National Nature Reserve

G.R. NZ758328. Altitude 1700' - 2400' (500 - 800m)

Observations were made on the duration of the spawning season and development of spawn at this site. The reserve is the largest in England and consists of 4000 hectares of gently rolling blanket bog. Spawning took place in all pools. Large quantities of spawn were laid in shallow pools that were often

temporary. The spring of 1971 was dry and all pools at Moorhouse showed drastic changes with a majority drying up entirely. Most pools had a dominent flora of Sphagnum sp. but Juncus sp. was also commonly found.

5.0 Descriptions of the spawning areas

Spawn was laid in most cases near or touching the surface of vegetation that provided cover for the spawning frogs. Spawn was laid in most cases in a compact mass with clumps of eggs being laid on top of previously laid eggs. At the Field Station and Waldridge Fell sites one or two masses were found apart from the main spawn areas. At Brasside th eggs were all laid in a compact mass less than three feet across. At Moorhouse, spawning followed roughly the same pattern as at the lowland sites, but afforded many exceptions. Many masses of spawn were found away from major spawning areas, some was laid in pools with a bare silt or gravel bottom and in one instance spawn was laid attached to the marginal vegetation of a very deep pool. The lowermost masses at this site were exceptional in that they were over two feet below the surface.

5.1 Discussion

Savage (1935, 1961) porposes that the attraction of mature frogs to a specific spawning ground is due to edours given off by the algal flora. At Waldridge Fell, four artificial pools were dug just before the breeding season opened. Spawning occurred only in the natural pools. At Brassside the frogs had a choice of eight pools and spawned in two only. Licht (1969b) has described the breeding behaviour of two ranids and also in a later work (Licht 1970), has given details of selection of egg laying sites emphasising the differences between the two species that he

studied. It is likely that the site chosen for spawning in Rana temporaria is one affording maximum exposure to sunlight whilst giving the spawning frogs a good degree of cover. It is not yet known what attracts the first males to the breeding areas. Licht (1969b) describes how males of R. aurora make their way to the breeding areas silently and accumulate there for some time before chorusing begins. It is already known that ranids can orientate themselves well from a variety of stimuli (Oldham 1967). On this basis it is thought possible that the frog populations studied made their way to the spawning areas partly by memory.

5.2 The chronology of spawning

From the time of selection, visits were made to the Waldridge Fell Site at three to six day intervals. Spawn was first found on the 21st of February and subsequently the site was visited at intervals of up to 24 hours. Spawning ceased on March 13th, the total length of the breeding season thus being 20 days. Spawn was discovered at Brasside on the 13th March, at which time it was thought that spawning had ceased at this site. Spawn was found at the Field Station Pool on March 22nd and spawning had definitely ceased at this site by that date.

Results of counting the number of egg masses laid per day at the Waldridge Fell Site are given in Table 1. These are displayed as an histogram, together withthe maximum and minimum temperatures for the days in question in Figure 1.

5.3 Discussion

The question of the simultaneity of spawning seasons in anura has been discussed by Blair (1961) who found well marked mechanisms to confine breeding for each species to a certain time. Savage

however, (1961) finds the breding of Rana temporaria to vary over fairly long periods in the South of England. In the present study there seems good evidence that breeding commenced and finished at approximately the same dates in at least two of the study sites. Licht (1969b) found a strong correlation between temperature and breeding. In the present study the first egg masses appeared after a short period of rising temperatures and no further masses appeared when the temperature subsequently dropped. Further egg masses were only laid when the temperature began to rise again on the 7th March. It is, therefore, concluded that in the present study there is some evidence that the commencement of spawning is dependent on a certain threshold temperature being exceeded, which in the present study was about ^{o}c. If this temperature effect exists then it would have a strong correlating effect on the breeding seasons of different populations of frogs.

5.4 Separation of Spawning Areas

On Table 1 the areas where spawn was found freshly laid on different days is laid down. It is seen that early in the breeding season the eggs were laid in a pool termed "Track Pool". Later following an interruption in breeding activity caused by cold weather masses of eggs were found at what is termed the "usual" breeding ground. These areas are marked on Sketch Map 1. They were on different sides of the marsh. Frogs marked by toe-
cl clipping were found solely at the Track Pool during the first period of egg laying. Many males were found congregated ind track pool. However, on the recommencement of spawning following

the cold spell, egg masses were found at the "usual spawning ground and captured frogs showed that a movement of male frogs had taken place from the first spawning area across the marsh. For the period 7th to 11th March, frogs taken at Track Pool were either unmarked individuals or ones present before. On the 12th, egg laying again occurred at Track Pool and declined at the "usual" spawning area, and male frogs that had been first captured at the "usual" spawning areaswere found in Track Pool.

At Brasside two breeding groups formed, one very much larger than the other and 30m apart.

5.5 Discussion

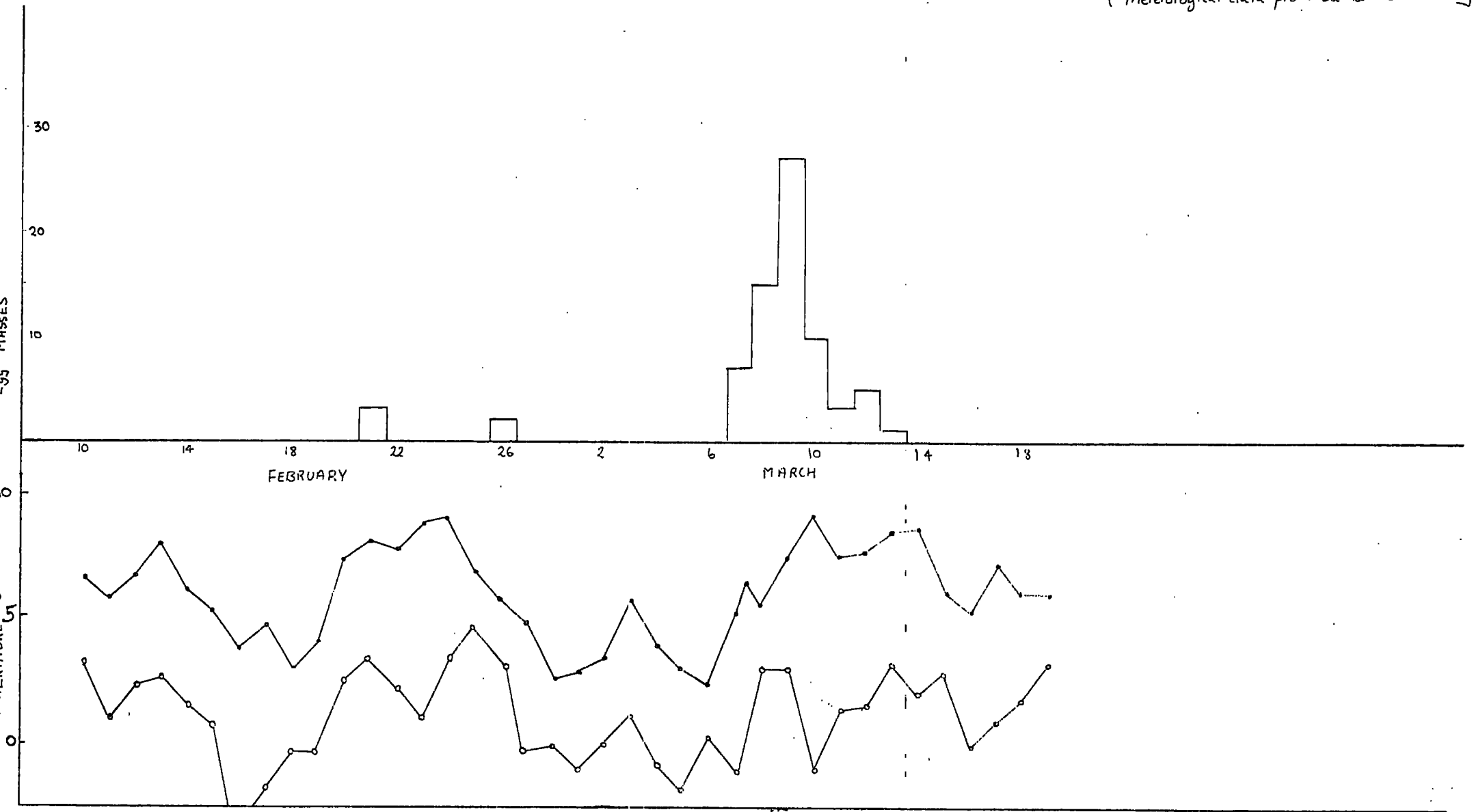
It is unlikely that the behaviour of the frogs observed at the study area at Waldridge is unique. The movement of male frogs between two spawning areas is indicative of the strong power of calling frogs to draw in other males to the breeding group. Oldham (1963) found breeding groups that remained separate only a few yards from each other. However, in this case one group was at the bottom of a pool, the other was calling in air vegetation nearby. The reason why the frogs moved back to the previously abandoned Track Pool after breeding intensity was declining at the"usual" site, is not known.

DATE	NO. MASSES LAID	SITE
February 21	3	Track Pool
26	2	- do -
March 7	7	Usual site
8	15	- do -
9	27	- do -
10	10	- do -
11	3	- do -
12	4	Track Pool
	1	Usual site
13	1	Track Pool

TABLE 1 The location and timing of spawning at Waldridge Fell Marsh, 1971.

Figure 1. RELATIONSHIP OF BREEDING TO AIR TEMPERATURE AT WALDRIDGE FELL

(meterological data from Durham Observatory)



Studies on the adult population

6.1 Methods

After its selection the site at Waldridge Fell was visited at three to six day intervals until breeding activity commenced. Subsequently the site was visited at least daily, until the cessation of breeding activity had been confirmed. Adult frogs were caught by hand unless in more than a few inches of water. The dense vegetation prevented the use of a pond-net. When a frog was caught it was placed into a polythene bag until it could be weighed, measured, marked and released. The frog was weighed and measured in this bag since this avoided transferring the frog when it might escape. The bag did not register on the scale which was accurate to 0.5gm. and weighed to 500gm. The nose-vent measurement was determined by allowing the animal to sit on the palm of the hand in the bag and placing a metal rule along the back. If the animal reacted by hunching it was induced to straighten out by gently pressing with the rule along the back. Only one measurement of each individual was made. Under the conditions it was decided that the extra accuracy given by taking the mean of three measurements such as carried out in the study of Raney and Ingram (1941) was not needed, the purpose of the study being to gain as much data and, therefore, to measure as many frogs as possible in the time.

The toes of each frog were examined for previous marks as it was captured and if it had not been previously marked the distal phalanges or digits were amputated in the manner described by

Martof (1953a). Care had to be taken not to damage the web of the hind feet which bled copiously if cut.

In order to confirm thattthe marking procedure described caused no mortality, the survival of four marked frogs was observed in a vivarium placed outdoors. for the duration of the study (February 25th to July 10th). These animals were fed on woodlice and earthworms. A marked frog released into the breeding population was observed on 20th May in good condition. See Plate 4.

The behaviour of male frogs at the spawn site was observed both at close range, by standing quietly near to the spawning areas. The frogs that had dived to below the vegetation would gradually come to the surface and resume their activity, taking no notice of stationary objects. Binoculars were also used. At night, as Savage (1961) suggests, the frogs are less likely to be frightened and were observed in the light of a torch.

6.2 Results

108 frogs were caught of which 14 were female. The total numbers of females as indicated by the spawn laid in the field plus that laid in the laboratory was 87. In the final sample of frogs taken on March 13th after marking had been going on for 20 days, 6 marked frogs were found out of a total of 23. Thus if this was a representative sample, about 25% of the male frogs were marked by the end of the study, giving an estimated population of 370 frogs with a sex ratio of about 3.25σ:1φ.

The sizes and weights of the frogs caught are given in Table 2 & 3 for male frogs, plotted in Fig. 2.

No.	Length	Weight	No.	Length	Weight	No.	Length	Weight
1	52	29	30	72	39	58	59	23
2	72	45	31	59	26	59	67	40
3	78	46	32	60	24	60	66	31
4	71	46	33	69	39	61	69	44
5	63	29	34	68	80	62	69	36
6	59	36	35	68	54	63	54	19
7	66	36	36	66	30	64	67	32
8	64	36	37	61	29	65	72	47
10	52	29	38	73	41	66	62	29
111	74	50	39	67	38	67	69	47
12	68	41	40	70	42	68	56	28
13	61	23	41	61	28	69	67	36
14	62	26	42	71	42	70	63	35
15	54	20	43	63	31	71	70	40
16	65	32	44	71	42	72	53	26
17	64	35	45	65	34	73	55	18
18	60	28	46	61	26	74	55	23
19	58	22	47	60	24	75	65	27
20	65	28	48	78	60	76	62	25
21	59	23	49	67	30	77	65	37
22	66	37	50	61	28	78	61	34
23	68	42	51	62	29	79	65	28
24	60	26	52	76	46	80	54	23
25	64	23	53	66	30	81	72	37
26	70	38	54	59	34	82	75	44
27	67	34	55	60	32	83	67	27
28	66	38	56	69	34	84	70	38
29	62	37	57	62	37	85	65	31

Table 2 The weights andllengths (gms. and mm.) of 85 male frogs trapped at the breeding ground at Waldridge Fell between February 21st and March 13th.

No.	Length	Weight
1	69	37
2	79	50
3	67	23
5	77	46
6	66	28
7	64	23
8	82	54
9	77	48
10	65	24
11	69	31
12	76	50
13	67	32

TABLE 3 The lengths and weights of 13 femalesfrogs taken at the spawning grounds of the Waldridge Fell study area.

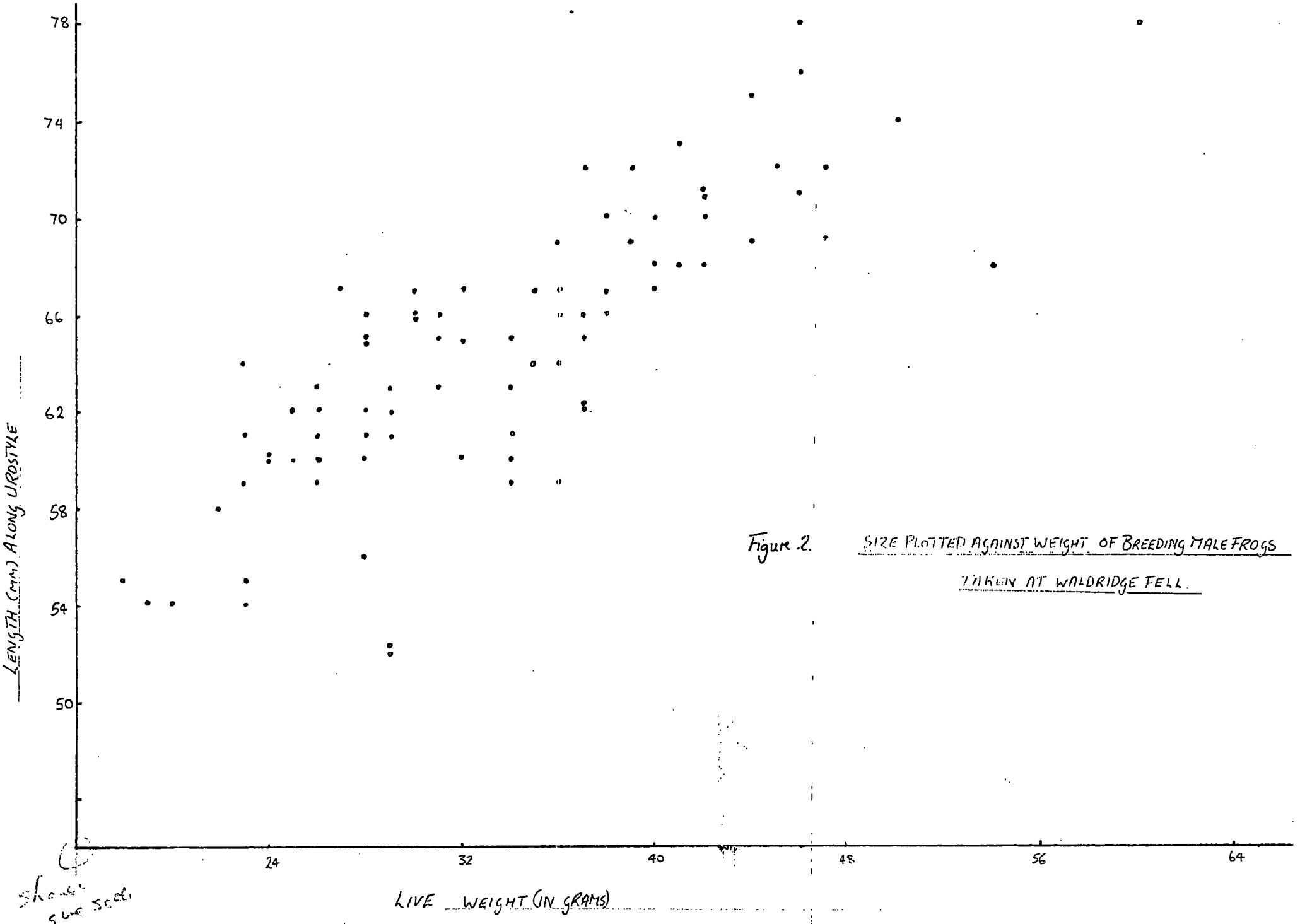


Figure 2. SIZE PLOTTED AGAINST WEIGHT OF BREEDING MALE FROGS TAKEN AT WALDRIDGE FELL.

23c

and The logarithms of individual weights are plotted against length in Figure 3.

The smallest male frog caught measured 55mm nose/vent and weighed 18 gms. The largest male measured 78mm long and weighed 60 gms. The mean length of 85 male frogs was 64.6 mm. and the mean weight was 33.5 gms.

The smallest female frog caught measured 64 mm. in length and w weighed 23 gm. The largest female frog caught measured 82 mm. long and weighed 54 gm. The mean lenth of 13 female frogs was 71.1 mm. and the mean weight was 36.9 gm.

The size-frequency of the frogs caught and also the weight-frequency of these frogs are plotted in Figure 3.

6.3 Discussion

The sex-rationof natural frog populations of Rana temporaria is not adequately researched. Oldham (1963) found a sex-ratio in the populations that he was studying of over 2 males to every female. In the present study it was found that the ratio of males to females probably exceeded 2:1. Many instances of disproportionate sex-ratios in anura are given by e.g. Blair (1943), Anderson (1954), Smith (1954), Jameson (1956), Pyburn (1958), Cunningham (1962), and Turner (1960). A common explanation for the different numbers observed of each sex is that the female spends less time on the spawning ground, and is more retiring than the male. However, in Oldham's (1963) study, the total number of spawn masses was less than half the number of

of Rana Temporaria

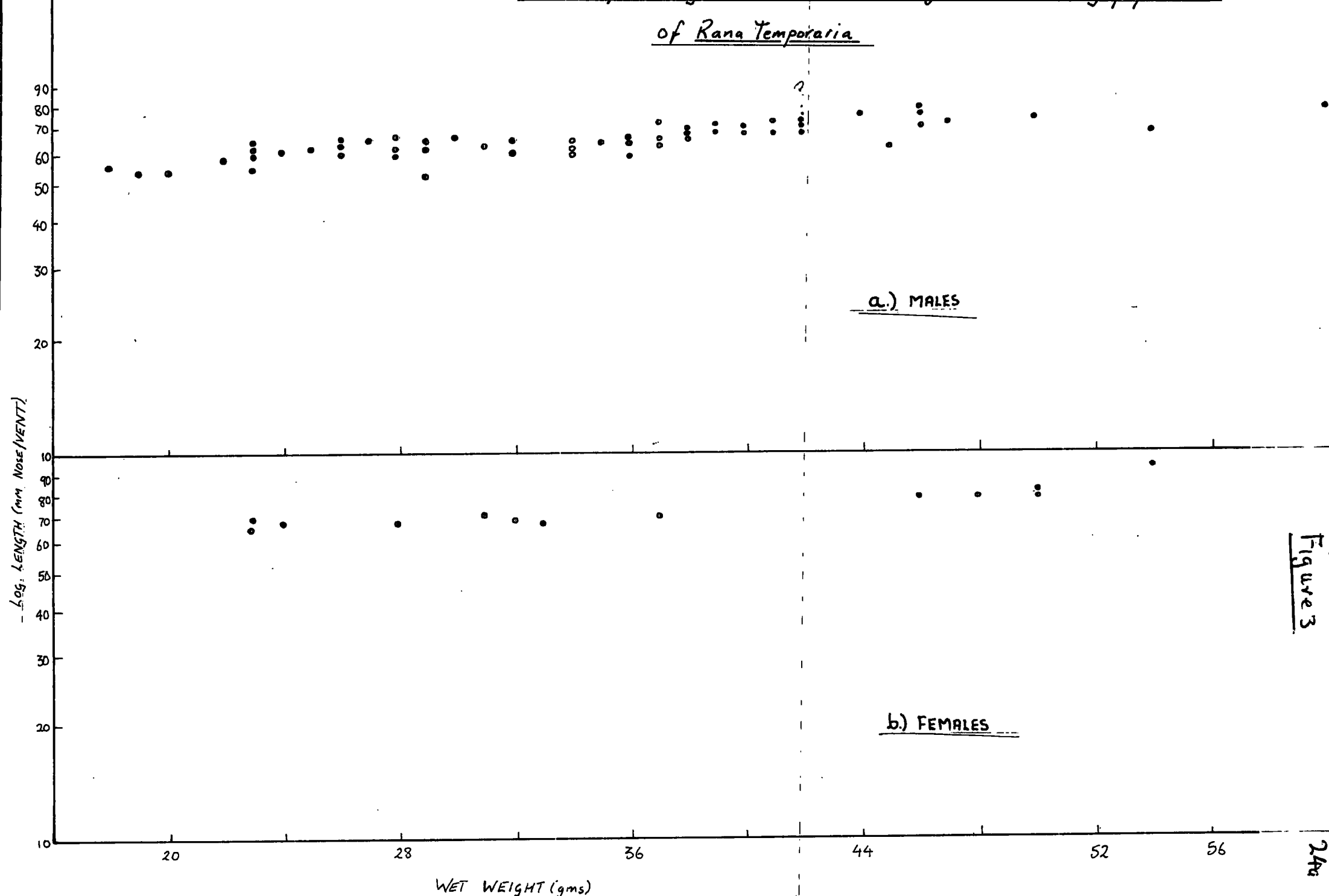
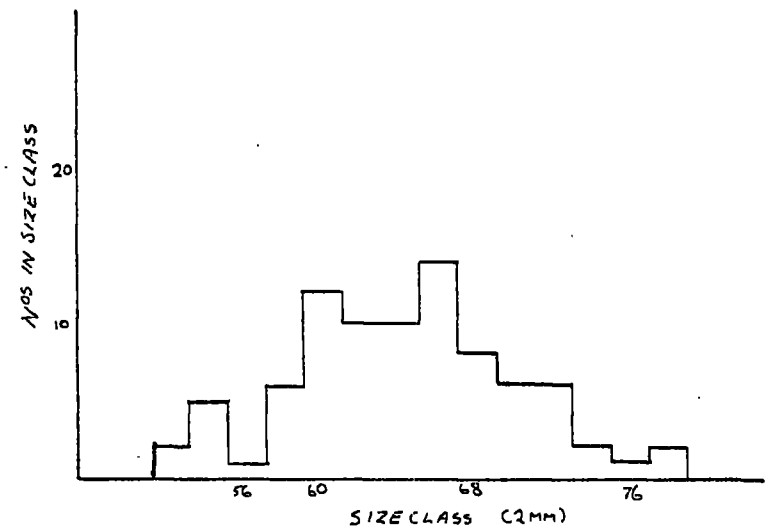
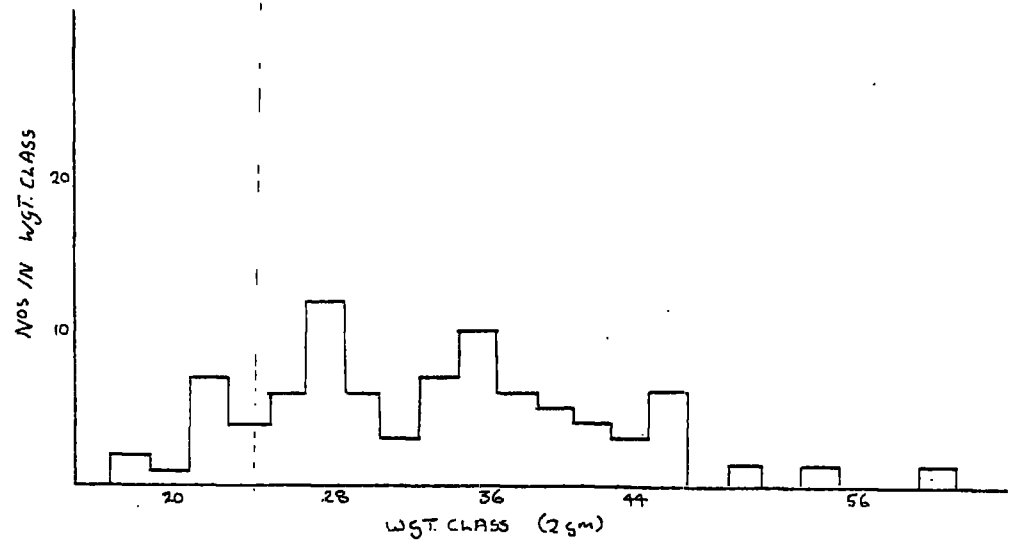


Figure 3

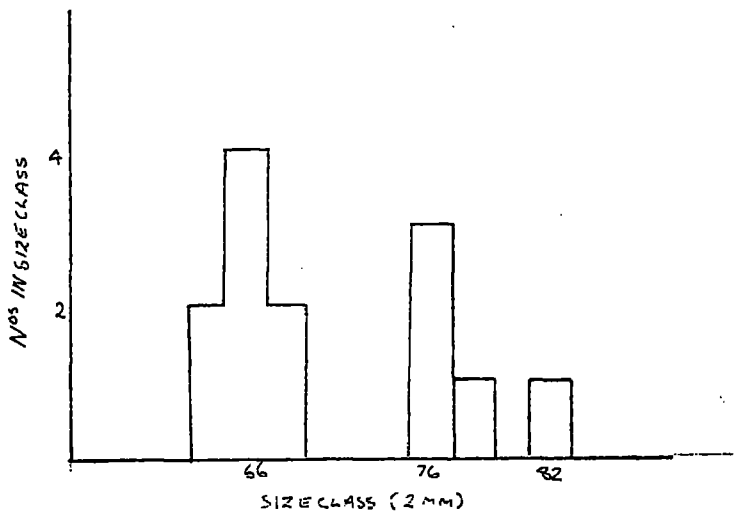
FIGURE 4. DISTRIBUTIONS OF SIZE AND WEIGHT OF CAPTURED FROGS



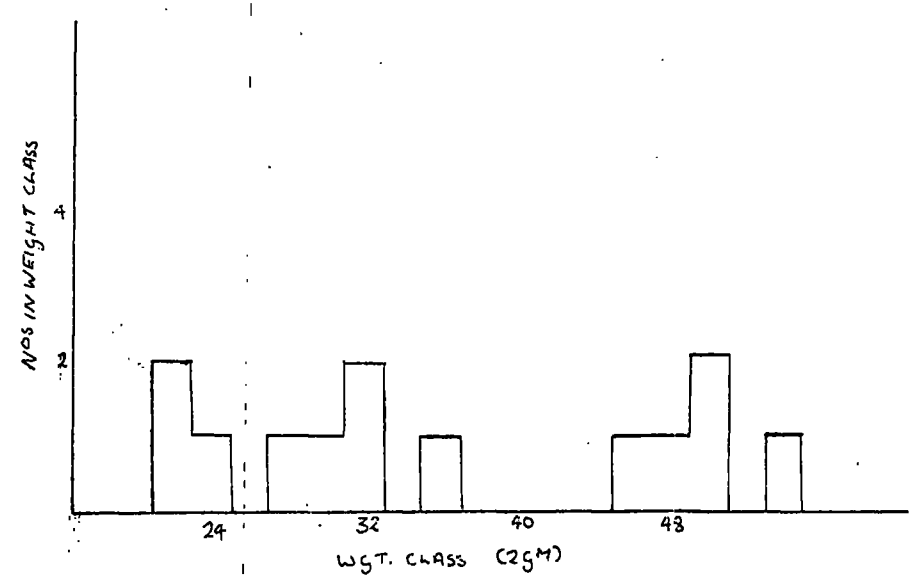
a) SIZE FREQUENCY MALE FROGS



b) WEIGHT FREQUENCY MALE FROGS



c.) SIZE FREQUENCY FEMALE FROGS



d.) WEIGHT FREQUENCY FEMALE FROGS

males caught. In the present study the evidence is less conclusive but strongly suggests that there were more males than females. It has been found by Smith (1950), Anderson (1954), Turner (1960) in Bufo bufo, Microhyla carolinensis and Rana pretiosa, the males all achieve sexual maturity a year ealier than the females. Thus one more year class is represented at the breeding grounds which may also account for the disproportionate sex ratio found.

6.4 The size-frequency of the male frogs

As shown in Figure 4a the size-frequency distribution of 85 male frogs taken from the breeding population at Waldridge Fell is a normal type of distribution. The normality of any distribution may be readily checked by plotting cumulative frequencies on normal probability paper after the method of Harding (1949). This procedure was carried out for this and the other distributions represented in Figure 4. The line obtained approximates to a straight line and thus represents a normal distribution. It is, therefore, not possible to distinguish modes within the size-frequency that may have represented age classes.

6.5 The weight-frequency of male frogs

As shown on Figure 4b the weight frequency distribution of 85 male frogs taken from the breeding population at Waldridge Fell shows several distinct modes when grouped as displayed. When Harding's probability paper analysis was carried out, the curve produced could be resolved into three distinct lines each representing a mode within the distribution.

However,,breeding male frogs accumulate a large and possibly variable amount of water in their sub-cutaneous lymph glands which, at present, prevents any assumption being made from the weight distribution. The method of Kolmogorov-Smirnov ( ), can give confidence limits for a distribution and test for significant deviations from it. In view of the complicating factor mentioned this test was not applied.

666 The size and weight distribution of female frogs

The distributions of the sizes and weights of the 13 female frogs for which reliable data is recorded are shown as histograms on Figure 4. The sample as grouped is not normally distributed. However, the small size of the sample prevents further analysis due to the possibility that the sample may not be representative.

6.7 Differences between males and females sampled

Caution must be applied when comparing the samples of males against the sample of females. There is a significant difference between the means of male and female lengths ($P = < 0.001$) and no significant difference between the means of male and female weight ($P = > 0.3$). The sample of females might have been biased by the inclusion of a number of large frogs. Also the fact that the male weight is greatly increased during the breeding season. (Up to 30% increase according to the data given by Wilson (1950)) by accumulating body water, whilst the female has a large and possibly variable percentage of her weight as eggs at this time is also a complicating factor in comparing the two sexes. The difference between the means of male and female nost-to-vent-length is about 6 - 7 mm. This difference is validated in a

larger sample, would be strong evidence for the hypothesis that females matured later than males in this species, since there is no evidence that the pattern of growth varies between the sexes (March 1937a).

6.8 Growth rates of Rana temporaria under natural conditions

The sole records for growth rates in this species is recorded in the papers of Flower (1925, 1936) and Wilson (1950). These are records of the growth of individuals kept in captivity and although of some interest in themselves, cannot be valid estimates of growth under naturally occurring conditions (Turner 1962). In all cases recorded for anura it has been found that the annual growth decreases with the size of the animal. Flower (1936) describes the growth of some young frogs that he raised under what may have been semi-natural conditions. The largest frog at four years old was 63 mm along the nost-vent measurement.

In the experiment that both Wilson (1950) and Flower (1925) describe, a male frog was kept until it was 12/ years old at which; age it had ceased to grow, having reached the length of 79 mm. A female kept under the same conditions attained the age of 8/5 years and measured over 80 mm.

It has already been shown that the age distribution of the sample of male frogs is normal and thus either there was only a single age group of males breeding in the site during the study, or the growth rates vary a great deal and have blurred the actual polymodality of this distribution. The first theory is unlikely since a differ-

ence of 23 mm. growth is difficult to attain in a single growing season in Great Britain. The maximum growth ever recorded for Rana temporaria is the instance described by Wilson (1950) when the male frog reached 65 mm. in 1.5 years. In the absence of concrete evidence it is permissible to theorise. There is some evidence, put forward above, that male frogs may mature earlier than female frogs. If this is so, then the smallest frogs found in the sample of males may be two years old or have completed a season and a half's growth. Young frogs transform at between 11 and 15 mm. in length (present study) so that the smallest frogs in the sample would have grown some 40 mm in the full season and the half season in which they have been spawned. For other species of anura of similar size the usual amount of growth until the first hibernation is some 5 - 10 mm. Observations by Ashby (1969) indicate a good deal of growth occurring in young frogs metamorphosing early in the year. If it is assumed that the young frog reaches a size of 21 - 24 mm. before it emerges for its first full season, then the growth taking place until it migrates to the breeding grounds some 10 months later is some 34 mm. Growth thereafter, following the pattern of other anuran species, would slow and if we assume a mean growth of 5 mm. per yer (based on captive frogs and Turner's (1962) collected data, then the eldest and largest frpgs in the sample taken would be 78 mm., when six or seven years old.

This sort of hypothesising helps to put the problem into perspective. However, the variable individual growth rates in field

populations of anura make it difficult to either confirm or deny the theory.

6.9 Mortality

If indeed the size-distribution is a true representation of several age groups whose sizes overlap, then the pattern of mortality can be examined, since if any age group is selectively removed this would affect the normality of the distribution. The curve remains normal and thus the yearly recruitment into the breeding population cannot be much greater than the size of the age-class above it. In the populations studied, recruitment of young frogs was several hundred into populations that contained only one or two hundred mature frogs. It is, therefore, thought that the pattern of mortality in Rana temporaria is one of very heavy larval mortality and then a subsequent reduction of immatures by a large percentage of the total, possibly over the first winter. Mortality is then continued at a low level after maturity is reached.

Causes of mortality are not known thoroughly for any anuran species. The frogs taken in the present study often had toes missing and occasionally whole feet. Haapenen (1970) describes some of the wounded frogs that he trapped. The cause of these wounds is not known. Female frogs are often reported found dead with ventral wounds, similar to those described by Turner (1960) in his study of Rana pretiosa in North America, caused by males fighting over females at the spawning grounds. No dead females were observed in the present study in lowland sites. However, four females were found dead on the moors at Moorhouse, one with a ventral slash

probably caused by a male. Twice struggling masses of males, attempting amplexus were observed at the spawning site, in a manner described by Savage (1961). A cause of mortality, probably important although not yet confirmed, is that of passerine birds feeding on emergent frogs. Burgess (1950) observed this to occur in Scaphiophus larvae.

6.10 Breeding behaviour

Licht (1969b) thought that the breeding behaviour of Rana temporaria as described by Savage (1961) was similar to that of another northern frog Rana aurora. However, Rana aurora lays its eggs in deep water and has a largely submerged chorus. In some instances Rana temporaria may behave in the same way (Savage, 1961, Oldham, 1963). However, in the present study, it was found that, in the breeding population studied, the males congregated in shallow water where there was submerged vegetation as cover. They called in air for long periods of time, with their white throats prominently dispalyed. Any movement of another male nearby would cause a male to move towards that male and attempt amplexus. The male approached would either hop away or sit still whilst uttering a high pitched release call. In only one case, was spawn found deep underwater. Females taken were all in amplexus, a fact that suggests females are quickly grasped upon entering the breeding group and after spawning, quickly depart. The post-spawning cessation ofaactivity mentioned by Ashby (1969) was also noticed in the present study.

Calling was at a low level thoughout the time of observation. The loudest chorus was on a warm sunny afternoon. Underwater

calling was not observed. Although Licht (1969b) reported this habit as belonging exclusively to Rana aurora it has been observed for Rana temporaria by Boulenger (1897) and Ashby (pers. comm).

The Number of Eggs Laid

7.1 Method

In order to estimate the number of eggs laid at the study sites, the approximate number of eggs in 30 individual egg masses was determined by a volumetric method. Fifty eggs were counted by hand and the volume of these eggs and their jelly was measured in a measuring cylinder. The total volume of the egg mass was then measured and the number of eggs calculated from the volume of 50 eggs previously obtained. Each mass had to be treated separately as the jelly continues to take up water for some days after the oviposition and therefore, the volume of individual eggs and the egg masses that they are in, varies according to the length of time that they have been laid. Egg masses measured came from Waldridge Fell.

The number of egg masses laid at each study site was determined by separating the masses by hand and counting them. The masses are adhesive when freshly laid and care had to be taken not to confuse large masses with two smaller masses adhering together. It is thought that there was a possible error of two masses at the site at Brasside and of three at the Field Station site.

7.2 Results

The results of the estimations for 30 egg masses are given in Table 4. The mean number of eggs per mass is 1322.4, ranging from 773 to 2326. The standard error of the mean is 243.6.

The number of egg masses at Field Station = ~~86~~ 93 ± 3

The number of egg masses at Brasside Site = 46 ± 2

7.3 Calculation of the number of tadpoles hatching at the two study sites

As described, the mean number of eggs per mass was determined by a volumetric method. The number of egg masses laid at each site was counted by eye with a good degree of accuracy. If some assumptions are made about the percentage of unfertilized eggs and the level of embryonic deaths, the number of tadpoles at hatching can be estimated.

Herreid & Kinney (1966) found the mean number of fertilized eggs in the species Rana sylvatica to be about 86.7%. Their experiments show that very cold water (below 5^{o} C.) may inhibit fertilization. The size of the egg masses that they studied was on average smaller than those found in the present study (mean no. = 778 as opposed to 1322) but since this is the only study available in which a field study has been carried out, their figure has been applied to the present data. However, their figure of 50% mortality in the prehatching phase is not applicable, except at the study areas at Moorhouse. It is thought that mortality in this phase was slight in the two lowland sites and that a 5% adjustment would suffice for this.

Thus the hatching number of tadpoles = no. egg masses x 1322
x .87 x .95
at either site.

At Brasside number of tadpoles hatching = 50250 $\pm$ 9111

At Field Station number of tadpoles hatching = 36890 $\pm$ 6627

7.4 Discussion

From the number of egg masses counted it is possible to estimate

Mass No.	No. Eggs
1	1,454
2	2,038
3	2,888
4	1,649
5	1,136
6	1,348
7	773
8	1,690
9	1,245
10	1,240
11	1,082
12	1,200
13	910
14	877
15	840
16	2,326
17	987
18	853
19	1,278
20	795
21	832
22	865
23	1,455
24	1,560
25	1,820
26	1,690
27	1,415
28	1,205
29	1,323
30	1,600

Table 4 The number of eggs per spawn mass of Rana temporaria.

the numbers of eggs laid in each pool with a fair degree of accuracy. It is thought from observations in the field and from culturing egg masses of this species that egg mortality is not usually high possibly between 0 and 10 per cent. If this is taken into account, the number of tadpoles entering the pool from the egg masses at Stage 20 of their development may be estimated, as a basis for population studies.

The mean number of eggs per mass contrasts with that observed by Boulenger (1897) which was between 1500 and 2000 on the basis of 6 masses counted. Heron-Royer ( ) gives the mean numbers of eggs per mass as over 2000. The lower estimate of Boulenger is well within the 5/2 fiducial limits of the present mean estimation (± 2 S.E.).

The distribution of numbers of eggs per mass grouped in size-classes of 100 is laid out as a histogram in Figure 4. It was thought that there was a strong likelihood that the number of eggs laid by each female increased yearly as she grew larger and hence the distribution of numbers of eggs per egg mass might give information on the age - distribution of female frogs. As seen in Figure 4, the numbers fall into no distinct pattern but have a distinct mode around the 800 point and there are possibly one or two modes between 1200 and 1800. If the smallest numbers of eggs are laid by females in their first year of breeding then the distribution found is highly convincing the largest numbers of masses (10 out of 30) coming from this group. An experiment designed to give additional information on this subject is

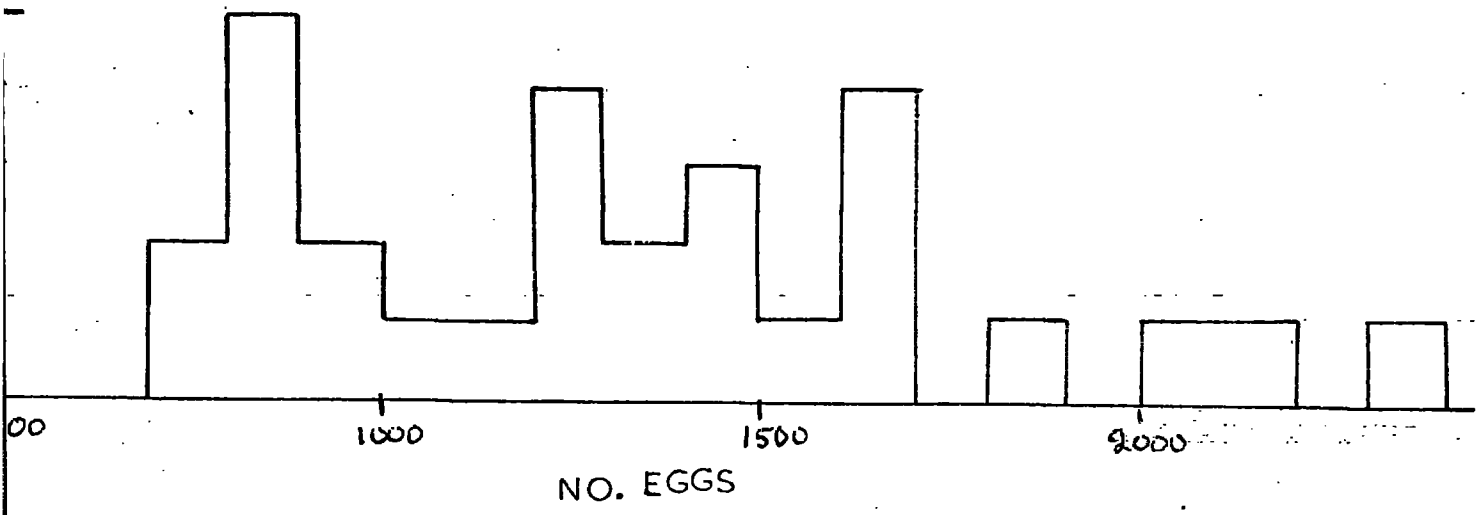


Figure 5 . The distribution of number of eggs in 30 masses of frog spawn taken from Waldridge Fell.

No. of female	Prespawning weight gm	Postspawning weight gm	Weight loss	% Weight (Postspawning) = Sex products
81	48	27	21	78
62	24	14	10	71
83	31	20	11	55
85	50	29	21	72
75	33	18	15	83
0	46	26	20	77
61	48	28	20	71
77	23	16	7	44

Table 5 The loss in weight of 8 female frogs kept under similar conditions at field temperatures until they spawned.

described below.

7.5 The weight loss of Female frogs after spawning

Method

14 female frogs were captured from the breeding population at Waldridge Fell and brought back to the laboratory where after weighing and measuring, their feet were marked in the manner described above. They were then paired with males and placed under glass vessels in about 0.5" of tapwater in an old sink. The vessels were necessary to prevent escape after spawning and to aid identification of the spawn laid by individual frogs. After four days had gone by with no spawn being laid the tapwater was replaced by pondwater. The first mass was laid the following night. After all the animals had spawned all but one were released at the Field Station (males also).

7.6 Results

Reliable data was only obtained for 8 females, one female died before spawning occurred, two others lost so much weight that it was considered that the marking had been confused and, therefore, the frogs could no longer be distinguished. The remaining three frogs variously escaped, or spawned, before the experiment had been set up in the manner described above and the weight decrease could not be reliably determined. The data from the remaining eight frogs is set out in Table 5.

7.7 Discussion

The mean weight loss of the females was 69% of their post-spawning weight. After spawning the female frog looks very emaciated and weak due to this great loss in weight. However,

the female termed O was kept in a vivarium for the duration of the study and quickly gained 5 gms. in weight on a diet of earthworms. She did not show any signs of putting on further weight or bf developing eggs before her death when she was accidently crushed by a rock in the vivarium. The designation 0 refers to the fact that the majority of both her feet were missing and she, therefore, had no toes that could be clipped.

The results show that the largest females lost a great deal more weight than the smaller ones. Frog number 81, 61 and 0 all over 40 gms. in weight before they had spawned lost over 20 gms. The largest frog 85, lost 21 gms., Frogs 83 and 75 lost 11 and 15 gms. respectively on spawning whilst the smallest frogs Nos. 62 and 77 weighing 24 and 23 grams. before spawning, lost 10 and 7 gms. respectively.

7.8 Conclusion

There are no comparable experiments on other anurans in the literature. In the experiment described, large females lost more weight during spawningthan smaller female frogs. Although there is some weight loss during this period due to utilization of stored food reserves it is probable that the weight lost was directly proportional to the weight of the sexual products. The spawn laid by these animals was marked and left in a refrigerator at 5^{o} C. for two weeks. When time was available for it to be counted, much had decomposed and so this evidence needed for confirmation of this theory is lacking. It is thought that the evidence is sufficient to state that large frogs, which may be older, lay more eggs than smaller frogs, which may be younger. The possibility of carrying out a survey on the age-distribution

of the female component of a frog population by counting the numbers of eggs per mass for the total masses laid is thus entirely feasible.

8.0 The development of the eggs, embryonic mortality

The eggs of Rana temporaria were found laid on vegetation either with the upper surfaces of the jelly exposed to the air or with a few cm. of water covering them. As the jelly took up water it became more flaccid, so that after the fourth day it usually subsided below the surface although it may have been formerly projecting above. On one case the spawn was found attached to vegetation in a deep pool so that some masses were over 2 feet (60 cm) below the surface. Savage (1961) and Oldham (1963) give details of other atypical sites for spawn.

The diameter of the egg was determined by stripping off the outer envelope and viewing the egg through a microscope fitted with a graticule eyepiece.

The mortality occurring in the first phase of larval development inside the jelly was assessed by counting eggs that did not develop in laboratory cultures and by examinations for eggs that were obviously not developing in the field. The field examinations failed in their object because by the time of examination the jelly had become so fluid that large quantities could not be examined due to handling difficulties.

Results

The diameter of the egg of Rana temporaria was determined to be 2.01 mm., SD. 0.08.

Mortality in the jelly envelope ranged from 50 to 1200 eggs to 260 in a mass of 1500 eggs. Field mortality was examined and

thought to be slight although counts were impossible to make.

8.1 Discussion

Licht (1971) thought that the habit of laying eggs in shallow water and in compact masses is an adaptation developed by anuran amphibia so that maximum use is made of the sun's energy in the development of the eggs. Species with these habits lay early in the year often just after regular frosts have ceased. Herreid & Kinney (1967) had come to the same conculusion and along with Savage (1950) and Licht (1971) prove that the formation of the egg mass is important in retaining heat. From these studies it is apparent that Rana temporaria is a typical early breeding amphibian and highly adapted to breed during short northern summers.. Douglas (1948) has shown that of three species of anuran, Rana temporaria developes quickest at the lowest temperatures.

In the present study it was found that most egg masses were laid in shallow water exposed to direct sunlight for much of the day.

Herreid and Kinney (1966) found up to 50 per cent mortality occurring in the eggs of Alaskan Rana sylvatica but could not attribute this toaany specific causes. In the present study mortality was thought to be low until the tadpoles hatched. At Moorhouse there was a higher incidence of embryonic mortality indicated by the appearance of a grey fungus in the jelly. Up to 90% of eggs were infected.

In conclusion the breeding behaviour of Rana temporaria is such that the eggs are deposited early in the year and the place of

oviposition and the structure of the egg mass is such that the eggs receive all the thermal energy available to them, so that the larvae have a good chance of metamorphosing before the growing season ends. Rana temporaria has the most northerly limits of distribution of any ranid and is found above the Artic circle (Hock 1956). Its adaptations may thus be the most developed of its type.

9.0 Investigations of tadpole growth and numbers

Little work has been carried out on larval populations of anura. Turner (1962) thought this was because the methods had yet to be devised that could provide accurate data. Herreid and Kinney (1966) have done much to rectify this situation and the present work is on the same lines, although the paper mentioned had not been read when the work was carried out.

Between the time of hatching of the spawn at the study sites at the Field Station and Brasside, and climax metamorphosis of the larvae the sites were frequently visited and sampled, in order to obtain as full a picture as possible of the events taking place in the two pools. On average visits were weekly although two unavaidable absences occurred when samples were delayed for periods of 9 and 11 days respectively.

9.1 Methods

A pondnet was used in a standard way to obtain a numerical estimate of tadpole numbers. Quantitative sampling using a metal tube to enclose an area of pool was used to give a conversion factor whereby the net samples could be covnerted into absolute numbers.

9.2 The standard net sample (SNS)

A standard pondnet with a polygonal opening of some 30 $cm.^2$ was used in a standard way by placing a metre rule on the surface of the water and sweeping the net three times along its length, keeping the edge of the net as closely applied to the bottom as

possible. The contents of the net were then turned out into a white enamel dish and any tadpoles extracted.

Before standard netting was started a series of samples had been taken to provide material for studies on the growth of tadpoles from hatching and standard netting did not begin until day 81. April 1st being taken as Day 0 when at Brasside over 50% of the tadpoles had hatched. These previous sampling had revealed the pattern of tadpole distribution within the pools and on this basis it was decided that the whole pool at Brasside could be treated as a single unit but that the pool at the Field Station would have to be spearated into two on the basis of the two very different types of substrate in this pool.

Because of the small size of both pools, it was considered not necessary to randomise sampling by dividing the areas up into sections and choosing these randomly. Instead the whole area of the pools was aampled by 10 SNS. The repeated net sampling caused the vegetation to become damaged and care had to be taken not to uproot areas of vegetation.

From the date of hatching 30 tadpoles were removed from each population at apprximately weekly intervals for the study of growth rates. After Day 81 the bulk of these 30 tadpoles were obtained from the 10 SNS carried out. If 30 were not taken then netting was continued in a non-standard way until 30 had been taken. These tadpoles were removed to the laboratory where they were killed by immersion in dilute formalin and preserved for later measurement.

9.3 Quantitative Sampling

In order to covert the SNS figures into estimates of absolute numbers, quantitative sampling was carried out on Day 81 at both sites using an aluminium tube. This was quickly pressed into the bottom of the pool so that its lower edge sank up to 3" into the bottom mud trapping any tadpoles present in the area enclosed. The tube (30 cms. in diameter) was then secured and vegetation inside was cut free, the entire contents were then dredged out using a handnet. The dredgings were turned out into a white enamel dish and tadpoles present were counted. It was not thought that any tadpoles escaped as the tube was pressed down.

9.4 Method of measuring sampled tadpoles

As described above, tadpoles were trapped weekly, brought into the laboratory, killed and stored in dilute formaldehyde solution (4%). No loss in weight or shrinkage was observed. On measurement the tadpoles were taken from the preservative solution and placed under a binolcular microscope when they were assigned a atage in development using the stages given by Witschi (1958) for Rana pipiens that he has adapted from Pollister and Moore's (1939) scheme for Rana sylvatica. The stages are illustrated and described in the Appendix of this present study. Excess moisture was then blotted off and the animal was weighed on a Mettler balance accurage to 0.001 g.m. being laid on a foil boat for this purpose. The body dimension was discovered by placing the tadpole on a piece of cm/mm graph paper. Care had to be taken

DATE	FIELD STATION				BRASSIDE				COMPARISON OF MEANS	
	mean wgt(gm)	S.E.	t	p	mean	S.E.	t	p	t	p
8.4.71.	-	-	-	-	.006	.0002	-	-	-	-
17.4.71.	.010	.0009	-	-	.022	.001	10.0	.001	6.6	.001
28.4.71.	.030	.0016	10.2	.001	.042	.002	6.5	.001	3.9	.001
6.5.71.	.042	.003	3.4	.001	.083	.007	5.2	.001	5.1	.001
13.5.71.	.135	.007	11.9	.001	.138	.008	4.8	.001	0.2	.8
20.5.71.	.170	.013	2.3	.02	.298	.013	9.8	.001	6.5	.001
29.5.71.	.225	.013	2.8	.01	.206	.012	4.8	.001	1.0	.3
3.6.71.	.320	.020	3.8	.001	.281	.020	3.1	.01	1.3	.2
14.6.71.	.460	.016	5.3	.001	.447	.022	5.4	.001	0.4	.7
21.6.71.	.503	.024	1.4	.2	.455	.026	0.2	.9	1.3	.2
27.6.71.	.597	.023	2.8	.01	.454	.022	0.05	-	4.4	.001
6.7.71.	.588	.020	0.3	.8	.421	.017	1.1	-	6.2	.001
12.7.71.	.434	.023	4.9	.001	.384	.016	1.35	-	1.5	.2

Table 6 The changes in weight of tadpoles at two sites, means of 30 individuals and standard error of means. The probability of there being significant differences between successive means and between the means of the two populations on the same date has been computed using t-values.

DATE	FIELD STATION				BRASSIDE				COMPARISON BETWEEN SITES	
	mean length	S.E.	t	p	mean length	S.E.	t	p	t	p
8.4.71.	-	-	-	-	4.0	.005	-	-	-	-
17.4.71.	4.0	.010	-	-	4.1	.007	0.8	.4	1.2	.3
28.4.71.	5.6	.016	8.1	.001	5.8	.018	8.5	.001	1.0	.3
6.5.71.	6.3	.016	3.0	.01	7.0	.016	4.8	.001	3.0	.01
13.5.71.	8.8	.017	10.2	.001	8.3	.019	5.0	.001	1.7	.1
20.5.71.	9.8	.019	3.9	.001	9.5	.027	3.5	.001	0.8	.5
29.5.71.	10.6	.024	2.4	.05	10.0	.028	1.1	.3	1.5	.2
3.6.71.	11.8	.023	3.7	.001	10.9	.029	2.1	.05	2.5	.02
14.6.71.	12.9	.013	3.9	.001	12.9	.020	5.4	.001	0.2	.9
21.6.71.	12.6	.018	1.4	.2	13.0	.025	0.5	.6	1.4	.2
27.6.71.	13.9	.010	5.9	.001	13.3	.013	0.7	.5	3.5	.01
6.7.71.	13.6	.014	1.3	.2	12.5	.009	4.8	.001	6.7	.001
12.7.71.	13.0	.013	3.2	.01	12.9	.014	2.4	.02	0.6	.6

Table 7 The changes in body length of two populations of tadpoles, means of 30 individuals and standard error of means. The probability of significant differences occurring between successive means and between the means of the two populations on the same date have been computed using t-values.

DATE	FIELD STATION				BRASSIDE				COMPARISON OF SITES	
	mean	S.E.	t	p	mean	S.E.	t	p	t	p
8.4.71.	-	-	-	-	22.0	0	-	-		
17.4.71.	23.0	0.0	-	-	24.7	0.15		.001		.001
28.4.71.	25.0	0.0		.001	25.0	0.0		.001	0	100.00
6.5.71.	24.9	0.04		.001	25.4	0.03		.001	7.8	.001
13.5.71.	25.16	0.05	2.9	.01	25.7]	0.04	6.17	.001	8.3	.001
20.5.71.	26.0	0.11	6.9	.001	26.2	0.11	4.11	.001	1.5	.2
29.5.71.	27.8	0.06	14.0	.001	26.5	0.11	1.6	.2	9.6	.001
3.6.71.	27.0	0.07	7.0	.001	27.4	0.13	4.9	.001	2.7	.01
14.6.71.	27.5	0.09	4.2	.001	28.1	0.10	3.8	.001	4.3	.001
21.6.71.	27.8	0.08	2.5	.02	28.2	0.16	0.3	.8	1.8	.1
27.6.71.	28.4	0.08	5.2	.001	28.7	0.15	2.4	.2	1.69	.1
6.7.71.	29.0	0.13	3.6	.001	29.8	0.25	3.5	.001	5.0	.001
12.7.71.	30.7	0.27	5.5	.001	30.2	0.29	1.1	.3	1.16	.3

Table 8 The changes in the state of development of two populations of tadpoles, means of 30 individuals from each population, standard error and t-values computed. The significance of differences between successive means at each site and between the means of the two populations on the same date have been computed.

Figure 6

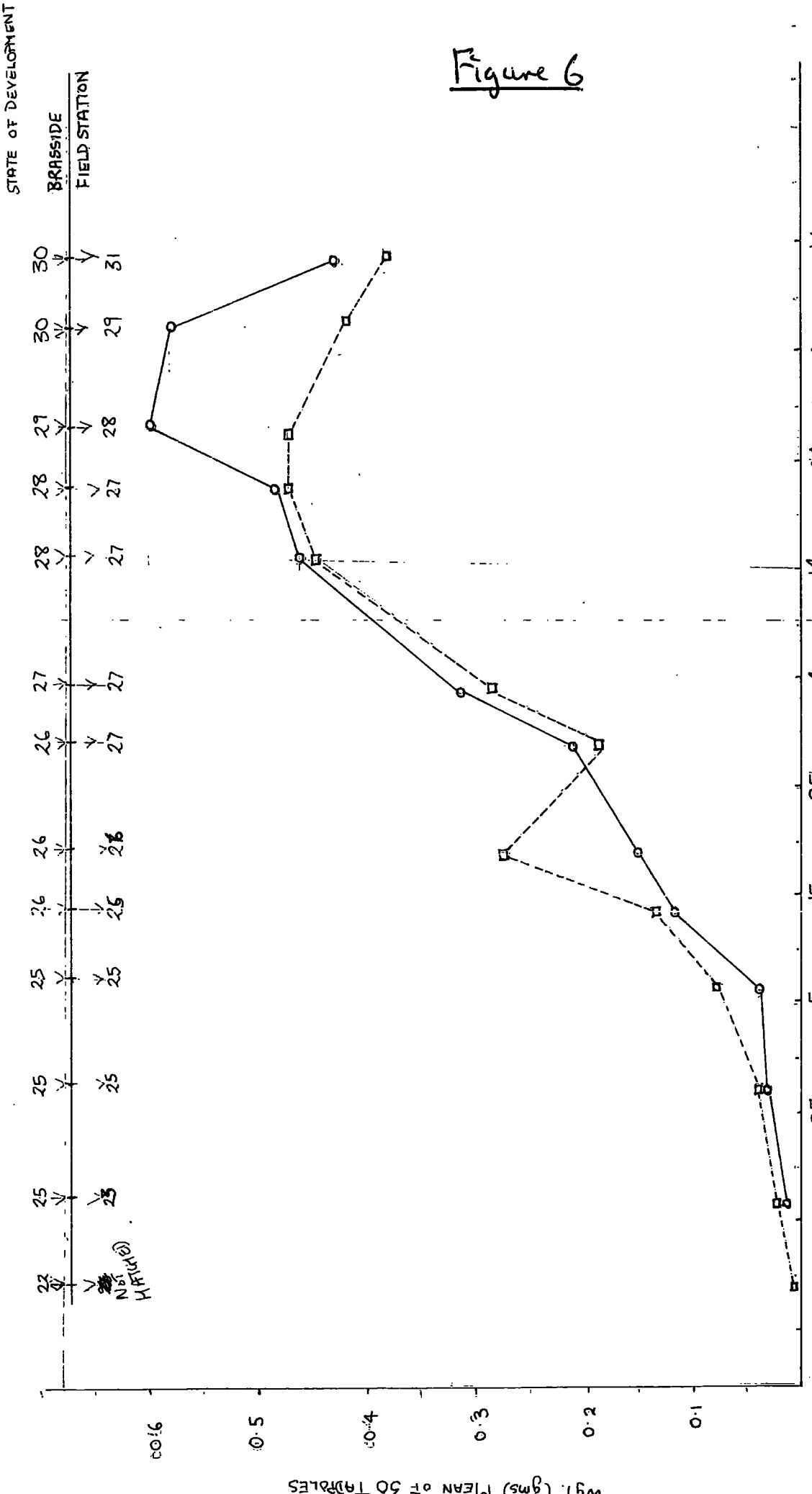


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FIGURE 6. GROWTH OF TADPOLES AT TWO SITES IN LOWLAND

because the smallest tadpoles in particular rapidly dehydrated if not kept moist.

9.5 Results of Growth studies

These are laid out in condonsed form in Tables 6, 7, and 8. Differences between successive samples have been tested for significance using the test known as Student's t test, after first using the variance ratio method to test for the normality of the samples. Differences between the two sites on the same date have also been computed using the same.method. T values and P levels are given.

These results are also plotted in Figure 6.

9.6 Conclusion

Both populations began their life as fre-living organisms by growing very slowly and growth continues in the familar exponential fashion with the major increases in both weight and length being found between the dates of 27 May to 14 June. The stage of development that grows fastest is seen to be Stage 27. An abrupt decrease in the average weight of tadpoles taken from Brasside on the 27th May is not immediately explicable. The mean weight subsequently falls below that of the Field Station population which hatched about one week later. In both populations there is a decline in the weight of individuals as theysstop feeding prior to metamorphosis. The graph of the increase in body length is more regular than that of mean body weight and shows a regular

increase in body length until climax metamorphosis is reached, at which point the mean length apparently decreases a little.

9.7 Discussion

The pattern of growth observed is ~~most~~ not markedly different from that described by Savage (1961) for southern populations of this species, or that shown by Alaskan populations of Rana sylvatica tadpoles (Herreid and Kinney (1966)). Savage (1961) attributes drops in the mean weight of samples of tadpoles to starvation which he finds fairly common in the pools that he studied. The drop in the mean weight of Brasside tadpoles taken on the 27th May is significant ($P = < 0.001$) compared to both the preceding sample and the succeeding sample ($P = < 0.01$). However, the mean length of the sample shows a significant increase on the preceding mean ($P = < 0.001$) but the sample taken on the 29th May shows no significant increase ($P = < 0.3$). Possibly the drop in mean weight while the mean length of tadpoles shows no such decrease but subsequently slows, indicates the onset of adverse factors in the Brasside Pool. Prior to this drop in weight growth had shown a typical exponential increase which if the Field Station population is taken to be normal should have continued for another two weeks before changing to an exponential decrease in growth rate.

As found for Alaskan populations of larval Rana sylvatica in the study of Herreid and Kinney (1966), growth is most rapid for this

species during the stages 26 and 27 and after the tadpoles have reached stage 28 the ir growth rate slows and finally reverses as the tail is re-absorbed and the fore-limbs emerge.

The mean maximum dimensions for the two pools are: max. wt. = .597 gm. for Field Station and .455 for Brasside, this is a significant difference (P = 0.001) and body length wqs. max. = 13.9 mm. Field St., & 13.3. Brassidepopulation (P = 0.01). Both mamimum dimensions were reached during stage 28 in Development.

10.0 Results of Population Estimations

Results of the quantitative sampling carried out to determine the officiency of the SNS sampling method are to be found in Tables 9 and 10. The SNS sample results taken on the same day at similar areas within each pool are also laid out in these tables.

From these results a conversion factor was calculated so that SNS sample figures could be converted into an estimate of absolute numbers of tadpoles in either pool. The Field Station site contained two widely differing habitats classed as vegetation and bare silt. Separate conversion factors were calculated for these two areas and they were treated separately in the ensuing weeks.

The Conversion factor was calculated in the following way:

if mean no. of tadpoles in SNS samples = a

and the mean no. of tadpoles in the sampling tube = b

and the area of the sampling tube = c

then the mean no. tadpoles/unit area in quant. sample $= \frac{b}{c}\ m^2$

$= x$

then conversion factor $= \frac{x}{a}$

$= y$

The conversion factor is applied by multiplying the mean number of tadpoles in any set of SNS samples by this factor.

The results of population estimations using the SNS method

The means of the SNS samples and the result of applying the appropriate conversion factor to them are laid out in Table 11. The estimates of population numbers are graphed logarithmically in Figure 7. It is seen that there is by this method of estimation a much smaller number of tadpoles in the two pools than at the time of hatching.

Area veg.	No. Tadpoles	Area silt	No. Tadpoles
a	6	1	3
a	6	2	6
a	4	3	13
b	6	4	20
b	3	5	11
b	2	6	2
c	5	7	5
c	2	8	3
c	1	9	6
d	6	10	2

Table 9(a) Results of quantitative sampling at Field Station on 20th May. For details of areas where samples were taken see Sketch map.

Area veg.	No. Tadpoles	Area Silt	No. Tadpoles
a	10	1	21
a	6	2	8
a	12	3	17
b	6	4	24
b	6	5	25
b	11	6	3
c	9	7	19
c	32	8	20
c	3	9	22
d	1	10	17

Table 9 (b) Results of standard net sweeps at Field Station on 20th May.

Area	No. Tadpoles
1	5
2	0
3	3
4	1
5	1
6	5
7	4
8	11
9	2
10	3

Table 10 (A) Results of Quantitative sampling at Brasside on 20th May. For details of sampling areas see Sketch Map.

Area	No. Tadpoles
1	11
2	5
3	3
4	3
5	5
6	1
7	4
8	3
9	2
10	3

Table 10 (b) Results on Standard Net Sweeps at Brasside on 20th May

10.1 Another method of population estimation

In view of the indirect nature of the method of estimating the population it was decided to carry out another estimation at both pools using the mark-recapture technique devised by Lincoln (19) and Peterson (19). The needed to be fulfilled if this method is to be accurate are discussed by Ricker (1949).

Method

A marking method was devised that was permanent and easily recognisable and was unlikely to be lost during the period of the experiment. This marking method consisted of clipping the end of the tail so that a clean cut took off the tip of the notochord. In the laboratory tadpoles marked in this way swam normally, did not bleed and fed normally. Several tadpoles marked thus survived for eight days with no mortality although mortality under field conditions could not be tested. Tadpoles with damaged tails and often extensively wounded, were often seen in the field. The mark could only be lost if the animal was eaten or had its entire tail removed. Two larvae trapped had lost their tails and had only a bleeding stump remaining. They were not recaught. The cause of the wounds was not discovered.

On the 27th June samples of tadpoles were taken at the study sites by taking 10 SNS sweeps as previously described and then continuing to sweep the pools for a period of 45 minutes.

All tadpoles caught during this time including the SNS samples were then marked as stated and replaced into the pools. Twenty four hours later the procedure was carried out again except that the tadpoles collected were brought back into the laboratory and examined after they had been killed by immersion in a dilute formalin solution.

10.2 Results

The results of this mark-recapture experiment are laid down on Table 12. The number of tadpoles recaptured was small being 10% and 14% of the total captured. However, it is thought that the numbers recaptured are sufficient to allow a calculation of the population numbers which are given in Table 12. These estimates which are only valid if all the conditions for this type of mark - recapture experiment were fulfilled at both sites, are 3850 for the Field Station and 916 for the pool at Brasside.

10.3 Discussion

The population estimates given by the mark-recapture experiment differ markedly from those obtained at the same date by the SNS method. These differing totals are given together in Table 13.

The mark-recapture results at both pools show a large under-estimation of population totals being made by the SNS method. Or conversely they show that the mark-recapture estimate has over-estimated the population at Brasside by over 200% and that at the Field Station by over 400%.

Since the experiment could not be repeated due to the lack of time available, the reliability of both methods of estimation

must remain suspect. For the purposes of this study the SNS estimates have been used. It must be held in mind that the population at Brasside may have been underestimated by 200% and that at the Field Station by 400%.

SITE	DATE	SNS means		TOTAL NOS. CALCULATED	AREAS USED
Field	20.5.71.	17.6	9.6	5842	Max. area =
Station	29.5.71.	12.6	7.8	4366	veg. - 37 m^2
	3.6.71.	8.0	2.2	2220	silt - 35.5 m^2
	14.6.71.	4.6	5.0	2033	
	21.6.71.	2.9	0.7	636	
	27.6.71.	2.6	3.0	896	Min. area =
	28.6.71.	2.8	0.6	731	veg. - 39 m^2
	6.7.71.	2.5	0.7	655	silt - 16.5 m^2
	12.7.71.	0.8	0.5	209	
Brasside	20.5.71.	4.0		2549	Max. area =
	29.5.71.	2.6		1657	51.5 m^2
	3.6.71.	5.2		3250	
	14.6.71.	2.0		1274	
	21.6.71.	1.9		728	Min. area =
	27.6.71.	1.2		460	31.0 m^2
	28.6.71.	0.9		345	
	6.7.71.	0.7		268	
	12.7.71.	0.4		153	

Table 11 Results of weekly SNS samplings and total estimated nos. of tadpoles present in the two study pools. Details of the areas of the pools are used in the calculations also given.

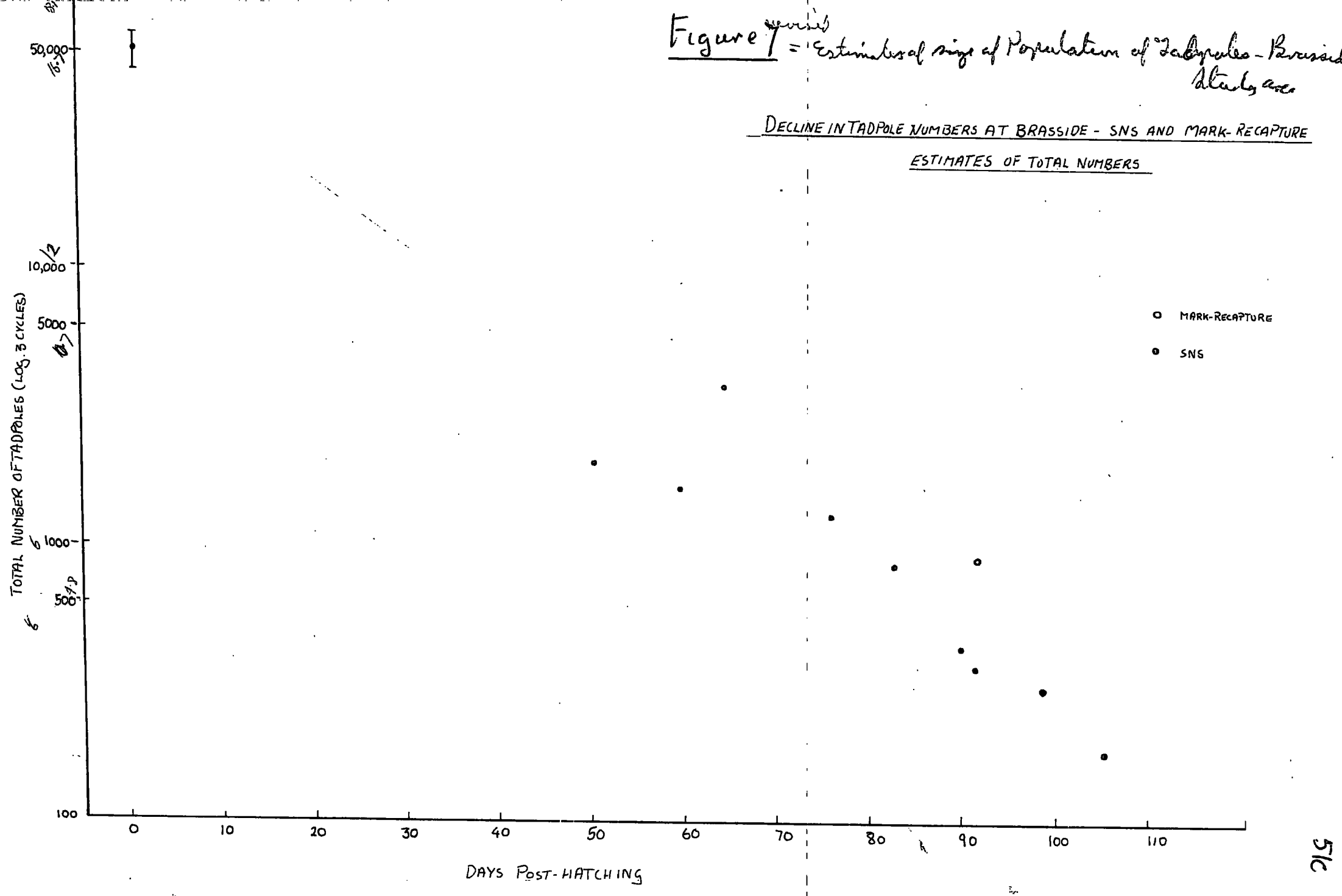
	Field Station	Brasside
No. tadpoles captured and marked 27th July	50	32
No. Tadpoles captured 28th July	77	28
No. tadpoles captured that were marked	8	4
Total No. tadpoles present if conditions for Lincoln Index fulfilled	3,850	916

Table 12 Results of Lincoln Index. Experiment carried out on 27th and 28th July

Site	Mark-recapture estimate 28 June	SNS estimate 27 June	SNS estimate 28 June	Mean SNS	% diff. methods
Brasside	916	460	345	402.5	227.6
Field Station	3850	896	731	813.5	473.4

Table 13 The differences between individual estimates of population at the two study sites.

Figure 7 = Estimates of size of Population of Tadpoles - Brasside Study area.



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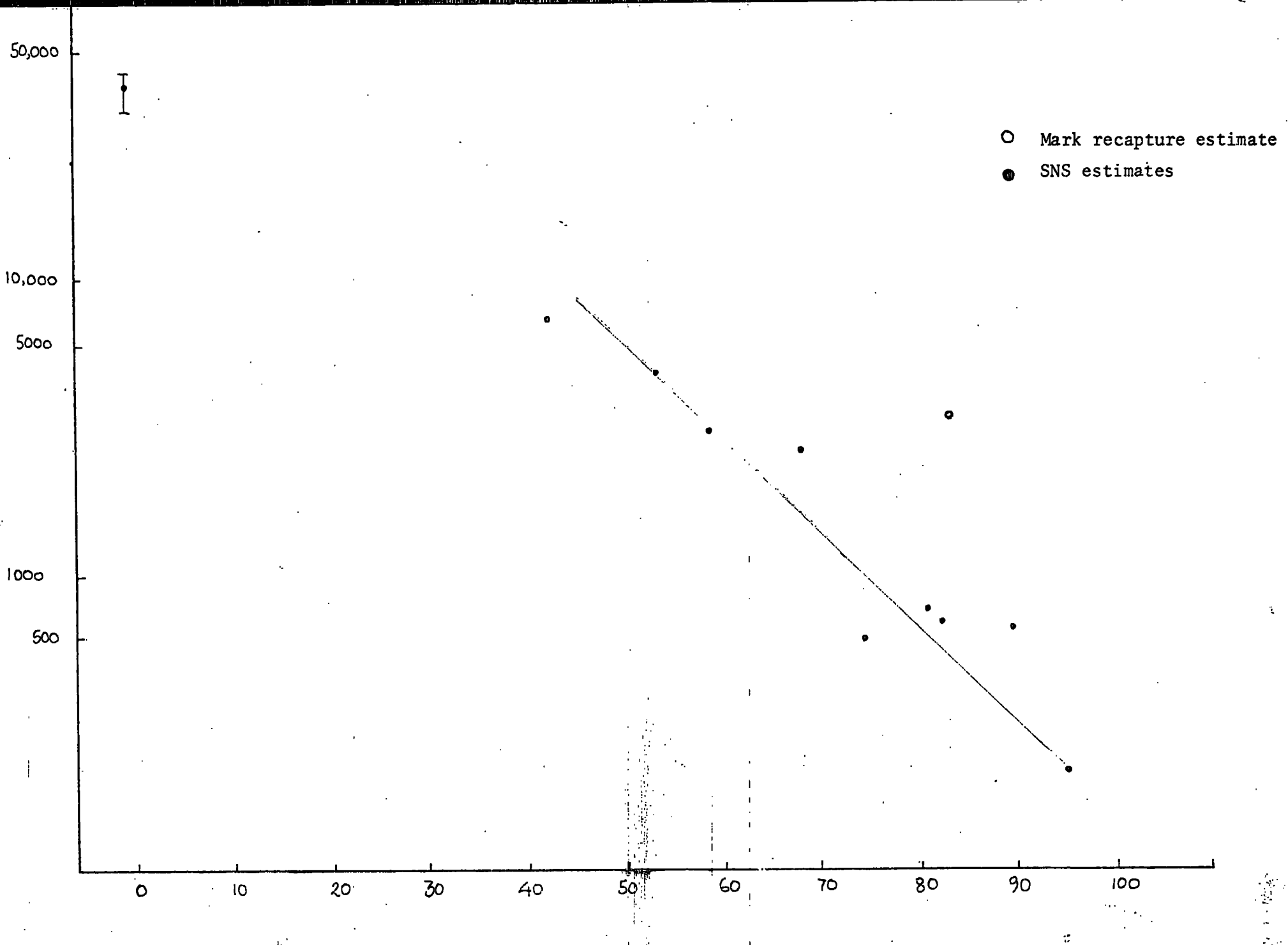

Figure 8 Estimates of Size of Population of Tadpoles - Field Station Study Site

11.0 The decline in the tadpole populations at the study sites

The results of the populations estimates by either the SNS method or the Lincoln Index (mark-recapture) show that the populations of tadpoles had decreased to very low levels in both pools by the time of climax metamorphosis. At Brasside even if the estimate giving maximum numbers is used, the population apparently suffered 99.994% mortality whilst at the Field Station site mortality was about 99.98%.

The causes of this high level of mortality are not known. The large numbers of predatory beetles in both pools were an obvious probable factor and to this end various organisms that may have played a part in the population decline were studied.

11.1 Predation Studies

Methods

Organisms found at the two study sites were brought into the laboratory for experiments to be carried out on their ability to capture Rana temporaria tadpoles and to determine their maximum rate of consumption of tadpoles of various sizes. The organisms were taken in the same net sweeps that provided SNS data and were not specially trapped. It was thus thought that they were inhabiting the same areas of the pools as tadpoles.

To test whether they were taking tadpoles the organisms were starved for 24 hours and then placed in 500 ml. or 1000 ml. beakers full of tapwater. Small tadpoles at Stage 25 of

Species of Predator	No	Duration of Expt.	Prey Size	No. Eaten	Mean/ Predator	Rate of feeding/hr
Dytiscus marginalis (adult)	1	24 hrs.	Stage 26,	30	30	1.25
Dytiscus marginalis (larva)	4	"	9 mm, 0.3gm	69	17.25	0.7
Agabus sp.	2	"		2	1	.05
Agabus sp.	2	"		3	1.5	.06
Colymbetes fuscus	2	"		14	7	0.3
Notonecta glauca	1	"		10	10	0.4
Triturus cristatus	1	"		39	39	1.6
Triturus helveticus	2	"		21	10.5	0.4
Dytiscus marginalis (adult)	1	58 hrs.	Stage 27,	22	22	0.38
Dytiscus marginalis (larvae)	5	"	13.5mm, 0.5gm	143	28.6	0.49
Agabus sp.	2	"		2	1.0	0.02
Colymbetes fuscus	1	"		3	3.0	.05
Triturus cristatus	1	"		28	28	.48
Triturus helveticus	9	"		27	3.0	.05

Table 14 The number of tadpoles eaten by various species of predator present in the two study pools. The size of the tadpoles fed was attempted to be ~~simulated~~ made even. column "Prey Size" gives the average sizes.

metamophosis were then introduced five per beaker. Animals that had not eaten any tadpoles in 36 hours were then eliminated. These included damsel fly larvae, Pyrrhosoma sp. and some coleopterous larvae. The remaining organisms that had been proved to be capable of capturing tadpoles were then starved for 48 hours after which they were placed into smaller aquaria than previously, again filled with tapwater. Tadpoles of approximately the same size were then placed into the aquaria and the number of tadpoles in each predator's environment was kept as constant as possible by the addition of further tadpoles as those present in the aquaria were eaten. The number of tadpoles eaten was recorded over one day and one night.

The organisms used were then starved again for five days and the experiment repeated using larger tadpoles for a longer time.

11.2 Results

The species of predator used and the numbers of tadpoles eaten are given in Table 15, together with the calculated rate of consumption of different sizes of tadpole. The consumption rate of an Agabus sp. present at both sites had been calculated using newly hatched tadpoles at Stage 22 of metamorphosis, and found to be a maximum of 5 tadpoles of this size per day.

11.3 Discussion

If the approximate levels of predator populations are known some hypotheses may be tested. The SNS sweeps gave a good relative estimation of the abundance of predators at both sites. Agabids were found in every sweep, often in high numbers, Dytiscus

Species of Predator	Possible Nos.	Duration of Active predation	Laboratory Feeding Rate/Hr.	Max. Number possibly eaten (assume 10hr. act)
Dytiscus marginalis (adult)	10	Throughout life of tadpole.	0.75	7,500
Dytiscus marginalis (larvae)	500,	- do -	0.5	25,000
Triturus helveticus	150	Many leave pool in July	0.2	1,500
Agabus sp.	10,000	Only during early life of Tad. (21 days)	0.8	1,600,000

Table 15 Hypothetical rates of predation using estimated numbers of predators in Field Station pool. The densities of predators are calculated from SNS recoveries.

Day	Nos. in Population (Estim.)	Apparent Decline	Apparent Mortality (%)
1	36890 ± 6627	-	-
50	5842	31048 ± 6627	86
59	4366	1476	25
63	2220	2146	48
74	2033	187	0.8
81	636	1397	69
87	896	+ 260	+29
88	731	165	18
95	655	76	1
101	209	446	68

Table 16 (a) The decline of the tadpole population at Field Station Site

Day	Nos. in Population (Estim.)	Apparent Decline	Apparent Mortality (%)
1	50250 ± 9111	-	-
50	2549	47701 ± 9111	95
59	1657	892	35
63	3250	+ 1593	+96
74	1274	1976	61
81	728	546	43
87	460	268	37
88	345	115	25
95	268	77	22
101	153	115	43

Table 16 (b) The decline of the tadpole population at Brasside Pool.

marginalis larvae were taken in 1 in 10 SNS and Triturus helveticus more rarely. Adult Dytiscus marginalis were rarely caught but this species is rarely active by day. Other species of Insecta known to feed at least occasionally onttadpoles were not estimated. Nepa cineraa was common at the Field Station site but was rarely trapped in the net. Table 16 illustrates the hypothetical situation if all the assumed predators in the Field Station all ate tadpoles at the mean maximum rate observed in the laboratory (mean of two sizes of tadpole). From this it seems that the level of predation by Agabus sp. might be the most significant factor in reducing the populations of tadpoles to the very low levels seen. However, all Agabids present cannot feed on the tadpoles present. For much of the time when this predator can take tadpoles at the maximum rate, the tadpoles are not dispersed over the pool but aggregated into a compact mass at the spawning ground where predator/tadpole contacts will be reduced. This may well be the explanation of this behaviour and the reason why the tadpoles persist in this behaviour when conditions at the spawing grounds are adverse (Savage 1935).

If the estimations of mortality taking place (based on the SNS estimates) are now consulted (Tables 16 (a) and (b)) then it is seen that the bulk of the mortality apparently observed in both populations takes place while the tadpoles are under 50 days.old. Thus, it is the younger and smaller tadpoles that suffer the heaviest mortality. The action of predators in removing tadpoles

from the populations will be maximal about day 25 to 30 when they disperse from their aggregations, because then they are exposed to many more predators including the sedentary Nepa cinerea. The pattern of mortality, see Figure 7, is strongly suggestive of heavy predation a large percentage of the population being removed each week. However, this could not be confirmed without confirmation about field rates of predation and conclusive evidence for consumption of tadpoles in the field, such as could be given by a serological method (e.g. Reynoldson and Davies 196).

Differences in the apparent mortality at the two sites studied may be related to the differences in faunal composition between the two sites. The number of species was greater in the well-established pool at Brasside. Individual species were more abundant. The only newt species in the pool studied at Brasside was T. cristatusa far more voracious species than T. helveticus which was the only newt inhabiting the Field Station site. The Field Station pool contained fewer species which may be related to the slow colonisation of aquatic habitats (Macan 1966). Evidence for other factors than predator pressure affecting the tadpole populations was gained in the study. Tadpoles at Brasside were hatched earlier and gained weight more rapidly than those at the Field Station until Day 55 after hatching when they showed a decrease in weight. Subsequently this population grew to a lower maximum weight than the Field Station and metamorphosed

at a smaller size. Herreid and Kinney (1966) found populations of Rana sylvatica crashed to 4% of the original population. The decline noted here is considerably greater. Savage (1961) states that populations of Rana temporaria are laid in marginal situations where the chances of survival are usually around 1% for any individual and that whole populations are commonly eliminated by the drying up of their habitats.

If, however, 200 tadpoles metamorphosed successfully at the Field Station and 100 at the Brass pool then for replacement of the population, expectation of survival will be about 0.5 for the Field Station and near 1.0 at Brasside. These figures strongly suggest that the number of tadpoles metamorphosing at Brasside would not replace annual mortality since females of this species do not become mature until three years old, according to Smith (1951) and Ashby (1969).

12.0 Laboratory growth results

12.1 Methods

Rose (1960) used a prepared laboratory diet of pelleted rabbit food in his experiments. A test on the usefulness of such prepared diets was carried out with a mass of spawn obtained in Feburary from Waldridge Fell. The spawn developed rapidly and hatched with about 80% success. Initially in pondwater the tadpoles were transferred to tapwater when the water became foul. These tadpoles were fed on the pelleted diet SG1 prepared by Oxoid Ltd. which was the most similar food to that used by Rose, that was available. The composition of this diet may be found in the Appendix.

Following the success of this pilot culture which produced over 300 small frogs after fifty-two days, it was decided to set up a controlled series of cultures. These were set up in the following fashion. The vessels used were 1 l. glas crystal dishes which allowed good visibility, were readily handled and easily cleaned. The dishes were filled with tapwater to a level 1 cm. below the rim. If over-filled, tadpoles could easily fall over the edge and out of the culture as they came to the surface to breathe. The cultures were kept in the laboratory at temperatures of between 12 and 20^{o} C.

Into these dishes a number of tadpoles were placed at an early stage in their development (Stage 22, see Appendix). Tadpoles from a single egg mass were used in order to maintain as great a degree of comparability as possible. At the time of transfer the tadpoles had not yet received their first meal.

A weighed amount of Oxoid Ltd.'s SG1 diet was given to each culture at intervals, when all food previously placed in the culture had been converted into faeces. By this method it was hoped to gain some idea of how much food each culture utilized and, therefore, calculate the efficiency of conversion of food to tadpole biomass.

The culture medium rapidly developed algaland bacterial growths that necessitated it being changed every two to three days in order to prevent additional sources of food building up in the cultures. Only two-thirds of the water was changed at a time so that the feacal material lying on the bottom was not disturbed.

When any tadpole died it was replaced from a parallel culture being fed on SG1 under the same conditions. Deaths were easily noticed since the number of tadpoles in all but the densest culture could be counted in situ. During Stage 28 onwards of the climax metamorphosis the tadpoles were quickly weighed and measured in the same way as Field samples. If replaced quickly into water no mortality resulted.

12.2Results

The results of growing tadpoles inccultures at varying densities are displayed in Table 17. It is seen that the tadpoles at the lowest densities did best and attained a maximum weight over twice that attained in the most crowded pulture. Tadpoles in all cultures grew normally and the experiment was stopped when tadpoles in the uncrowded cultures had 100% metamprphosed. Metamorphosis at the temperatures of the experiment occurred in the uncrowded cultures 48 days after the cultures were set up. The cultures at the lowest

density reached the greatest weight observed for tadpoles in either lab or field during the duraction of this study.

The size of the culture grown at a density of 30 tadpoles to a culture was comparable to that found in field populations at the two study sites (maximum weight 0.51 gm., maximum body length 13.1 mm.). In contrast the size of the most crowded culture was very small, below the mean size found in field populations in this study, the weight at maximum was only a mean of 0.3 gm. and the mean length was only 11.00 mm. The uncrowded cultures metamorphosed first followed by the 30 cultures in the main. However, many tadpoles reached climax metamorphosis in the densest culture even though they were considerably smaller than the other tadpoles that metamorphosed. Lack of time prevented this experiment from being continued until all tadpoles had metamorphosed.

12.3 Discussion

Although many authors (e.g. Atkin 1966, Adolph 1931a, 1931b, Lyn and Edelman 1936, Richards 1962, Rose 1960, Rose and Rose 1961, Rugh 1934, Wilder 1924 and Ung 1878) have cultured tadpoles of many species in order to analyse the adverse effects of crowding on growth and development, little work has been carried out on the larvae of Rana temporaria. The work of Douglas (1939) was concerned with the development of the embryo and although Savage (1950), (1961), has carried out extensive studies on the behaviour, ecology and physiology of tadpoles he does not describe a method for successfully maintaining a large proportion of tadpoles to metamorphosis. He does, however, comment (Save 1961)

that an attempt to rear tadpoles on pure algal culture failed when the tadpoles were apparently arrested at a stage in metamorphosis before the climax metemorphosis of forelimb development and tail resorption. In the present study a method for rearing large numbers of tadpoles to and through metamorphosis has been devised. The diet is solely vegetable in origin and therefore dispels the theory that tadpoles need a meat diet or meat supplement to metamorphose successfully. Some older books stress this point and state that in the wild, tadpoles of Rana temporaria shift to a carnivorous diet prior to climax metamorphosis.

Apart from this, the experiments described above confirm the already incontrovertible evidence of the adverse effects of crowding in tadpoles. Recently Brockelman (1969) has made an attempt to extend this type of experiment to the field and found that clearcut effects of this type are not distinguishable under field conditions. Predation has a greater effect than crowding in his experiments.

Other deductions may be made by examining the amount of food consumed by individual cultures. The amount of food ingested to weight of tadpoles produced is given in Table 17 and is seen to be far higher in uncrowded cultures than in crowded ones, being 0.9 as opposed to 0.1 gm. SG1 diet per gm. tadpole (wet weight). The reason for this difference is not known. Possibly the increased activity of the crowded tadpoles leaves them less time for feeding and thus the crowding effect is in reality starvation. There was a greater amount of faecal ingestion in the crowded cultures and this may have increased the efficiency of utilization of food. Conversely this would also have increased the inhibitory effects of algalike cells (Richards 1962), if these exist in this species.

In the field faeces must be normally lost and not deliberately recycled.

Dedd tadpoles provided a source of highly digestible food and were normally completely eaten before they were found. The number of tadpoles dying per culture is therefore included in Table 17. Another possible food source is primary production by algae, and bacterial growth might provide food of a higher digestibility than SG1.

12.4 Growth under field conditions compared to actual field growth rates

12.5 Method

Tadpoles were cultured by the method described above outside the laboratory under a temperature regime resembling that occuring in the field. Tadpoles were taken from the field populations and weighed. They were then fed on SG1 diet so that there was excess food at the bottom of the cultures. After nine days tadpoles were again sampled from the field populations at all study sites and weighed and measured, together with the cultured tadpoles. The culture medium was clean spring water taken from Waldridge Fell. Culture densities were 30 tadpoles per litre since growth in tap-water at this density most closely approximated field growth, however an uncrowded culture (S) was kept with Waldridge Fell tadpoles.

12.6 Results

The results of this experiment are laid out in Table 18, together with comparisons between the means of field and cultured tadpoles. It is seen that tadpoles from the Field Station grew very little over this period whether in cultures supplied with excess food or

in the Field Population. There are no significant differences between the mean weight of tadpoles at the beginning of the experiment and at the end. In contrast tadpoles from Brasside grew rapidly in culture and showed a significant increase in weight ($P \leq 0.01$) whilst the field population showed a significant decrease over this period compared to the initial average weight. Tadpoles given excess food in the culture had a significantly heavier mean weight than tadpoles in the field population ($P \leq 0.001$). At Waldridge Fell, tadpoles at densities of 5 and 30 fed on SG1 to excess, showed no significant difference in their mean weight after nine-days and did not differ significantly from the mean weight of the tadpoles before they were placed into the culture. However, the sample of tadpoles taken from the field showed a significant increase in the mean weight of tadpoles ($P = 0.01$). There is also a significant difference between the culture maintained at a density of 30 tadpoles ($P \leq 0.02$).

12.7 Conclusion

There is no overall pattern to the results. Tadpoles from the Field Station apparently did as well in the field as in a culture supplied with excess food. Tadpoles from Brasside study site apparently did far better when supplied with excess food putting on nearly 30% weight in nine days whilst the mean weight of tadpoles in the field declined. At Waldridge Fell where tadpoles were in fact found to achieve larger sizes than at the other sites growth was significantly better in the field than in culture.

12.8 Tests on the toxicity of tapwater

12.9 Method

Four cultures were set up, two using tapwater as the culture medium and two using clean pondwater taken from Waldridge Fell. One of each type of medium was placed in the laboratory and one of each outside where it was subjected to temperatures resembling those occurring in the field. Thirty tadpoles trapped at Waldridge Fell study site on the same date were placed into each culture, after previously weighing by the method described above. After 13 days during which excess SG1 diet was supplied to the cultures, the tadpoles were weighed again and any differences noted.

12.10 Results

The results of the two weighings together with the standard error of the means and tests of the significance of any differences between them are to be found in Table 19. It is seen that significant growth only occurred in one culture, that with tapwater as a medium at field termperatures ($P < 0.001$). Slight increase in the mean weight of the culture using pondwater was recorded but was not significant ($P < 0.2$). Tadpoles kept in cultures kept at laboratory temperatures declined in weight.

12.11 Conclusion

No adverse effect of tapwater on growth was recorded. Declines in mean weight of tadpoles kept in either pond water or tapwater at laboratory temperatures may be attributed to the onset of climax metamorphosis accelerated by the higher temperatures of the laboratory. The existence of toxic effects on very young and embryonic tadpoles was not determined but in view of the

Culture	Dens.	Wt. Food Eaten (gms.)	Mean Max. Weight T.poles	Mean Max. L'gth Tadpoles	Mean Wt Food/Gm Wet Wt. Biomass	No. Died	% Met. 25.6.71	Mean Wt. Young Frogs
1	5	3.4	0.8	17.0	0.85	1	100	0.45
2	5	3.3	0.71	15.8	0.93	3	100	0.42
3	5	3.4	0.80	16.0	0.85	0	100	0.43
4	5	3.5	0.73	16.6	0.96	1	100	0.41
5	30	6.8	0.50	13.0	0.11	13	10	0.23
6	30	6.7	0.44	12.8	0.09	16	23	0.24
7	30	6.6	0.47	13.1	0.10.13	13	20	0.29
8	30	6.7	0.48	13.0	0.13	10	27	0.29
9	30	6.7	0.51	13.0	0.12	12	30	0.28
10	100	13.0	0.30	11.0	0.11	28	10	0.25

Table 10 The growth of Rana temporaria tadpoles in standardised cultures at various densities. Weights where not stated are in grams live wt. and measurements in mm. along the body only.

	No. of Culture	Specification of Sample	Mean Wt $\bar{w}$	S.E. of Mean	Value of t	P	Value of t	P
20th May	1	Field Station (field sample)	.21	.026				
					1.3	.2		
29th May	2	Field Station fed on SG1 (excess)	.25	.015			.48	.7
					1.3	.2	(1,3)	
29th May	3	Field Station (field sample)	.22	.014				
20th May	4	Brasside	.22	.020				
					3.0	.01		
29th May	5	Brasside fed on SG1	.30	.014			3.8	.001
					3.8	.001	(4,6)	
29th May	6	Brasside field sample	.20	.021				
20th May	7	Waldridge	.25	.016				
					0.8	.3		
29th May	8	Waldridge fed on SG1 x 5	.28	.015			3.7	.01
					0.16	1.0	(7,10)	
29th May	9	Waldridge fed on SG1	.27	.021			.95	.3
							(8,10)	
29th May	10	Waldridge Field Sample	.35	.028				

Table 18 Growth of tadpoles in pondwater supplied with excess food (SG1) compared over 9 days with the growth of similar tadpoles in the field.

No. of Culture	Date	Culture Medium & Temp.	Mean Wght of Tad-poles	S.E.	Sign. of 13 days	
					t	P
1	3.6.71	pond/field	0.38	0015	0.14	0.9
1	16.6.71	- do -	0.40	0021		
2	3.6.71	pond/lab.	0.43	0017	1.10	0.3
2	16.6.71	- do -	0.40	.019		
3.	3.6.71	tap/field	0.28	.010	4.80	0.001
3	16.6.71	- do -	0.37	.015		
4	3.6.71	tap/lab.	0.36	.018	2.30	0.05
4	16.6.71	- do -	0.32	.007		

Table 19 Growth of tadpoles in tapwater and pondwater at two temperature regimes, with significance of differences arising.

high success rate of the culture method using tapwater, it is thought that no such effects occurred with Durham tapwater. It is thought that the heavy metals used in controlling algal growth act at the respiratory surfaces. Tadpoles from an early age rely on atmospheric air for much of their respiration (Savage 1961) and hence may not be so susceptible to these toxins.

12.12 The relevence of laboratory studies to field studies

The highly artificial nature of most density studies with the exception of Brockelman's (1969) work, gives little insight into the nature of these effects in the field or whether they do indeed occur. Savage (1961) page 35) gives a suggestive instance where tadpoles were common one year in a pond and grew badly with few surviving to metamorphosis. In the next year far fewer tadpoles hatched and the survivors grew much better. The controls for the laboratory studies described above show that tadpoles grew in the field at equivalent rates to tadpoles on a diet of SG1 except at Brasside and that tapwater did not apparently affect their growth. Thus it is feasible that density effects noted in the laboratory may occur in the field. In the present study about 50,000 egggs were laid at the Brasside study site with an area of approximately 84 square meters, whilst 37,000 eggs were laid at the study site at the Field Station where the surface area of the pool was, at maximum approximately 150 square metres. Growth apparently was a little better at the Brasside site until Day 57 after hatching when a pronounced decline in the average weight of individual tadpoles appeared. The average weight

never subsequently exceeded that of the tadpoles at the Field Station and the number of tadpoles reaching climax metamorphosis was apparently less than half those reaching this stage at the Study site at the Field Station. It is not known whether a population crash occurred during the decline in weight at the Brasside site. If it did then the events described above indicate starvation occurring in the pool due to over-population. Population estimates were not taken until Day 81. Thus the experiment carried out giving excess food to tadpoles from Brasside between the dates of 20th May and 29th May is of great interest. The decline in weight of the field population was noted on the 17th May and the tadpoles had begun to put on weight again by the 27th although they had still not reached their previous mean weight.

The rapid gain in weight of the tadpoles brought into culture with excess food points to their being in a condition of starvation. What the conditions were that brought on the onset of adverse alimentary conditions is not known. However, there is some indication that this population over-ate its food supply and subsequently declined to a low level at which growth was slower than in other pools studied.

13.0 Calorimetric Studies

Because the frog has a larval stage that is aquatic and herbivorous but then in the adult stage is terrestrial and carnivorous, it was considered that a study of the efficiency of utilization of food by the tadpole might yield intersting results.

13.1 Method

Tadpoles were fed on a diet of Oxoil Ltd. SG1 pelleted laboratory diet as previously described. The cultures were kept with and excess of food in tapwater at between 12 and 20° C.

Faeces were collected by placing well fed tadpoles from this culture into an aluminium seive in a small vessel filled with tapwater. The majority of the faeces produced fell though the seive and accumulated at the bottom of the container where they were periodically collected. The water was filtered in order to concentrate the faeces which were then placed into anooven at 60°C. Collection and concentration were carried out as often as possible in order to reduce the growth of bacteria on the a faeces, which might affect the result of the analysis. Tadpoles in the seive were exchanged frequently with fed tadpoles and the material was slowly accumulated in the oven until there was judged to be sufficient. The faeces were left in the oven for three days and removed to a dessicator in which SG1 pelleted diet had also been placed. Both samples were left until they

achieved a constant weight.

Calorimetric analysis was then carried out using an oxygen microbomb calorimeter in the manner described by Philippson (1964). The material to be analysed was pressed into a pellet and replaced into a dessicator until needed. The micro bomb system was then calibrated by using pellets of anhydrous benzoic acid of known weight and calorific content. These were used in the following way:

A pellet was placed onto the pan of the microbomb secured under a length of platinum wire stretched between the terminals of the firing circuit. The bomb was then screwed together and flooded with oxygen via a non-return valve to a pressure of twenty atmospheres. The pressurized bomb was then placed underwater in order to check that it had been properly sealed and to cool it. If there were no leaks it was then dried and placed on a ring of thermocouples. A metal cover was then placed over the system to prevent environmental fluctuations from affecting the thermo couples. Upon the chart recorder producing a straight line indicating that the bomb was at a steady state where heat was neither being lost, nor being gained, the pellet was ignited by passing a current through the platinum wire. Heat given off by the combustion was registered by the thermocouples and recorded by a deflection on the chart recorder. The procedure was carried out for ten weighed pellets of benzoic acid, tadpoles faeces, SG1 diet and whole tadpole body in turn and mean deflections calcul ated. Pellets were weighed directly before their use in the bomb.

Pellet Type	Pellet Weight	Deflection Recorded	Heat Equivalent (cals)	Cals/ Division
Benzoic acid	0034	61.7	152.4	2.43
	.021	52.8	131.2	2.48
	.022	38.7	144.5	2.46
	.024	60.6	153.7	2.54
	.015	40.2	98.34	2.45
	.020	52.5	130.9	2.49
	.020	51.0	126.5	2.48
	.026	65.0	165.1	2.54
	.027	67.5	174.5	2.58
	.023	54.0	147.3	2.73
				$\bar{x}$ = 2.52

Table 20 (a) Calibration of Recorder

Pellet Type	Pellet Weight	Deflection Recorded	Heat Equiv. (cals)	Cals/Gm. Dry Weight
Tadpole (whole body)	.023	46.1	116.2	5095
	.021	37.4	93.5	5169
	.025	47.7	119.3	4713
	.019	33.75	90.1	5969
	.021	41.5	103.8	4940
	.023	44.5	111.3	4754
	.021	40.5	101.3	4644
	.026	51.3	128.3	4970
	.028	52.1	130.3	4651
				$\bar{x}$ = 4990

Table 20 (b) Results of calorific analysis of tadpole biomass.

Pellet Type	Pellet Weight	Deflection Recorded	Heat Equivalent	Cals/Gm. Dry Weight
Faeces from	.0204	31.5	78.8	3860
SG1 Diet	.0208	29.6	74.0	3558
	.0167	26.3	65.8	3937
	.0221	37.8	94.5	4276
	.0248	39.2	98.0	3951
	.0204	29.3	73.3	3590
	.0254	40.0	100.0	3937
	.0223	35.8	89.5	4013
	.0239	40.3	100.5	4205
	.0127	20.3	50.8	3996
				$\bar{x}$ = 3932
SG1 Diet	.0285	47.4	118.5	4156
	.0321	52.3	130.8	4073
	.0256	44.7	118.8	4365
	.0385	55.3	138.3	3591
	.0329	52.8	132.0	4021
	.0257	40.9	102.3	3978
	.0308	48.0	120.0	3896
	.0296	49.2	123.0	4155
	.0270	50.8	127.0	4703
	.0271	46.5	116.3	4290
				$\bar{x}$ = 4122

Table 21 Results of calorimetric analysis of tadpole food and faeces

The calorific content of benzoic acid is known and thus the deflections produced by weighed amounts of this substance were used to calibrate the recorder.

13.2 Results of Calorimetric Analysis

Tables 20 and 21 give the readings taken from the chart recorder and the calculated calibration of the recorder, together with the calculated heat released by combustion of the three substances analysed. The calorific content of each substance per gram of dry weight was then arrived at by proportional calculation. The mean ($\bar{x}$) of ten individual combustions was then taken to be the mean calorific content of that substance.

13.3 Conclusion

The readings from the pellets of benzoic acid calibrated the recorder as giving a deflection of 2.5 divisions on the chart for every calorie given off on combustion.

The calorific content of whole tadpole biomass on this basis = 4.9 Kcals per gm. dry weight, that of sG1 diet = 4.1 KCals/ gm. dry weight and that of faeces = 3.9 Kcals/gm. dry weight.

On the basis of these figures the apparent assimilation efficiency of the tadpoles fed on this diet may be estimated.

13.4 Apparent assimilation efficiency

The apparent assimilation efficiency will be equal to

$$\frac{\text{Kclas food - Kclas faeces}}{\text{Kcals Food}} \times 100$$

$$= \frac{4.1 - 3.9}{4.1} \times 100$$

$$= 4.9\%$$

13.5 Discussion of results of Calorimetric analysis

The value given by the analyses described above for the apparent assimilation efficiency of SG1 diet is very low. Newell (1965) found that growth of bacteria on faeces increased their food value to molluscs and it is thought that this would have raised the calorific content of the faeces so that the apparent assimilation efficiency would seem to be lower than it is. However, Savage (1961) comments onthe low efficiency of assimilation of algae eaten by this species. Faeces are produced continually and this reflects the continual feeding activity of the tadpoles. The paesage time through of carmine particles though tadpoles with a mean gut length of 80 mm. was determined to be 5 hours. In a similar experiment Savage (1961) recorded six hours. The efficient ruminent herbivores take up to 48 hours to process their food. The assimilation efficiency of poikilotherms may vary according to their feeding rate (Dawes 1960), Brown (1946) and with the quality of the food (Hoo and Freankel (1966a)). It seems possible that the combination of a rich food source (in the field tadpoles take in much detritus with their food), in great excess and possibly with the complicating effect of bacterial growth have given a low estimate. It is interesting to note that tadpoles grown on the same diet in uncrowded cultures used more food to produce a given unit of biomass than tadpoles in more crowded cultures. (See section).

The efficiency of assimilation of an adult ranis closely related

to Rana temporaria has been calculated by Mazur and Chlodny (1969) as being 80. 6% on a diet of earthworms and slightly less on the more normal diet of insects. The efficiency of assimilation of Triturus vulgaris/helveticus tadpoles (these species are indistinguishable) as young larvae has been determined as 90/4% by Avery (1971b), the tadpoles being fed on a diet of Enchytraeid worms.

If the low assimilation efficiency of Rana temporaria tadpoles found in the laboratory is reflected in the field, then it is probable that on metamorphosis and attainment of a higher trophic level the efficiency of utilization of food will increase - an interesting verification of a basic assumption of some workers on the trophic-dynamic theory of ecology.

14.0 The production of tadpoles at the Field Station study site

14.1 Method

The data gained during the field study of the population inhabiting the study site at the Field Station was used to compute the production of tadpole biomass during the period April 17 to July 12. The method used and a detailed account of the steps taken during computation of this figure are to be found in Ricker (1970).

The number of tadpoles in the population on the first four dates for which data are given are estimated from the known rates of decline of the population. The number of tadpoles hatching is estimated to ± 8000 and thus these estimates will have the same order of confidence.

The estimates used in the rest of the calculation are gained from SNS data which as already shown may be under estimates of up to four times the actual figure.

Table 22 gives the full data used.

14.2 Results

The result of calculating the production of this population is that 823 gms. (wet weight) of tadpole biomass are estimated to have been produced, on the basis of SNS estimates. If mark-recapture estimates were accurate then this figure may be quadrupled.

14.3 Conclusion

The amount of production by this population of tadpoles is not

large in spite of the large numbers of hatching tadpoles. The majority of production (over 50%) on the basis of the population estimates takes place during the first weeks of the tadpoles free life in the pool. This must be largely absorbed by predators. (Over 99% of all the tadpoles present disappear from the population. Thus this 823 gms. was largely diverted into the next trophic level of the pool. Note that there is a net loss in tadpole biomass as the tadpoles reach climax metamorphosis.

The large numbers of eggs laid by frogs may be a device whereby the survival of some tadpoles through the highly vunerable egg and post-hatching stages is assured. The high production of the young tadpoles is not purely to benefit the predators in the pools but rather so that some excess production is left for the young frogs to be produced from.

Date	Mean Wt.	Inst. Growth Rate	Stock Nos.	Stock Biomass	Mean Biomass	Production (Gms Wet Wt.)
	w	G	N	B	B	P
April 17	.010		35,000	350		
		0.998			490	489
April 28	.030		21,000	630		
		0.042			596	25
May 6	.042		13,500	563		
		0.166			889	147
May 13	.135		9,000	1215		
		0.033			1104	36
May 20	.170		5,840	993		
		0.031			987	30
May 29	.225		4,366	982		
		0.070			846	59
June 3	.320		2,220	710		
		0.021			822	27
June 14	.460		2,033	935		
		0.018			637	13
June 21	.533		636	339		
		-0.001			438	8
June 27	.597		896	535		
		-0.051			460	- 0.5
July 6	.588		655	385		
					237	- 13
July 12	.434		209	91		

$\leq P$ = 823 gms.

Table 22 Estimation of production of tadpole biomass (wet weight) in Field Station Pool. For explanation of method see Ricker (1970) and text.

15.0 The Ecology of Rana temporaria at Moorhouse

The ecology of Rana temporaria at this site was very different to that found in the lowland sites studied. The facts observed may be summarized as below:

15.1 Breeding

Breeding was first observed on March 30th, 38 days after the date of first breeding at Waldridge Fell and 18 days after the cessation of breeding activity at this site. The last confirmed date of breeding was about 25th April although spawning may have gone on longer, since gravid females were found after this date. Breeding took place in areas of shallow water and around the margins of deeper water (see above). The majority of egg masses were laid in water that was temporary. Egg mass of the largest spawning ground observed must have contained many hundreds of egg masses.

15.2 Adult population

The adult population was at a high density and frogs were perhaps the commonest vertebrate on the moors besides meadow pipits. The behaviour of adult and juvenile frogs was similar in most respects to that of lowland frogs. However, frogs were often seen moving over the blanket bog or amongst heather in a way not seen in the apparently more retiring populations of lowland frogs. Perhaps this observation was a result of the higher densities of frogs.

15.3 Growth of tadpoles and larval mortality

Mortality of the eggs and embryos was at a high level as indicated by the grey fungal infection found on dead or dying eggs (Licht

1969b). Over 50% of all eggs were dead, a condition resembling that occurring in Rana sylvatica eggs in Alaska as found by Herreid and Kinney (1966). The effects of heat, frost, fungal infection are difficult to distinguish but temperaturs are unlikely to reach. 25°C in most eggs which is the upper limit of temperature tolerance. It is felt that the fungus only infects dead or dying eggs but there is no proof for or against this point of view. This leaves the effect of frost, the lower lethal temperature for eggs of this species as determined by Douglas (1948) is about 4°C. If temperatures are long below this level then severe egg mortality may result. Exposed eggs will tolerate as long as 12 hours of complete freezing and still develop normally in some cases. The mortality of eggs and tadpoles due to dehydration was also severe. The spring and summer of 1971 has been warm and fairly dry. The majority of the pools in which eggs were laid had disappeared by May 5th. In the remaining standing water, tadpoles grew rapidly. A sample of tadpoles obtained from Bog Eng on June 2nd was after about 50 days growth, comparable in size to lowland tadpoles after 40 days. These tadpoles were at Stage 27 of metamorphosis. The first post-metamorphosis frogs were notices in late June and thus the development time for moorland tadpoles is about the same or slightly less than that of lowland tadpoles. In this context it would be of great interest to see what growth was made by these small frogs before the winter hibernation.

15.4 Conclusion

In conclusion, large differences were observed between the behaviour and population ecology of frogs at Moorhouse and at lowland sites studied. The breeding season commenced later and carried on for a longer period of time than at lowland breeding grounds. Several peaks of breeding activity were noticed, also noted by Curry-Lindhahâ (1958), this may be related to conditions at the breeding grounds or be related to the large distances that some frogs must travel to arrive at the breeding grounds.

Mortality of eggs and tadpoles was very great the deaths being largely due to catastrophic factors such as desiccation and possibly freezing. The level of the frog population was much higher than than found in lowland areas studied.

16.0 Summary

1. The breeding behaviour of the common frog Rana temporaria (1) was observed and the frogs at the selected spawning site were measured. Subsequently the size frequency of these frogs was analysed.

2. The average number of eggs per spawn mass was determined and found to be 1322 ± 243 (S.E.).

3. The number of eggs laid at two spawning grounds was calculated and a standard method of sampling was adopted so that the dynamics of these tadpole populations could be followed through the life history of the tadpoles.

4. Sampling at roughly weekly intervals gave the data needed for a production estimate and for a comparison between the pools studied.

5. A culture method for Rana temporaria tadpoles was devised and tadpoles were grown successfully at both laboratory and field temperatures, on a purely vegetable diet. The assimilation efficiency of tadpoles fed on this diet was calculated.

6. The production of the tadpole population at one site was calculated on the basis of the data obtained and the net production was found to be about 800 gms. of tadpole biomass.

17.0 Acknowledgements

My thanks and sincere appreciation to Dr. K.R. Ashby my supervisor in this study, to Mr. T.C. Dunn for aid in finding the sites, to Mr. Tyndale for access to the site at Brasside, to all concerned with the 1970/71 M.Sc. course, both staff and students who all helped in some way to make this project feasible. My especial thanks to Mr. P. Williamson for his continued generosity and acute criticism of this work, and to my wife who has suffered long without complaint.

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The stages of tadpole used in the Text (After Witschi 1958)

No.	Diagnostic Characters
22	Newly hatched, external gills, nostrils, mouth and eyes not yet developed.
23	Large external gills, eyes and mouth not yet fully functional, adhesive glands strongly developed.
24	External gill resorbed, active swimmer, feeder.
25	First Trace of hind limb seen as bud.
26	Hind limb bud grows longer.
27	Hind limb begins to differentiate into parts.
28	Hind limb small but completely developed.
29	Fore limbs developed under operculum.
30	Fore limbs visible through skin, body wall thickens. Gut cannot be seen. Mouth more froglike.
31	Fore limbs emerge, head skeleton developed, resorbtion commences at tip of tail.
32	Resorbtion well advanced and tail dark and fragile, animal may be totally terrestrial at this stage.
33	Tail stump partially or completely resorbed. Animal is now a young frog and unable to exist in a totally aquatic environment.

For sketches of these stages see Figure 0.

LABORATORY ANIMAL

DIETS

Manufactured to the highest standards of quality

by:

HERBERT C. STYLES (BEWDLEY) LTD.,

MARKETED BY:

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Reprinted, September, 1966.

~~95~~
97a

FOR RATS, MICE AND MONKEYS.

The 'Oxoid' Breeding Diet.

This new Diet, of especial value in the mouse breeding unit, has been formulated with regard to the modern concepts of animal nutrition and fertility. It is high in protein and Vitamin E and fully supplemented with other vitamins and minerals. Details of this new formulation are given overleaf.

Modified Diet 41B.

Based on the published formula by Bruce and Parkes, this Diet contains the full vitamin supplement which replaces the Cod Liver Oil of the original Diet 41. An additional feature, characteristic only of the 'Oxoid' Diet, is the inclusion of the 'MINSAL' mineral supplement.

FOR RABBITS AND GUINEA PIGS.

Diet S.G.1.

This Diet has been developed by Short and Gamage at the National Institute for Medical Research (B.M.J., 1959, 1, 512; J. Animal Tech. Assoc., March, 1959) where it has been adopted as the standard ration for Rabbits and Guinea pigs. The Diet has been found satisfactory for the breeding and growth of Guinea Pigs and Rabbits if supplemented for Guinea Pigs by fresh greenstuff and hay, and for Rabbits by hay only.

Modified Diet 18.

The formula is based on Diet 18 of Bruce and Parkes (J. Hyg. 1947, 45, 70.). It differs from the published formula in that the ground nut cake has been replaced by soya meal, and a trace elemented mineral supplement replaces the salt and chalk.

THE 'OXOID' BREEDING DIET - For Rats and Mice.

A new Diet, designed to ensure litters of good size, with higher weaning weights and reduced mortality.

In the nutrition of Laboratory Animals there is a need for a Diet specially formulated to meet the more exacting requirements of Breeding stock. It is well recognised that diets suitable for maintenance do not necessarily give ideal results with breeding stock.

The new 'Oxoid' Diet is the culmination of a long period of research and practical trials. It takes account of the critical requirements of the breeding animal, and in its formulation particular attention has been devoted to achieving a high level of digestible protein. The diet is fully supplemented to cover all known requirements of minerals and vitamins, especially Vitamin E, which has been shown to be of particular importance to the breeding animal.

The ingredients used are guaranteed to be of the highest quality obtainable as follows:-

Barley Meal, Maize Meal, Whole Wheat Meal, Wheat By-products, English White Fish Meal, Extracted Soya Bean Meal, English Dried Skim Milk Powder, Unextracted Dried Yeast, Pure Cane Molasses, Minerals and Vitamins.

CALCULATED ANALYSIS.

Crude Oil	2.6 %
Crude Protein	20.4 %
Crude Fibre	2.7 %
Digestible Oil	1.9 %
Digestible Crude Protein	17.6 %
Digestible Fibre	1.2 %
Digestible Carbohydrate	48.8 %
Metabolizable Energy	2825 cals per kilo.
Lysine	1.0 %
Methionine	0.4 %
Cystine	0.4 %
Tryptophane	0.2 %
Valine	1.0 %
Leucine	1.3 %
Isoleucine	0.9 %
Threonine	0.6 %
Phenylalanine	0.9 %
Histidine	0.5 %
Arginine	1.2 %
Tyrosine	0.6 %

Fe	214 p.p.m.
Mn	46 p.p.m.
Cu	30 p.p.m.
I	6 p.p.m.
Co	1 p.p.m.
Zn	6 p.p.m.
Vitamin A	2434 i.u./lb.
Vitamin D_3	670 i.u./lb.
Vitamin E	21.8 mgm/lb.
Thiamine	2.6 mgm/lb.
Riboflavin	3.4 mgm/lb.
Niacin	24.5 mgm/lb.
Pantothenic Acid	8.2 mgm/lb.
Choline	621.0 mgm/lb.
Biotin	0.3 mgm/lb.
Folic Acid	0.4 mgm/lb.
Pyridoxine	3.9 mgm/lb.
Inositol	100.0 mgm/lb.
Vitamin B_{12}	12.8 mcgm/lb.
Ca : P	1 : 1.1
Ca	0.8 %
P	0.8 %
Na	0.5 %
Cl	0.7 %
Mg	0.2 %

97c

PERCENTAGE COMPOSITION OF DIETS.

Ingredients.	Modified Diet 41B.	Diet S.G.1.	Modified Diet 18.
Bran	-	40	15
Middlings	-	18	-
Sussex Ground Oats	40	12	-
Barley Meal	-	-	20
Wholemeal Flour	46	-	-
Soya Meal	-	-	15
Linseed Cake	-	-	10
Meat and Bone Meal	-	-	8
White Fish Meal	8	10	-
Dried Grass Meal	-	20	30
Dried Yeast	1	-	-
Dried Skim Milk	3	-	-
Mineral Supplement	1	-	2
Vitamin Supplement	1	-	-

N.B. No Groundnut Meal or Cake is used in any 'Oxoid' Diet.

CALCULATED NUTRIENTS.

	Modified Diet 41B.	Diet S.G.1.	Modified Diet 18.
	%	%	%
Crude Protein	15.91	20.33	23.60
Crude Fibre	5.05	9.05	9.53
Oil (Ether Extract)	3.17	4.18	3.07
Calcium	0.84	0.89	2.02
Phosphorus	0.67	1.05	1.17
Chlorine	0.34	0.23	0.71
Sodium	0.23	0.15	0.47
Potassium	0.50	1.06	1.01

MINERAL SUPPLEMENT (MINSAL LTD., NORTHWICH, CHESHIRE).

CALCULATED ELEMENTARY ANALYSIS.

	%
Calcium	21.55
Chloride	18.21
Sodium	11.79
Phosphorus	3.58
Magnesium	1.19
Iron	0.93
Manganese	0.026
Copper	0.023
Iodine	0.023
Cobalt	0.006
Potassium	0.006

VITAMIN SUPPLEMENT.

	Per Kilo Diet
Vitamin A	3928 I.U.
Vitamin D_3	982 I.U.
Thiamine	0.5 mgm.
Riboflavin	1.5 mgm.
Nicotinic Acid	2.5 mgm.
Ca-D-pantothenate	0.5 mgm.
Vitamin B_{12}	3.4 mcgm.
Choline Chloride	25 mgm.
Vitamin E (alpha Tocopherol Acetate)	1.2 mgm.
Vitamin K (Menadione)	0.5 mgm.

INGREDIENTS.

The raw materials employed are of the highest quality and have been so selected to conform with the accepted tenets of animal feeding and to ensure that batch to batch variation is reduced to a minimum.

Bran	English milled
Middlings	English milled
Sussex Ground Oats	Thin husks
Barley Meal	Best quality, free from impurities.
Wholemeal flour	English wheat, bold plump kernels.
Linseed Cake	Expeller flakes ground into meal. 8% oil. 30% protein.
Meat and Bone Meal	45 - 48% protein. Maximum oil 4%.
White Fish Meal	Minimum protein 66% Maximum oil 4%
Dried Grass Meal	High protein and carotene content averaging 17% protein and 290 mg. carotene per kilo.
Dried Yeast	Unextracted. Protein 46%
Dried Skim Milk	Roller dried.

MOUSE BREEDING PERFORMANCE - a comparison of three different Diets.

Diet	No. of Breeding Pairs	No. of Litters	No. of young at		Average litter size at birth.	Average litter size at weaning.	% Weaned per litter.	Mean weight at weaning (g.)
			Birth	Weaning				
41B	50	63	484	380	7.7	6.0	78	12.4
A Competitor's Breeding Diet	50	73	469	361	6.4	4.9	77	14.3
'Oxoid' Breeding Diet	50	132	1083	912	8.2	6.9	84	13.8

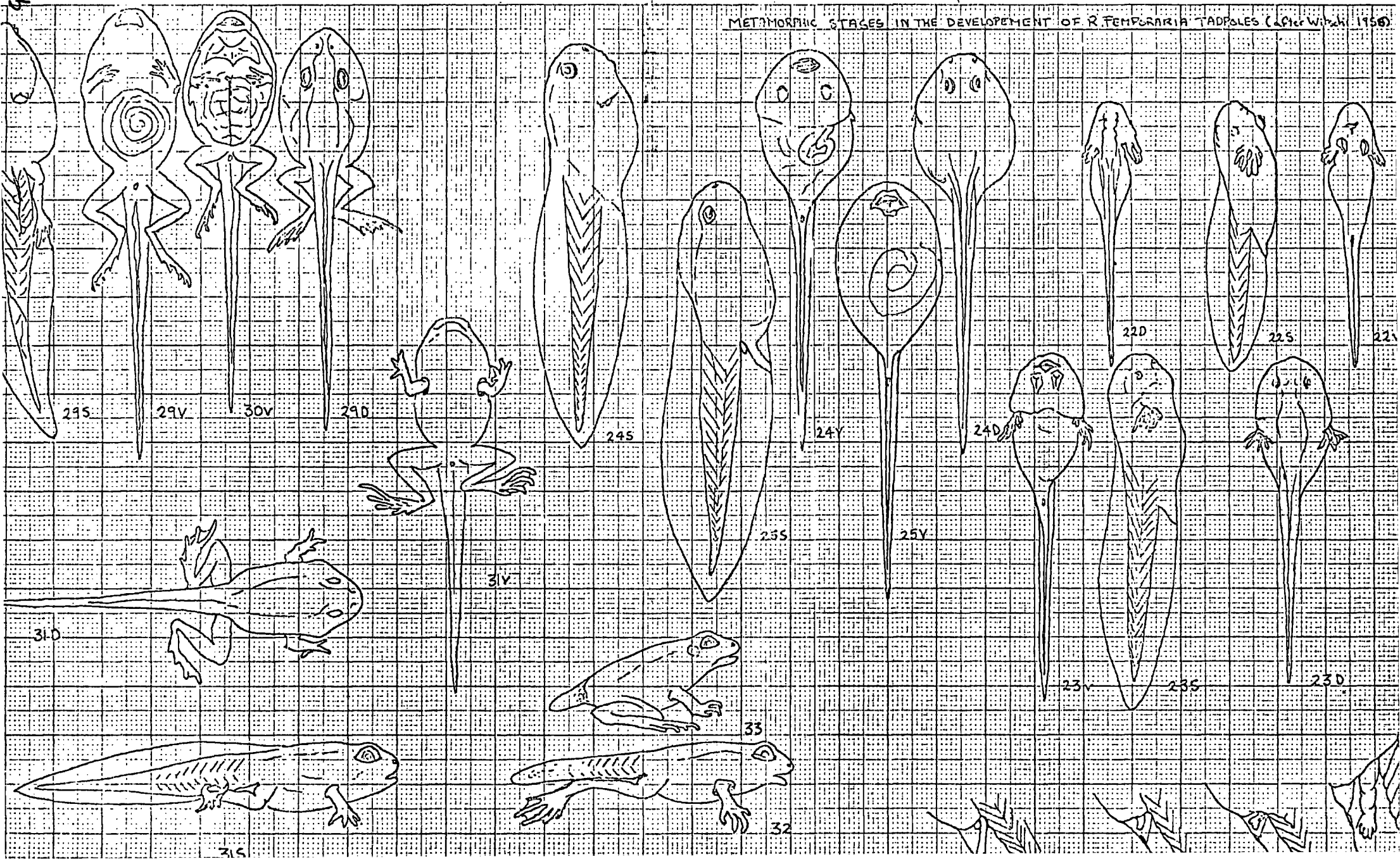
Breeding performance of 3 groups of 50 Tuck T.T. mice taken at random from records for a period of three months during which time they were fed exclusively on diets listed but otherwise maintained in similar conditions.

Figures supplied by courtesy of Mr. W.R. Kingston, Breeding Unit, Research Department,
Fisons Pharmaceuticals Limited,
Holmes Chapel, Cheshire.

The stages of tadpole used in the Text (After Witschi 1958)

No.	Diagnostic Characters
22	Newly hatched, external gills, nostrils, mouth and eyes not yet developed.
23	Large external gills, eyes and mouth not yet fully functional, adhesive glands strongly developed.
24	External gill resorbed, active swimmer, feeder.
25	First Trace of hind limb seen as bud.
26	Hind limb bud grows longer.
27	Hind limb begins to differentiate into parts.
28	Hind limb small but completely developed.
29	Fore limbs developed under operculum.
30	Fore limbs visible through skin, body wall thickens. Gut cannot be seen. Mouth more froglike.
31	Fore limbs emerge, head skeleton developed, resorbtion commences at tip of tail.
32	Resorbtion well advanced and tail dark and fragile, animal may be totally terrestrial at this stage.
33	Tail stump partially or completely resorbed. Animal is now a young frog and unable to exist in a totally aquatic environment.

For sketches of these stages see Figure 0.


METAMORPHIC STAGES IN THE DEVELOPEMENT OF R. TEMPORARIA TADPOLES (after Witsch 1956)
29S
29V
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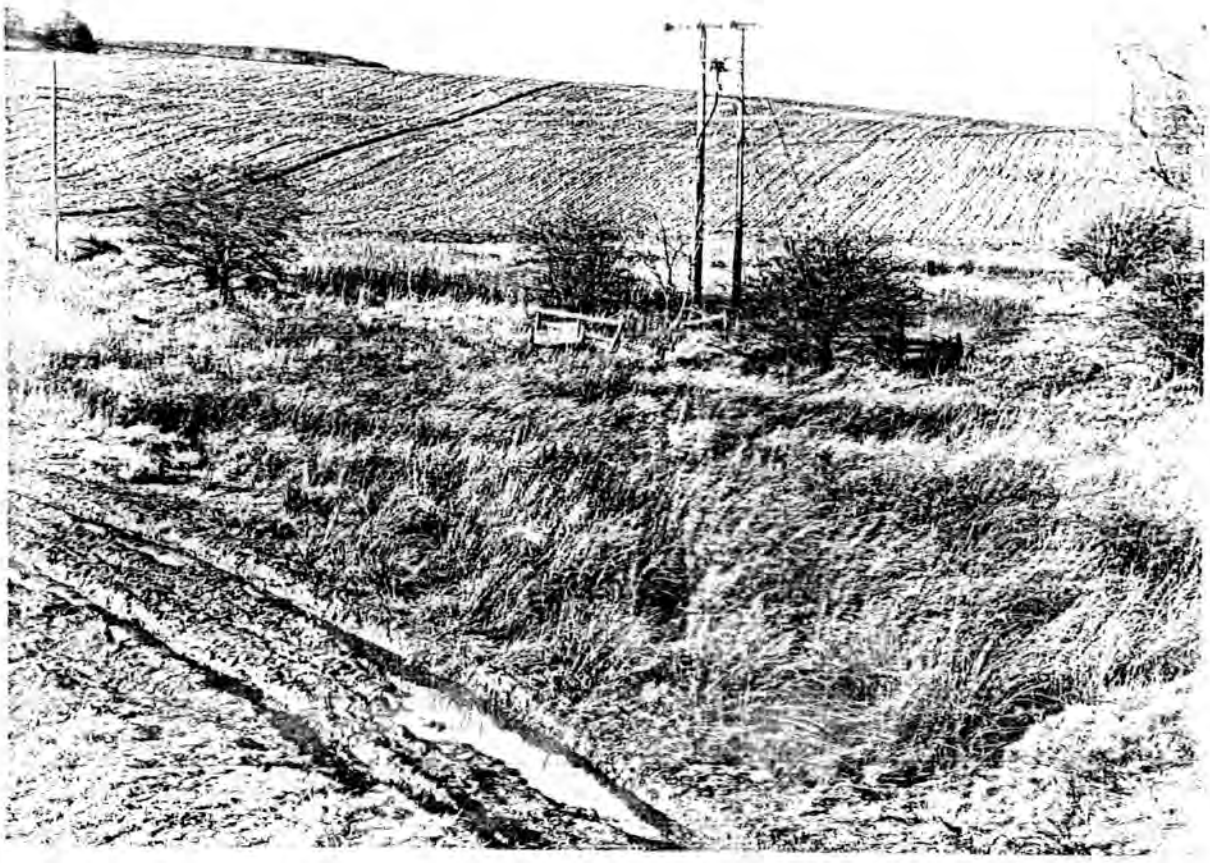


Plate 1 Waldridge Fell Study Area

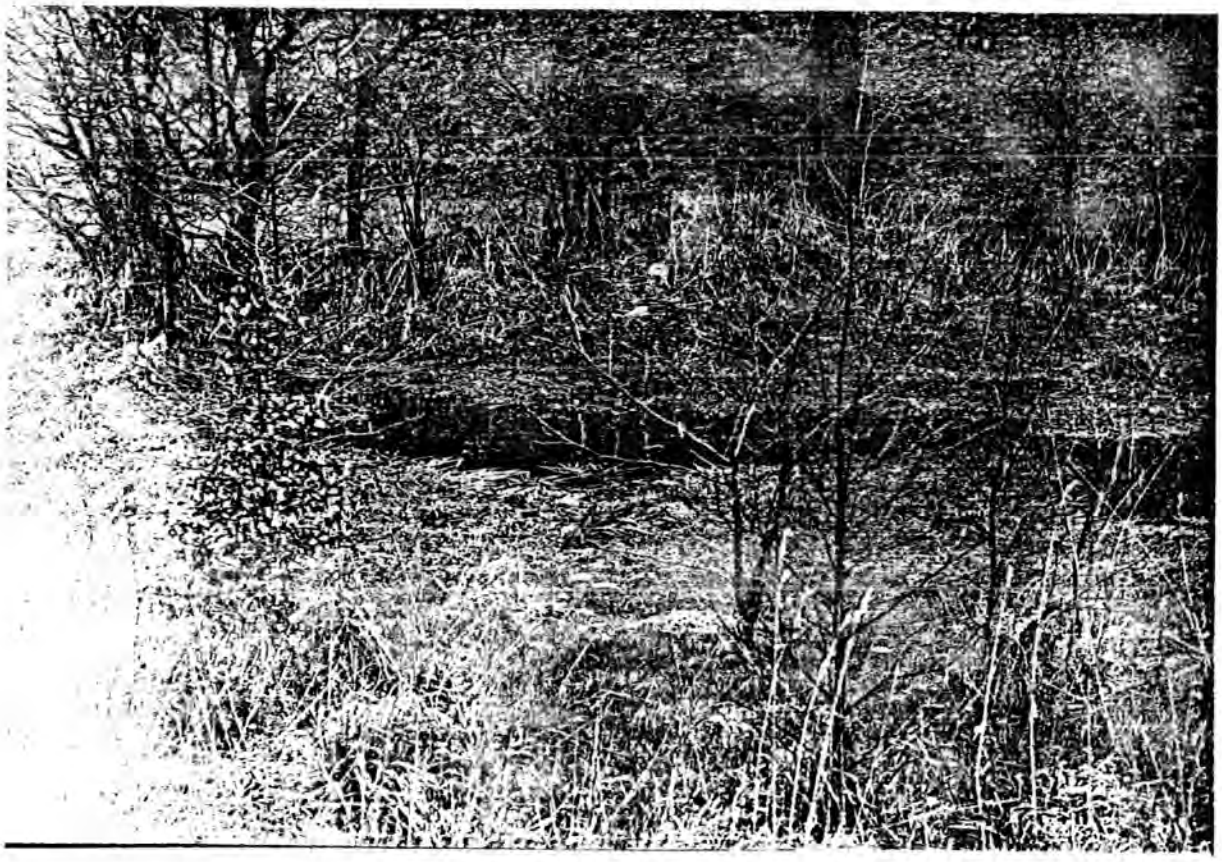


Plate 3 Field Station Study Area

Plate 2 Brasside Study Area

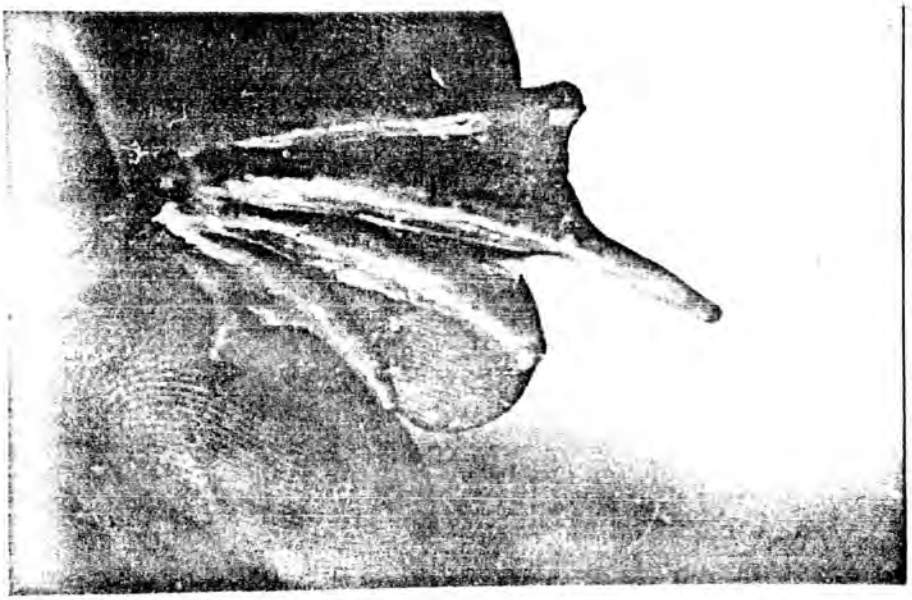
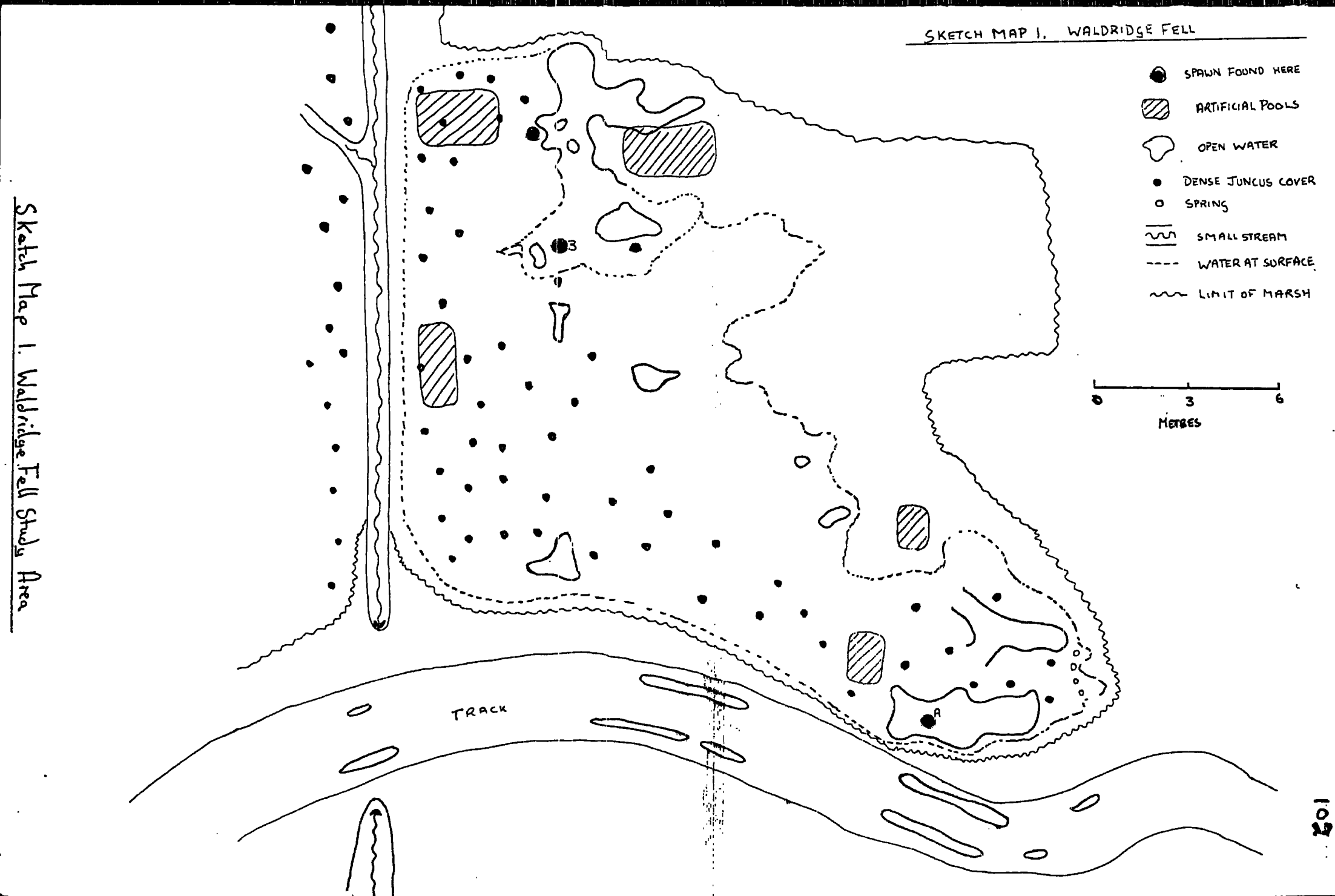
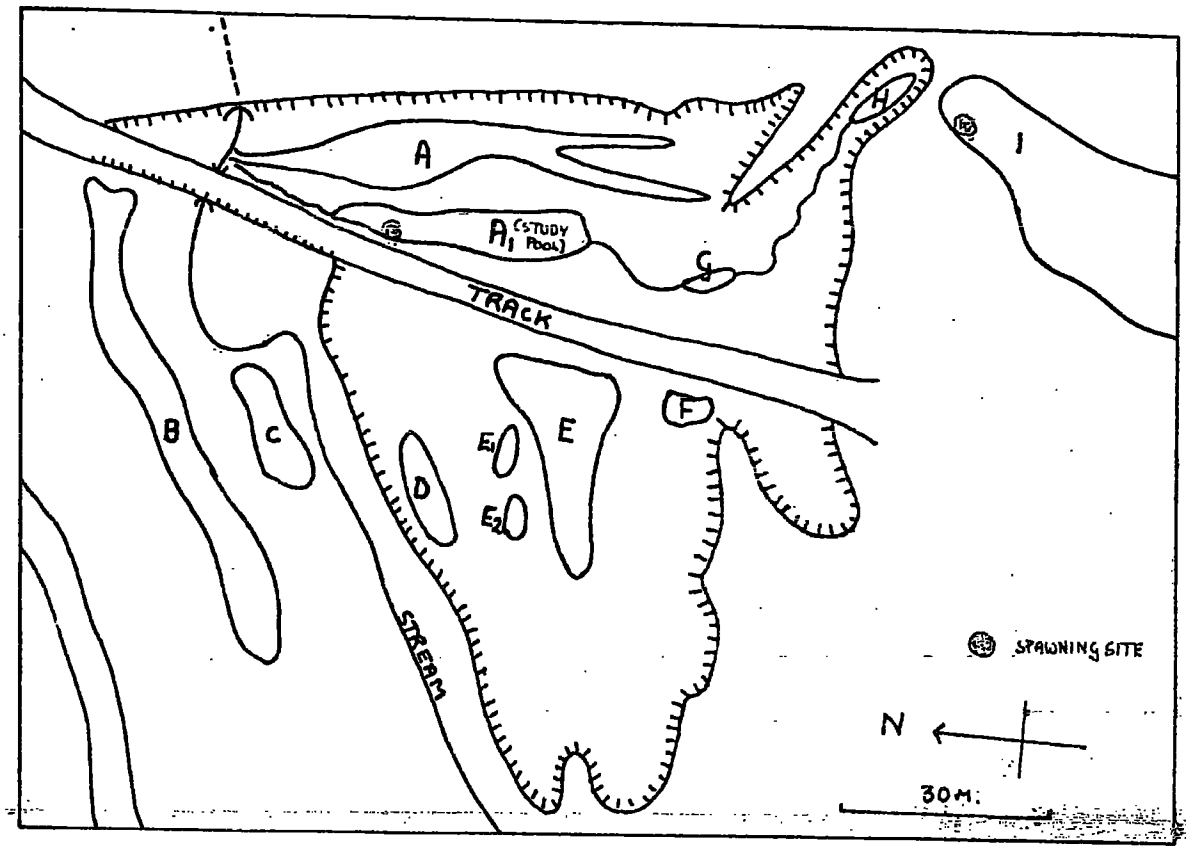


Plate 4 Frog's Hind Foot three months after marking

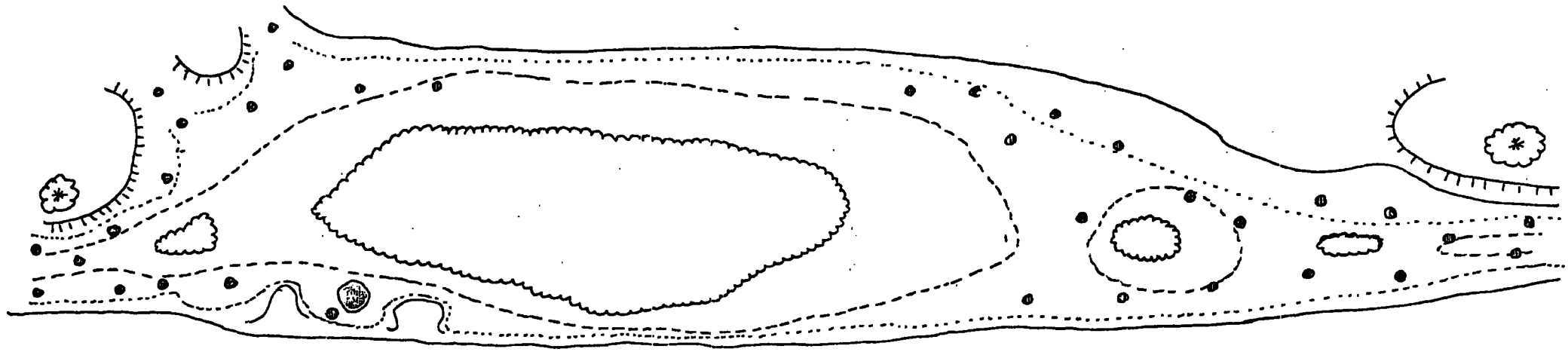
SKETCH MAPS



Sketch Map 1. Waldridge Fell Study Area



ebb map 2 The Brasside Pond System (After Morphy 1965), showing the two sites where Rana temporaria spawned



MAXIMUM EXTENT OF POOL

LIMIT OF POOL 17·4·71

LIMIT OF POOL 12·7·71

OPEN WATER 12·7·71

HIGHER GROUND

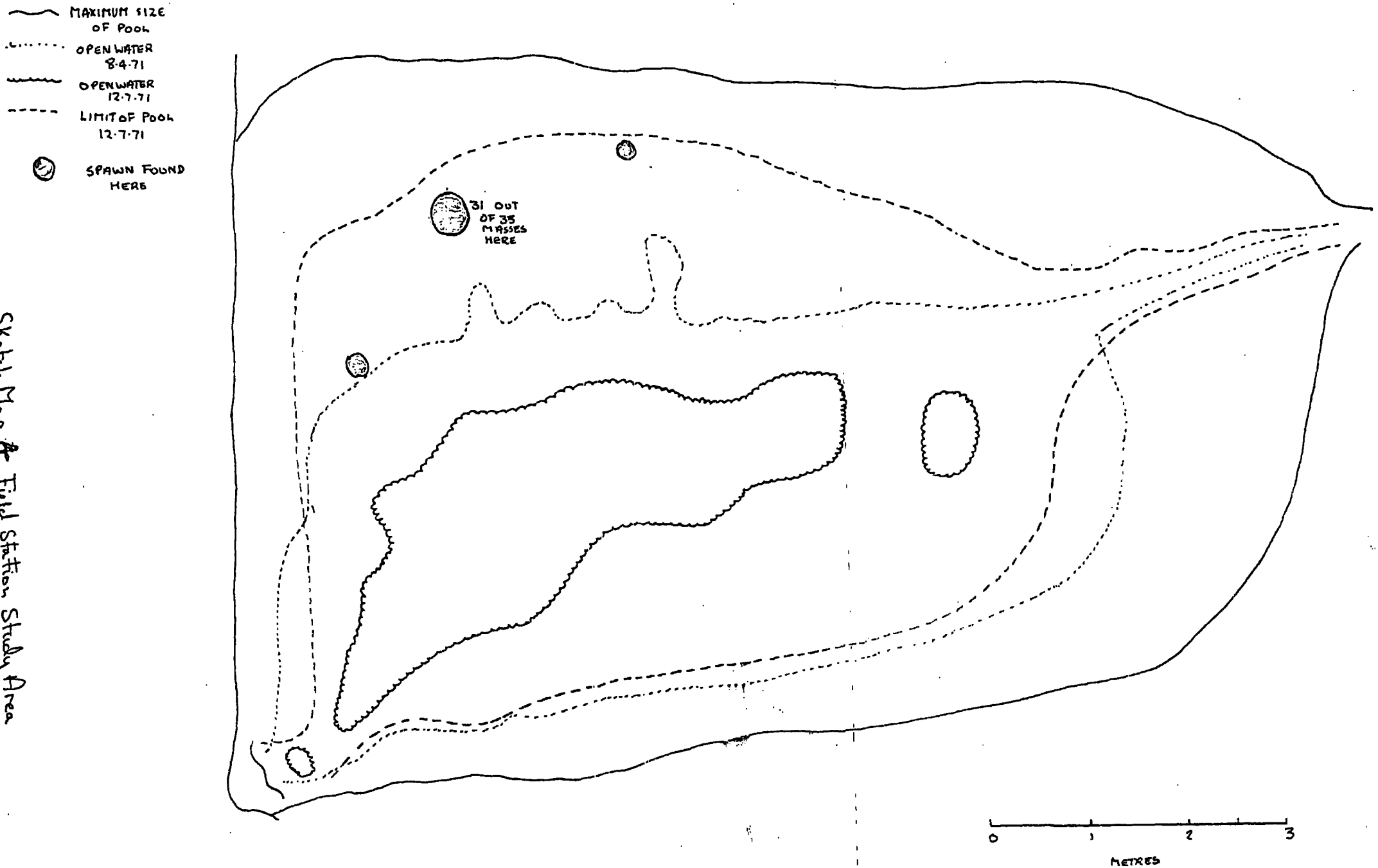
BUSH

DENSE JUNCUS GROWTH

SPAWN FOUND HERE

SKETCH MAP 2. BRASSIDE POOL (A1)

SKETCH MAP 3 FIELD STATION POOL



Sketch Map A Field Station Study Area