The population dynamics of the crested newt (Triturus Cristatus Cristatus (Laurenti)).

Thesis

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THE POPULATION DYNAMICS OF THE CRESTED NEWT (*TRITURUS CRISTATUS CRISTATUS* (LAURENTI))

A thesis submitted for the
degree of Master of Philosophy
by
Andrew Bielinski B.Sc.
to the Department of Biology
of the Open University, on
26th April, 1985

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No part of this thesis has previously been submitted by myself for a degree or any other qualification to this or any other University or similar institution. The work presented is entirely my own.

A. Bielinski

26th April 1985

"I must not omit to tell you......that my people, every now and then of late, drew up with a bucket of water from my well, which is 63 feet deep, a large black warty lizard with a fin-tail and yellow belly. How they first came down at that depth, and how they were ever to have got out thence without help, is more than I am able to say."

Gilbert White, 1788.
The Natural History of Selbourne

ABSTRACT

This thesis describes studies carried out on the crested newt, *Triturus cristatus*, and the smooth newt, *T. vulgaris*, at two localities in the vicinity of Milton Keynes, Buckinghamshire, between 1980 and 1983. The first study site was a pond within the grounds of the Open University at Walton Hall and the second was some 8 miles away from this near the village of Milton Bryan.

At Walton Hall crested newts were intercepted during migration to the breeding pond using drift fencing and pitfall traps and by picking animals up off the road during evening searches. In this way it was found that movement was significantly correlated with daily temperature, but not with daily rainfall. In addition, it was observed that males entered the breeding pond significantly earlier than the females.

At Milton Bryan a program of mark-recapture analyses was carried out on both species as the basis for the study of their population dynamics. Animals were trapped using static underwater traps and marked using toe-clips and the recording of belly-patterning. Both species were found to show variable population sizes from year to year. The sex ratio in *T. vulgaris* showed an excess of females in all years, whilst that of *T. cristatus* varied from an excess of males in some years to equality in other years. Annual survival of male and female crested newts was calculated as 0.36 for each sex.

From data on weight change during the season it was found that the majority of individuals of both sexes lost weight whilst in the water. Annual growth in the crested newt was found to be highly variable, but positively correlated with body size; smaller individuals had larger increments of growth than larger individuals. However, animals of the same size did not necessarily grow by the same amount. Size-frequency distributions of both species are analysed and morphometric characteristics compared with data from other populations. The problems associated with the the extrapolation of these types of data into age-distributions are discussed, with reference to the data on growth. It is concluded that length cannot be used as reliable indicator of age in _T. cristatus_. From the size-frequency data it was found that the numbers of juveniles appearing at a breeding site may be highly variable from year to year. The implications of this for the dynamics of crested newt populations are discussed.

Data are also presented from the dissection of preserved animals. These relate gonad size to body size in both species. It is shown that both testes weight and ovary weight are positively correlated with body weight and snout-vent length and that females display size-specific fecundity i.e. larger females produce larger ova and greater quantities of ova than smaller individuals. These findings are discussed

with reference to other species of urodele and with regard to the life history tactics displayed by other species.

CONTENTS

Chapter 2. Methods

LIST OF TABLES

LIST OF FIGURES

Between Pages

CHAPTER 1. INTRODUCTION.

1.1 Classification and brief literature review.

The tailed amphibians belong to the order Urodela. This is a large group comprised of three super-families, the Cryptobranchoidea, Salamandroidea and Sirenoidea (Webb et al, 1981). Goin & Goin (1962) classify the former two at the sub-order level. However, both classifications identify the Salamandroidea as containing five families: the Salamandridae, Ambystomatidae, Plethodontidae, Amphiumidae and Proteidae.

Those amphibians referred to as newts belong to the family Salamandridae. There are some 14 or 15 genera in the family which are confined to Europe, the United States of America and parts of Asia. Wake & Ozeti (1969) studied the evolutionary relationships within the family and identified four groups within each of which animals shared broadly similar features. This was based on the comparison of 40 characters, ranging from morphometric features to feeding mechanisms. The largest of these groups contained nine genera. These were *Triturus*, *Taricha*, *Notophthalmus*, *Euproctus*, *Neurergus*, *Paramesotriton*, *Cynops*, *Hypselotriton* and *Pachytriton*. Of these, only *Triturus* and *Euproctus* occur in Europe, although other members of the family are found; namely, *Salamandrina*, *Salamandra*, *Chioglossa* and

Pleurodeles.

There is some argument as to the number of species in the genus *Triturus*. Smith (1951) follows the classification of Lantz (1927) who recognized nine species, with eighteen subspecies. Steward (1969), however, identifies eight species comprised of twenty-seven subspecies after that of Mertens and Wermuth (1960). The differences between these two taxonomies arise from the inclusion of the Caucasian species *T. vittatus* in the classification of Lantz and the discovery of further subspecies in the last 30 years. Frazer (1983) gives the same nine species as Smith (1951), but recognises 32 subspecies. These extra subspecies have arisen through further splitting of *T. vulgaris* and *T. alpestris*.

In the British Isles, however, the situation is rather less complicated with only three native species occurring. These are the great crested newt (*Triturus cristatus cristatus*, Laurenti), the smooth newt (*T. vulgaris vulgaris*, Linn.) and the palmate newt (*T. helveticus helveticus*, Razoumowski). Only the first two species occur in the study area and thus it is with these that the work is concerned.

Until recently few detailed studies of either of these species were available in the literature, although their general natural history had been documented for some time. The species were probably first described in the British

Isles by Dr Christopher Merrett, a physician, in 1667 (Smith 1951). This was followed by writings from persons such as John Ray, in 1693, and John Morton, in 1712. It was not until 1800, however, that they were clearly identified as being different from lizards. In 1839, Bell's 'A History of British Reptiles' was published and gave much better descriptions of the biology of these animals than had previously been available (Frazer 1983). However, the major contribution to our knowledge of the British newts, prior to modern research, unarguably arose through the work of G.A. Boulenger who wrote extensively on all branches of herpetology (Smith 1951).

Apart from the work of Boulenger and occasional papers such as that by Cummings (1912) on distant orientation by newts, the biology of this group was largely ignored in the first half of this century, until the publication of 'The British Amphibians and Reptiles' by Malcolm Smith in 1951. This remains one of the most authoritative books available on the subject. Information is given on the life cycles of all three newt species native to Britain, with descriptions of courtship display, metamorphosis, distribution, etc.

Creed (1964) published work carried out on crested newts in the New Forest and detailed various aspects of the metamorphosis of this species.

The most thorough studies of the ecology of smooth and crested newts in Britain have appeared in the last twelve or so years. Bell (1973, 1974a, 1977) and Bell & Lawton (1975) published work on the population dynamics of the smooth newt. This study was carried out on a series of ponds in Oxfordshire over a three year period. Many aspects of the life history are detailed, from development of the egg, through descriptions of the larval stage to analysis of the growth, survival, fecundity and age-structure of the adult population.

The sexual behaviour of the smooth newt has been very fully described by Halliday (1972, 1974, 1975) in much greater detail than had previously been attempted. He identified four separate phases of display through which a pair must proceed for successful spermatophore transfer to take place. More recently this work has been continued by Paul Verrell (1983b, 1984a, 1984b 1984d) who has, in addition, studied aspects of the sexual behaviour of the American red-spotted newt, Notophthalmus viridescens (Verrell 1983a). More recently, both of these workers have made a study of the breeding dynamics of smooth and crested newts at a pond in Buckinghamshire (Verrell & Halliday in press a, b).

The characteristics of newt breeding sites were investigated by Cooke & Frazer (1976) who gave the preferences of the three species for pH, pond size, density of vegetation and other physical properties. Similar information has been provided by Beebee (1977b, 1979, 1981) in his studies of amphibian habitats in Sussex. Much of this work has arisen through concern over the decline of amphibians in Britain in recent years, particularly in the case of the crested newt and the natterjack toad, *Bufo calamita*. This decline has been documented by Prestt et al (1974) and by Beebee (1975, 1977).

Studies of the ecology of *T. cristatus* and *T. vulgaris* in Europe have followed the lines of those in Britain though often in less depth. Hagström (1974, 1975, 1976, 1977, 1979a, b, 1980) has studied both of these species in Sweden. However, most of the papers cited are rather short and often repetitive. Dolmen (1980, 1981) has described the distribution of both species and homing behaviour of smooth newts in Norway. Studies of growth in adult crested newts have been carried out by Glandt (1981), who has also investigated the abundance of the genus *Triturus* in mid-Europe.

Our knowledge of the ecology and behaviour of *T. cristatus* and *T. vulgaris* in the British Isles, then, is somewhat patchy, with certain aspects being more fully documented than others. In particular, the population ecology of the crested newt has been very neglected. The aim of this study was to provide a more complete picture of the ecology of this species through the monitoring of one or more populations in the Milton Keynes area. It was hoped that information would be gathered on the timing of spring and autumn migrations, through the use of drift-fencing and pitfall traps, whilst populations within the ponds would be censused using mark-release-recapture analyses. In addition, preserved animals would be used to investigate the reproductive systems of males and females and the feeding habits of both species. Hopefully, the work would lead to practical suggestions for the conservation of the species. Smooth newts were to be studied also to provide comparative data for studies on the species by other workers.

The introduction of the 1981 Wildlife and Countryside Act requires that a licence be obtained for any studies of crested newts. This was kindly granted for this study by the Nature Conservancy Council.

1.2 Description of species.

The smooth newt is now probably the commonest amphibian in the British Isles. It is found in a variety of localities within its range. Smith (1951) reports that it tends to be replaced at higher altitudes by *T. helveticus*. However, it is now thought that water acidity is a more important factor in the distribution of the species (Cooke & Frazer, 1976).

T. vulgaris is a small species, adults generally ranging between 70 and 90mm total length. There is considerable sexual dimorphism during the breeding season. At this time the males develop a prominent, continuous crest along the back and tail and have large, dark spots on the upperparts and belly. The underside is usually bright orange or yellow. Females are much more drab, lacking the crest and large spots and generally having less colour on the belly. Both sexes exhibit a great deal of variation in ground colour (Arnold and Burton, 1978).

The great crested newt, as its name suggests, is a much larger species, with adults ranging from about 90 to 150mm total body length. It is an unmistakeable animal, with both males and females possessing strongly granular skin of a dark- brown or black colouration. It is this granular skin which gives rise to its other common English name of the 'warty newt'.

Both sexes have white stippling on the side of the head and body, with bright orange or yellow underparts heavily patterned with black blotches. During the breeding season the male also has a high, strongly denticulated dorsal crest and a silver-white band running along either side of the tail. Unlike *T. vulgaris* the crest in *T. cristatus* is not continuous, but has a gap at the base of the tail.

The life histories of both species are broadly similar and very simply are as follows. In the British Isles adults start to enter the breeding ponds in late February or early March, generally at night (Smith 1951). Males actively court females through a complex display sequence. This courtship behaviour is fully described for the smooth newt by Halliday (1974). Fertilization is internal, following the picking up of spermatophores by the female. Eggs are laid singly on vegetation such as water starwort (*Callitriche palustris*) (Smith 1951).

The embryos develop over three to four weeks after which the tadpoles emerge. These are carnivorous throughout life, feeding on zooplankton, insect larvae etc. Following metamorphosis the juvenile newts leave the water to find refugia in which to survive the winter and the time prior to returning to the pond to breed (Frazer 1983). Most adults leave the water sometime between August and October, although some have been reported to overwinter in ponds

(Smith 1951, Verrell & Halliday, in press b).

1.3 Description of study areas.

A number of ponds in the Milton Keynes area were visited during the winter of 1979/80 with a view to determining their suitability as study sites. The majority of these were rejected for a variety of reasons.

First, many ponds were found to lack one or both of the species involved in the study. Secondly, the rapid expansion of the new city at the time meant that some sites were likely to disappear before the end of the study. Finally, disturbance by children was a factor, since traps were liable to vandalism if left for any length of time. After eliminating those ponds which were deemed unsuitable two sites were chosen and trapping commenced in January 1980.

The first of these sites is a pond within the grounds of the Open University (O.S. grid reference SP886370). This has been in existence for at least sixty years, appearing on Ordnance Survey maps dating back that far. However, it is not known whether it has undergone alteration at all during the building of the University. There is no inflow or outflow and although rather deep (some 2.5m at its deepest)the pond has been known to dry up in exceptionally dry summers, as in 1976. The location of the pond is shown in Figure 1. The southern edge slopes very steeply, whilst the other three sides shelve more gently. The distribution of the most abundant plant species at the site is indicated in Figure 2. Briefly these are *Lemna trisulca*, *Potamogaton natans*, *P. crispus* and *Ceratophyllum demersum*. The latter two are particularly used in the pond by female newts to lay their eggs on.

The pond is fairly isolated within the grounds of the university as may be seen from Figure 1. It is immediately surrounded by pollarded willows (*Salix* sp.) an area of lawn and a road. Beyond this are buildings or car parking areas. Although the nearest undeveloped land is only some 100m away to the south and the west, animals approaching from the west would have to cross the River Ouzel, whilst those moving from the south have a large car park to contend with, as well as the ring road. The nearest ponds are some distance away as indicated in Figure 1.

The site supports a diverse invertebrate fauna as may be seen from Appendix 1, which also shows the vertebrates observed at the site. The 3-spined stickleback, (*Gasterosteus aculeatus*), occurs here in large numbers and is likely to be a major predator of the eggs and larvae of both newt species, although their actual impact has not been assessed. A heron (*Ardea cinerea*) visited the pond sporadically during 1981 and may have preyed on the adults

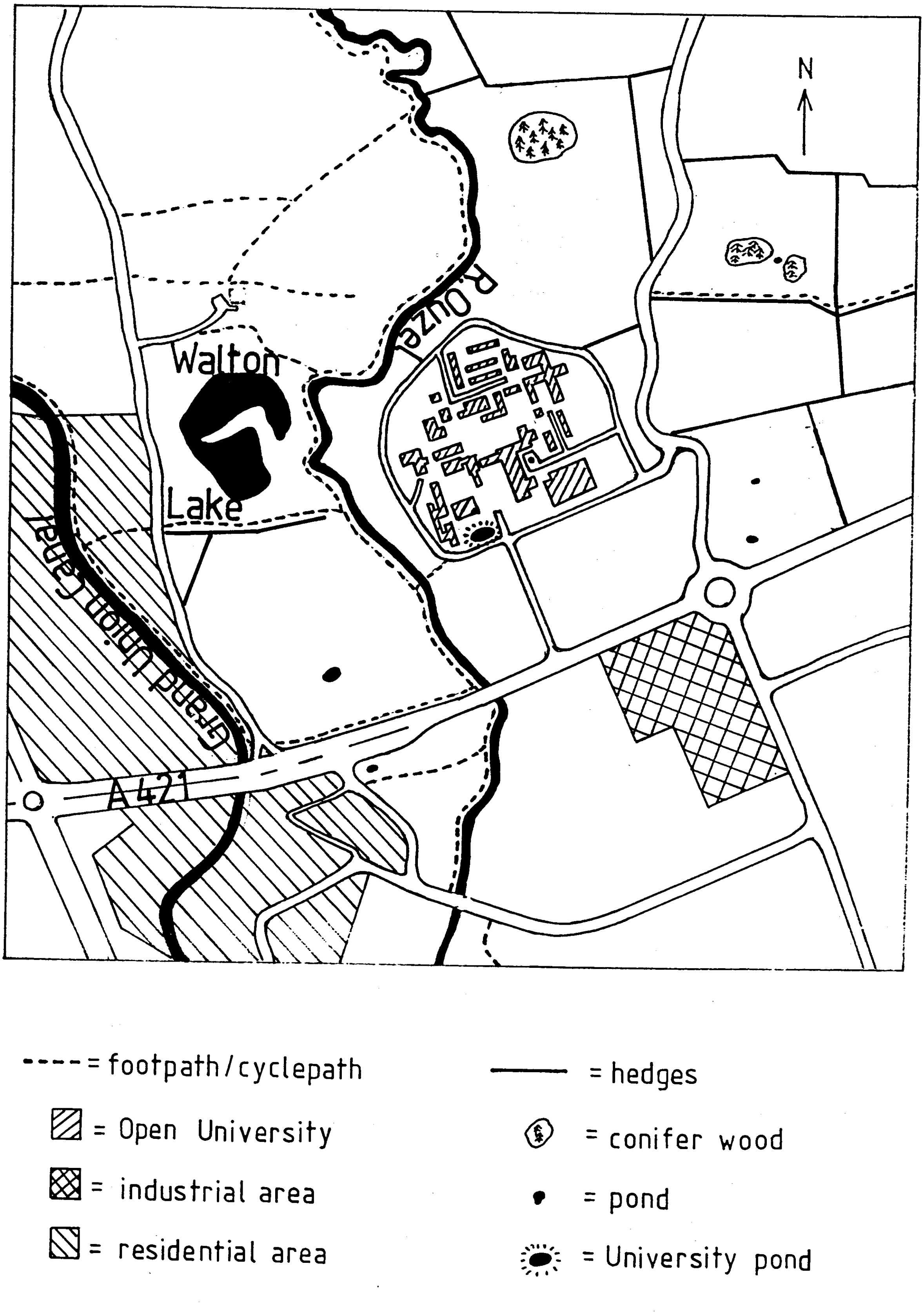


Figure 1. The location of the University pond at Walton Hall. (not to scale)

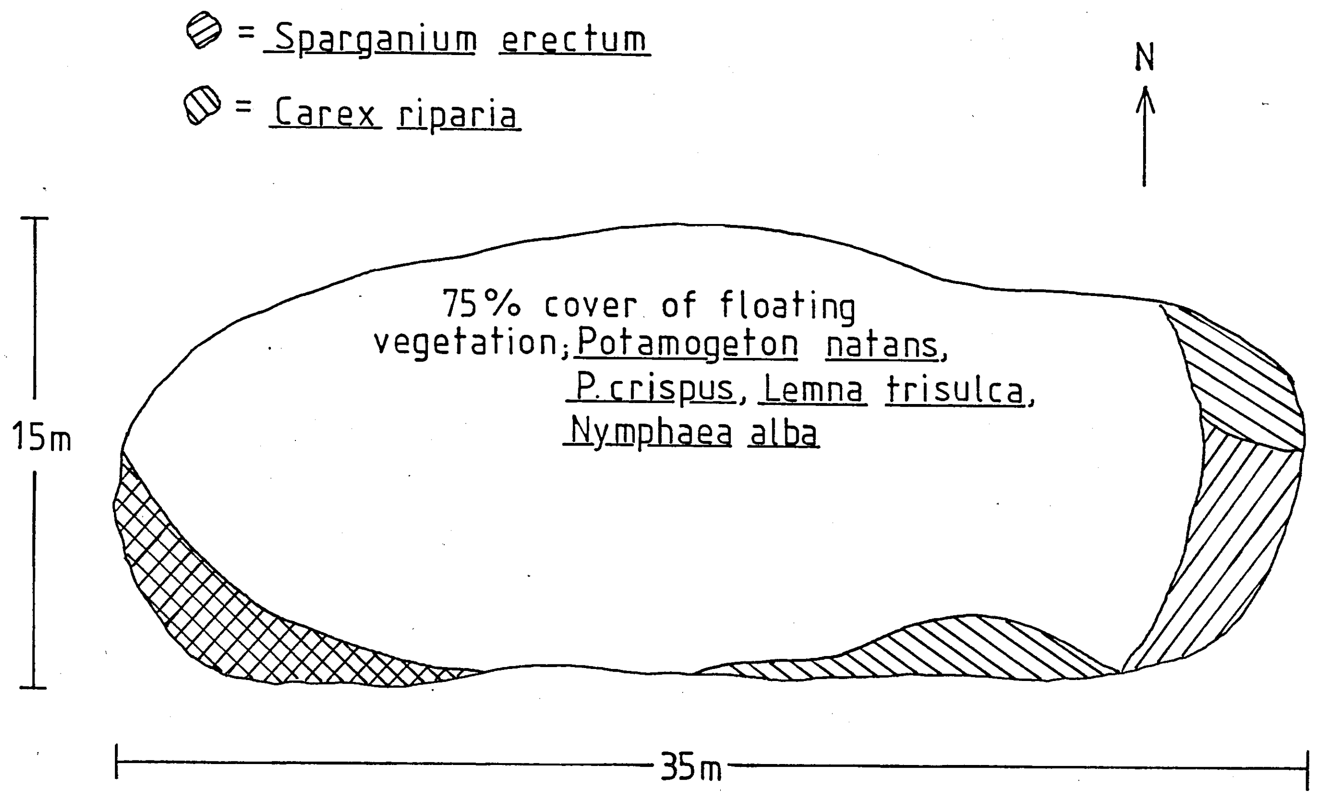


Figure 2. The distribution of the major aquatic plant species in the University pond.

of both species, although frogs are the favoured amphibian prey (Cramp & Simmons, 1977).

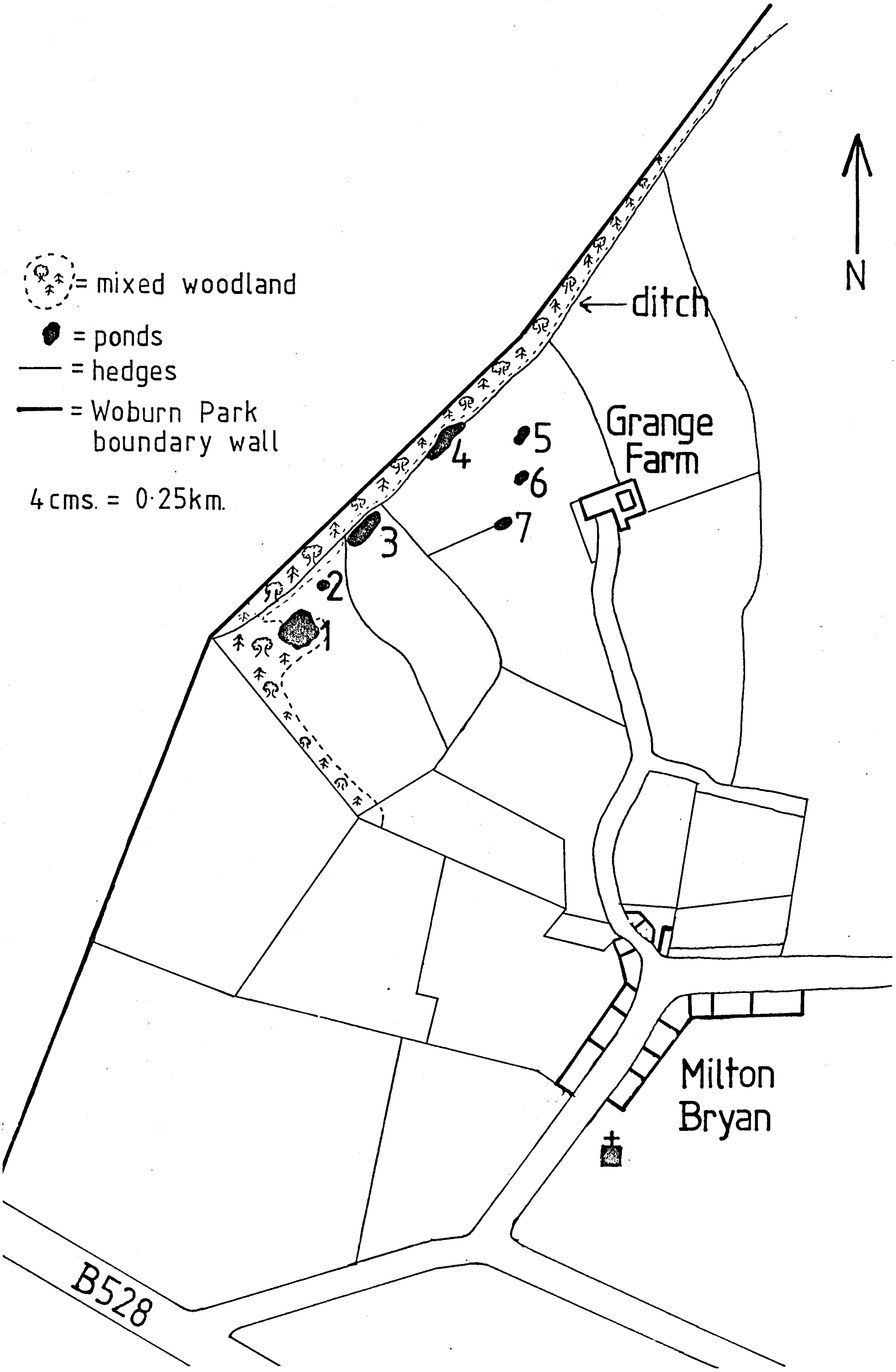
The second study site is a series of seven ponds near Grange Farm near the village of Milton Bryan, Bedfordshire (O.S. grid reference 971308). These are on land owned by the Bedford Estate and permission to work there was granted by the steward (formally Mr N. Street and latterly Mr D.C. Thompson). The distribution of the ponds is shown in Figure 3. Their origin is unknown, but they appear on Ordnance Survey maps dating back to the turn of the century.

It was found that ponds 2, 4, 5 and 6 dried up completely each year. Neither species of newt was found in these four small ponds, apart from six individual smooth newts in pond 6 in 1980. Ponds 3 and 7 remained filled throughout the year but did not support any newts. However, populations of _Bufo bufo_ and _Rana temporaria_ bred annually in pond 3. Trapping was therefore discontinued in all ponds except pond 1 from 1981 onwards.

Pond 1 was by far the largest of the seven, being some 1110m^2 in area and having an average depth of 0.38m. An outline of the pond showing the distribution of the main plant species is given in Figure 4.

As may be seen from this figure the pond is surrounded by mixed woodland and pasture. The woodland is mostly

Figure 3. The location and distribution of the ponds at Milton Bryan. The main study pond is indicated by the figure 1.



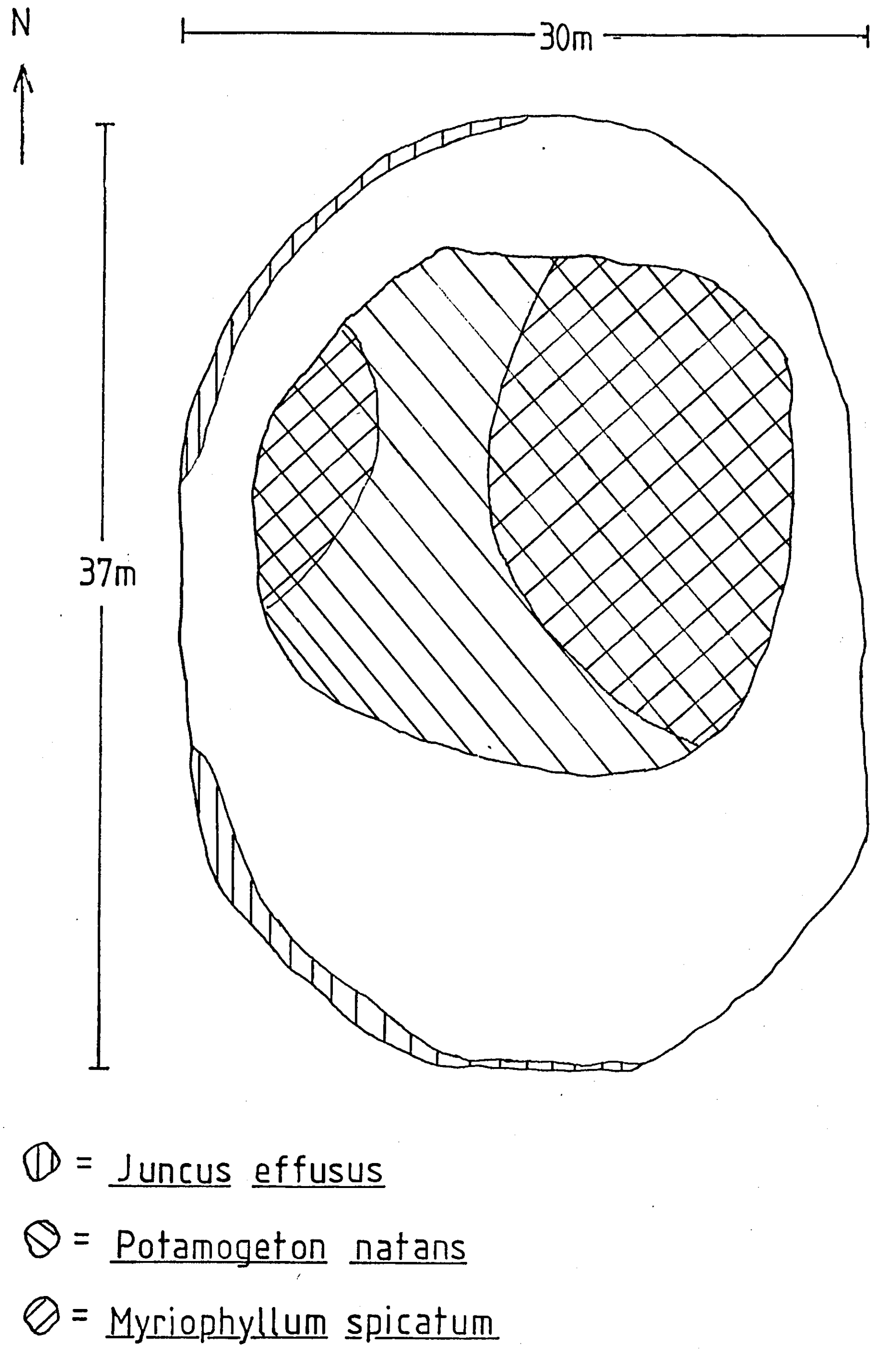


Figure 4. The distribution of the major aquatic plant species occurring in the main study pond at Milton Bryan.

willow (*Salix alba*), ash (*Fraxinus excelsior*) and Norway spruce (*Picea abies*). It is largely open in character, with very little in the way of a shrub layer. Beyond the wood to the east are arable fields of various crops. The pasture closest to the pond is rather damp and formed largely of tussock-forming grasses, such as *Deschampsia cespitosis*. This area contains a considerable amount of encroaching scrub, comprised of hawthorn (*Crataegus monogyna*), and dogrose (*Rosa canina*). These are also the main components of the hedgerows near the pond. Beyond this damp area the pasture is rather more improved neutral grassland.

The invertebrate species in this pond were very similar to those at the Walton Hall site and are listed in Appendix 1. The major difference is the number of species of dragonflies and damselflies present at Milton Bryan; five species were found here as opposed to one at Walton Hall. No fish occurred at this site, unlike Walton Hall. A herd of cattle was present for most of the study period. This tended to churn up the edge of the pond somewhat, thus damaging the vegetation.

Cooke & Frazer (1976) studied the characteristics of the breeding sites of the British newts. Briefly, smooth newts are rarely found in ponds having a pH of less than 6, and have a preference for heavily vegetated sites with surface areas in excess of 100m2. They also prefer metal rich waters, particularly those with a high calcium content. Crested newts tend to prefer larger, deeper ponds than smooth newts, with areas of more open water in them. Their pH preference is not known.

Beebee (1977), in a study of amphibians on chalk uplands in Sussex, found that both newts were more abundant in those ponds which were associated with gorse (Ulex) scrub, and were absent from areas of exclusively arable farming. The presence of a suitable vegetation structure for the terrestrial phase of the newt's life cycle is obviously of major importance.

The two main ponds in this study broadly conform to the requirements set out above. The University pond is very deep and has areas of both vegetation and open water. The pH was measured on a number of sampling occasions during the 1981 breeding season, giving an average of 7.6 (at an average temperature of 7.0°C), which would be expected, given the alkaline nature of the clay soils in the area. However, there is little suitable cover for terrestrial animals in the immediate vicinity of the pond. During 1980, a large mound of earth near the pond was used as a refuge by juvenile crested newts; this, however, was removed after a few months. The effect of this on the juvenile population is not known.

The main study pond at Milton Bryan is not particularly deep, but again it has open water and dense vegetation. The pH here was 7.8 averaged over the 1981 breeding season. Furthermore, it had a high calcium content of 56ppm and a potassium count of 3ppm (analysis carried out by Pam Gray of the Systems Department at the Open University). The surrounding woodland and pasture offer a large number of refugia for terrestrial animals. Surprisingly, however, searches during the autumn and winter failed to find either species on land.

CHAPTER 2. METHODS

2.1 Trapping methods.

A number of techniques are available for the investigation of amphibian populations, of which three are recommended for studying newts at their breeding sites: netting ponds during daylight, searching by torchlight after dusk and setting traps in the water. A further method, particularly applicable for long term studies, is to use a combination of drift-fencing and pitfall traps (see Storm & Pimentel 1954, Twitty 1966, Gill 1978a, Cockburn et al 1979 and Gibbons & Semlitsch 1981). In most situations this is probably the most efficient technique available; Gill (1978a) was able to intercept some 90% of a population of American red-spotted newts (*Notophthalmus viridescens*) entering a breeding pond using such a method.

The method or methods used in any particular study depend largely upon the nature of the ponds under study, and also to some extent on whether the data required are qualitative or quantitative.

Netting by daylight was ruled out for both sites in this study on two counts. First, both ponds were heavily vegetated; intensive sampling over a season or more would have led to considerable habitat damage. Secondly, the depth of the pond at the University meant that only the very edge would have been accessible for sampling.

As stated in chapter 1, there was a herd of cattle present at the Milton Bryan pond for most of the spring and summer. This meant that any drift-fencing erected would have been trampled very quickly. Furthermore, the number of fallen trees around the pond would have prevented the site from being fenced off entirely. Therefore only aquatic traps were used here. These are described in the next section.

The University pond appeared to be an ideal location at which to use drift-fencing. Permission to erect one was granted by the University estates office and the fence was built during the spring of 1980. It was constructed of plastic sheeting attached to wooden stakes and supported at the top edge with fencing wire. The overall structure was 23cm in height with a further 15cm dug into the ground to prevent animals from burrowing under. The drop traps consisted of plastic waste bins (23cm x 23cm x 30cm) sunk into the ground at various points, as shown in Figure 5.

Initially the method proved reasonably successful, with a steady trickle of animals being caught. Unfortunately, the presence of the fence caused problems for the gardening staff during lawn-mowing and damage to the fence occurred on a number of occasions. Finally, during August 1980 the fence

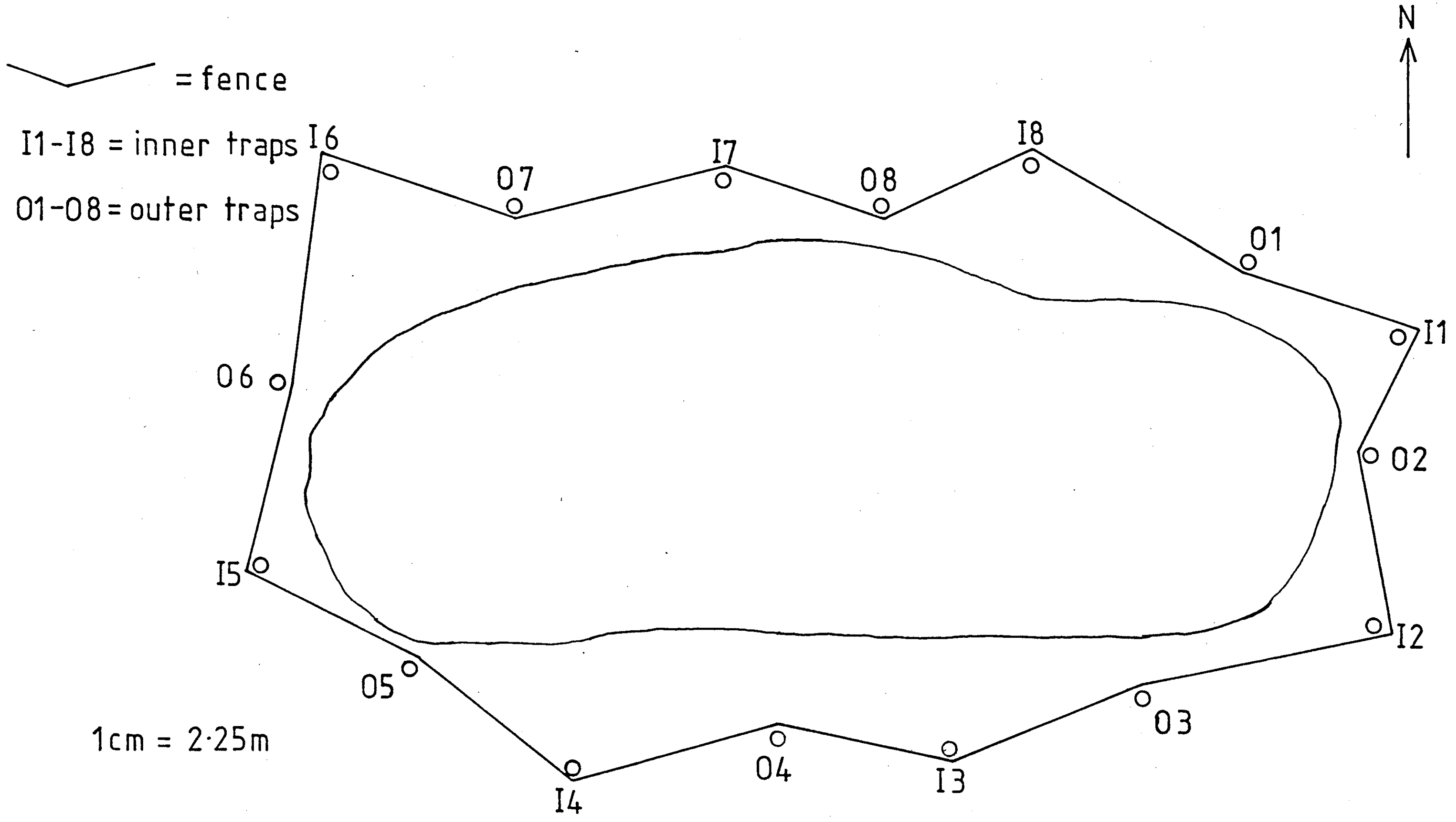


Figure 5. The layout of the drift-fence/pitfall trap system used at the University pond during 1980.

was completely uprooted by vandals. It was replaced the following season in a modified form. This was devised so as to facilitate the lawn-mowing activities of the gardening staff. It took the form of discrete 'V' shapes of fencing. These were arranged with the mouths of the 'V's facing away from the pond so as to channel incoming animals into the drop-traps. These could be turned around to face the pond in order to capture animals leaving the pond in the autumn. However, this design proved to be almost totally unsuccessful and the method was abandoned at the end of 1981.

The aquatic traps used in the study are shown in Figures 6 and 7. The former was designed by Graham Bell and K.T. Marshland and used by Bell during his PhD study (Bell 1973). The second was developed by Breder (1960) for trapping fish fry.

Both types were used at each site. The steep-sided nature of the University pond meant, however, that only a small area could be trapped. Consequently, captures were very few. Furthermore, any smooth newts captured were removed for behavioural studies, so a population study of this species was not attempted here. These factors resulted in trapping being terminated at this site from the end of 1981.

Of the two traps, the 'Bell' type appeared to be the most successful. It consistently caught more newts than the other type. This can be seen for 1981 and 1982 from Table 1 . Trap

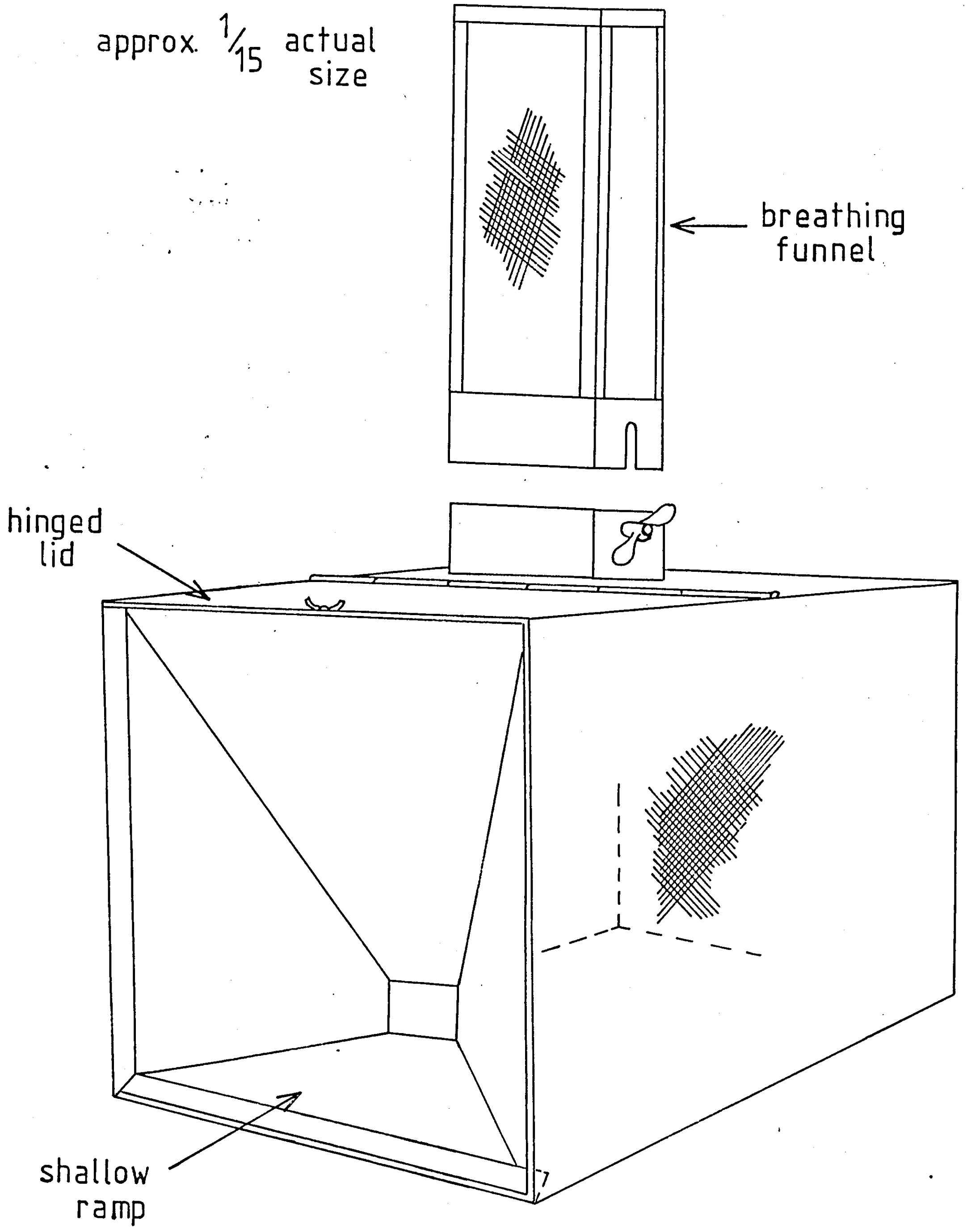


Figure 6. The underwater newt trap designed by Graham Bell.

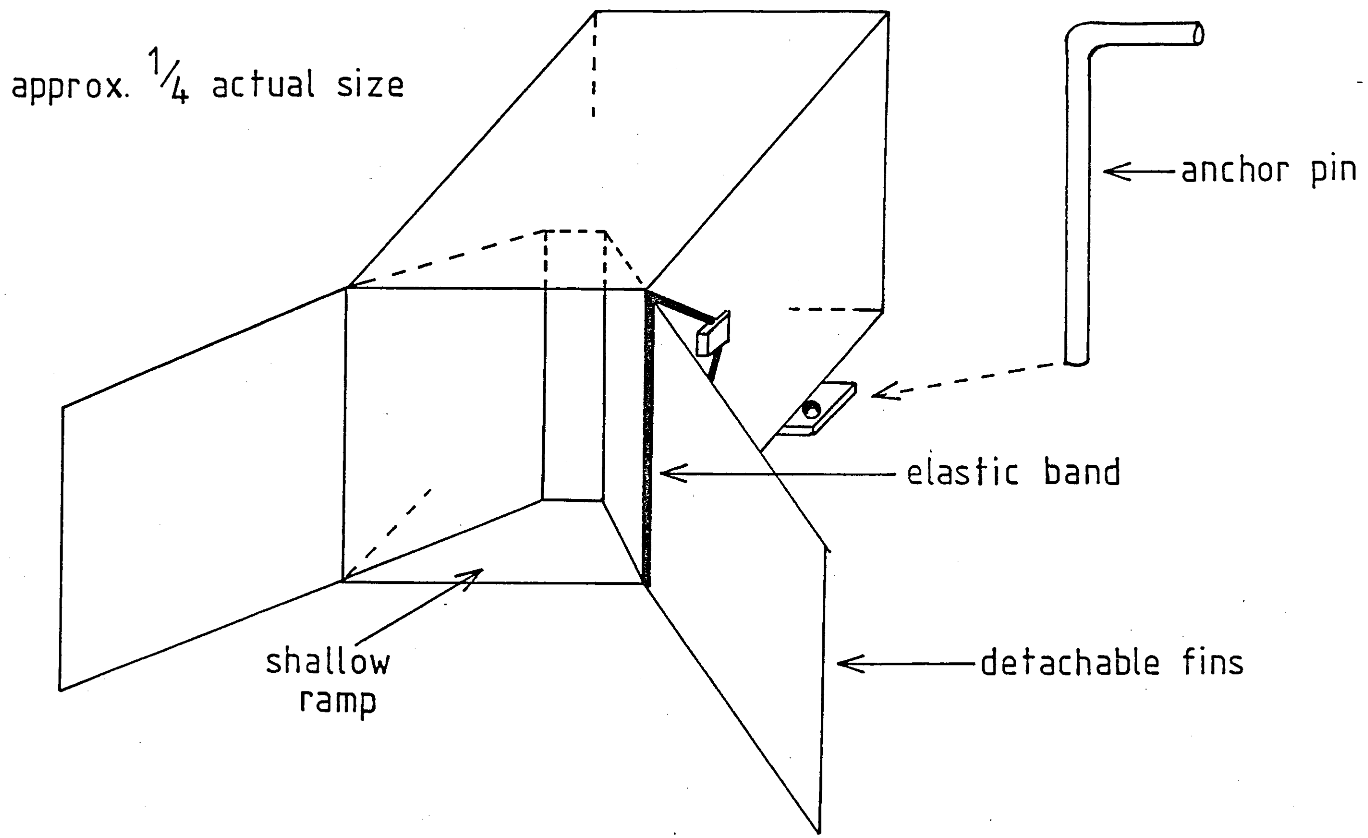


Figure 7. The fish-fry trap designed by Breder. This was the type predominately used at Milton Bryan.

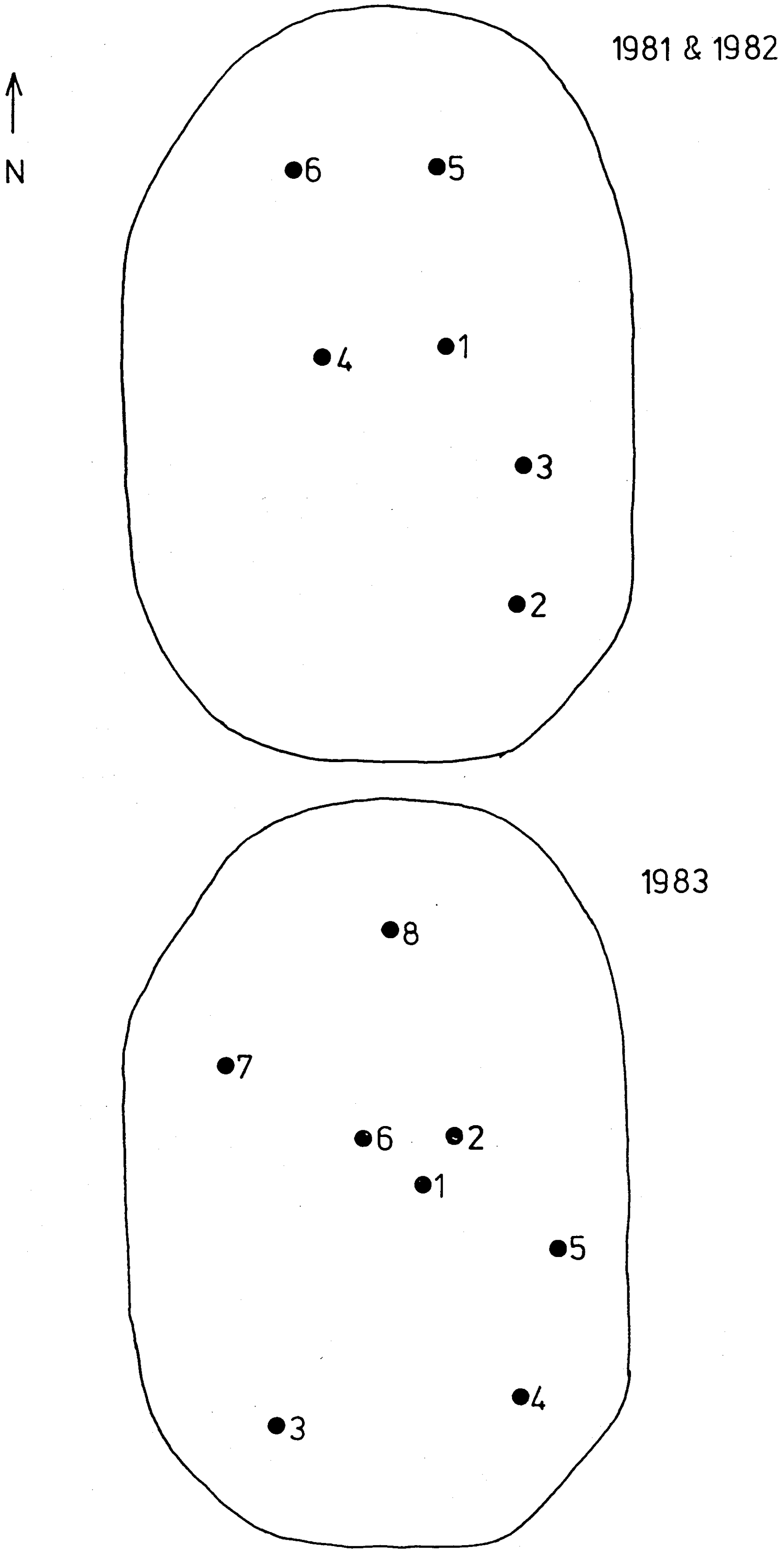


Figure 7a: The arrangement of the aquatic traps used at Milton Bryan in 1981, 1982 & 1983

1 is the 'Bell' type and the remainder are Breder's design. Trap 1 caught as many animals as the others combined. It was positioned in approximately the same place in the pond in each of these years.

YEAR	SPECIES	SEX	N	% OF TOTAL NUMBER CAUGHT PER TRAP					
				1	2	3	4	5	6
1981	_T. crist_	m	234	55.3	8.8	10.3	11.4	7.3	6.9
1981	_T. crist_	f	227	56.7	5.7	8.5	16.2	6.8	6.1
1982	_T. crist_	m	165	42.5	13.1	14.4	10.0	12.5	7.5
1982	_T. crist_	f	63	41.7	18.3	15.0	10.0	8.3	6.7
1981	_T. vulg_	m	118	69.7	4.2	5.9	4.2	7.6	8.4
1981	_T. vulg_	f	58	58.6	10.3	8.6	3.4	5.3	13.8
1982	_T. vulg_	m	56	70.9	10.9	1.8	5.4	9.2	1.8
1982	_T. vulg_	f	31	60.0	3.3	10.0	6.7	20.0	0.0

N = number of animals caught per year m = males f = females
Table 1. Distribution of captures per trap at Milton Bryan, 1981 and 1982.

This inequality in catching capacity is probably due in the main to its larger size, since animals found both equally easy, or difficult, to escape from. This was investigated by separately placing the traps in an aquarium with ten newts and periodically counting the numbers of newts in each trap. After 3-4 hours all the newts had moved into the traps. Subsequently, during an approximately 24 hour period, no animals were found outside the 'Bell' trap and only one outside the other type.

However, the Breder trap produced greater mortality, due to its lack of a breathing funnel. This was only important during May and June when dissolved oxygen levels were probably low. A few mortalities occurred, about 12 animals in all, during late May and early June 1981.

Traps were checked every 2 or 3 days on average early in the season and every 2 days later in the year when animals may have suffered due to lower oxygen levels. The traps were left in situ throughout the year and checked occasionally during the autumn

Figure 7a shows the arrangement of the aquatic traps at Milton Bryan during 1981, 1982 and 1983. In 1981 and 1982 trap 1 was the Bell type of trap, the remainder being of Breder's design. In 1983 traps 1 and 2 were of Bell's design. During 1981 and 1982 traps 2, 5 and 6 were situated in less weedy areas of the pond than the other traps, whilst in 1983 traps 3, 4, 7 and 8 were in similar positions. As may be seen from Table 1 there was little difference in the number of animals caught in the various Breder traps in 1981 and 1982. The pond at Milton Bryan varied little in depth, being fairly uniform from about 1 metre from the bank. This suggests that the habitat characteristics at this site were having little effect on the numbers of newts being caught, possibly reflecting the mobility of the animals and the relatively small size of the pond. However, during 1983 trap 3 caught no individuals at all; this area was almost entirely weed-free. and winter. No animals were found in them on these visits, however.

2.2 Marking methods.

The methods of population estimation used in this study were modifications of a technique usually attributed to Lincoln (1930), although Le Cren (1965) suggests credit is also due to Petersen. Very simply, they require that a sample is taken from a population, that the individuals are marked in some way and then returned to the population. Further samples are taken and the proportion of marked animals noted. Calculations of population size may then be made using whichever formulae are applicable to the method being used.

The main requirements for marking animals in such studies are that the marks should not affect the longevity or behaviour of the individuals concerned and that they remain discernible for as long as the study is in progress. In many instances this is straightforward but, for amphibians, there are surprisingly few methods available. These are reviewed by Honegger (1979) and Ferner (1979). Three widely used methods were considered for this particular study: subcutaneous injection of ink using a Panjet inoculator, freeze-branding and toe-clipping.

Bell (1973) found that the first method was not really suitable for small urodeles;the ink disappeared after a year and some animals shed the tail distal to the dye-mark within a fortnight of being marked. Furthermore, it would probably have been of little use in such a heavily pigmented animal as *T. cristatus*.

Freeze-branding also appears to be a rather poor method for marking newts since the marks disappear after a fairly short period of time (Taber et al 1975).

Toe-clipping is a popular technique for marking amphibians. There are two drawbacks with it, however. First, a study on Fowler's toad (*Bufo woodhousei fowleri*) has shown that there may be an effect on mortality, indicated by the fact that the probability of recapture decreased with the number of toes removed (Clarke, 1972). Thus, for most of this study only one toe was removed per individual in order to reduce any deleterious effect to a minimum. Secondly, regeneration of digits occurs after a few months and marks may disappear after about a year. Bell (1973) could identify only half his marks confidently after this time. Twitty (1966), however, found that in species of *Taricha* regenerated toes were recognizably smaller than normal ones for a period of several years. This was found to be the case with crested newts in this study. Regeneration in smooth newts, though, was rather more rapid and complete.

Heatwole (1961) showed that the regeneration of limbs and digits in the salamander *Plethodon cinerea* was completely inhibited by applying 0.1N beryllium nitrate solution to the wound. However, this substance is extremely toxic to humans (beryllium causes oedema and even death) and great care must be taken when using it. Therefore, the use of the technique in this study was rejected. The chemical does not appear to have a deleterious effect on salamanders at the concentrations used by Heatwole. Of fourteen individuals treated only one died of unknown causes and this was not attributed to the beryllium nitrate since the individual in question had been subjected to the lowest concentration used in the study (0.05N).

Digit removal was combined with a method described by Hagström (1973) for the identification of individual animals. He photographed the belly patterning of smooth and crested newts and found these to be unique to individuals. His apparatus for this was somewhat cumbersome, however, so in this study patterns were simply copied onto pre-drawn newt outlines. Polaroid photographs would have been even more convenient, but rather expensive when large numbers of animals are involved. Some workers have used photocopiers for this purpose where ponds have been convieniently situated (Glandt, 1981). Some represenative examples of belly patterns are shown in Figures 8 and 9.

This combination of methods was extremely successful for recognizing individual crested newts, but less so for smooth newts. This was primarily due to the rapid regeneration of

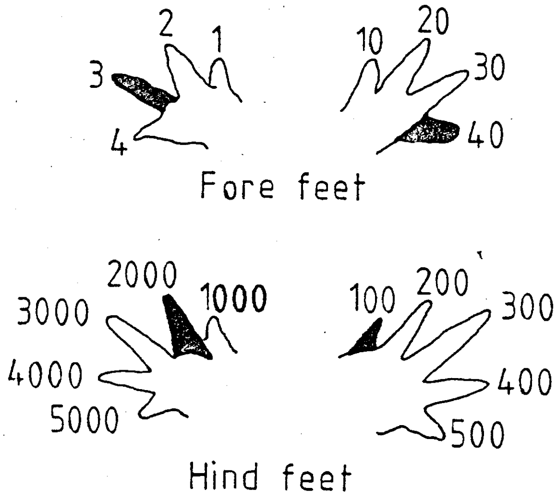


Figure 10. The coding system used for toe-clipping T. vulgaris at Milton Bryan during 1983. The shaded toes indicate those which were removed in this individual: this animal would be coded 3412.

digits in the latter species. Therefore, during 1983 a different marking regime was used for the latter species. Digits were assigned a number, as shown in Figure 10. By removing one to four toes (one from each foot) it was possible to uniquely mark somewhere in the region of 4000 animals, or 8000 if numbers were duplicated for males and females. In fact some 400 animals were marked using this system. The method is based on the system used by Twitty (1966) for marking western newts, *Taricha rivularis*. This itself was derived from the technique devised by Martof (1953) for use on the frog *Rana clamitans*.

Upon capture animals were weighed (except in 1980) to the nearest 0.1g using a Pesola spring balance (supplied by the British Trust for Ornithology). Two measurements of length were also taken, snout to tip of tail and snout to cloacal vent. Both of these were taken to the nearest millimetre. Snout-vent length is sometimes referred to as "standard length" or SVL (Bell 1977, Semlitsch 1983). The height of the dorsal crest in male crested newts was also measured to the nearest millimetre. This was done by flattening the crest and measuring from its base to its highest point.

Bell (1973) measured length to an accuracy of 0.1mm by anaesthetizing animals and using Vernier callipers. This was ruled out for this study on three counts. First, an accuracy of 0.1mm is doubtful, not least because newts are soft-bodied and the male cloaca varies in size with time. Secondly, the procedure may have a deleterious effect on the animals. Finally, it would have been very time-consuming to do this in the field, where all measurements were made.

In summary, the trapping and marking methods used in this study were as follows: aquatic animals were caught using underwater traps, whilst terrestrial animals were intercepted during migration to the pond with drift-fencing and pitfall traps; all individuals were marked with toe-clips and individual recognition facilitated by the recording of belly patterns. I envisaged that the main problems with the use of underwater traps were likely to be low sampling intensity, unequal catchability of males and females and the possibility that some animals would escape from the traps. In addition it is not possible to obtain accurate information about immigration and emigration using this method. The use of drift-fencing and pitfall traps has fewer problems; there is the initial effort of erecting the structure which is time consuming and some animals will inevitably climb over or under the fence. The major drawback with the use of toe-clips was likely to be the regeneration of digits before the end of the study period making identification of recaptured animals difficult.

CHAPTER 3 RESULTS

This chapter presents the results of of the studies carried out at Milton Bryan and Walton Hall. Sections 1 & 2 relate to the use of and the results of mark-release-recapture analysis of crested and smooth newts at Milton Bryan. Section 3 presents an analysis of the size-frequency distributions of these species at this site, whilst section 4 uses data from recaptured individuals to study weight changes, growth and the length of time spent in the pond by these individuals. In section 5 data from preserved animals is given; these relate gonad size to body size in both species and, in particular, how this relates to female fecundity. Section 6 deals with the influence of climatic variables on the migration of *T. cristatus* at the Walton Hall pond. Finally, section 7 is an analysis of the stomach contents of the preserved animals used in the gonadal analysis.

3.1 Mark-recapture analysis: testing the assumptions.

There are a number of assumptions underlying all methods of mark-release-recapture analysis. These must be satisfied as far as possible if such methods are to be valid. For most studies the assumptions are as follows:

1. The longevity and behaviour of animals should not be affected by marking, and marks should be recognizable throughout the study period.
2. Individuals of both sexes and all age groups should be caught in the proportions in which they occur in the population. Furthermore, the position of animals in the habitat should not affect their chances of capture. That is to say, there should be 'equal catchability'. There is an amendment to this, which is basically an extension of the first assumption. This is that the susceptibility of an animal to capture is not affected by any previous captures.
3. Marked animals should become randomly mixed in the population.
4. Sampling should be at discrete time intervals, the total time being large compared with the time involved in taking a sample.

Part of the first assumption has already been dealt with in Chapter 2, section 2, in which it was shown that marks were recognizable throughout the study period. However there were no data to show whether marking had had an affect on mortality. It is hoped that any such effect was minimized by the removal of only one toe per limb.

In a study of a Manx shearwater (Puffinus puffinus) population, Orians and Leslie (1958) describe a method of testing for the effect of previous captures on an individual. This was done by comparing the actual and expected variances of a series of recaptures of individuals known to be alive throughout the study period. A number of recaptures made during 1983 were suitable for such an analysis in this study. The results of this are rather inconclusive but, on the whole, it appears that the susceptibility of an animal to capture is not affected by previously having been captured. The worked examples are given in Appendix 2.

Bell (1973) found that he captured males and females in different proportions, and that these were different to those occurring in the population. This may be due to males and females behaving differently in the pond. Gauss (1961) reported male crested newts as having territories or home ranges within ponds, whilst females tended to wander to a greater extent . Dolmen (1980) reports a similar situation with his study population, through showing that males were recaptured in the same place more often than females. In order to counteract any such effect in this study the sexes of both species are treated as separate populations and estimates produced accordingly.

Analyses were made using chi-square in order to ascertain whether individuals were being recaptured in the trap in which they were last captured. This was found not to be the case (see Appendix 2) and it may be concluded that marked animals become randomly dispersed in the population after release.

For assumption 4 the sampling time may be regarded as the time between visits to the traps (usually 2 or 3 days) or the time time taken to process (i.e. weigh, measure and draw) one animal. In both cases, these periods are very short compared to the total study period of 5 to 8 months, so either may be regarded as the sampling time.

On the whole, therefore, the requirements for the use of a mark-recapture analysis appear to have been satisfied and the results following in the next section valid.

3.2.1 Results of population analysis.

The following results are based on a mark-release-recapture analysis carried out over four seasons, from 1980 to 1983. Population estimates have only been produced for the Milton Bryan site since the data from Walton Hall were not suitable for such an analysis.

After preliminary sorting the raw data were processed using a computer program developed at Manchester University. The program produces three population estimates for any one set of data, each of which is derived from a different method of analysis. These are the Lincoln Index method, the Fisher & Ford method and the Jolly-Seber stochastic method.

The first of these methods, also called the Petersen estimate, is the simplest mark-release-recapture technique available. It makes use of only two sampling visits to a population. It is also the method upon which the more sophisticated models are based. Briefly, it is derived as follows: a random sample of r individuals is taken from a population, marked so as to be recognizable in the future and returned to the population. A second random sample is then taken some time later of n individuals, of which m individuals are marked. If the total population size immediately before the first sample was N then the following equation should be true, assuming the proportion of marked animals to have remained constant:

$$\frac{m}{n} = \frac{r}{N}$$

from which we may derive an estimate for N, N', such that

$$N' = \frac{rn}{m}$$

This, however, requires that no births, deaths, immigrations or emigrations have occurred. Since this is not true for most populations the model is somewhat restrictive in its use. Therefore, more sophisticated models such as those of Fisher & Ford and Jolly-Seber may be used which take account of any losses or gains in the population during the study period. The full equations for and the rationale behind these other methods can be found in a number of texts, including Southwood (1978), Begon (1979) and Blower, Cook & Bishop (1981).

The Jolly-Seber method produces a very robust estimate of population size where the numbers of captures and recaptures are large. It also gives information about survival, immigration and emigration rates, thus making it a valuable technique. However, the nature of the analysis requires that the data are split into a number of subsets and so there are a number of points at which errors may arise. The Fisher & Ford method uses fewer subsets through the lumping of data and so makes more use of the data available. It is, therefore, particularly useful when captures and recaptures are rather few. It does, however assume a constant survival rate.

In situations where too few recaptures have been made for one to use either the Fisher & Ford or Jolly-Seber tests, and it is essential to obtain an estimate of some sort, then it is necessary to use the Lincoln Index or the "weighted mean" method. This is very similar to the Lincoln Index, in that it assumes no loss or gain to the population, but it differs in that it accumulates data over a number of days. The full derivation of the method is given by Begon (1979) but, very simply, the following procedure is used. An estimate of population size is made for each sampling occasion using the Lincoln Index. Because each of these is derived from different amounts of information, i.e. the number of captures and recaptures in a sample, some will be more accurate than others. Therefore, each estimate is weighted accordingly (by using the number of recaptures in the relevant sample) and an overall estimate obtained, along with the standard error. It is this weighting which makes the method preferable to obtaining an estimate by simply taking the mean of a number of unaltered Lincoln Index estimates. However, it is really only of use when all other methods are inapplicable. Bell (1974b) describes a method for estimating population sizes when no recaptures have been made. However, the validity of this method has been criticized on statistical grounds (Edwards 1974) and so has not been used, even to derive an estimate for the female smooth newt population in 1982 when only one recapture was made and Bell's method may have been of use.

The totals of animals captured at Milton Bryan are given in Table 2 along with the numbers of recaptures. The population estimates are shown in Tables 3 to 10.

YEAR	SPECIES	SEX	TOTAL CAUGHT	No. OF RECAPTURES
1980	*T. cristatus*	male	134	18
1980	*T. cristatus*	female	43	5
1980	*T. vulgaris*	male	183	15
1981	*T. cristatus*	male	264	36
1981	*T. cristatus*	female	227	29
1981	*T. vulgaris*	male	118	13
1981	*T. vulgaris*	female	58	3
1982	*T. cristatus*	male	165	19
1982	*T. cristatus*	female	63	7
1982	*T. vulgaris*	male	56	2
1982	*T. vulgaris*	female	31	1
1983	*T. cristatus*	male	445	149
1983	*T. cristatus*	female	394	98
1983	*T. vulgaris*	male	249	34
1983	*T. vulgaris*	female	163	9

Table 2. Total numbers of animals caught at Milton Bryan

In cases where two population estimates are derived, one from the Fisher & Ford method and one from the Jolly-Seber, the Fisher & Ford estimate has been taken as the most accurate. This is because where recapture data are scanty, or sampling intensity is low, Jolly's method tends to produce an overestimate of population size when compared to the actual size and to that produced using Fisher & Ford (Bishop & Sheppard 1973). Bishop & Sheppard determined this by using computer simulations of populations and varying the sampling intensities. Also, because the Fisher & Ford method combines samples, sampling errors should tend to cancel out and the overall sampling error should be minimized. In two situations the estimates derived from each method were in reasonable agreement, so a mean of the two was taken as the population size and it is this figure which appears in Table 3 . However, it is probably more correct to say that the population size lies between the estimates obtained from the two methods; i.e. between 1169.4 & 684.6 for the males and between 832.4 & 835.2 for the females. This refers to the male and female *T. cristatus* populations for 1983. Table 3 also gives the measurements of error for the estimates. In the case of the Fisher & Ford estimate the error is simply that arising from the calculation of the mean population size for any given year.

The nature of the analysis used in these two methods is such that estimation of population size on any one sampling day is dependent on recaptures having been made on the sampling days immediately preceding; without such recaptures gaps appear in the data. In order to reduce the number of these, capture and recapture data have been grouped into 5-day periods. However, gaps do still occur and these are shown as blank 'days' in the tables, a 'day' being one 5-day period.

YEAR	SPECIES	SEX	N	S.E.	SEX RATIO (Males:Females)
1980	*T. cristatus*	male	394.8	143.5	2.5:1
"	"	female	154.7*	56.6	
"	*T. vulgaris*	male	295.0	185.3	1:1.7
"	"	female	516.0*	364.8	
1981	*T. cristatus*	male	503.9	256.2	1:1.2
"	"	female	624.5	312.6	
"	*T. vulgaris*	male	142.6	83.4	1:3.2
"	"	female	456.3*	322.6	
1982	*T. cristatus*	male	423.9	245.1	3.1:1
"	"	female	134.5	94.8	
"	*T. vulgaris*	male	870.5*	786.0	
"	"	female			
1983	*T. cristatus*	male	794.0	344.0	1:1.1
"	"	female	868.6	321.3	
"	*T. vulgaris*	male	355.4	244.4	1:3.1
"	"	female	1113.5	168.8	

N = Mean population size *= Estimates calculated using the weighted mean method

Table 3: Overall population sizes for Milton Bryan 1980-83

YEAR	MAXIMUM POPULATION ESTIMATE males	females	total
1980	680	(154)	(834)
1981	1008	1150	2154
1982	1034	269	1303
1983	1459	1355	2814

Table 3a: Maximum population estimates for *T. cristatus* populations at Milton Bryan from 1980 to 1983.

As may be seen from Table 3 there are considerable fluctuations in the overall population sizes of both species from year to year. In 1980 and 1982 the estimates for crested newts were particularly low. This is also reflected in the absolute number of animals captured in these two years, as shown in Table 2. In 1980 the low capture rate may be related to the smaller number of traps used in that year (i.e. low sampling intensity). These fluctuations are primarily due to changes in the size of the female component of the population from year to year; the number of males in the population does not vary as dramatically.

These fluctuations may also be observed from looking at the maximum estimates for males and females. These are shown in Table 3a and are simply the maximum estimates for each sex as obtained from the calculation of the mean population size for each year. The corresponding values may be seen in Tables 5 to 9. These are interesting values, which open to a number of interpretations. It may be that the maximum estimate at any one time is the minimum number of individuals using the pond over the season as a whole due to turnover. Alternatively, the estimate may be a minimum for the number of animals using the pond because there may be a component of the population that does not get trapped.

The estimated sex ratio for both species also varies between years. For T. cristatus it ranges from 3 males:1 female in 1982 when overall numbers were small, to 1 male:1 female in 1983 when they were much higher.

These are, of course, overall sex ratios; there may be variation in this figure through the season as the population fluctuates. In addition, there is what Emlen (1976) describes as the 'operational' sex ratio which may be different again; this is the ratio of fertilizable females to sexually active males. Unfortunately, this latter ratio was not directly measurable in this study since it was not possible to clearly identify those animals which were sexually active. In particular, it is difficult to assess the number of females that are sexually receptive at any given time since a proportion of animals are likely to be unresponsive to male courtship due to having been already inseminated (Verrell, 1984).

In addition to the overall sex ratio I have looked at the variation in sex ratio through the season from comparisons of the male and female data in Figures 11 to 15. These are shown in Table 4. As may be seen there is a little fluctuation in these ratios through the season but, by and large, they agree with the overall ratios shown in Table 3. Variation in the sex ratio may have important consequences for the reproductive strategies followed by individuals within a particular population and this is discussed further in chapter 4.

The lowest numbers of smooth newts occurred in 1981. Again, as with the crested newt, the size of the population from year to year is highly variable. It was not possible to derive an estimate for the female <u>T. vulgaris</u> population in 1982 since only one recapture was made. The sex ratio

T. cristatus: 1981

DATE	MALES	FEMALES	SEX RATIO
26/3-30/3	404	633	1:1.6
31/3- 4/4	674	694	1:1.0
5/4- 9/4	1008	1128	1:1.1
10/4-14/4	492	850	1:1.7
15/4-19/4	464	491	1:1.1
20/4-24/4	458	558	1:1.2
25/4-29/4	348	465	1:1.3
5/5- 9/5	305	1150	1:3.8
25/5-29/5	281	1021	1:3.6

T. cristatus: 1982

DATE	MALES	FEMALES	SEX RATIO
8/3-12/3	93	6	15.5:1
2/4- 6/4	624	61	10.2:1
22/4-26/4	406	75	5.4:1
2/5- 6/5	372	269	1.4:1

T. cristatus: 1983

DATE	MALES	FEMALES	SEX RATIO
29/3- 2/4	680	1200	1:1.8
3/4- 7/4	960	420	2.3:1
8/4-12/4	660	940	1:1.4
13/4-17/4	750	450	1.7:1
18/4-22/4	1070	1350	1:1.3
23/4-27/4	820	950	1:1.2
28/4- 2/5	1460	500	2.9:1
3/5- 7/5	950	890	1.1:1

T. vulgaris: 1983

DATE	MALES	FEMALES	SEX RATIO
17/4-21/4	400	1059	1:2.6
22/4-26/4	341	910	1:2.7
1/6- 5/6	198	1317	1:6.6
11/6-15/6	196	1051	1:5.4

Table 4: Variation in sex ratios through the season for *T. cristatus* in 1981, 1982 & 1983, and for *T. vulgaris* in 1983.

estimates for *T. vulgaris* show an excess of females in all years where a ratio was obtainable; they range from 1 male :

1.75 females to 1 male : 1.32 females

The numbers of newts in the pond appear to vary through the year. These fluctuations are shown in figures 11 to 15. The data for T. cristatus in 1983 show these variations most clearly, but the pattern is repeated in other years. In 1983 numbers of crested newts began to increase from the end of February, reaching a peak in the middle of May and thereafter declining. This is seen to some extent, also, in the data relating the movement of animals to climate and time of year in chapter 3 section 6.

Gill (1978) estimated the annual survival of American red-spotted newts through determining the percentage of marked animals returning to breeding ponds from the previous year. Thus, if 60% of those animals marked in one year returned the following season, this was interpreted as signifying a 60% survival rate. This does not take into account, of course, those animals which are presumed dead, but which may appear in a future year. However, it is a valid approach when the sampling intensity of the population is very high. In studies such as that at Milton Bryan, where the sampling intensity is not very high or is uncertain, then it is necessary to use a more indirect method for the estimation of survival rate. It is possible to do this by using the Jolly-Seber method and treating each year of the study as one sampling occasion. In this way a survival rate of 0.36 is obtained for both male and

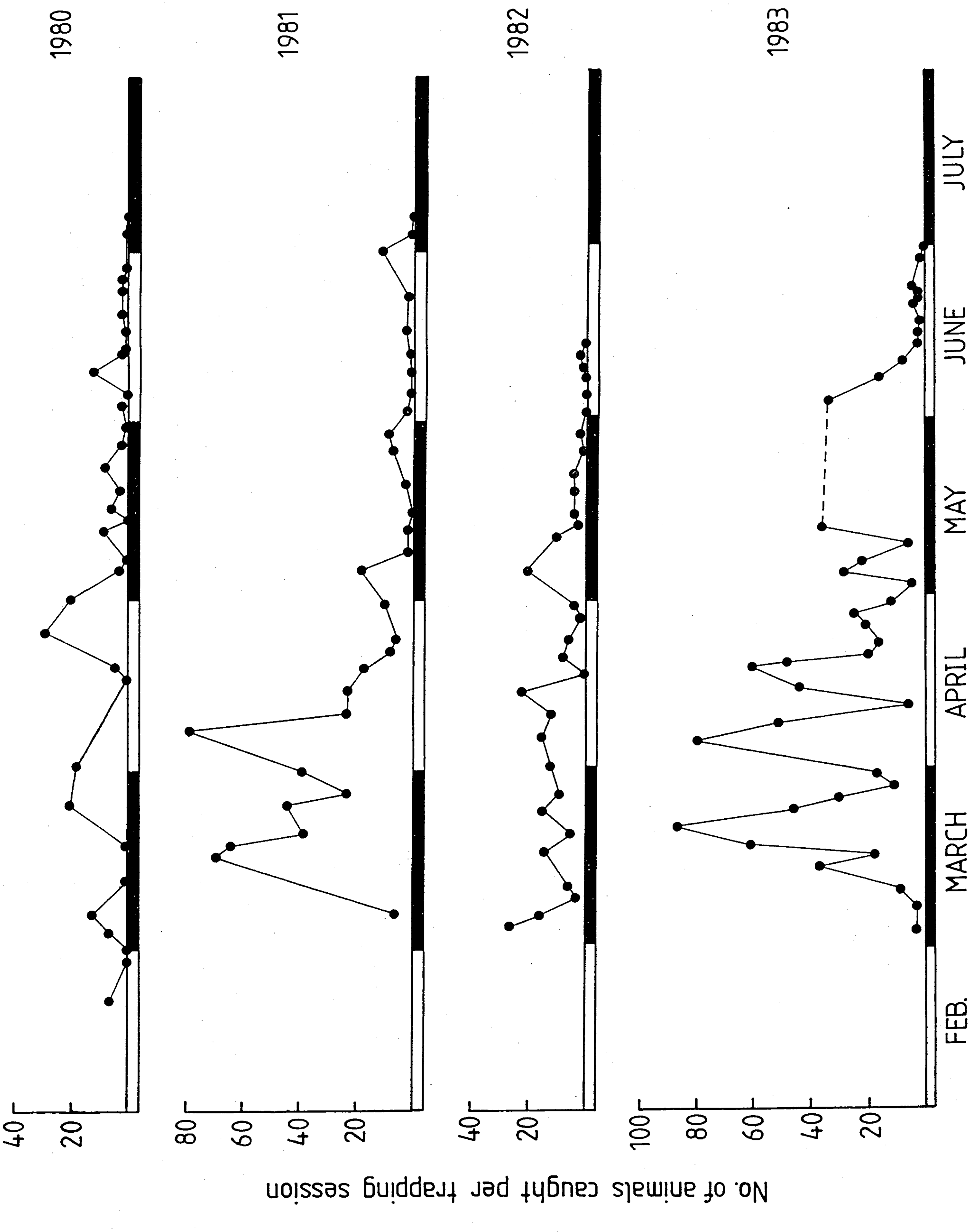


Figure 10a: The numbers of crested newts captured on each sampling occasion during 1980, 1981, 1982 & 1983 at Milton Bryan (males and females combined)

female crested newts between 1980 and 1981. The standard errors for these figures are 0.06 for males and 0.076 for the females. The calculations for these estimates are given in Appendix 3. As with Gill's method these are likely to be underestimates due to the reappearence of indivivuals which were presumed dead. I was unable to derive such estimates for smooth newts due to the aforementioned difficulty in identifying individuals from the previous season.

Figure 10a shows the numbers of crested newts taken on each sampling occasion during 1980, 1981, 1982 and 1983 at Milton Bryan (males and females combined). These reflect the overall population numbers in each year, with moree individuals being captured in 1981 and 1983 when the populations were at their highest. Thus, the number of captures may be used as an indication of population size, either over the season or on any particular sampling occasion.

In addition it is seen from the figure that the numbers of animals trapped tail off somewhat in the latter part of the season. The reason for this is not known, but has also been reported from other populations, such as that studied by Verrell & Halliday (in press a). It is possible that a behavioural change occurs at some point during the season, such that animals do not move about the pond as frequently at the end of the season as early in the season. The effect is observed for both males and females.

These data show up some of the problems associated with the use of mark-recapture techniques on populations of newts in large ponds. Although 8 traps were ultimately used at the Milton Bryan site, this intensity of sampling does not appear to have been sufficient to produce large numbers of recaptures and hence, more accurate population estimates. Therefore, either more aquatic traps should be used in such circumstances, or another method used. Gill's (1978) reports of 90% efficiency in trapping American red-spotted newts in his study area strongly recommend the use of drift-fencing and pitfall traps for population work on newts whenever this is feasible.

DAY	MALE POPULATION
1	---
2	---
3	---
4	---
5	---
6	---
7	155
8	---
9	340
10	---
11	---
12	---
13	---
14	---
15	680
16	---
17	359
18	592
19	383
20	232
21	---
22	---
23	467
24	294
25	509
26	427
27	300

Mean population size = 394.8
Overall "daily" survival = 1.0

Table 5: Population estimate for male *T. cristatus* in 1980 using the Fisher & Ford method.

DAY	MALE POPULATION	FEMALE POPULATION
1	---	---
2	---	---
3	---	---
4	946	---
5	404	633
6	674	694
7	1008	1128
8	492	850
9	464	491
10	458	558
11	348	465
12	---	---
13	305	1150
14	---	255
15	---	---
16	---	221
17	281	1021
18	---	---
19	163	---
20	---	---
21	---	363
22	---	---
23	---	---
24	---	289

Mean male population = 503.9 Mean female population = 624.5 Overall male "daily" survival = 0.92 Overall female "daily" survival = 0.96

Table 6: Population estimates for T. cristatus in 1981 using the Fisher & Ford method.

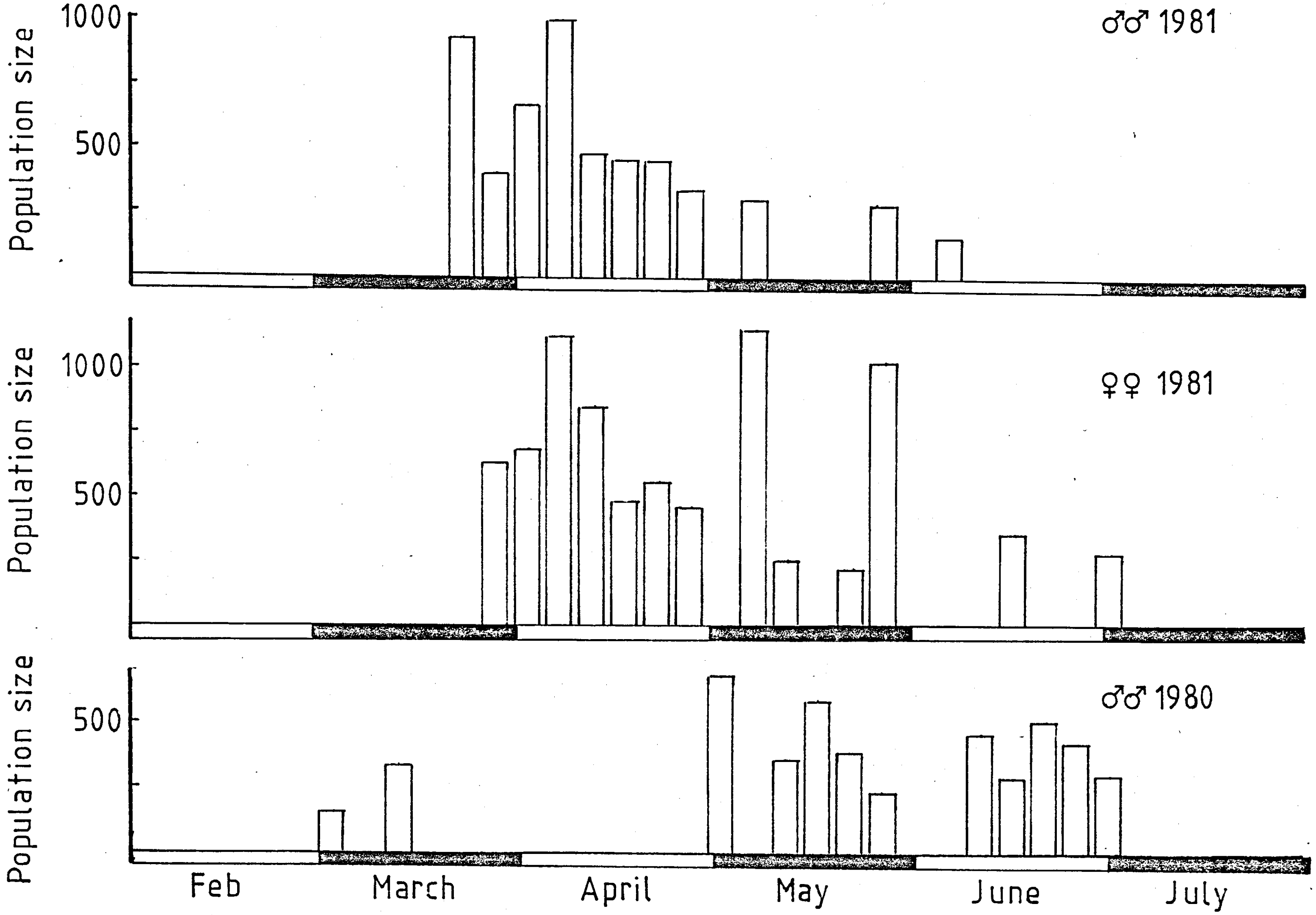
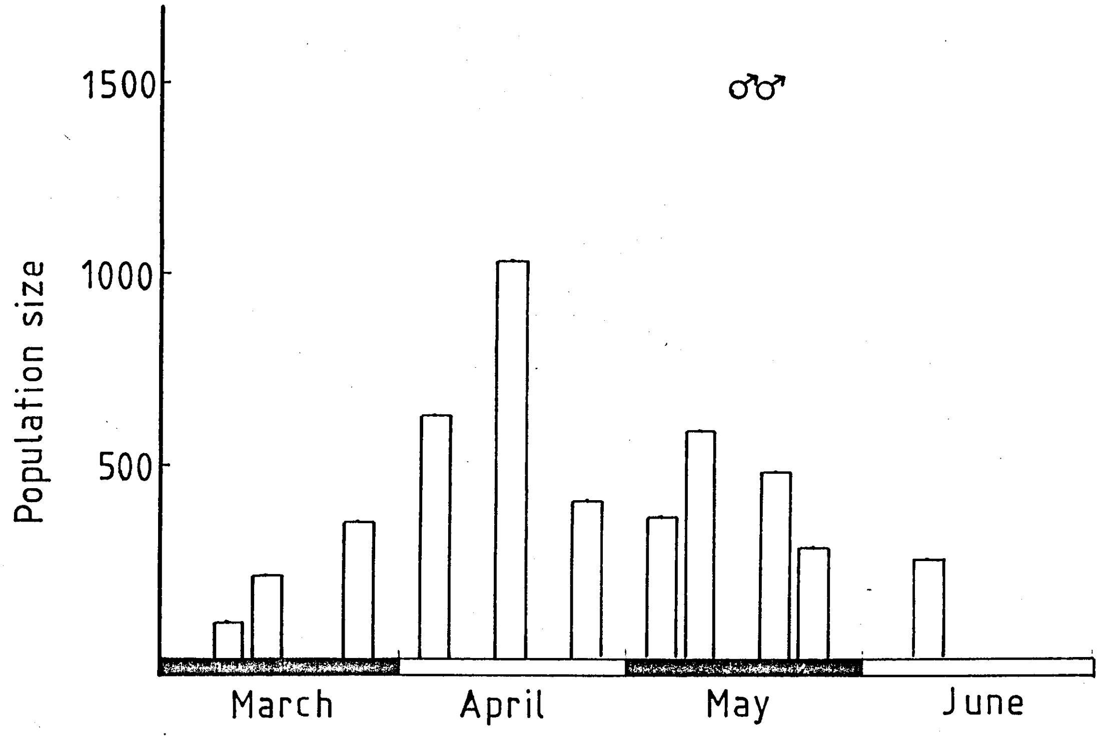


Figure 11: Variation in population size during the season for T. cristatus at Milton Bryan 1980 & 1981, based on the results of the mark-recapture analysis.

DAY	MALE POPULATION	FEMALE POPULATION
1	---	---
2	93	6
3	210	---
4	---	---
5	324	---
6	---	---
7	624	61
8	---	---
9	1034	---
10	---	---
11	406	75
12	---	---
13	372	269
14	590	---
15	---	204
16	478	---
17	281	---
18	---	---
19	---	---
20	253	---
21	---	192

Mean male population size = 423.9
Overall male "daily" survival = 1
Mean female population size = 134.5
Overall female "daily" survival = 1

Table 7: Population estimates for T. cristatus in 1982 using the Fisher & Ford method.



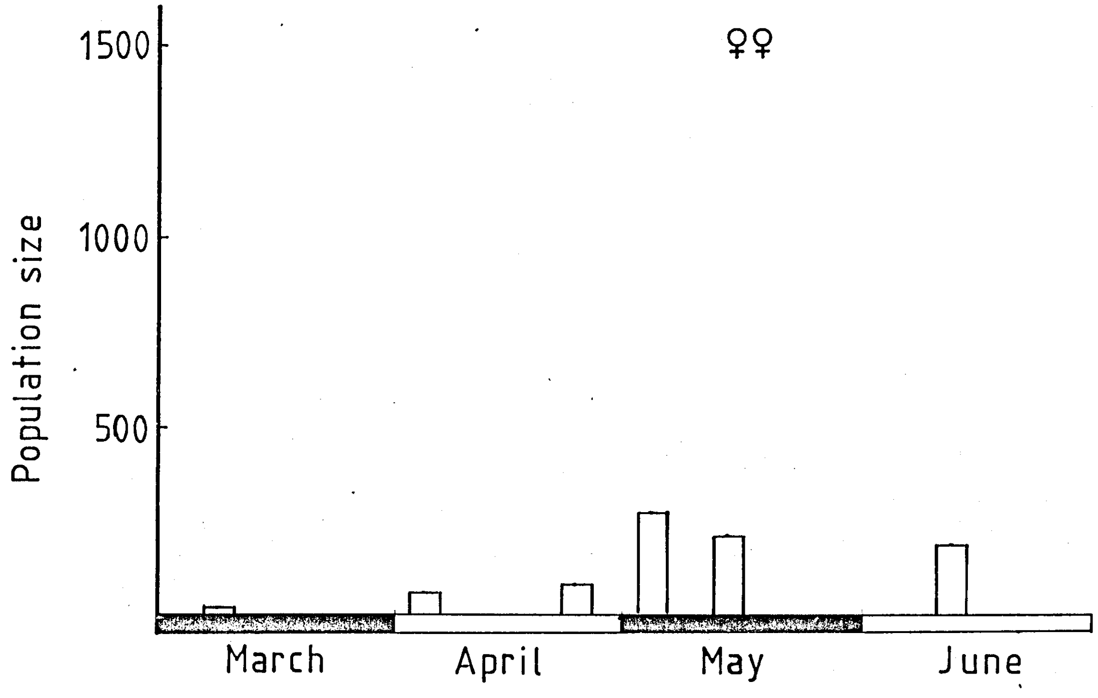


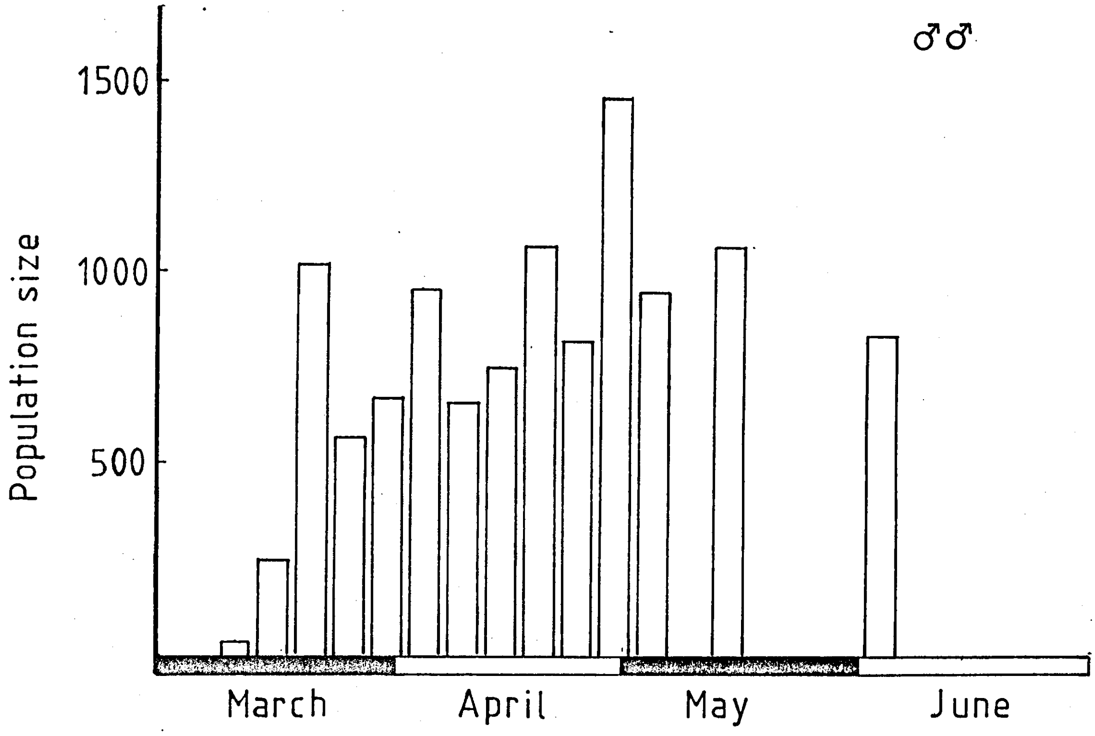
Figure 12: Variation in population size during the season for <u>T. cristatus</u> at Milton Bryan in 1982, based on the results of the mark-recapture analysis.

DAY	FISHER & FORD	JOLLY-SEBER			
	pop. size	pop. size	S.E.	survival	immig.
1	--------	--------	----	--------	-----
2	---28---	---38---	-30-	--1.29--	-----
3	--292---	--211---	147-	--0.67--	-185-
4	--987---	-1056---	488-	--1.25--	-793-
5	--737---	--395---	188-	--0.84--	-----
6	--685---	--661---	265-	--1.25--	-----
7	--954---	--957---	329-	--0.96--	-321-
8	--770---	--548---	163-	--0.74--	-----
9	--741---	--760---	291-	--1.33--	--33-
10	--985---	-1147---	496-	--1.34--	-126-
11	--976---	--673---	297-	--0.54--	--54-
12	-1297---	-1621---	1237	--1.77--	-431-
13	-1104---	--788---	480-	--0.59--	-----
14	-1160---	--------	----	--------	-788-
15	-1740---	--399---	262-	--------	-399-
16	--------	--------	----	--------	-----
17	--------	--------	----	--------	-----
18	--------	--------	----	--------	-----
19	-1352---	--330---	241-	--------	-----
20	-2103---	--------	----	--------	-330-
21	-1616---	--------	----	--------	-330-
22	-2899---	--------	----	--------	-330-
23	--------	--------	----	--------	-330-
24	-1803---	--------	----	--------	-----

Mean Fisher & Ford estimate = 1169.9
Estimated overall "daily" survival = 1.0

Mean Jolly-Seber estimate = 684.6
Estimated overall "daily" survival = 0.98

Table 8: Population estimates for male *T. cristatus* in 1983 using both the Fisher & Ford and Jolly-Seber methods. Overall population estimate (as shown in Table 3) is taken as the mean of the differences between the estimates from both methods.



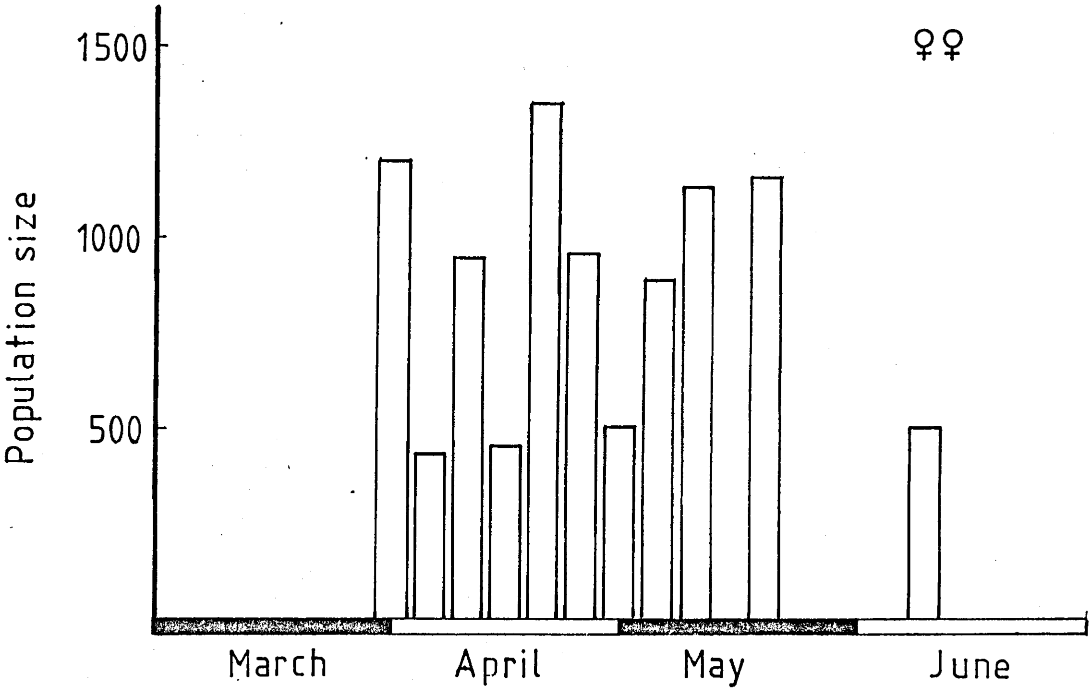


Figure 13: Variation in population size during the season for <u>T. cristatus</u> at Milton Bryan in 1983, based on the results of the mark-recapture analysis. The values presented here are the combined data from the Fisher & Ford and Jolly-Seber analyses.

DAY	FISHER & FORD	JOLLY-SEBER			
	pop. size	pop. size	S.E.	survival	immig.
1	--------	--------	----	--------	-----
2	--------	--------	----	--------	-----
3	--------	--------	----	--------	-----
4	--------	--------	----	--1.15--	-1464
5	--931---	-1464---	-981	--1.51--	-----
6	--339---	--533---	-428	--1.11--	--665
7	--686---	-1201---	-648	--1.00--	-----
8	--603---	--310---	-123	--0.37--	--769
9	-1499---	-1212---	-889	--1.43--	-----
10	-1015---	--900---	-425	--0.97--	-----
11	--795---	--221---	-110	--0.28--	--284
12	--665---	-1127---	-893	--3.82--	--250
13	-1343---	--933---	-561	--0.61--	--933
14	--------	--------	----	--------	-1059
15	-1262---	-1059---	-793	--------	-----
16	--------	--------	----	--------	-----
17	--------	--------	----	--------	-----
18	--------	--------	----	--------	-----
19	--785---	--227---	-124	--------	--227
20	--980---	--------	----	--------	-----
21	--------	--------	----	--------	-----
22	--------	--------	----	--------	--227
23	--666---	--------	----	--------	-----
24	--364---	--------	----	--------	-----

Mean Fisher & Ford estimate = 852.4
Estimated "daily" survival = 0.98

Mean Jolly-Seber estimate = 835.2
Estimated "daily" survival = 0.96

Table 9: Population estimates for female *T. cristatus* in 1983 using both the Fisher & Ford and Jolly-Seber methods. Overall population estimate (as shown in Table 3) is taken as the mean of the differences between the estimates from both methods.

DAY	1981	1980
1	---	---
2	---	---
3	---	---
4	---	---
5	---	---
6	303	441
7	114	---
8	126	---
9	111	---
10	---	---
11	59	---
12	---	662
13	---	---
14	---	340
15	---	---
16	---	485
17	---	136
18	---	---
19	16	---
20	15	170
21	---	---
22	11	179
23	---	---
24	---	129
25	---	113

Mean population size for 1980 = 295.0
Mean population size for 1981 = 142.6

Overall "daily" survival for 1980 = 0.93
Overall "daily" survival for 1981 = 0.78

Table 10: Population estimates for male *T. vulgaris* in 1980 & 1981 using the Fisher & Ford method.

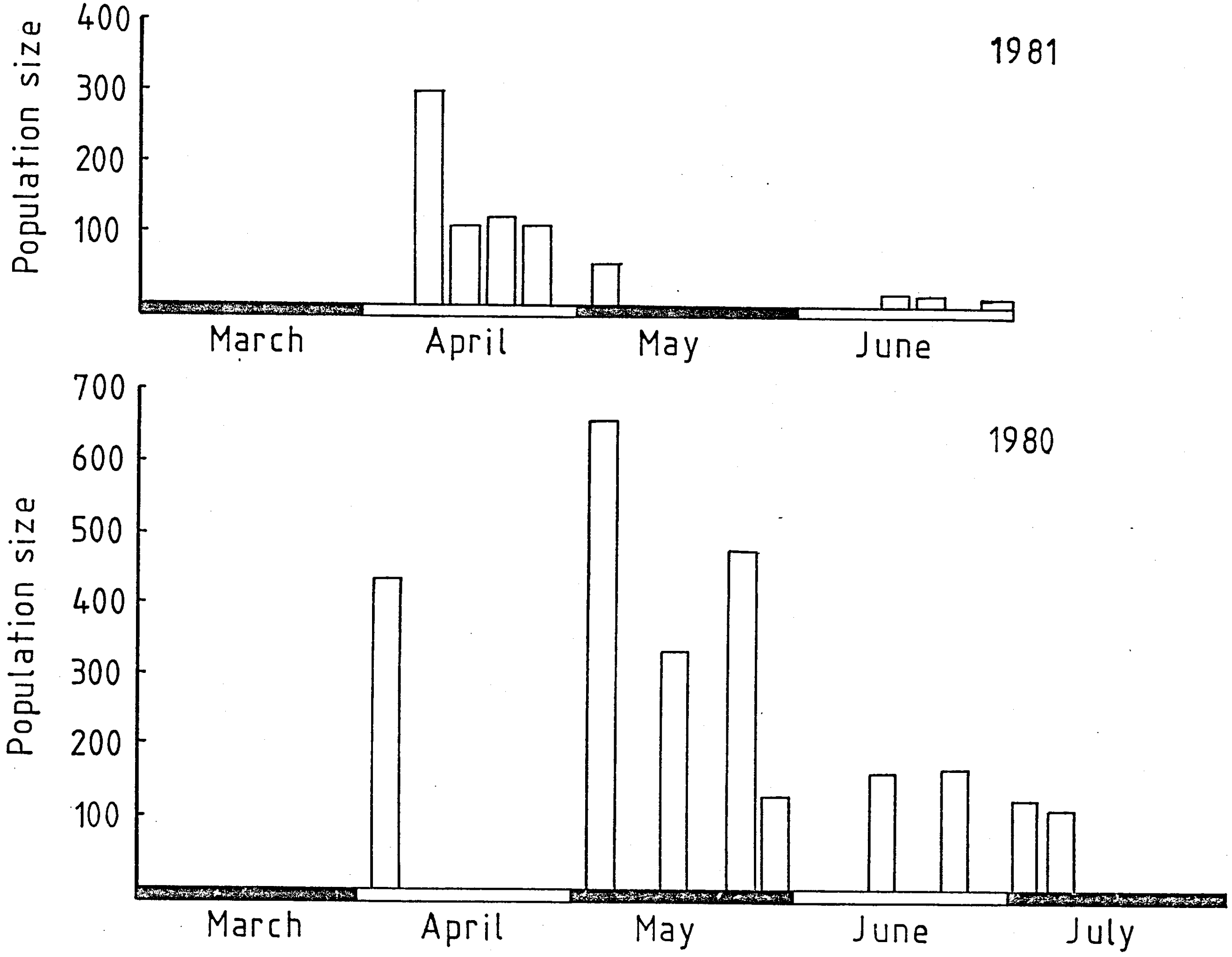


Figure 14: Variation in population size during the season for <u>T. vulgaris</u> males at Milton Bryan in 1980 & 1981 based on mark-recapture analysis.

DAY	MALE POPULATION	FEMALE POPULATION
1	---	---
2	161	---
3	575	---
4	1106	---
5	---	---
6	---	979
7	---	---
8	---	---
9	394	---
10	400	1059
11	341	910
12	516	---
13	313	---
14	---	---
15	175	---
16	---	---
17	---	---
18	---	---
19	198	1317
20	218	---
21	196	1051
22	185	---
23	198	---
24	---	1365

Mean male population = 355.4 Mean female population = 1113.5

Overall male "daily" survival = 0.92 Overall female "daily" survival = 1.0

Table 11: Population estimates for *T. vulgaris* in 1983 using the Fisher & Ford method.

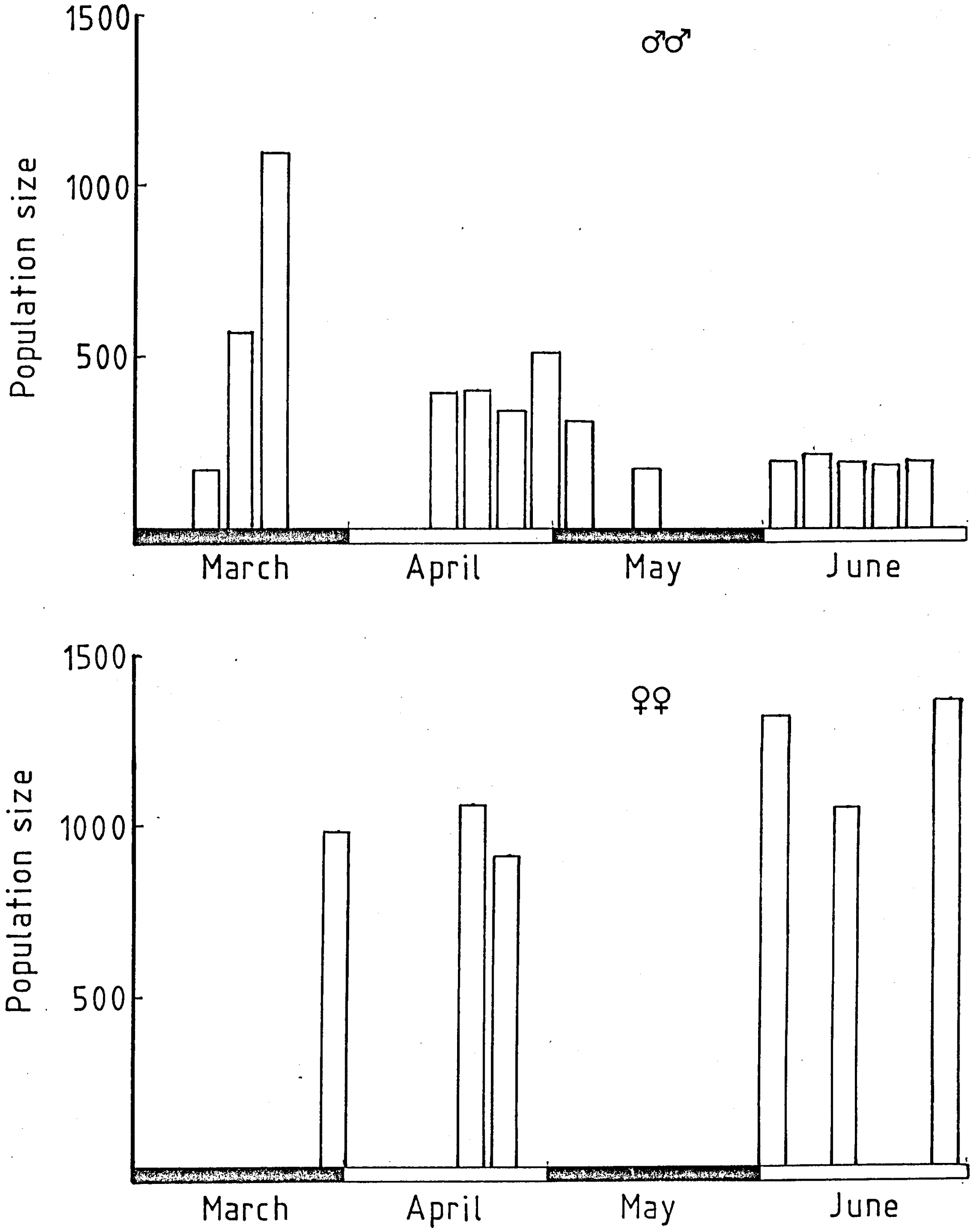


Figure 15: Variation in population size during the season for *T. vulgaris* at Milton Bryan in 1983, based on mark-recapture analysis.

3.2.2 Discussion.

The principal results arising from these data, then, are that the populations of both species at Milton Bryan fluctuate from year to year, that there is a variable sex ratio in crested newts from one year to the next, whilst that in smooth newts is more or less constant, and that annual survival rate in crested newts is the same for males and females.

Glandt (1982) remarks that in four mixed populations of Triturus in Germany fluctuations were observed in the sizes of all but one population over a four year period. He does not give any details, however, saying only that large populations only underwent small changes, whilst small populations displayed large as well as small fluctuations.

Bell's (1973, 1977) smooth newt populations showed yearly changes of the same order as those at Milton Bryan as did four species of Triturus in a four year study by Blab & Blab (1981) and Hagström's (1979) smooth and crested newt populations. Bennett (1970), working on Notophthalmus viridescens in Sandy Lake, New Hampshire found massive fluctuations from year to year. He was, however, dealing with very much larger populations than in this study. In contrast, Gill (1978b) found very little variation in his demic populations of this species within an area, although there were large differences between ponds. There is no evidence from this study that the populations in the immediate vicinity of Milton Bryan are stable, with the fluctuations occurring between ponds.

Bell (1977) found a preponderance of females in most of his smooth newt populations but, a near 1:1 sex ratio in crested newts. Similarly, Verrell & Halliday (in press a) obtained a 1:1 ratio for their crested newt population. In contrast, Blab & Blab (1981) and Hagström found proportions of males and females biased in favour of males in crested newts; Blab & Blab give a ratio of 1:1.6. The last authors found a 1:1 sex ratio for smooth newts with a very occasional excess of males. Harrison et al (1983) have results for smooth newts in agreement with the findings in this study, giving a ratio of 2.6 males to 1 female. Comparative work on *N. viridesescens* shows a consistent ratio of 2 males : 1 female (Gill 1978a).

Most authors report more or less constant sex ratios from year to year for given populations. Variable ratios have been recorded in palmate newts by van Gelder (1973) and also for *Ambystoma tigrinum* by Semlitsch (1983).

Hagström (1979) estimated survival of crested newts at between 0.7 and 0.8 for both sexes. This is higher than my findings for Milton Bryan but, given that I am probably underestimating there may not be too much discrepancy. Frazer (1983) quotes crested newts as having an annual mortality, of 42%, which is more in line with my findings, but does not say how he arrived at this figure. There is no reason, of course, why survival should be constant between populations. Hagström, in fact, found wide variation in the survival of smooth newts at two different localities. At one site it was estimated at 0.5 and at the other at only 0.06. This difference was attributed to differing predation pressures between sites. Bell gives survival of smooth newts as approximately 0.45 for males and 0.55 for females. This is a significant difference, which he explains as being due to differential mortality of males during breeding. This is reversed in _N. viridescens_ where male survival is reported as 5-8% greater than female survival.

Blab & Blab (1982) report that their populations build up in March and April to reach a peak in May. They did not find any major fluctuations within this period. The apparent within season variations in some populations at Milton Bryan are probably simply artefacts due to the techniques used in estimating the population sizes. If they were genuine fluctuations they would be difficult to explain other than that they arise from groups of animals moving into and out of the pond throughout the season. Such a phenomenon has not been recorded for either smooth or crested newts. Gill (1978a) found large numbers of red-spotted newts leaving the water for short periods during the night but, this was to rid themselves of leech infestation and they always returned to the water afterwards.

3.3.1 Analysis of size-frequency distributions.

The size-frequency distributions for the crested and smooth newt populations at Milton Bryan and Walton Hall are given in Figures 16 to 21. The means of these distributions, along with the standard deviations are given in Table 12.

From Table 12 it will be seen that body weight, total length and SVL are all variable to some extent. The measurement most commonly used in urodele ecology for studying size variation within and between populations is SVL (Sayler 1966, Semlitsch 1983). Therefore, it is this value that the size-frequency histograms are based on. Total length tends to be more variable due to tail damage. Weight will vary with the amount of food eaten, and animals also gain weight on entry into water, through hydration (Moriya 1982, Verrell & Halliday in press a, b).

The mean SVL of T. cristatus at Milton Bryan varies little from season to season (see Table 12a). This is true for both sexes. Not surprisingly, none of these variations are significant (using Fisher-Behrens test and 2-sample t-test). The Fisher-Behrens test is used for testing the null hypothesis that two population means are equal where the variances of the populations are unequal, which is why I have used it in a number of instances in this study. A description of the method is given by Campbell (1974). The Walton Hall population, in contrast, shows a decrease in mean SVL of both

a. Milton Bryan, 1980 to 1983.

YEAR	SPECIES	SEX	N	MEAN SVL + SD (mm)	MEAN TOTAL LENGTH + SD (mm)	MEAN WEIGHT + SD (g)	MEAN CREST + SD (mm)
1980	*T. cristatus*	male	113	65.0 + 4.6	108.3 + 7.8		6.3 + 2.7
1980	*T. cristatus*	female	38	68.3 + 5.6	118.4 + 10.2		
1981	*T. cristatus*	male	226	65.4 + 5.3	109.5 + 9.5	6.3 + 1.5	5.5 + 2.2
1981	*T. cristatus*	female	193	68.5 + 4.3	118.4 + 8.1	7.0 + 1.3	
1982	*T. cristatus*	male	147	65.4 + 4.8	109.0 + 8.2	5.8 + 1.3	4.9 + 2.1
1982	*T. cristatus*	female	57	69.7 + 4.8	120.7 + 8.6	6.9 + 1.4	
1983	*T. cristatus*	male	293	65.6 + 4.4	111.0 + 7.8	6.1 + 1.3	5.7 + 2.2
1983	*T. cristatus*	female	292	68.7 + 4.8	119.8 + 9.1	6.7 + 1.6	
1980	*T. vulgaris*	male	166	43.3 + 2.5	86.5 + 5.4		
1980	*T. vulgaris*	female	68	42.6 + 2.8	81.9 + 6.2		
1981	*T. vulgaris*	male	105	44.1 + 2.3	88.3 + 5.7	2.4 + 0.5	
1981	*T. vulgaris*	female	55	43.7 + 2.8	84.1 + 5.6	2.5 + 0.6	
1982	*T. vulgaris*	male	54	43.1 + 2.9	85.2 + 6.1	2.1 + 0.4	
1982	*T. vulgaris*	female	29	42.2 + 2.8	80.6 + 5.6	2.0 + 0.4	
1983	*T. vulgaris*	male	214	43.4 + 2.5	87.0 + 5.4	2.1 + 0.4	
1983	*T. vulgaris*	female	154	43.1 + 2.9	83.9 + 6.1	2.1 + 0.5	

b. Walton Hall, 1980 to 1983.

YEAR	SPECIES	SEX	N	MEAN SVL + SD (mm)	MEAN TOTAL LENGTH + SD (mm)	MEAN WEIGHT + SD (g)	MEAN CREST + SD (mm)
1980	*T. cristatus*	male	54	77.4 + 5.6	129.6 + 8.8		3.9 + 2.4
1980	*T. cristatus*	female	26	81.8 + 4.1	141.1 + 7.0		
1981	*T. cristatus*	male	37	74.5 + 7.6	124.6 + 12.1	9.3 + 2.7	3.2 + 1.3
1981	*T. cristatus*	female	14	79.6 + 6.1	137.6 + 10.4	12.3 + 3.3	

Table 12. Mean values of morphometric measurements taken of crested and smooth newts at Milton Bryan and Walton Hall

sexes from 1980 to 1981 (see Figure 12b). The decrease in males is significant ($p < 0.05$, Fisher-Behrens), but in females non- significant ($p > 0.05$, Fisher-Behrens).

In both populations females are significantly larger than males ($p < 0.01$, Fisher-Behrens and 2-sample t-test). In addition, the Walton Hall animals are significantly larger than those at Milton Bryan ($p < 0.01$, Fisher-Behrens).

Table 12a also gives the mean SVL's of the male and female smooth newts at Milton Bryan. There is more variation here than in the crested newt population. In this instance those animals which comprised the population in 1981 were significantly larger than those in 1980 and 1982 ($p < 0.05$ for each, Fisher-Behrens). The males are slightly larger than the females, but not significantly so ($p > 0.05$, Fisher-Behrens).

Figures 16 to 18 show the overall size-frequency distributions for male, female and juvenile crested newts at Milton Bryan for the years 1980 to 1983. The juvenile animals are of indeterminate sex and form a fairly distinct size class ranging from 35mm to 55mm SVL. It was not possible to sex any of these individuals. There is some overlap in size between juveniles and adults in this population. For instance, in 1983 two individuals were captured of 53mm SVL. This is within the juvenile size class, but both individuals were clearly identifiable as males. Bell (1979) regarded all individuals under 60mm in length as juveniles for the same reason, but in

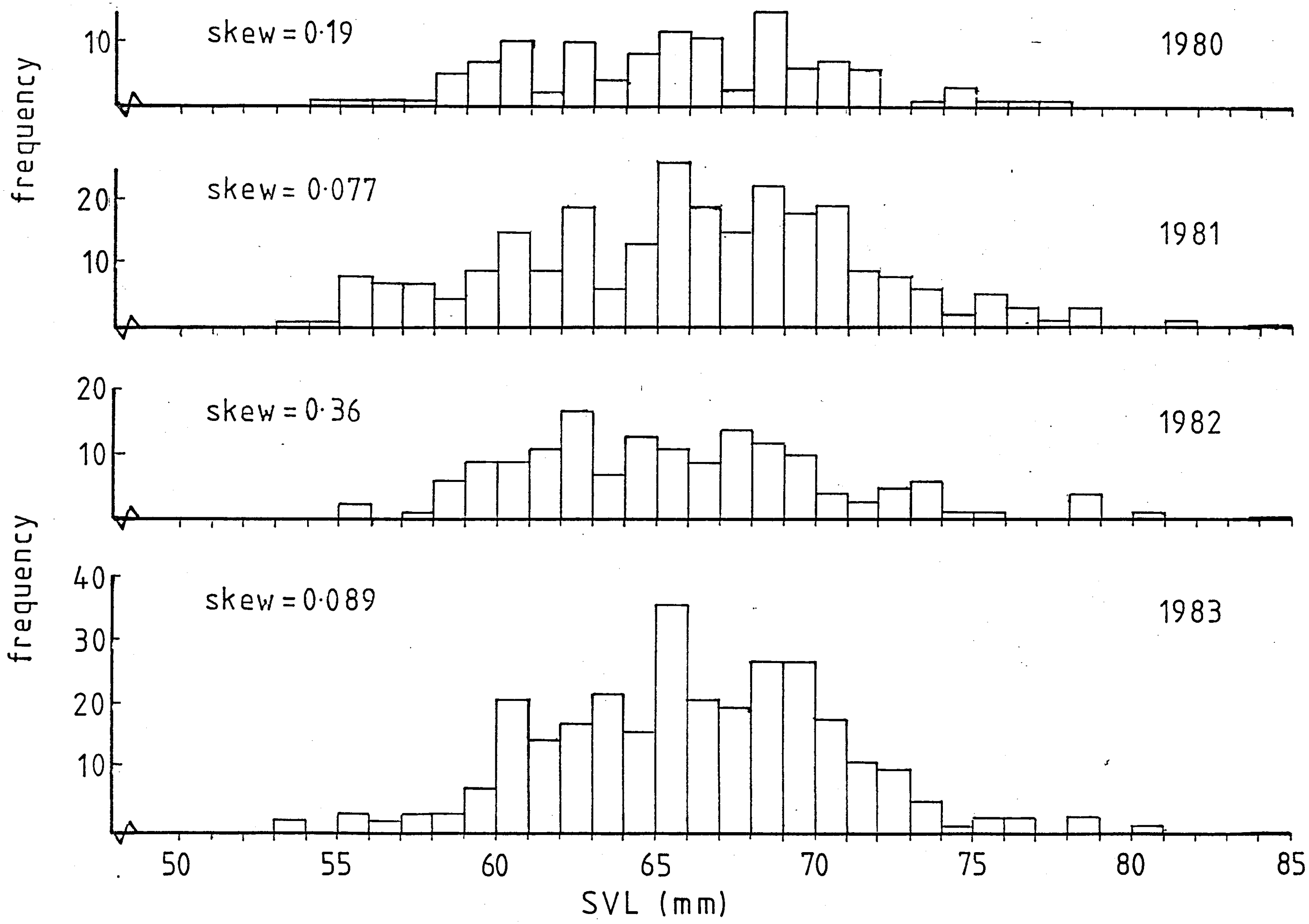


Figure 16: The size frequency distributions of the male T. cristatus population at Milton Bryan, 1980 to 1983.

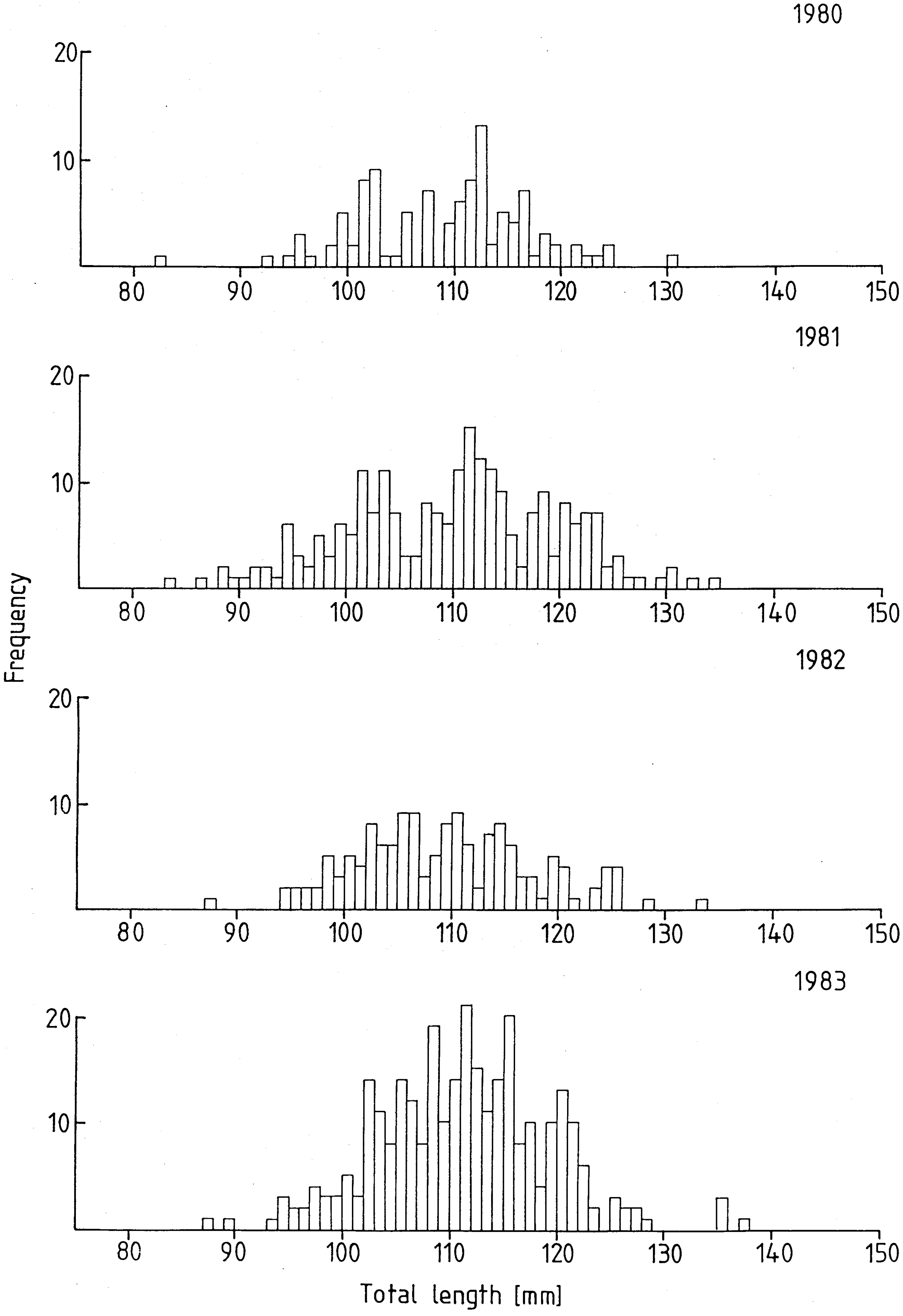


Figure 16a: The size-frequency distributions of the male *T. cristatus* population at Milton Bryan, 1980 to 1983, using total length as a measure

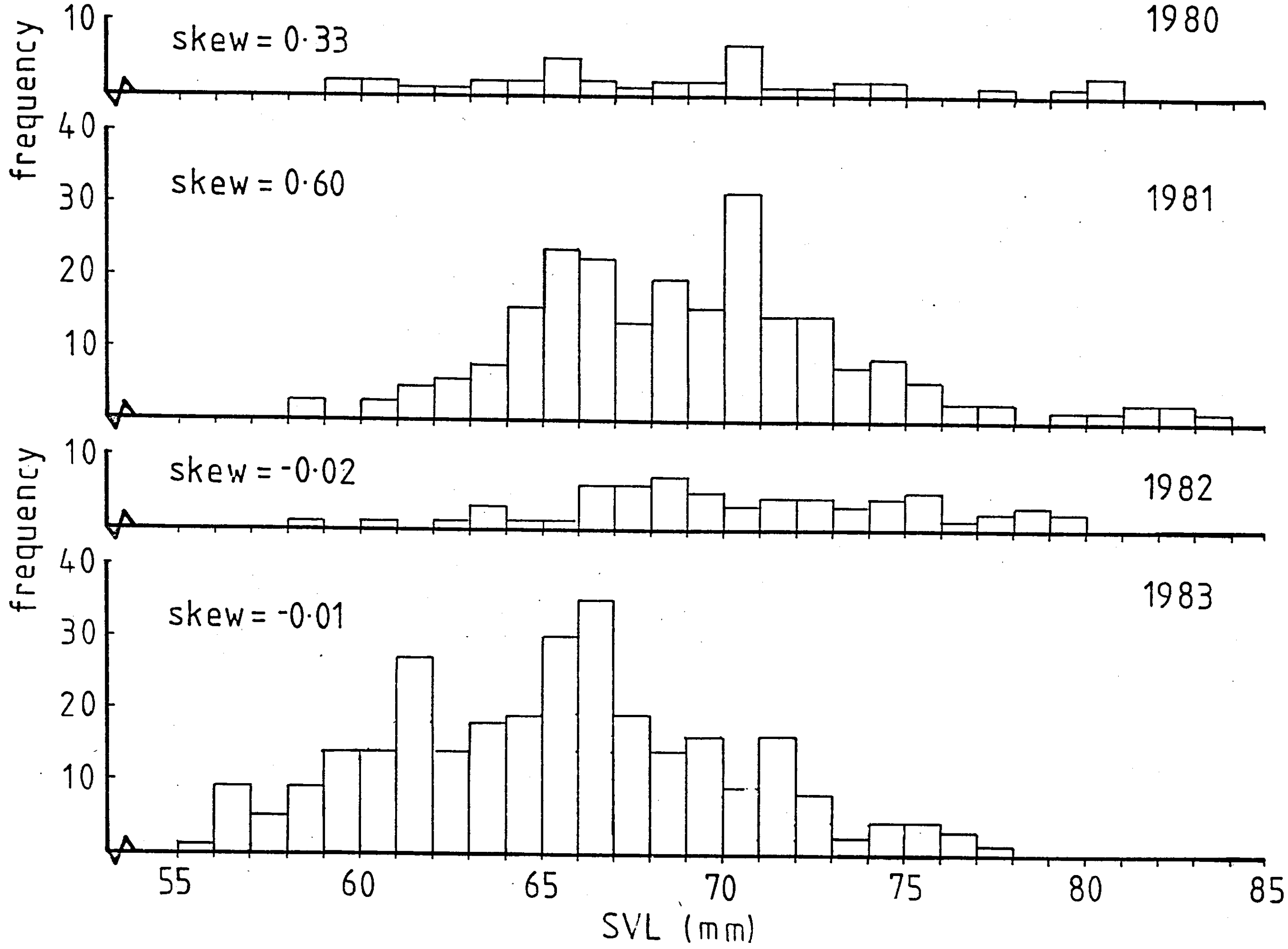


Figure 17: The size frequency distributions of the female *T. cristatus* population at Milton Bryan, 1980 to 1983.

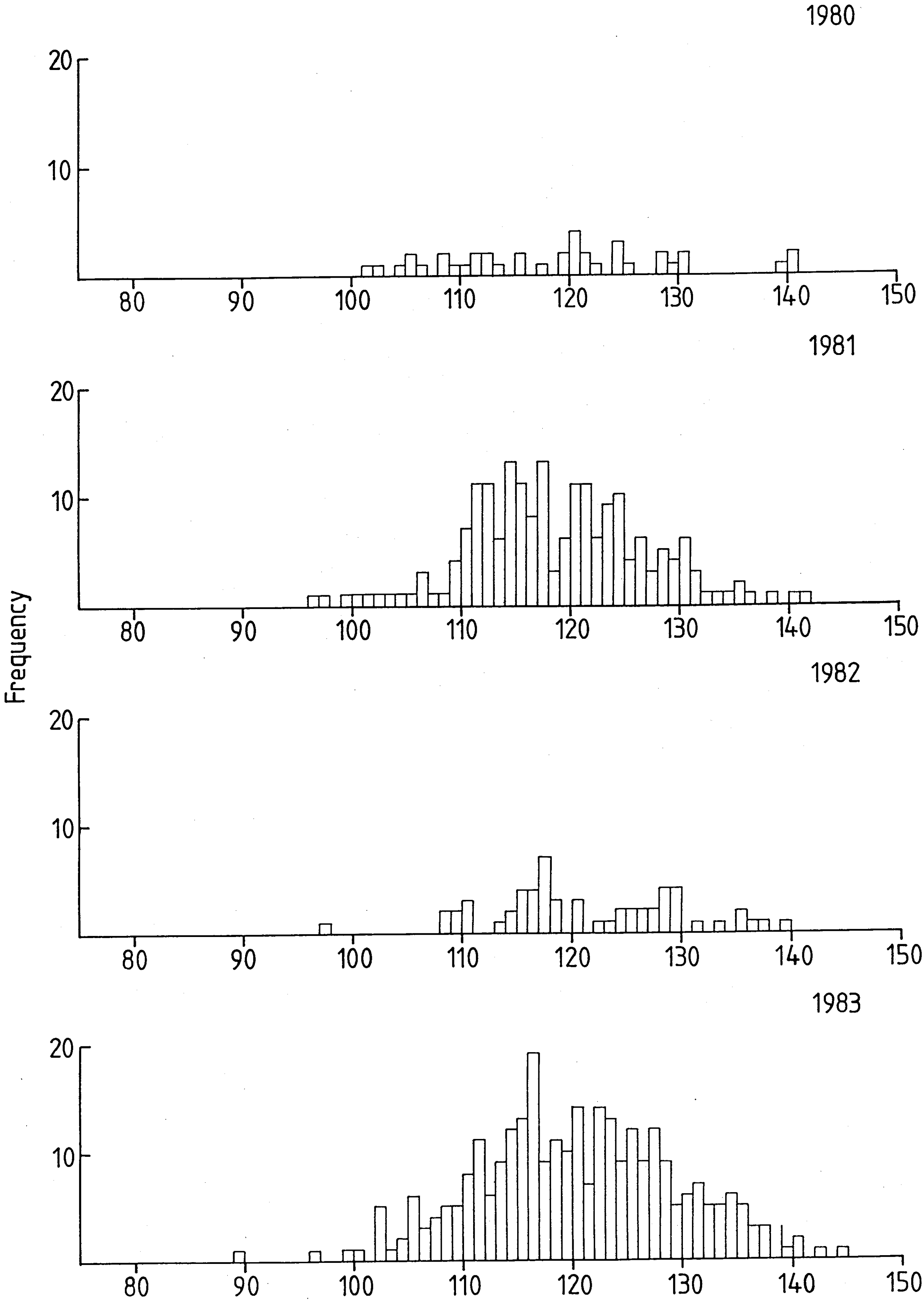


Figure 17a: The size-frequency distributions of the female <u>T. cristatus</u> population at Milton Bryan, 1980 to 1983, using total length as a measure

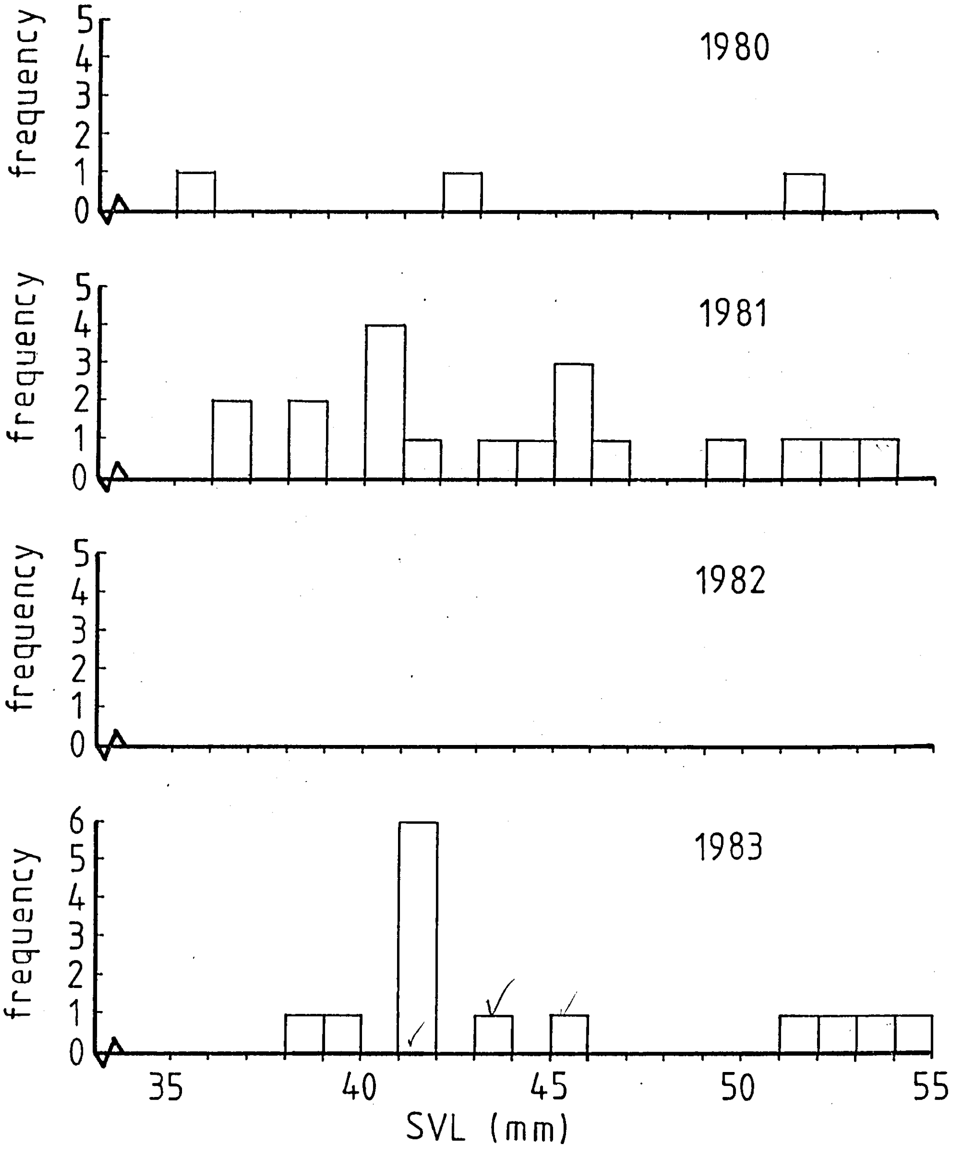


Figure 18: The size-frequency distributions of juvenile <u>T. cristatus</u> at Milton Bryan, 1980 to 1983.

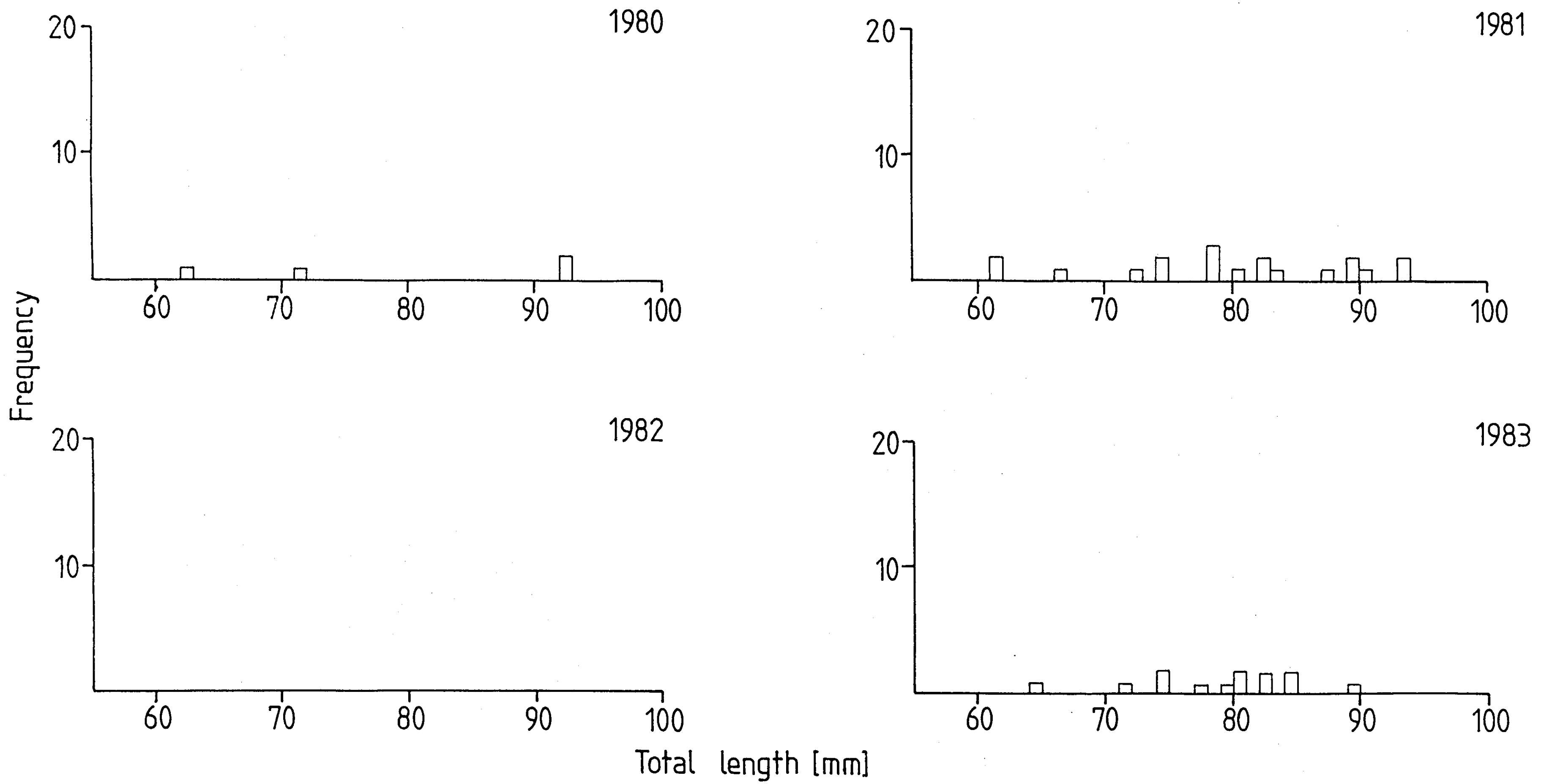


Figure 18a: The size-frequency distributions of juvenile _T. cristatus_ at Milton Bryan, 1980 to 1983, using total length as a measure

this study it was possible to sex any animal over 55mm in length. Furthermore, he included them in his female data, thus giving his female size-frequency histograms a distinctive, but erroneous, negative skew.

Figures 16a to 18a show the size-frequency distributions of the Milton Bryan population in terms of the total length of animals instead of SVL. This produces a similar result to plotting SVL distributions, but it is interestingg to look at the point at which animals are distinguishable as adults. Most males were identifiable from 90mm upwards, with a few individuals recognizable at smaller sizes than this. The juveniles occupied size ranges between 60mm and 93mm. Females were rarely found below 100mm total length. Cooke (pers comm) reports juveniles as having a total length of 90mm in the populations which he has studied.

It will be seen from the figures that the numbers of juveniles fluctuate from year to year; they are, in fact, absent from the 1982 population. These animals are thought to be about one year old and visiting the pond for the first time since metamorphosing, although they do not breed (Higginbottom 1853, Smith 1951, Verrell & Halliday in press a).

The principal variations in size distribution are in the frequencies of each size category. Some of this will be due to variations in the actual population size, such that more

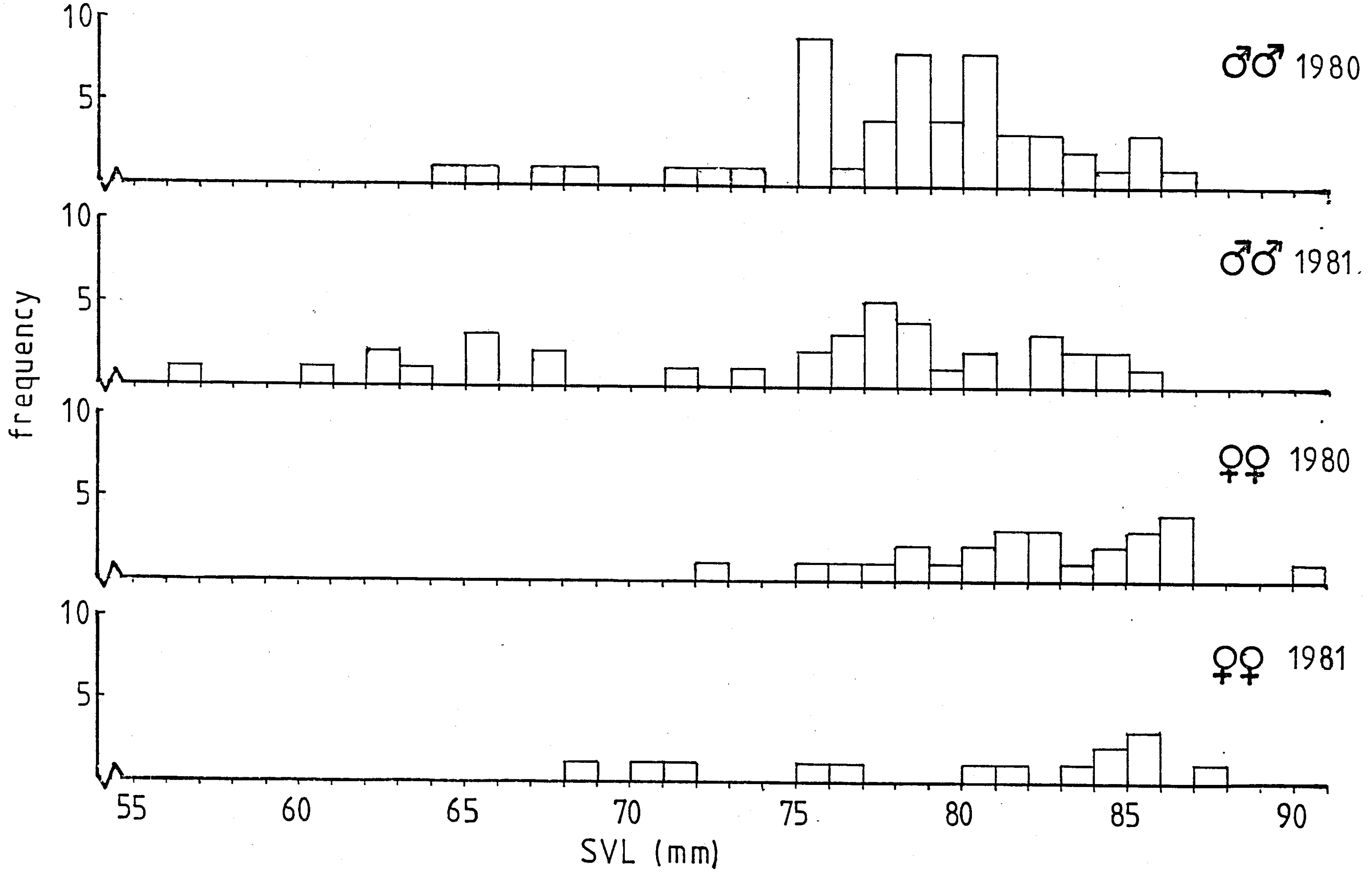


Figure 19: The size-frequency distributions of the male and female T. cristatus population at Walton Hall, 1980 and 1981.

animals occur per category when the population is large and fewer when it is small. There is some variation in the skew of the distributions (calculated using SPSS program; see figures). This value is a measure of the spread of values about the median and so tells us something about how the structure of the population is altering from year to year, that is to say, whether the population is comprised of more small animals in one season than another. Female crested newts show an increase in skew of the SVL distribution from 1980 to 1981, suggesting the presence of greater numbers of larger animals in this year. In 1982 and 1983 there is very little skew at all. The males show only a slight skew in 1980, 1981 and 1983 but, considerable positive skew in 1982, again suggesting the presence of more large individuals in that year. The skews for the total length data broadly follow this pattern also.

The size frequency data for the Walton Hall population are a little more patchy due to lower numbers of captures, but are broadly similar to that at Milton Bryan (see Figure 19).

Figures 20 and 21 show the size-frequency distributions for smooth newts at Milton Bryan. These are similar to those for the crested newt. No individuals were caught with a SVL less than 35mm and it was possible to sex all animals captured i.e. no juvenile smooth newts were found in the water at Milton Bryan.

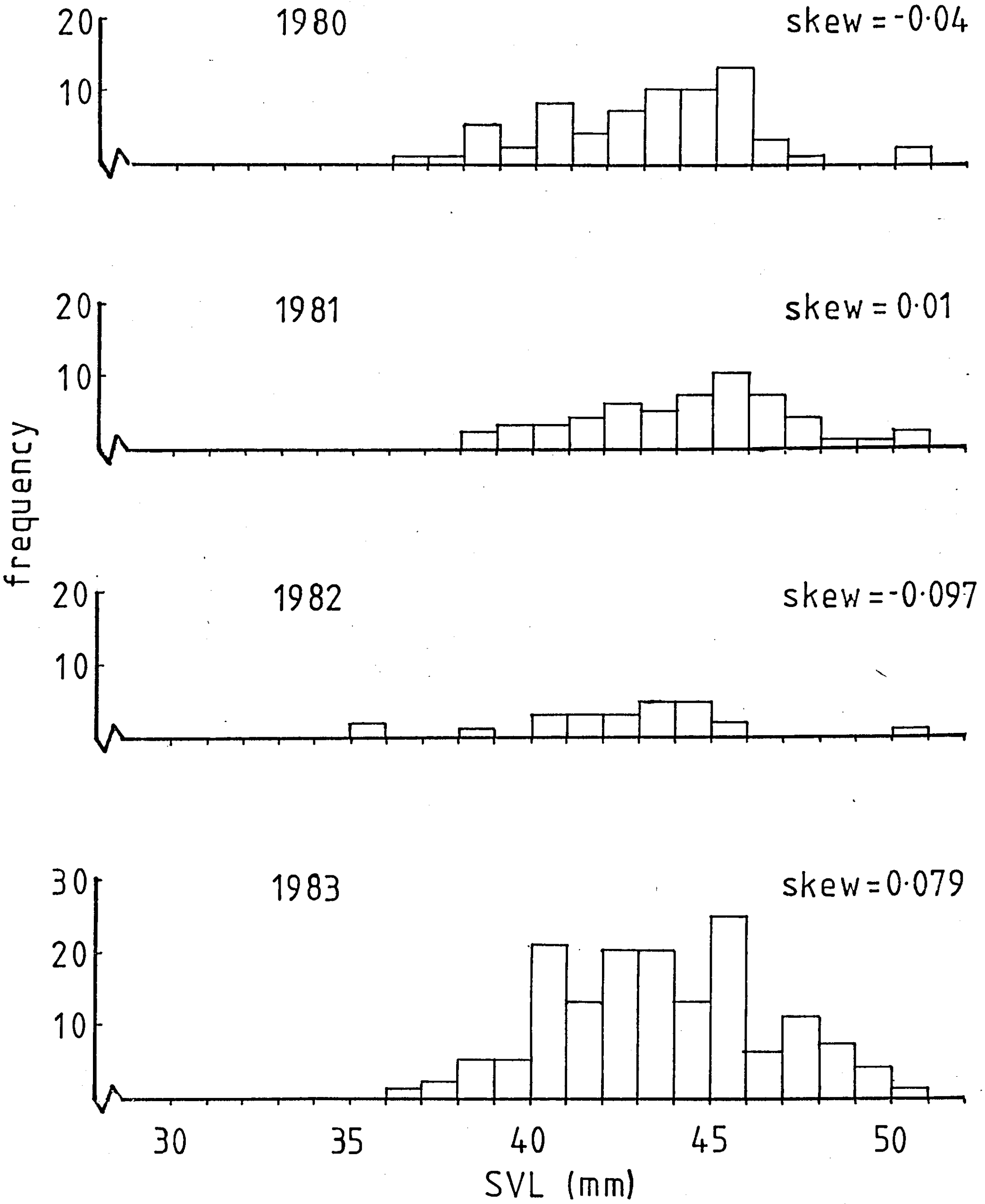


Figure 20: The size-frequency distributions of the female *T. vulgaris* population at Milton Bryan, 1980 to 1983.

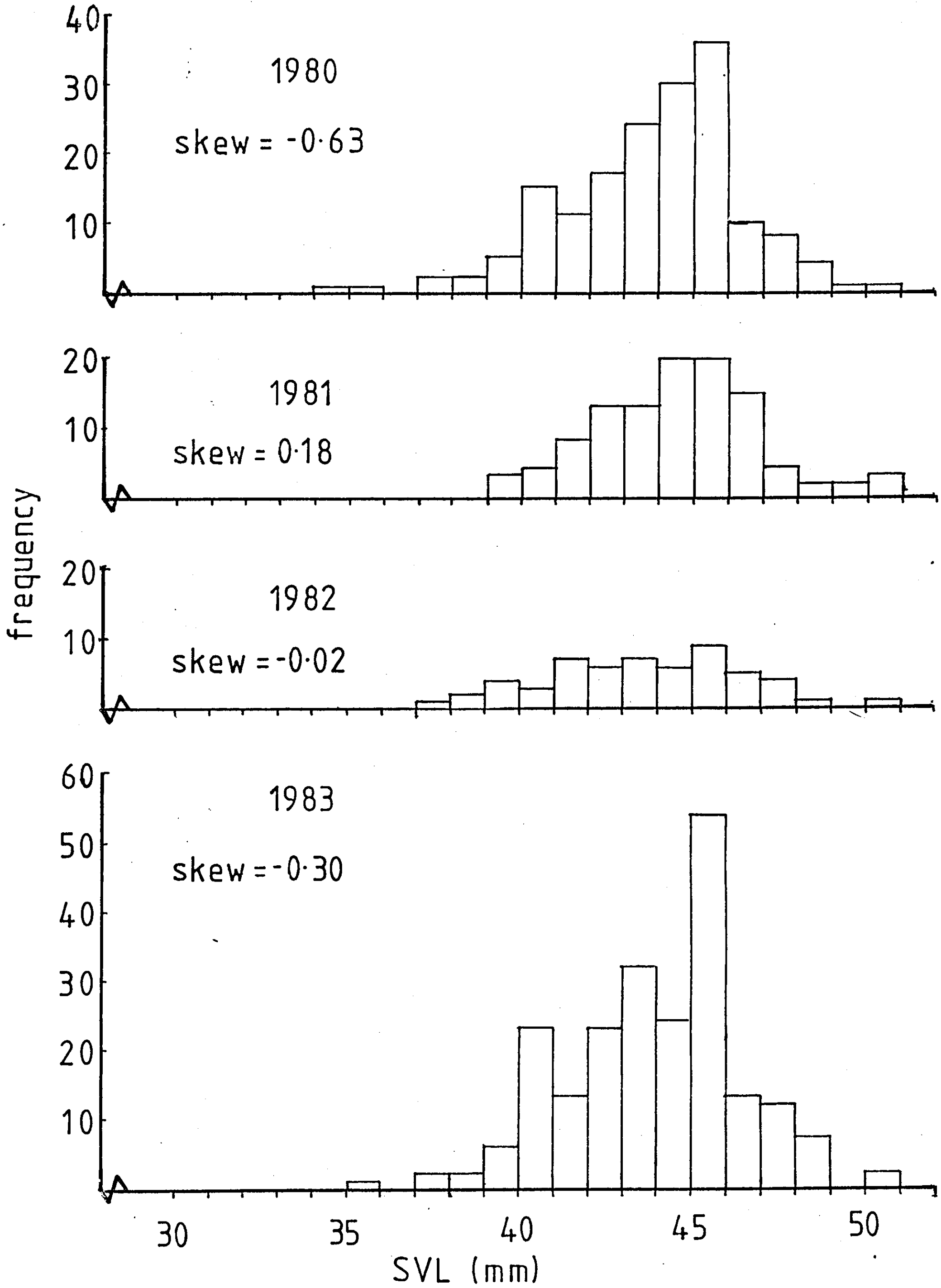


Figure 21: The size-frequency distributions of the male *T. vulgaris* population at Milton Bryan, 1980 to 1983.

The skew of each distribution is again given in the figures. As is seen, the females have very little skew to their distribution in all years, with little variation from one year to the next. The males are broadly similar, although a high negative skew occurs in 1980, suggesting the population consisted of more smaller animals in that year. 1983 also shows increasing skew to the left.

Frazer (1983) lists means, ranges and largest recorded specimens of smooth and crested newts in the British Isles. These are shown in Table 13.

	T. cristatus	*T. vulgaris*
mean total length of males	120mm	79mm
mean total length of females	111mm	76mm
range for males	110-140mm	50-93mm
range for females	128-157mm	50-93mm
largest recorded male	145mm	109mm
largest recorded female	162mm	100mm

Table 13: Means, ranges and largest recorded individuals in British specimens of *T. cristatus* and *T. vulgaris* (from Frazer, 1983).

From this and from Table 12 it may be seen that the male and female crested newts at Milton Bryan are, on average, at the lower end of the size range for the species, whilst those at the Walton Hall site are in the middle of the range. However, the largest individuals found at the University are approaching the the upper size limits recorded for this species in the British Isles. The male smooth newts at Milton

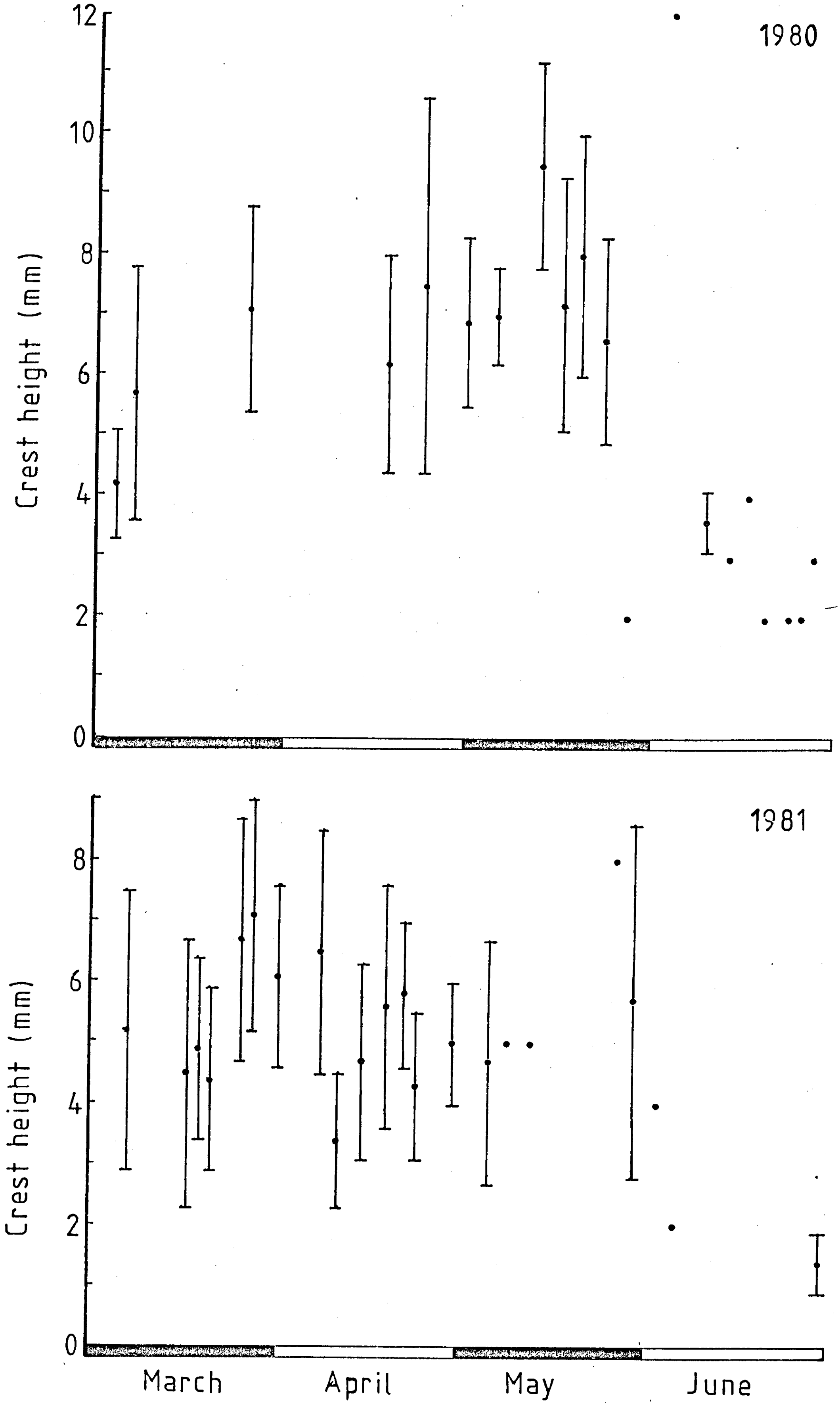


Figure 22: The variation in crest height of aquatic male *T. cristatus* at Milton Bryan during 1980 and 1981.

Values shown are means with standard deviations also given.

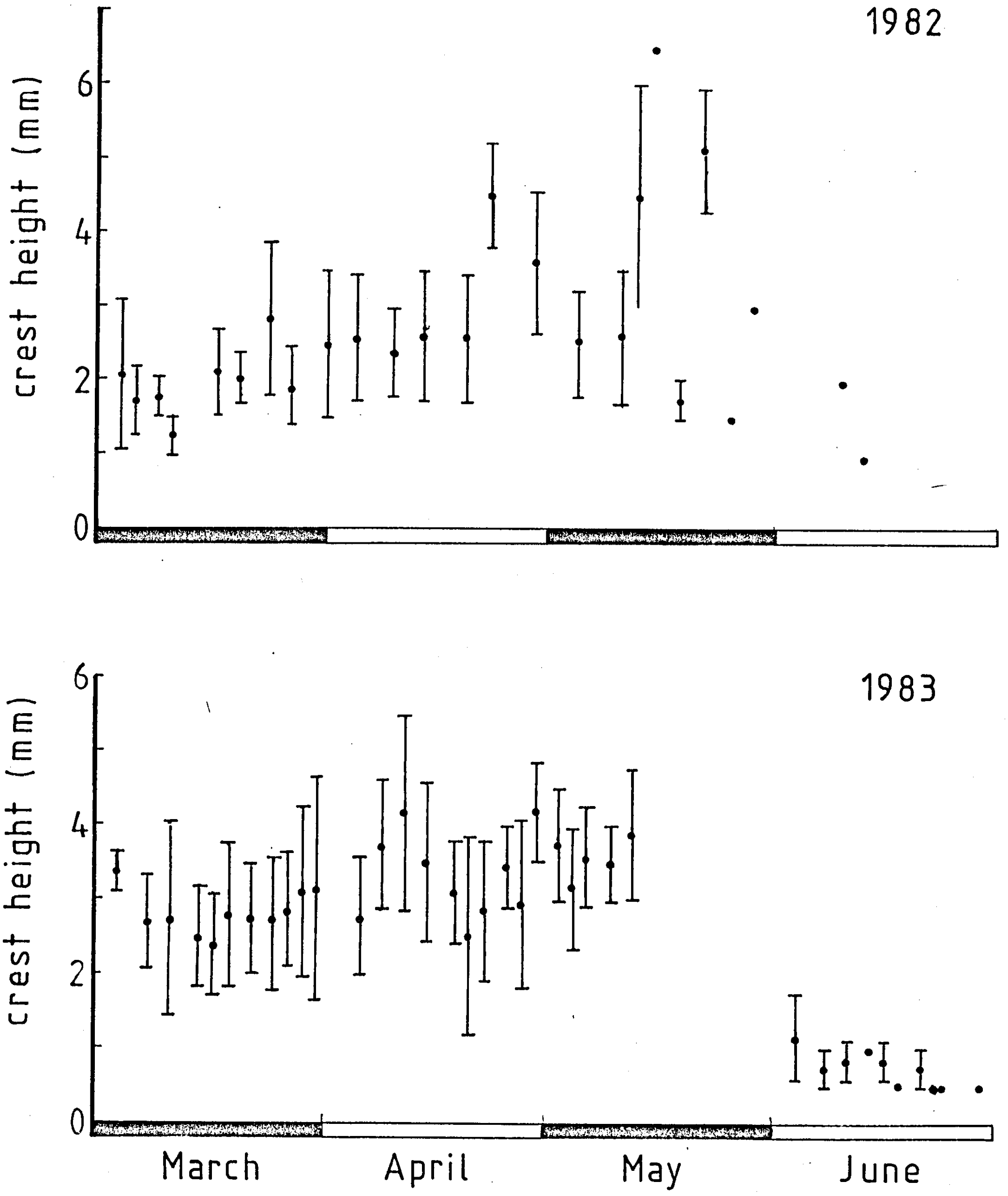


Figure 23: The variation in crest height of aquatic male T. cristatus at Milton Bryan during 1982 and 1983.

Values shown are means with standard deviations also given.

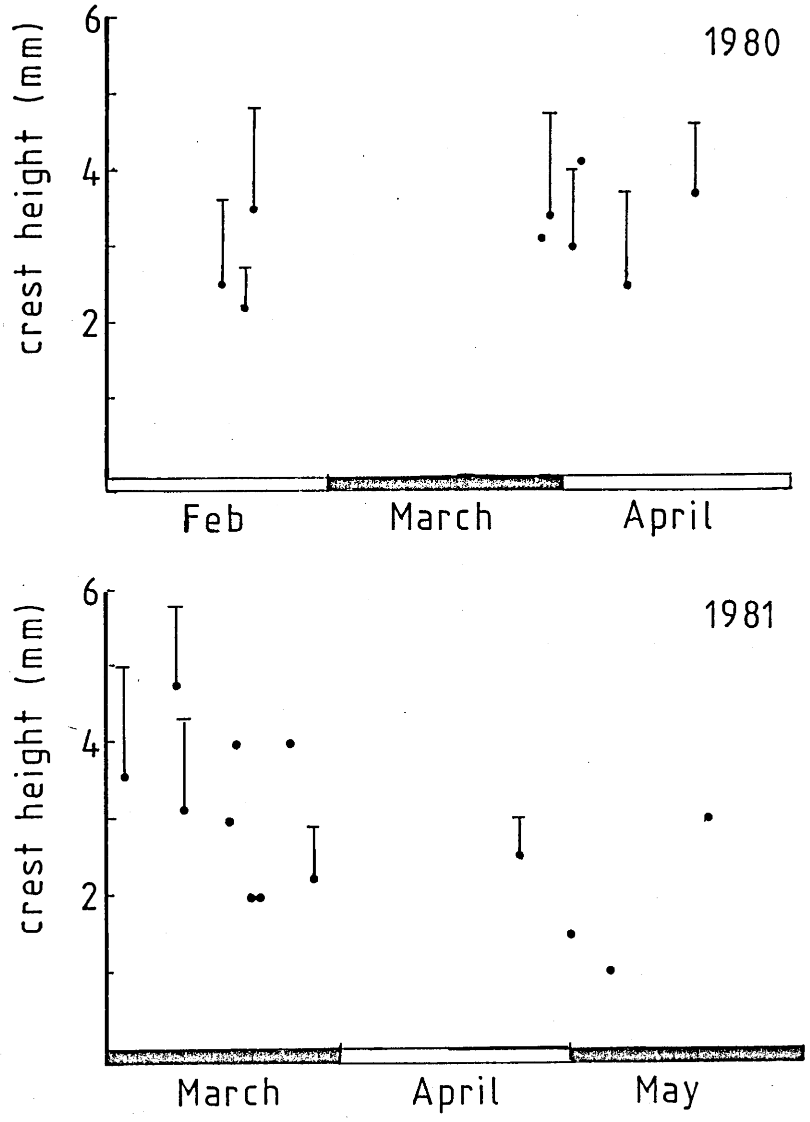


Figure 24: The variation in crest height of terrestrial male *T. cristatus* at the Walton Hall pond during 1980 and 1981. Values shown are means with standard deviations or individual figures.

Bryan are slightly larger than the average for British specimens, whilst the females are in the middle of the range.

Crest height in T. cristatus was thought to be a possible indication of the sexual state of the males. This is discussed further in section 4 on testes analysis. Here, the variation in crest height through the breeding season is investigated. Figures 22 and 23 show this for males at Milton Bryan. There is considerable variation, but on the whole it appears that a peak is reached in April or May. Figure 24 gives the equivalent data for Walton Hall. The majority of these animals had smaller crests, thus confirming the view that crests are developed on entry to the breeding site. Males leaving the University pond in August had completely lost their crests, but were still recognizable as males through the still visible white stripe on the tail.

3.3.2 Discussion.

The major problem in the interpretation of urodele size-frequency distributions is in relating them to the age structure of the population being studied, since no direct method for age determination exists for live urodeles. The usual technique is to dissect the raw data into size-classes using the method of Harding (1949). This involves the transformation of the size-frequency distribution into percentage-cumulative frequencies which are than transferred onto probability graph paper. Under this treatment a normal distribution appears as a straight line, a polymodal distribution as a series of straight lines separated by steps. Each size-class is assumed to consist of animals of the same age.

Bell (1973, 1977, 1979) used this method on the data he obtained from populations of smooth and crested newts. He then used this as the basis of his life-history analyses of the two species. The problem is that recent work has shown there to be only a very weak relationship between the age of a urodele and its body length.

The existence of growth rings in the parasphenoid bone of amphibians was first recorded by Senning (1940) and confirmed by Peabody (1961). Using these rings it was possible to age animals to within one year. More recently, the technique has been to use the femur rather than the parasphenoid (Castanet 1975, Smirina & Rocek 1975, Hagström 1977, Francillon 1979, 1980 and Dolmen 1981). Hemelaar & van Gelder (1980) and Gibbons & M^cCarthy (1983) have also successfully used the method on the phalanges of the anuran species Rana temporaria and Bufo bufo. This has the advantage that animals need not be sacrificed in order to be aged.

There is considerable variation in the results obtained in these studies. Gibbons & McCarthy found the number of rings to be highly correlated with body length. In contrast, Gittins et al (1983) found no such relationship in B. bufo. Similarly, Hagström (1977) failed to find a strong correlation between these scores in Triturus, whilst Verrell (unpublished data) suggests there is a relationship, but one which must be treated with caution. Since animals may be aged to within 1 year using this method it is clear that any results on age-structure of urodele populations derived from Harding's method must be interpreted with caution.

The variation in the skew of the distributions is comparable with that found by Bell (1977) in his smooth newt populations. However, the explanation he gives does not appear to fit with my data. He demonstrated that variation in skew was co-incidental with changes in the mean length of the population, which, he argues, is indicative of a change in the age structure. This is not necessarily the case at Milton Bryan. Comparing skew with mean SVL of male smooth newts from 1980 to 1981 one finds Bell's interpretation to hold true. There is an increase in mean body length associated with an increasingly positive skew. However, an increasing negative skew from 1982 to 1983 does not produce a decrease in mean SVL. Similarly, the skew of the female smooth newt distribution is more or less constant from year to year but there are significant changes in SVL between some years. The data on crested newts are also in disagreement with Bell's argument. Here again, there are variations in the skew of the male and female distributions but, apart from a little change in standard deviation, the mean SVL's are constant.

3.4.1 Analysis of weight change and growth from recapture data.

Quantitative information on phenomena such as the growth of adult smooth and crested newts and weight change during the breeding season is scarce in the literature. Hagström (1976) and Glandt (1981) provide some of the most recent data on growth. Such data are important if a complete profile of the biology of these species is to be obtained. For instance, information on growth rates of individuals coupled with other demographic data may give an insight into the capacity of a population to recover from perturbation due to environmental change, over-predation, pollution, etc.

The data obtained from the recapture of individual animals within a season and from year to year enables one to study a number of these factors and may also provide information about the time spent in a pond by various individuals. At the onset of this study little was known about the time spent in breeding ponds by the different sexes and so, information of this type would be of value.

Changes in the weight of an individual during the breeding season may be an indirect indication of the reproductive effort of that animal (particularly when coupled with data on ovary and testes weights), the extent to which it is feeding and so on.

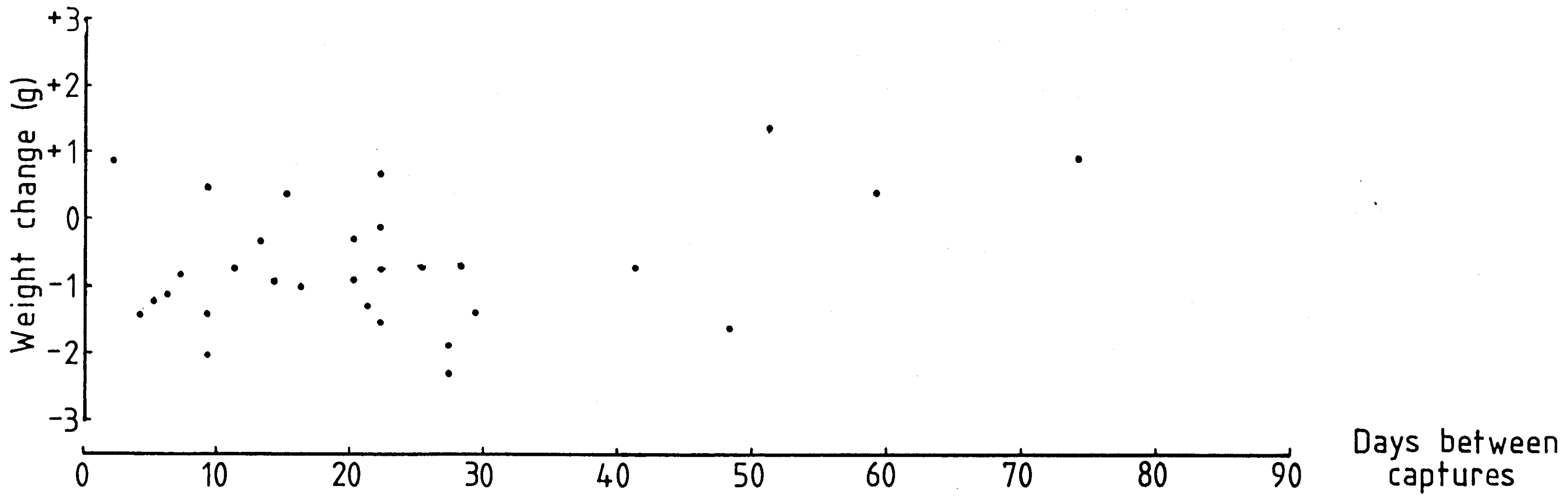


Figure 25: The relationship between weight change and the number of days between captures for male <u>T. cristatus</u> at Milton Bryan during 1981.

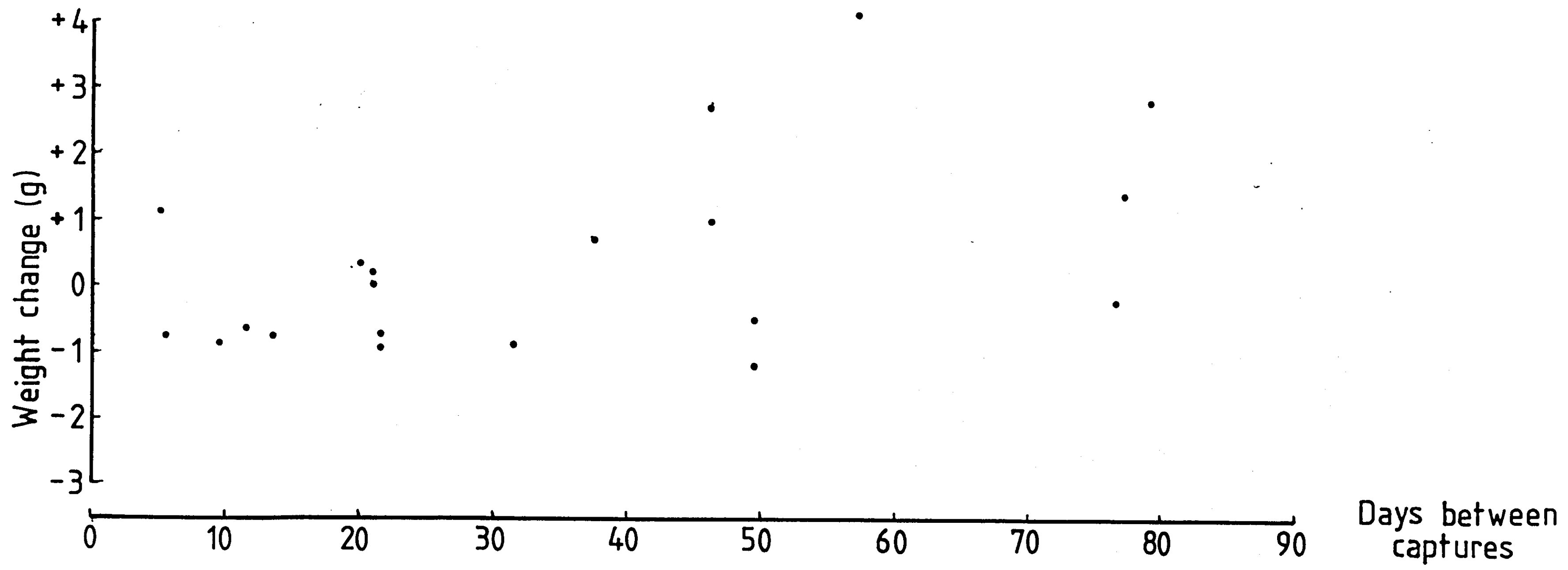


Figure 26: The relationship between weight change and the number of days between captures for male <u>T. cristatus</u> at Milton Bryan during 1982.

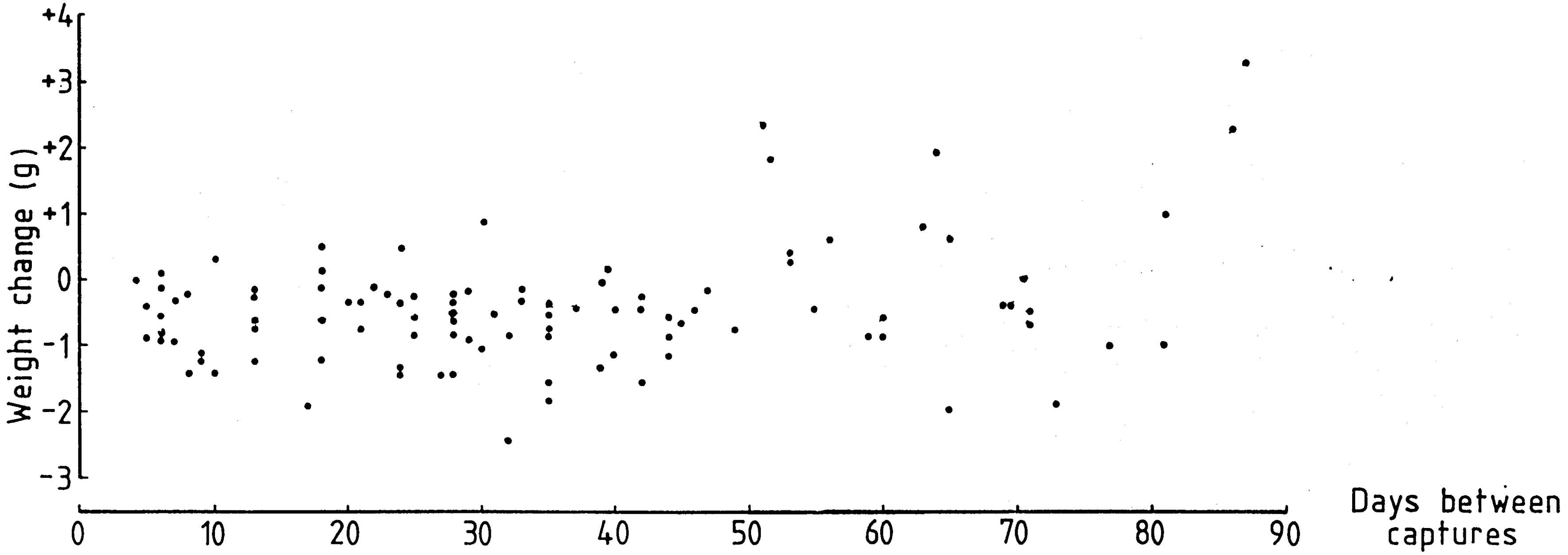


Figure 27: The relationship between weight change and the number of days between captures for male *T. cristatus* at Milton Bryan during 1983.

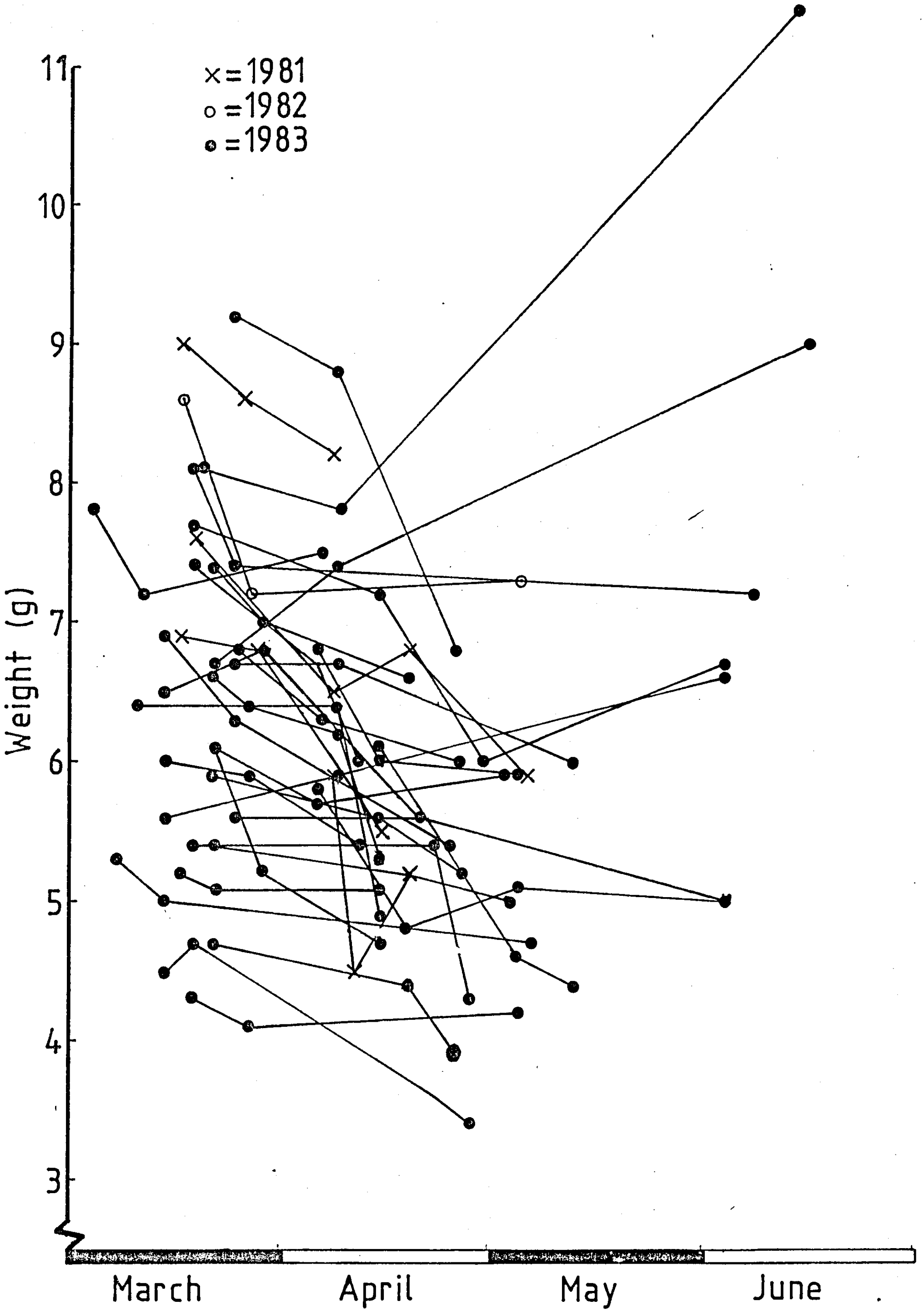


Figure 28: The change in weight of individual T. cristatus males at Milton Bryan during the 1981, 1982 and 1983 breeding seasons.

Figures 25 to 27 show the weight changes between captures of individual male crested newts in 1981, 1982 and 1983. There is considerable variation within each year, with some animals losing more weight over a short period than others, some gaining weight and others remaining fairly static. There are significant correlations between weight change and time between captures in 1982 and 1983 ($r = 0.5$, $N = 21$, $p < 0.05$ & $r = 0.32$, $N = 107$, $p < 0.05$ respectively Pearson). The correlation for 1981 is non-significant ($r = 0.29$, $N = 30$, $p > 0.05$, Pearson). In general, then, it appears that animals that are recaptured quickly have lost more weight than those with longer intervals between captures. This comparison, however, does not take account of the dates on which recaptures are being made. It may be that a general trend is being observed such as that animals are gaining weight early in the season and are losing it later or vice versa. Figure 28 shows the variation in weight of individual males recaptured a number of times during each year. The majority show a steady decline in weight. Eight show an increase, the timing of which is variable but, in each case this was preceded by an initial loss in weight.

The weight changes between captures for female crested newts are shown in Figures 29 and 30. Significant correlations are obtained for 1981 and 1982, but not for 1983 ($r = 0.50$, $N = 26$, $p < 0.05$, $r = 0.84$, $N = 7$, $p < 0.05$, $r = 0.09$, $N = 80$, $p > 0.05$ respectively, Pearson). The plots for those

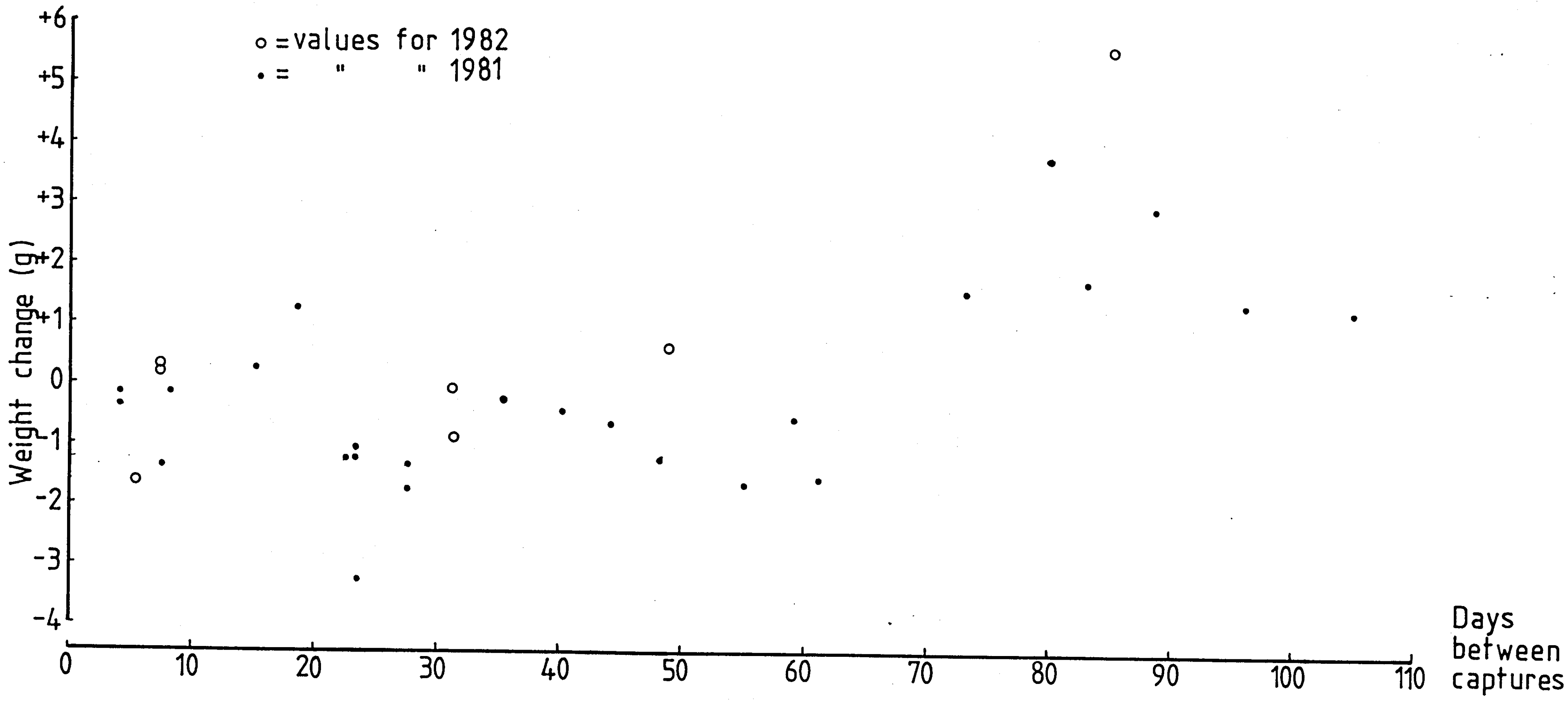


Figure 29: The relationship between weight change and the number of days between captures for female _T. cristatus_ at Milton Bryan during 1981 and 1982.

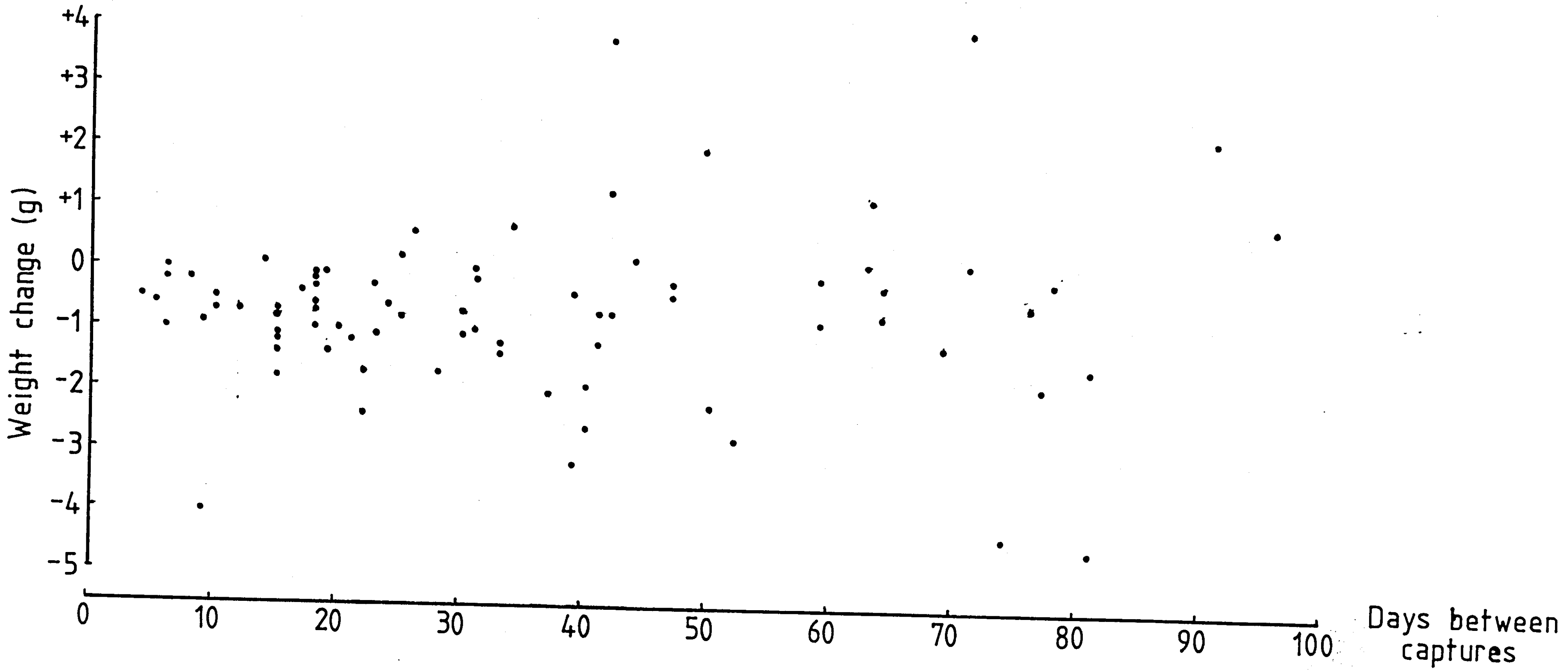


Figure 30: The relationship between weight change and the number of days between captures for female *T. cristatus* at Milton Bryan during 1983.

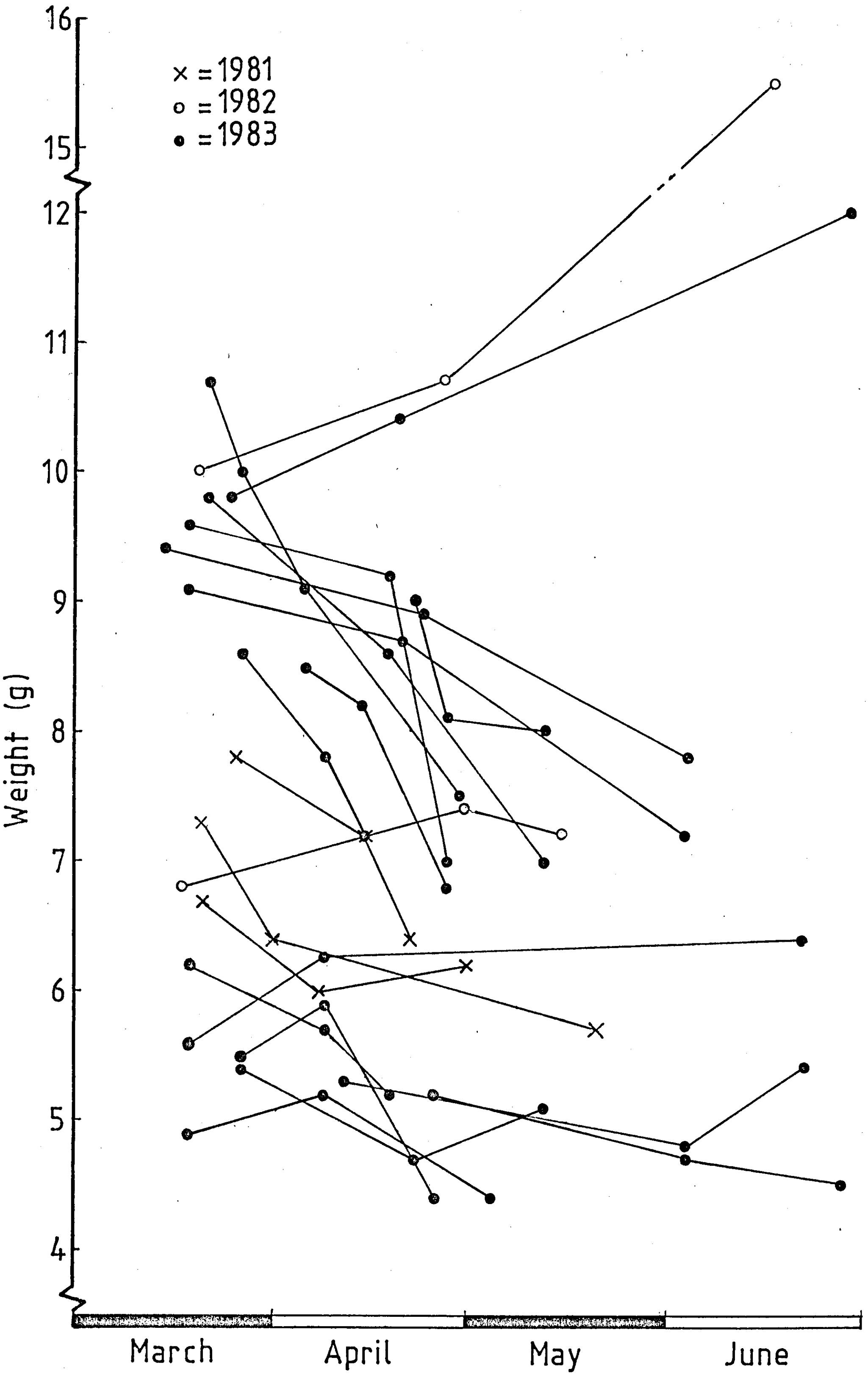


Figure 31: The changes in weight of individual T. cristatus females at Milton Bryan during the 1981, 1982 and 1983 breeding seasons.

individuals recaptured more than once are shown in Figure 31 . The general conclusions are the same as for the males. Again, the majority of animals show a steady loss of weight in the early part of the breeding season, with five increasing after a time.

In 1981 and 1982 the difference in mean weight loss between males and females was non-significant ($p > 0.05$, Fisher-Behrens test). In 1983, however, the difference was significant ($p < 0.01$, Fisher-Behrens). For females mean weight loss approximates to the mean weight of the ovaries (calculated from preserved animals, see section 4 of this chapter). For males, though, weight loss is far greater than is expected purely from the deposition of spermatophores (on the basis of testes weights; see section 5).

The results for male and female smooth newts are shown in Figures 32 and 33. Only data for 1981 and 1983 have been used since there were insufficient recaptures in 1982. For the males there are non-significant correlations between weight loss and recapture interval in both years ($r = 0.58$, $N = 11$, $p > 0.05$ & $r = 0.32$, $N = 22$, $p > 0.05$ repectively, Pearson). Only the data for 1983 reach significance in females ($r = 0.69$, $N = 10$, $p < 0.05$, Pearson). There was no significant difference found between mean weight loss for males and females in 1983. In 1981 all three females increased in weight. No animals were recaptured more than once so it was

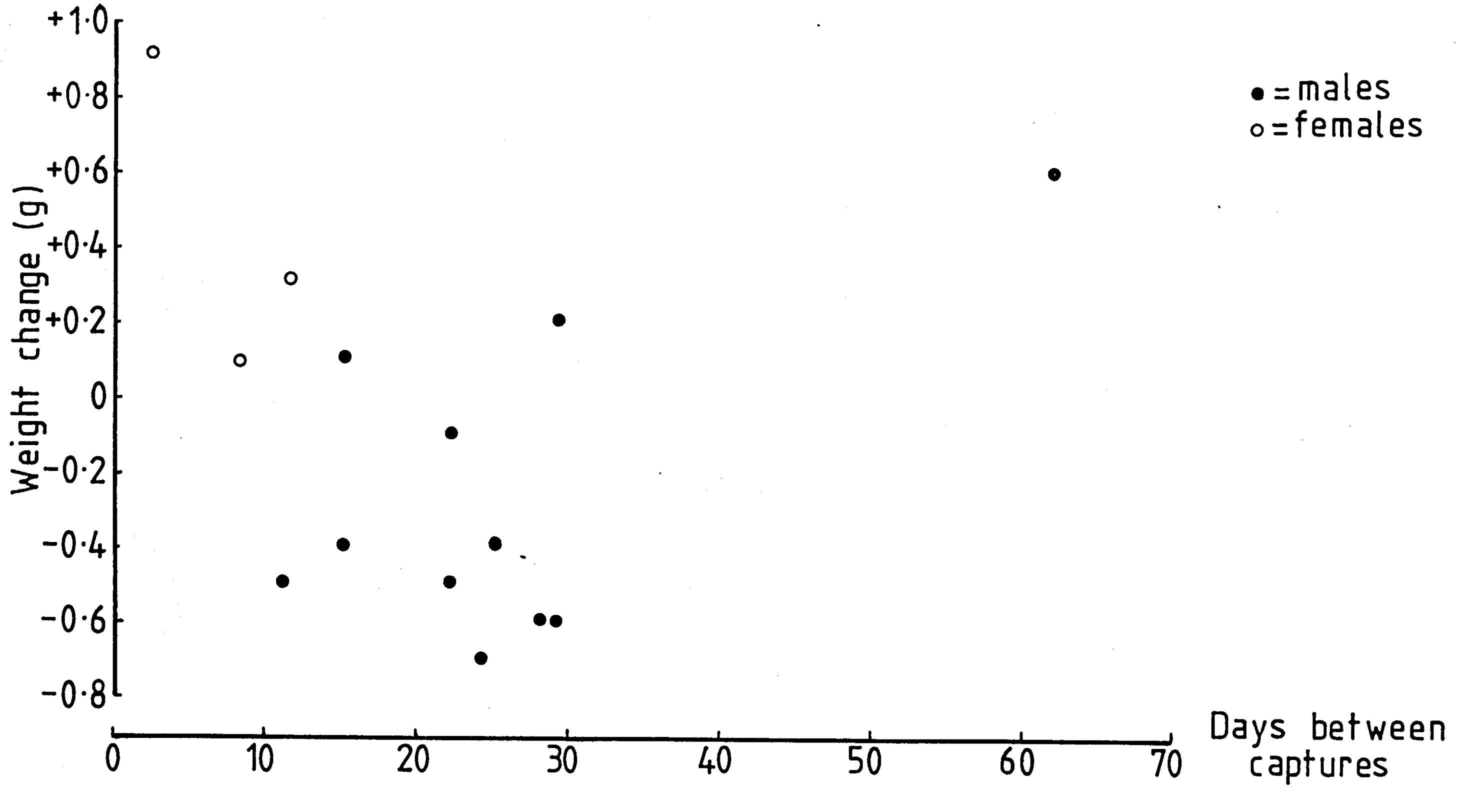


Figure 32: The relationship between weight change and the number of days between captures for male and female <u>T. vulgaris</u> at Milton Bryan during 1981.

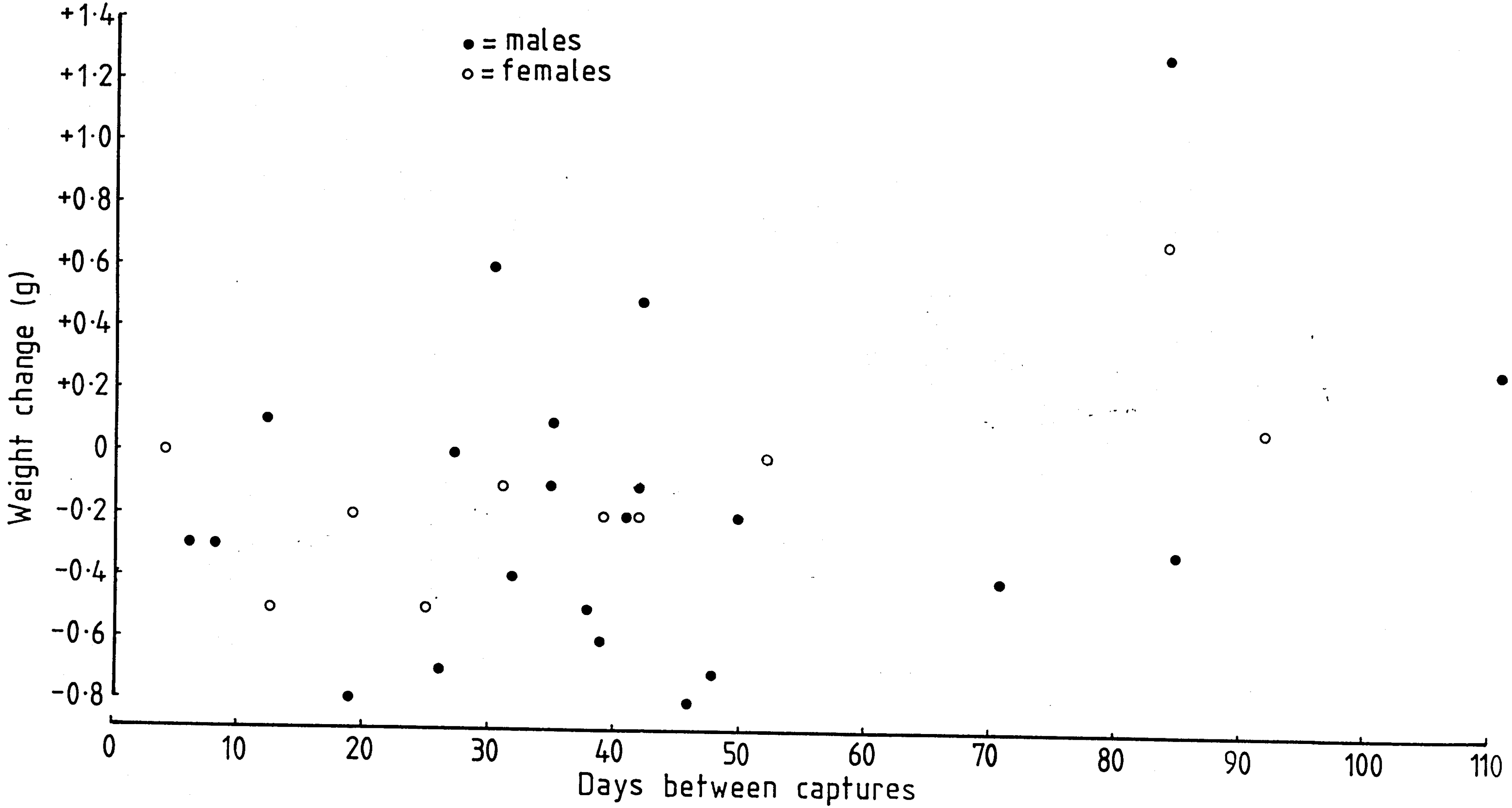


Figure 33: The relationship between weight change and the number of days between captures for male and female <u>T. vulgaris</u> at Milton Bryan during 1983.

not possible to plot weight change through the season for this species.

The magnitude of weight loss in the females is consistent with that expected from egg deposition but, males are again losing more than can be accounted for purely from the loss of sperm in depositing spermatophores.

YEAR	SPECIES	SEX	N	MRI	SD
1980	T. cristatus	male	18	49.8	35.3
1980	T. cristatus	female	5	27	2.8
1981	T. cristatus	male	30	22.6	16.8
1981	T. cristatus	female	26	38.2	29.4
1982	T. cristatus	male	21	34.0	23.1
1982	T. cristatus	female	6	27.7	27.9
1983	T. cristatus	male	107	33.7	20.9
1983	T. cristatus	female	80	34.6	23.2
1980	T. vulgaris	male	15	35.3	25.8
1980	T. vulgaris	female	5	51.4	28.8
1981	T. vulgaris	male	11	25.6	12.9
1981	T. vulgaris	female	3	7	3.7
1982	T. vulgaris	male	1	17	
1982	T. vulgaris	female	1	26	
1983	T. vulgaris	male	26	43.3	25.5
1983	T. vulgaris	female	9	42.4	28.0

Table 14: Mean recapture intervals (MRI) for T. cristatus and T. vulgaris at Milton Bryan, 1980 - 1983.

The mean recapture intervals for males and females of both species are given in Table 14. These give some indication of the period spent in the water, although exact periods cannot be determined without recording entry and exit of individuals to and from a pond. There is no significant difference for male and female crested newts in 1982 and 1983 but, there is for 1981 ($p < 0.05$, Fisher-Behrens); females appear to have remained in the pond longer than males in that year. The results for smooth newts in 1983 were non-significant.

There were also some differences between years. Male crested newts had a significantly longer MRI in 1980 than in 1981 ($p < 0.01$, Fisher-Behrens), whilst the difference between the 1981 and 1982 values are approaching significance. There was no difference between the 1982 and 1983 values for males and no significant differences were found for the female values. From this I would suggest that males may be spending different amounts of time in the water in different years whilst the females tend to spend roughly the same amount of time in a breeding pond in each year.

For smooth newts only the data for 1980 and 1981 are comparable. There was no significant difference for males, but the values for females did show a significant difference ($p < 0.01$, Fisher-Behrens).

Weight change over a season gives an indication of what is happening to an individual whilst it is in the pond. Weight gain or loss from year to year may also be of interest but, because weight will vary, due to reasons previously outlined, in order to study the growth of individuals it is necessary to look at changes in length. Since total body length may be more variable than SVL (for reasons previously mentioned in Chapter 2), it is variation in SVL which is used in this study.

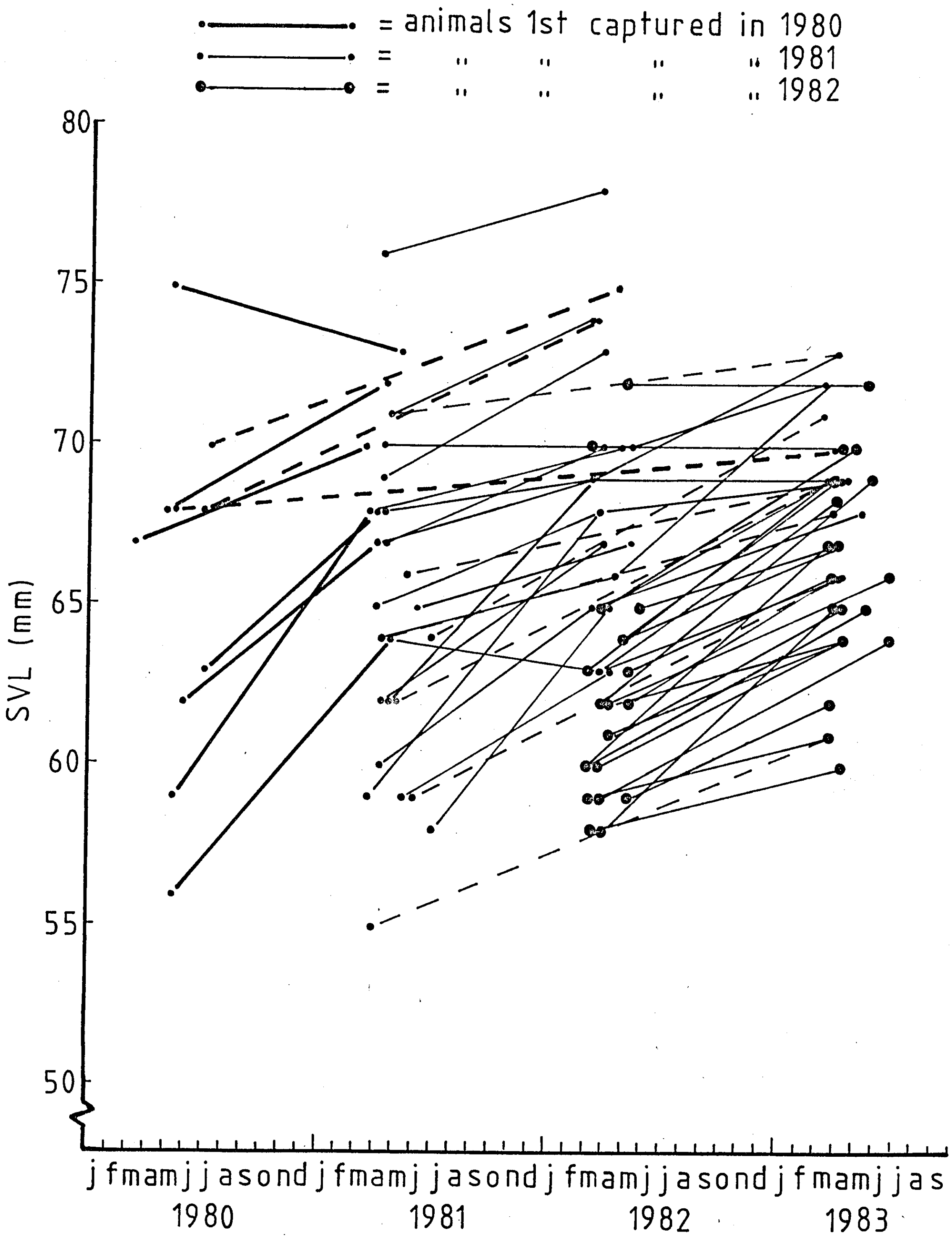


Figure 34: The changes in SVL of individual male T. cristatus captured in more than one year. Solid lines denote captures over successive years; broken lines denote captures over non-adjacent years.

Figure 34 is a graph of the change in SVL of individual male crested newts over a number of years. Figure 35 shows the equivalent data for female crested newts. No such information was available for smooth newts due to difficulties in the identification of individual animals from one year to the next.

The majority of animals show an increase in length. Some show no growth, whilst a very few decrease in size. When the weight and length of a recaptured individual were recorded it was not known what the previous values of these measures were until the new data were entered on that animal's record card in the laboratory. Upon entering new data on record cards I found that errors of more than 1mm either way in measuring recaptured animals were rare. Therefore, any change in length of 2mm or more should be an indication of true growth and not an error in measuring.

As may be seen from the slopes of the different lines individuals are growing by different amounts. It is also apparent that animals of the same size may increase by different degrees. In order to interpret these data more fully they have been converted to growth rates. This was done by dividing the changes in length by the time between captures and expressing the results in mm per 100 days.

When these are plotted against the SVL's of animals on first capture Figures 36 and 37 are obtained. From these it is

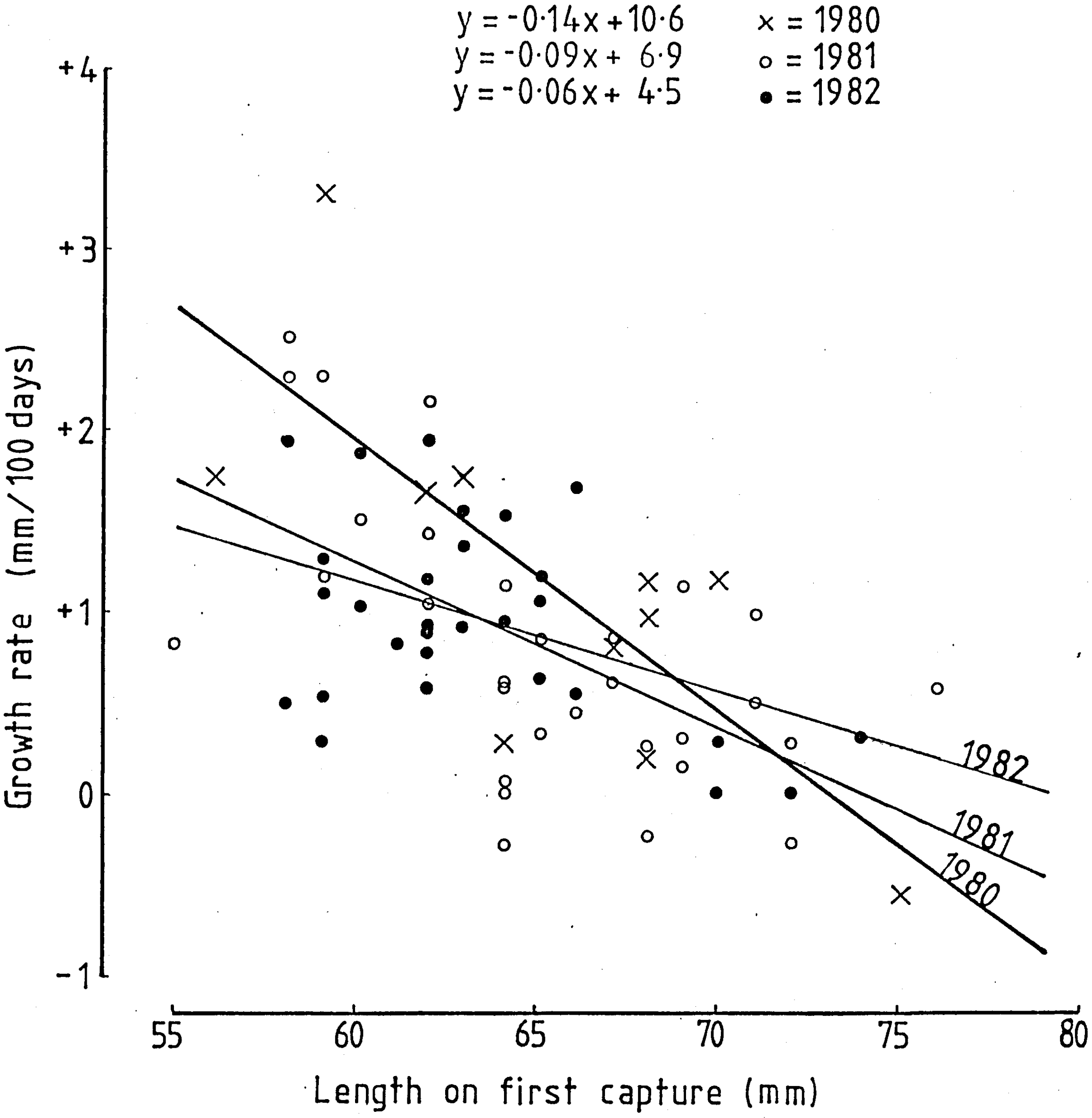


Figure 36: The relationship between growth rate and length on first capture of individual male T. cristatus captured between 1980 and 1983 at Milton Bryan.

1980/81 r = -0.76, N = 11
1981/82 r = -0.60, N = 30
1982/83 r = -0.43, N = 29

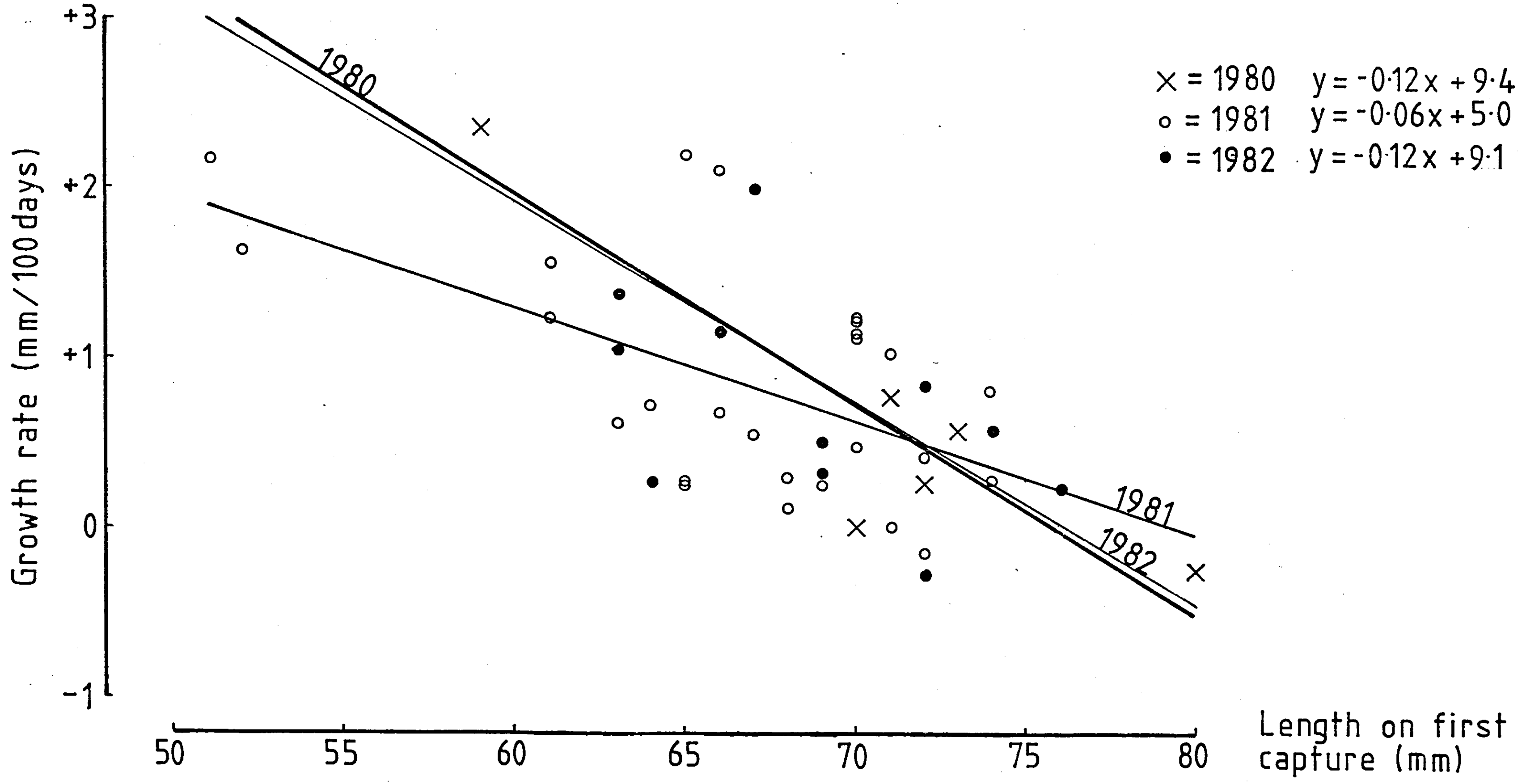


Figure 37: The relationship between growth rate and length on first capture of individual female <u>T. cristatus</u> captured between 1980 and 1983 at Milton Bryan.

1980/81 r = -0.91, N = 6; 1981/82 r = -0.53, N = 26; 1982/83 r = -0.61, N = 12.

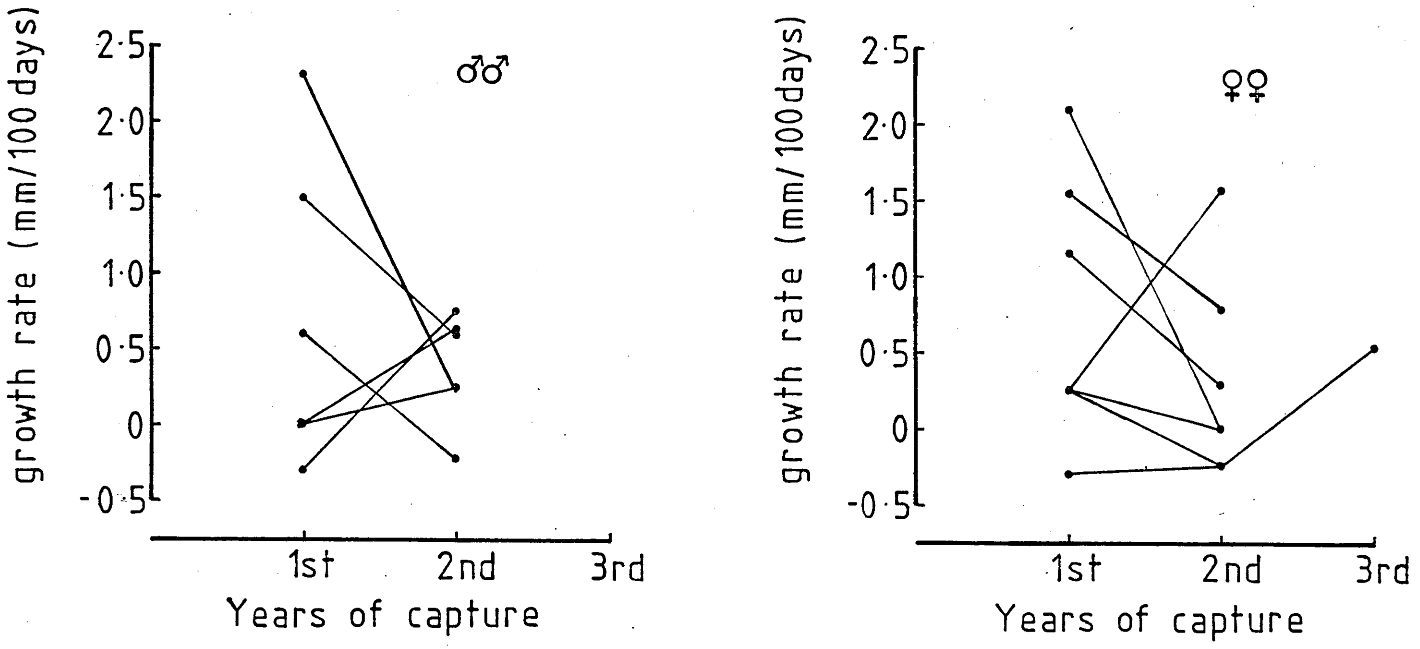


Figure 38: The changes in growth rate of male and female T. cristatus captured over more than two seasons at Milton Bryan.

apparent that smaller animals have higher growth rates, on average, than the larger individuals. Analysis of the relationship between original SVL and subsequent growth rate produces significant correlations for both sexes for all years. The correlations are shown in the figures.

This is further supported to an extent by Figure 38 which show the changes in growth rate of those males and females captured in more than two years. These data are rather 'noisy' due to the low sample size but, taking males and females together, the majority of individuals show a decrease in growth from one year to the next i.e. as an animal increases in size it's rate of growth slows down.

The same result is obtained if the data are analysed in terms of percentage growth rates. Significant correlations are obtained between percentage-growth rate and original SVL for both male and female crested newts in all years. For females these correlations are: 1980, $r = -0.91$, $N = 6$, $p < 0.05$; 1981, $r = -0.71$, $N = 26$, $p < 0.05$; 1982, $r = -0.57$, $N = 12$, $p < 0.05$, Pearson. For males the values are: 1980, $r = -0.84$, $N = 11$, $p < 0.05$; 1981, $r = -0.70$, $N = 30$, $p < 0.05$; 1982, $r = -0.57$, $N = 29$, $p < 0.05$, Pearson. Thus, larger individuals grow by a smaller increment of their length than do smaller animals.

3.4.2 Discussion.

A number of workers have recorded weight change in newts between entering and leaving breeding sites. Harrison et al (1983) found female smooth and palmate newts to be significantly lighter on leaving a pond in mid-Wales, whilst male smooth newts were significantly heavier. Egg load in palmates was calculated to be 13% of body weight so egg loss alone did not account for the weight change in females of this species.

Verrell & Halliday (in press a), working on crested newts, found immigrant males and juveniles to be significantly lighter than emigrants; females did not show any significant change. They showed, however, that no such difference occurred in smooth newts.

Gill (1979) found that male *N. viridescens* gained a moderate amount of weight during the breeding season, but lost weight during autumn and winter. Females of this species behaved in the opposite manner. He also demonstrated that body weights of both sexes were density dependent by experimentally manipulating the size of the population in a number of ponds.

In order to compare the data from this study with that from the above work it is necessary to extrapolate a little since only aquatic individuals were measured at Milton Bryan, so data on weights on entry and exit to the site are unavailable. Having made this proviso my results agree reasonably with those of the other workers. The data on males would appear, at first, to be anomalous. However, from the recapture intervals given previously it is clear that animals are spending some time in the water after the last recaptures I have for them and in this time are probably feeding intensively and so gaining weight. Verrell & Halliday's data suggest that animals which stay in the water for long periods gain weight, whilst those which only remain for a short period tend to lose weight. This is consistent with my finding that individuals with short recapture intervals tend to lose more weight than those with longer periods between recaptures.

The reason for the loss of weight initially is not completely known but, probably arises from a combination of factors. Some animals may lose weight if they are unable to feed whilst in a trap, particularly if this is for 2/3 days. There may also be density dependent weight loss as in Gill's population. Principally, however, the energy costs of reproduction are likely to be considerable and this is likely to manifest itself in the condition of the animal. Verrell (unpublished data) has evidence of loss of mass in a number of organs and in fat bodies in sexually active males of the smooth newt. This may account for the extra weight loss in males which is not attributable to spermatophore deposition.

Harrison et al (1984) estimated the period spent in a breeding pond by smooth newts as 100 days for males and 97 days for females. Hagström (1979) found these dates to be highly variable from one location to another. At one pond animals were only present in the water for a few days, whilst at another they remained for several weeks. Predation pressure is suggested as an explanation for this. Verrell & Halliday (in press b) have found male and female smooth newts to spend approximately 150 days in the water at a pond in Buckinghamshire, with crested newts at the same location slightly less time, around 90 days (Verrell & Halliday, in press a). Griffiths (1984) found female smooth newts to have shorter mean recapture intervals than males, concluding that females were spending less time in the water than were males. He calculated these values from the first and last captures of individual aquatic animals in the way I have done in this study.

Clearly, the time spent in a breeding pond by these species is highly variable and probably dependent on a number of factors, such as climate, predation, and food supply. This is discussed further in chapter 4.

The results of the study of annual growth increments in adult crested newts are in close agreement with those from other studies. Semlitsch (1983) found a slowing of growth rate in Ambystoma tigrinum on attainment of sexual maturity, as did Sayler (1966) for *Plethodon cinereus*. Glandt (1981) found that growth in *T. cristatus* occurred after the completion of reproduction for that season and upon return to the land. Certainly, no individuals at Milton Bryan were recorded as increasing in length whilst in the pond, although small increments may have been undetectable since measurements were not made to a high degree of accuracy. This periodicity of growth is evident in growth rings where it appears in zones of varying thickness (Hagström 1977, Dolmen 1982).

I have shown that growth rate is not size-specific; two individuals of, say, 70mm SVL do not necessarily attain the same length after a year's growth. This fact confirms the view that body length is a poor indicator of age in urodeles. Hagström (1975) and Glandt (1981) have also demonstrated this. Tilley (1974) found differential growth rates in populations of the terrestrial salamander *Desmognathus ochrophaeus* from different habitats. This leads to size differences at maturity which has implications for the fecundity of individuals, a fact which is discussed at greater length in the final chapter.

3.5 Analysis of testes and ovaries from preserved animals.

During 1981 a number of animals of both species were collected and killed in order to investigate the male and female reproductive organs and to analyse stomach contents. Individuals of various sizes were taken and at different times of the season so as to obtain a wide spread of data and investigate any changes in the state of the ovaries, testes and stomach contents with time. I attempted to keep the total number of animals killed to a minimum, particularly in the case of females, so as not to deplete the breeding population overmuch. Interestingly, there is evidence that removal of adults from a breeding pond may enhance larval survival in the pond (Snell, 1982). In this instance, the removal of newts from three garden ponds lead to an increase in the numbers of juveniles appearing in subsequent years. This may have arisen from a lowering of predation pressure and/or an increase in the availability of food for larvae. The phenomenon was observed for all three British species found in the ponds.

3.5.1 Testes analysis for T. cristatus.

Male crested newts were dissected and a number of measurements made on each, namely;body weight, SVL, crest height, testis weight and number of lobes per testis. These measures were taken in order to investigate the relationships between body size and the reproductive organs, and how these

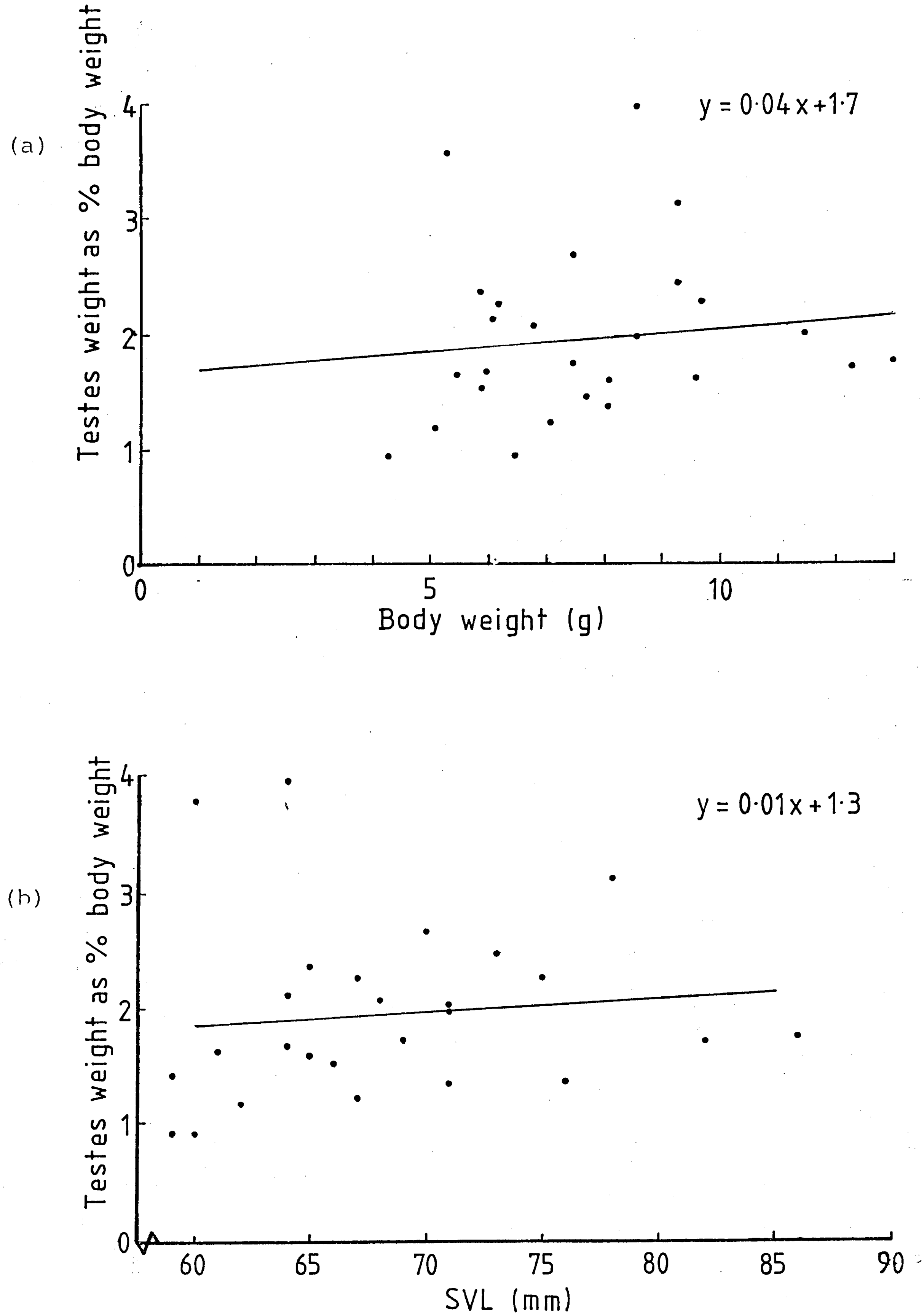


Figure 39: The relationships between body weight and normalized testes weight, and SVL and normalized testes weight in male *T. cristatus* at Milton Bryan.

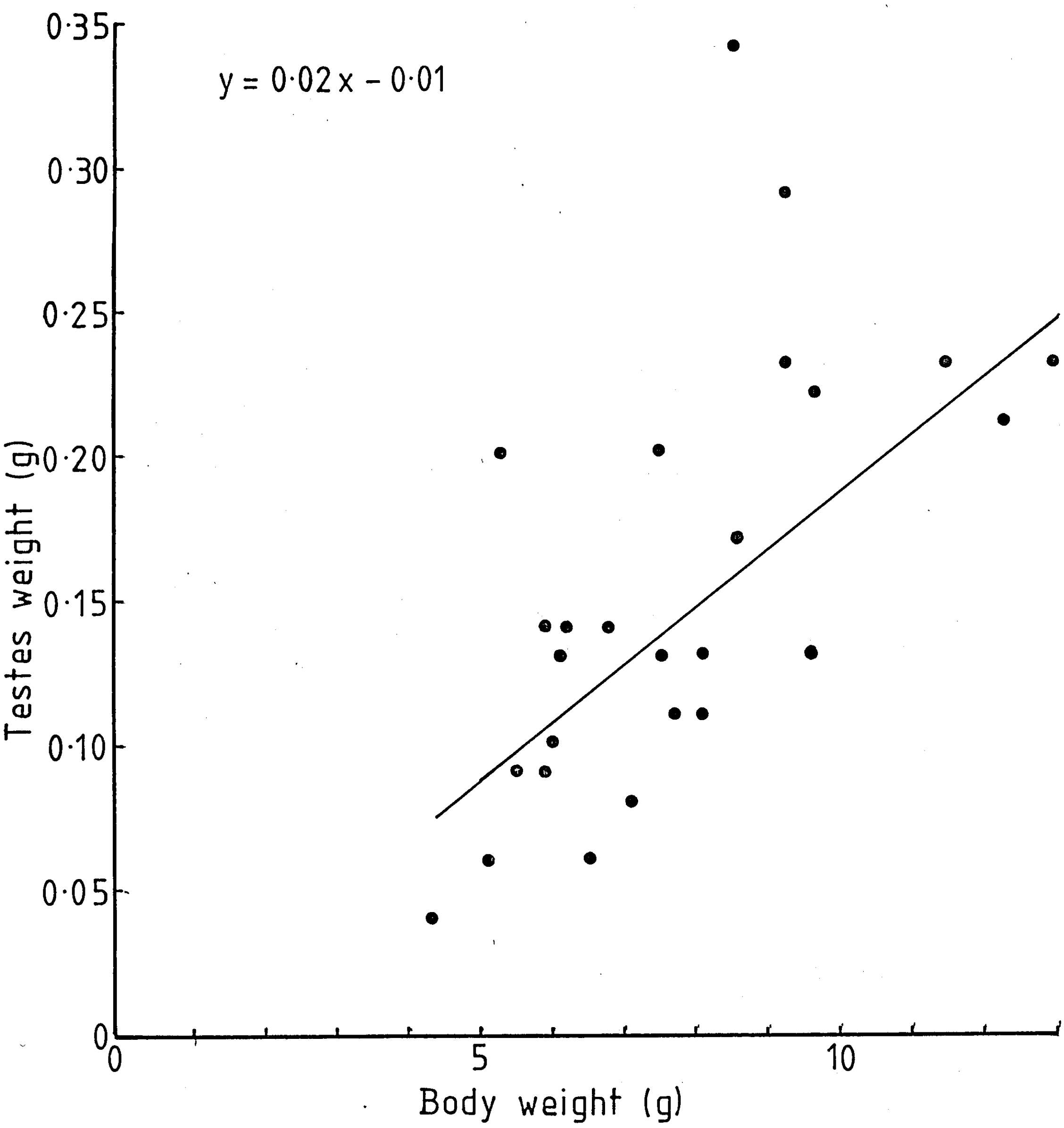


Figure 40: The relationship between body weight and non-normalized testes weight in male T. cristatus at Milton Bryan.

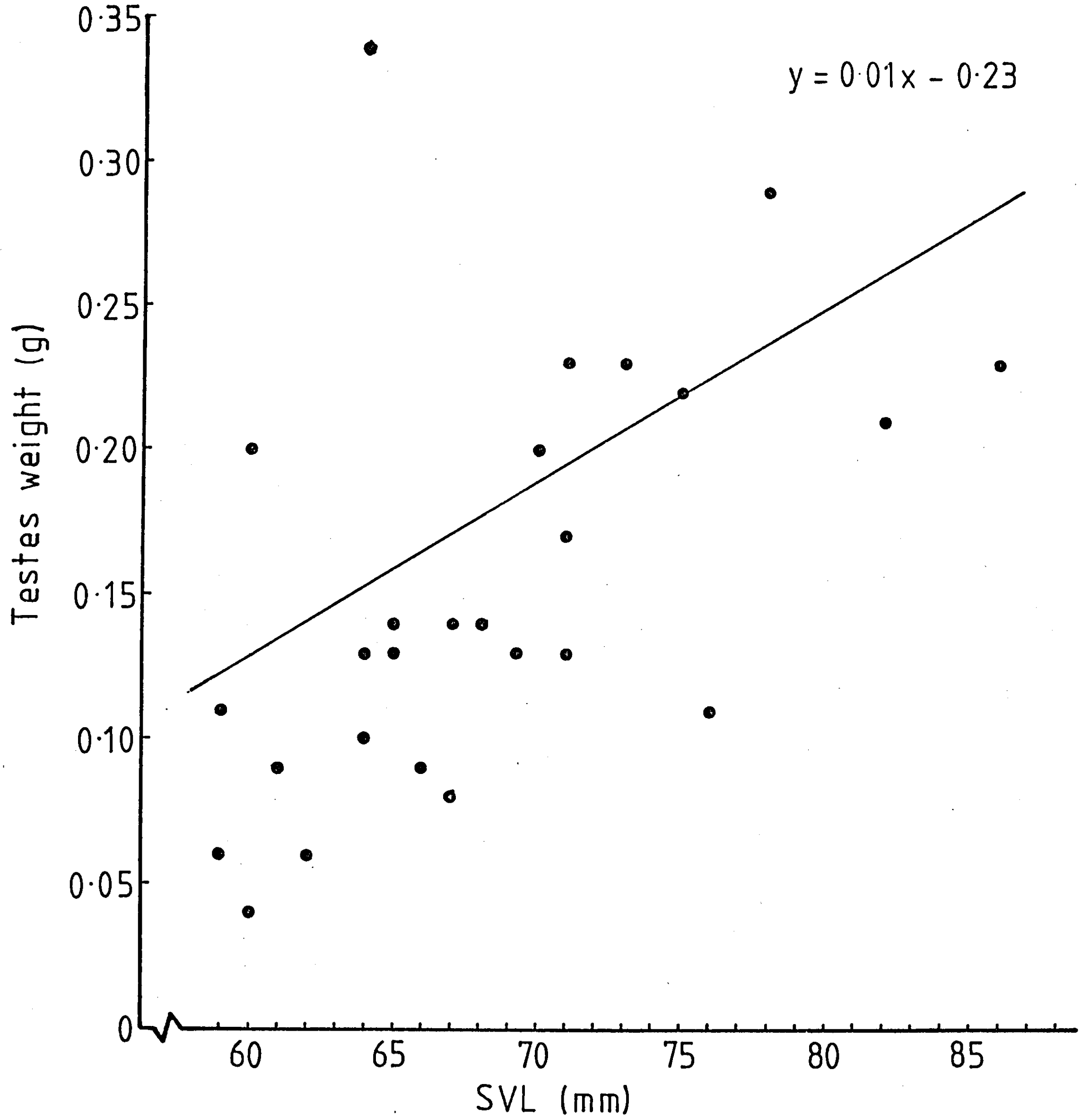


Figure 41: The relationship between SVL and non-normalized testes weight in male T. cristatus at Milton Bryan.

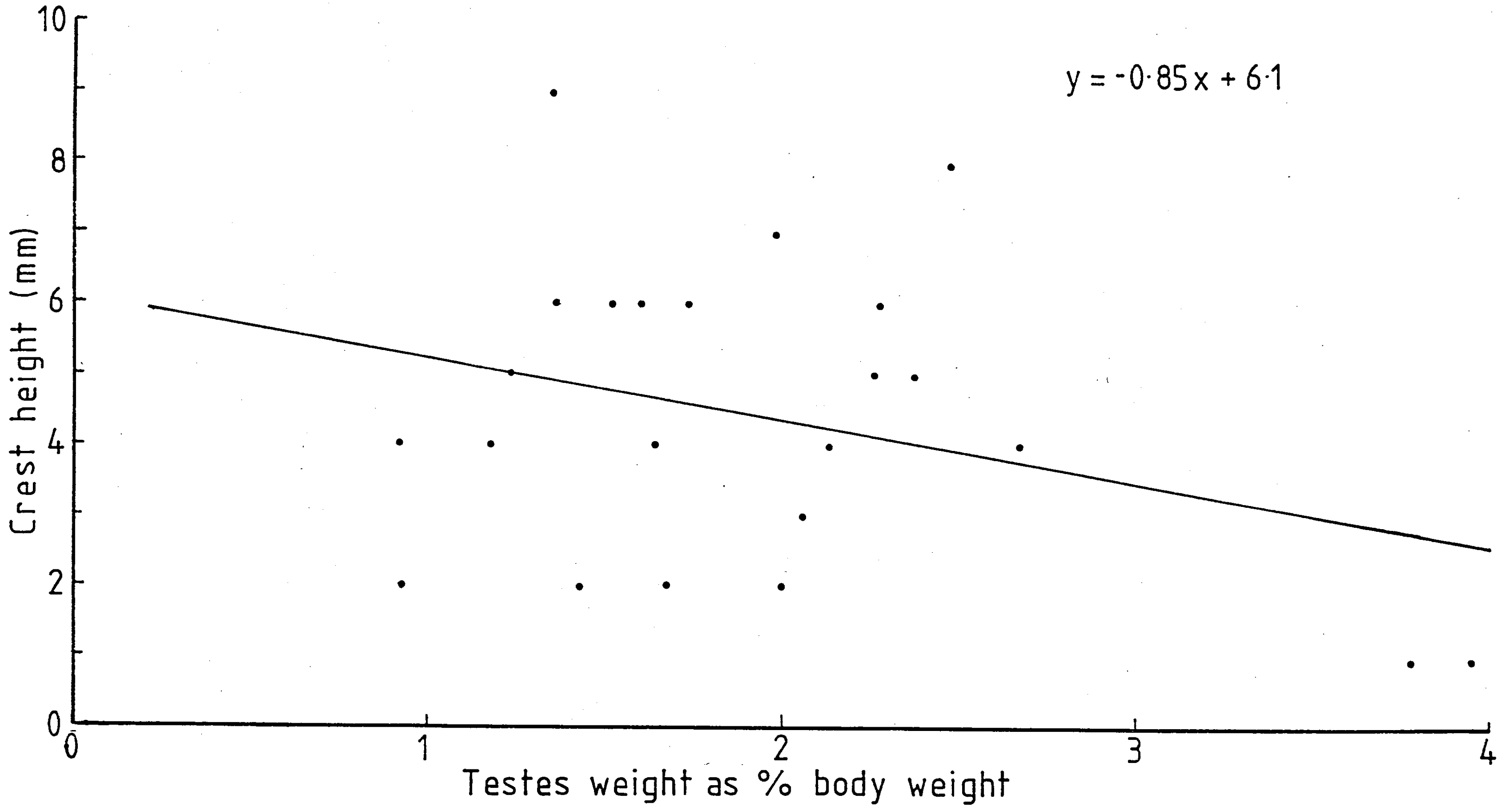


Figure 42: The relationship between normalized testes weight and crest height in male T. cristatus at Milton Bryan.

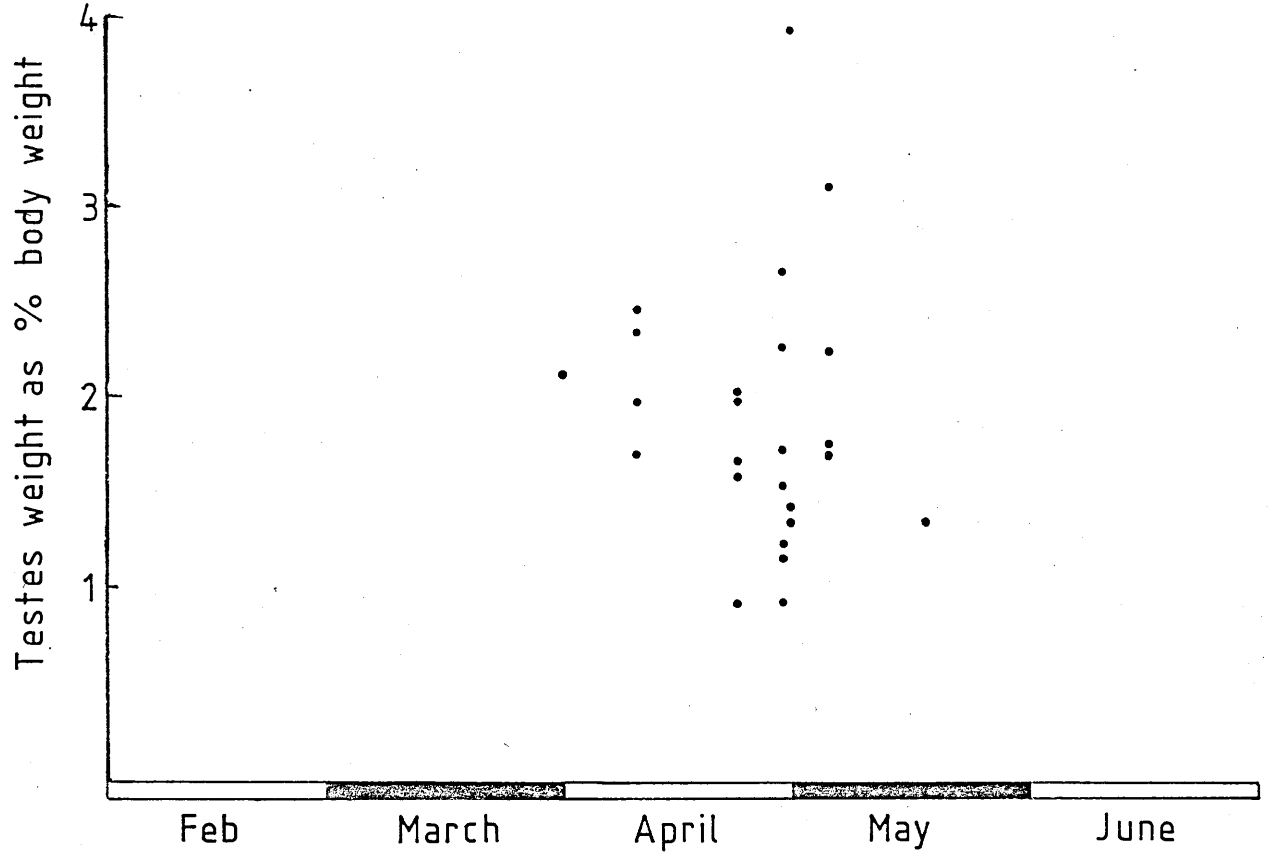


Figure 43: The relationship between normalized testes weight and date of capture in male _T. cristatus_ at Milton Bryan.

Better as tables?

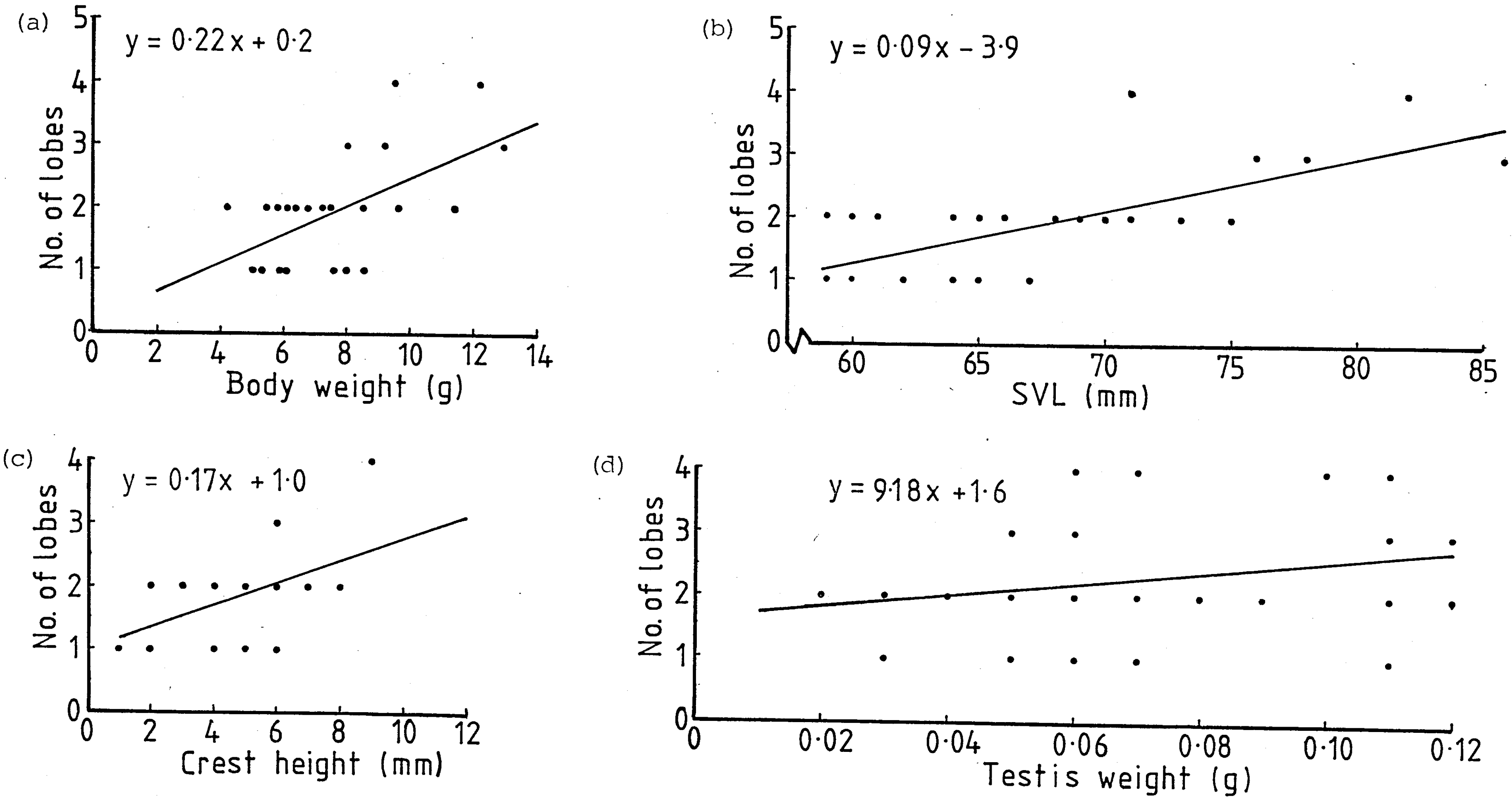


Figure 44: The relationships between the number of lobes per testis and (a) body weight, (b) SVL, (c) crest height and (d) testis weight in male *T. cristatus* at Milton Bryan.

may vary through the breeding season. Lobe number was recorded because this has been reported as a criterion for the ageing of some species of urodele (Organ 1961, Collins 1964, Spight 1967, Joly 1971, Sever 1974, Lofts 1976 and Dolmen 1982).

Figures 39 to 44 show the results of these analyses. There are non-significant correlations between testes weight and SVL or testes weight and body weight(r = 0.09 & 0.11 respectively, N = 26, $p > 0.05$, Pearson product moment correlation, Figure 39). In each case testes weight is the combined weight of both testes in an individual, and is expressed as a percentage of body weight . This procedure is the most common means of accounting for the effects of differential body size on gonad size. The ratio obtained is referred to as the Gonosomatic Index or GSI (DeVlaming et al, 1982). They refer data expressed in this way as 'normalized' and this is the term used in this study. Neither is there a significant correlation between testes weight and crest height (as measured on date of capture), (r = 0.30, N = 23, $p > 0.05$, Pearson). This latter relationship was investigated to see if it was possible to determine the sexual state of males indirectly through crest size.

If testes weights are not normalized, then significant correlations are obtained between this measure and both body weight and SVL (r = 0.64 & 0.54 respectively, N = 26, $p < 0.05$, Pearson).

Testes weights were also plotted against the date of capture (Figure 43). This shows a great deal of scatter and a non-significant correlation ($r = -0.29$, $N = 26$, $p > 0.05$, Pearson).

The number of lobes was noted for each testis and subsequently plotted against various measures, shown in Figure 44. These data may also be displayed in table form, as shown in Table 15, but the results are open to the same interpretation.

NUMBER OF LOBES	SVL (mm)	BODY WEIGHT (g)	TESTIS WEIGHT (g)	CREST HEIGHT (mm)
1	63.5 (2.8)	6.8 (1.2)	0.08 (0.04)	3.5 (1.8)
2	67.1 (4.9)	7.3 (1.9)	0.07 (0.03)	4.5 (1.9)
3	80.0 (4.3)	10.0 (2.1)	0.10 (0.04)	6.0
4	76.5 (5.5)	10.8 (1.3)	0.08 (0.02)	9.0

Table 15: Comparison of number of lobes per testis with mean SVL, mean body weight, mean testis weight and mean crest height for male _T. cristatus_ at Milton Bryan. Figures in brackets denote standard deviations for each value.

The correlations between lobe number and body weight and lobe number and SVL are significant ($r = 0.57$ & 0.69 respectively, $N = 26$, $p < 0.05$, Pearson), whilst that between lobe number and crest height is approaching significance. There is no significant correlation, however, with the weight of individual testes ($r = 0.29$, $N = 26$, $p > 0.05$, Pearson).

It was also found that a pair of testes does not necessarily consist of equally sized units. In 11 of the pairs looked at there was a difference of 0.01g (about 13% of average testis weight) between each testis and in three other cases differences of 0.02, 0.03 and 0.04. There was never any difference in the number of lobes in each testis of a pair, however.

3.5.2 Ovary analysis for T. cristatus.

Nineteen female crested newts were weighed, measured and dissected. The ovaries were removed and weighed. Following this the number of yolked oocytes per ovary was counted and a mean oocyte diameter determined for each individual. Diameters were measured using a scaled grid in the eyepiece of a microscope and 50 oocytes per ovary were measured in order to determine each mean. The relationships between the various measures are shown in Figures 45 to 55.

Ovary weight correlates non-significantly with both SVL and body weight ($r = 0.32$ & 0.13 respectively, $N = 19$, $p > 0.05$, Pearson), ovary weight being expressed as a percentage of body weight. Once again, however, if the non-normalized ovary weights are plotted then significant results are obtained ($r = 0.68$ with body weight and $r = 0.66$ with SVL, $p < 0.05$, Pearson.) The ovaries were found to comprise between 4.2% and 13.2% of body weight, with a mean of 8.4%.

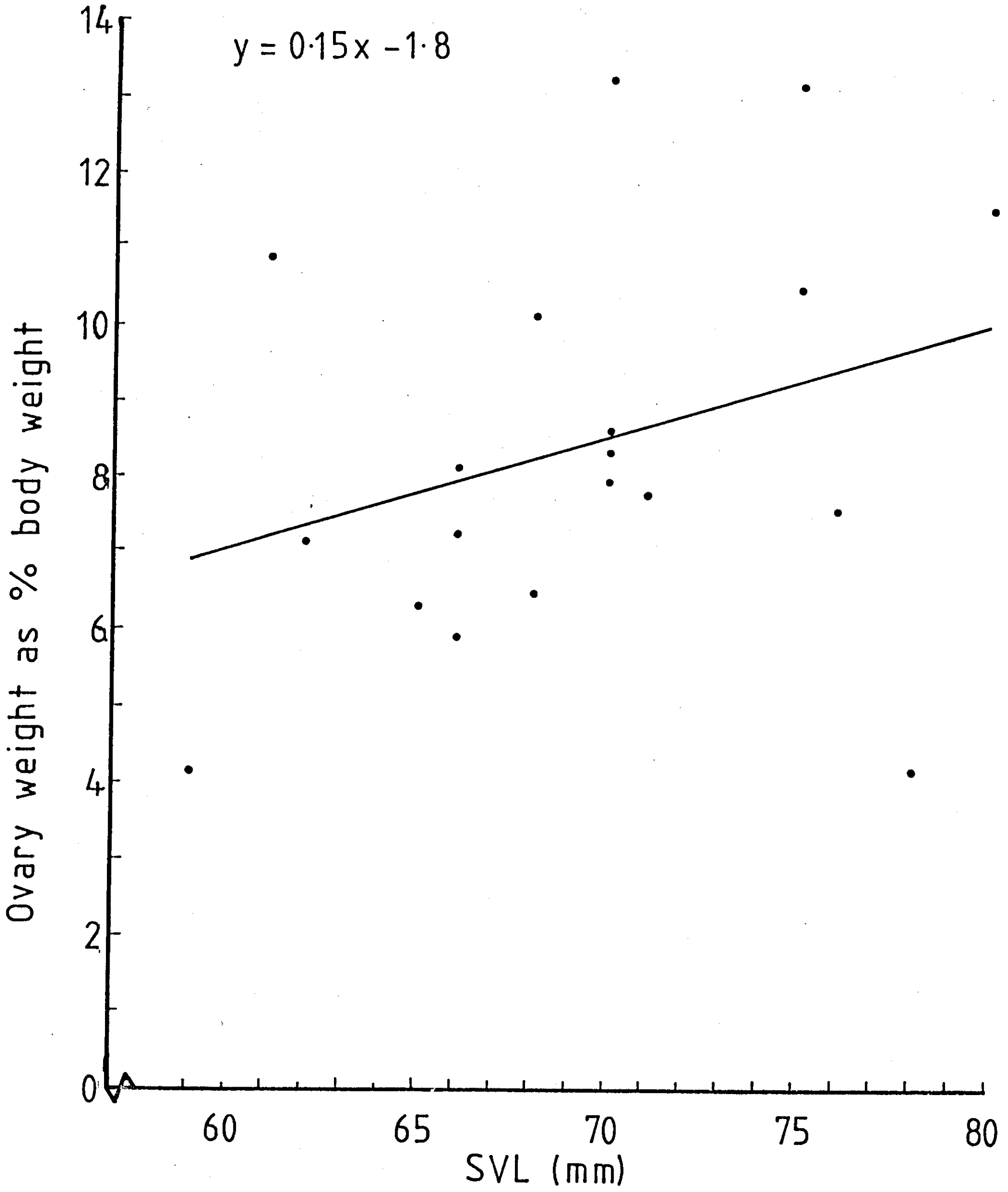


Figure 45: The relationship between normalized ovary weight and SVL in female T. cristatus at Milton Bryan.

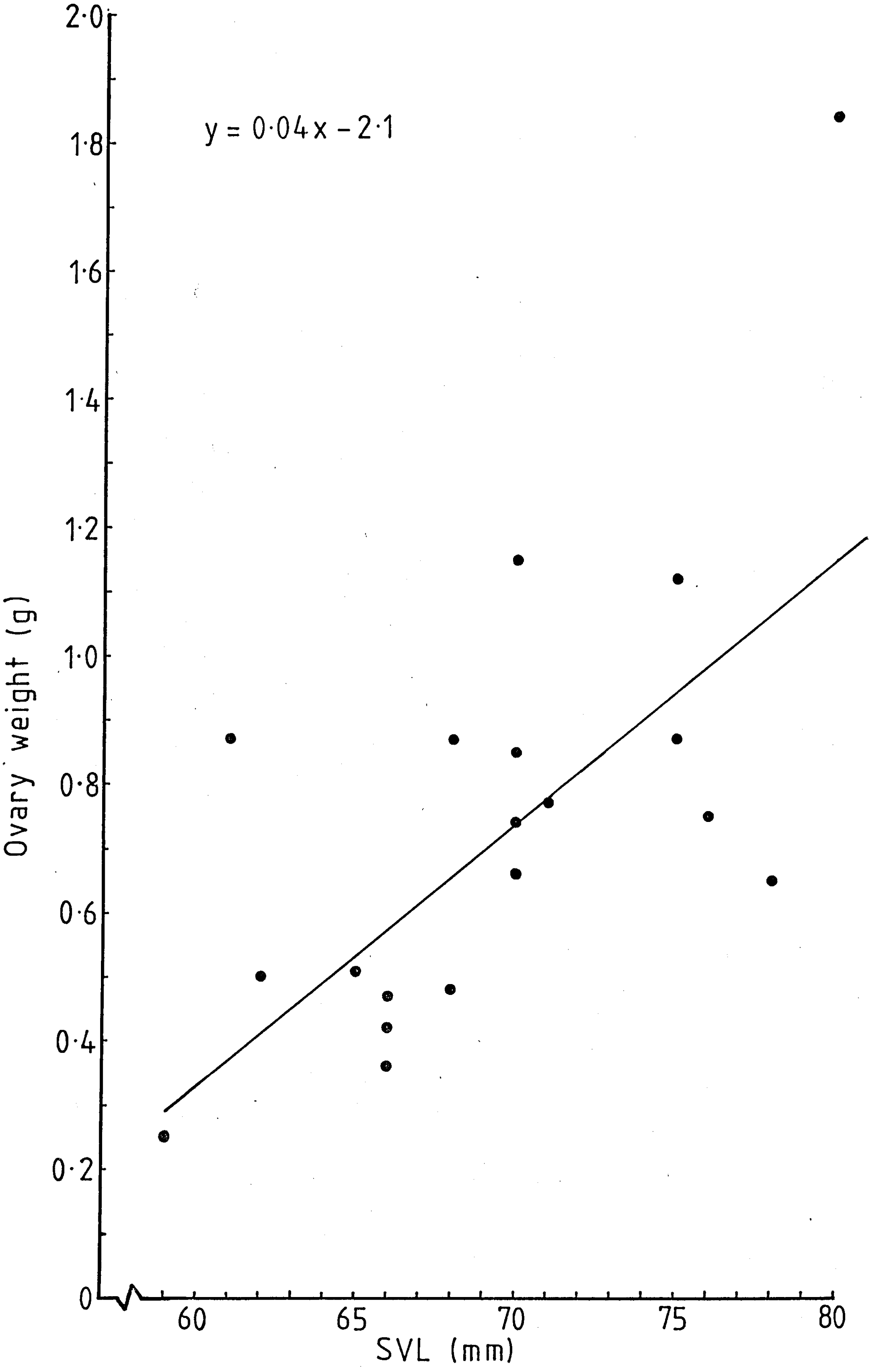


Figure 46: The relationship between non-normalized ovary weight and SVL in female T. cristatus at Milton Bryan.

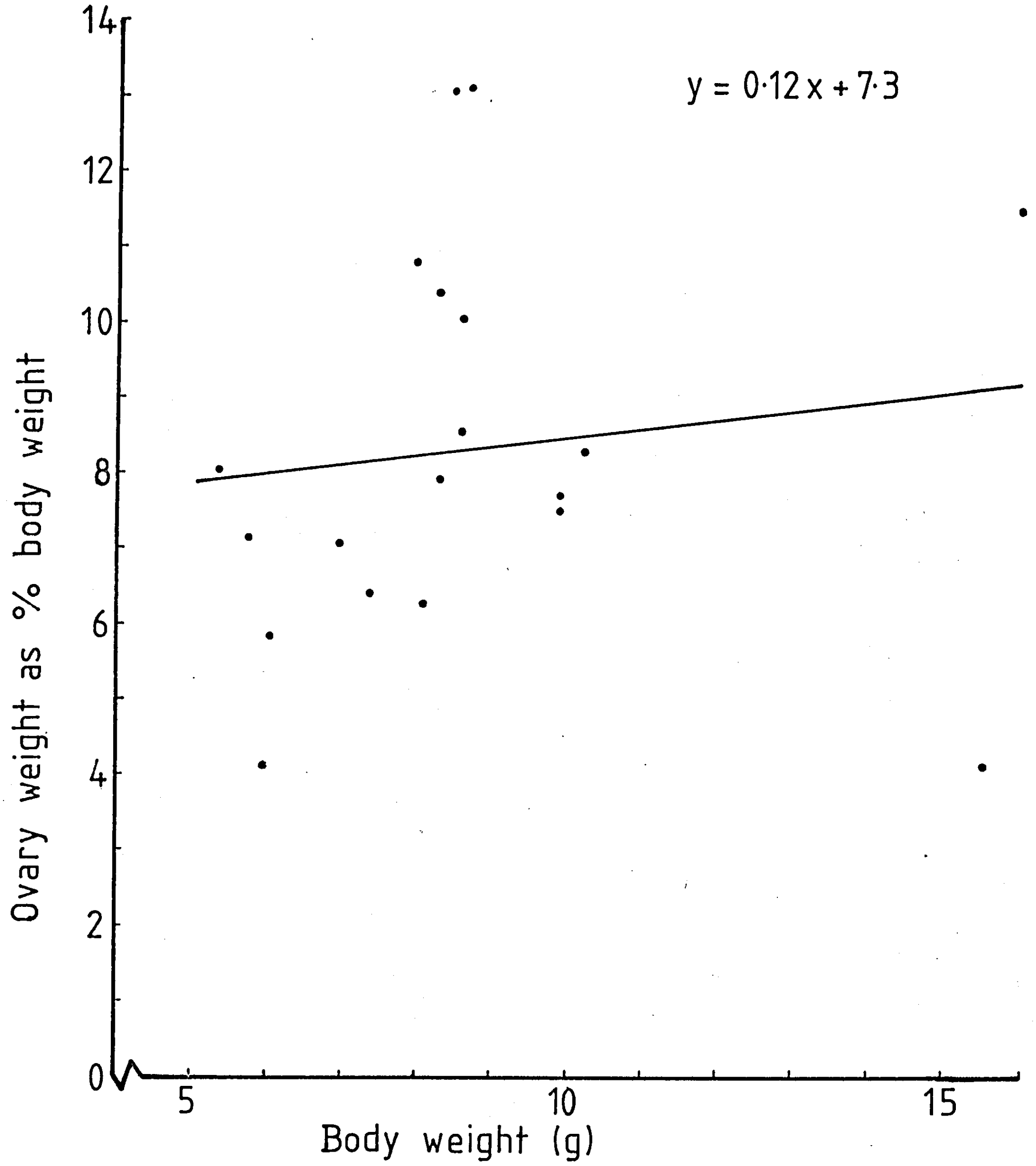


Figure 47: The relationship between normalized ovary weight and body weight in female T. cristatus at Milton Bryan.

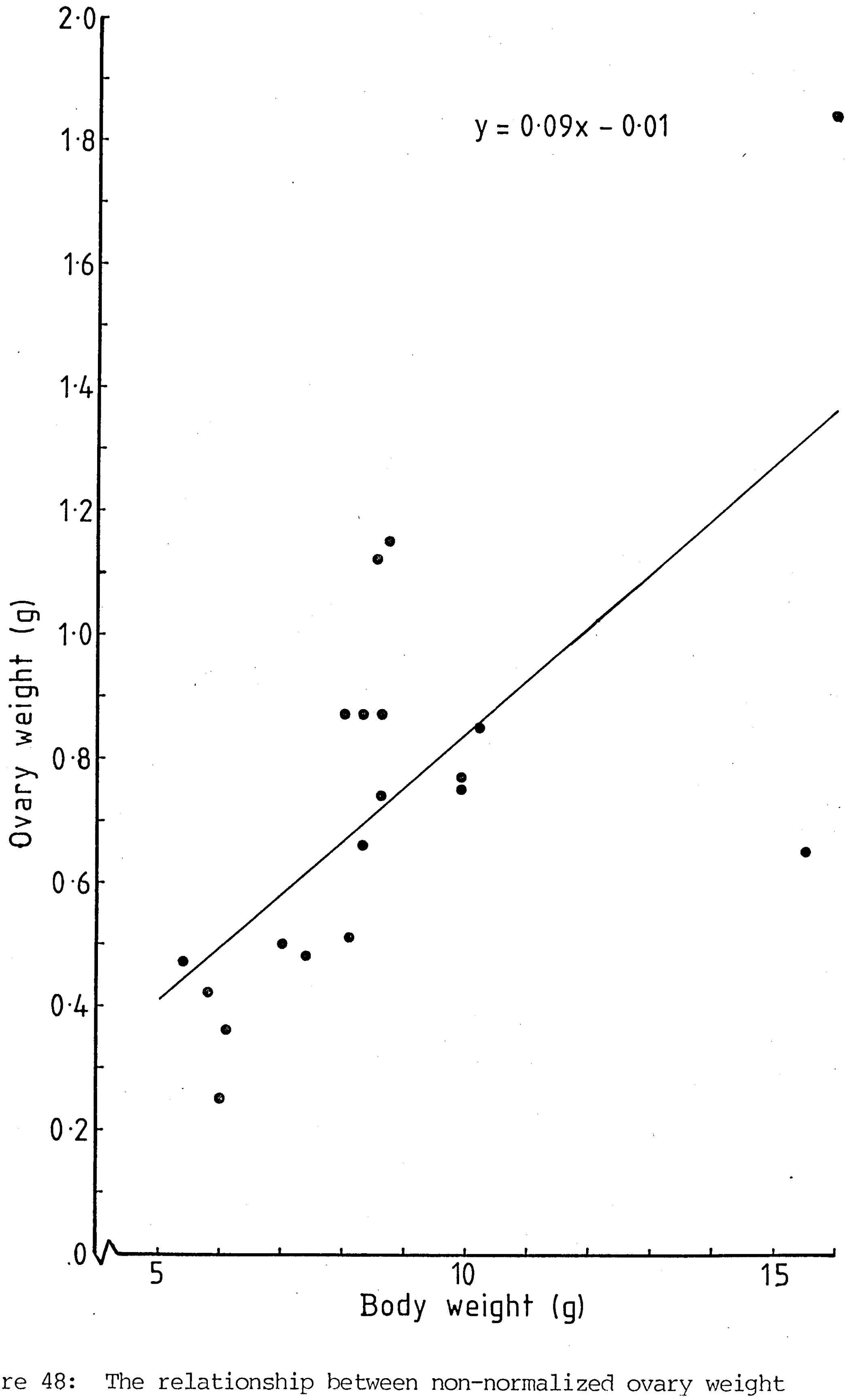


Figure 48: The relationship between non-normalized ovary weight and body weight in female T. cristatus at Milton Bryan.

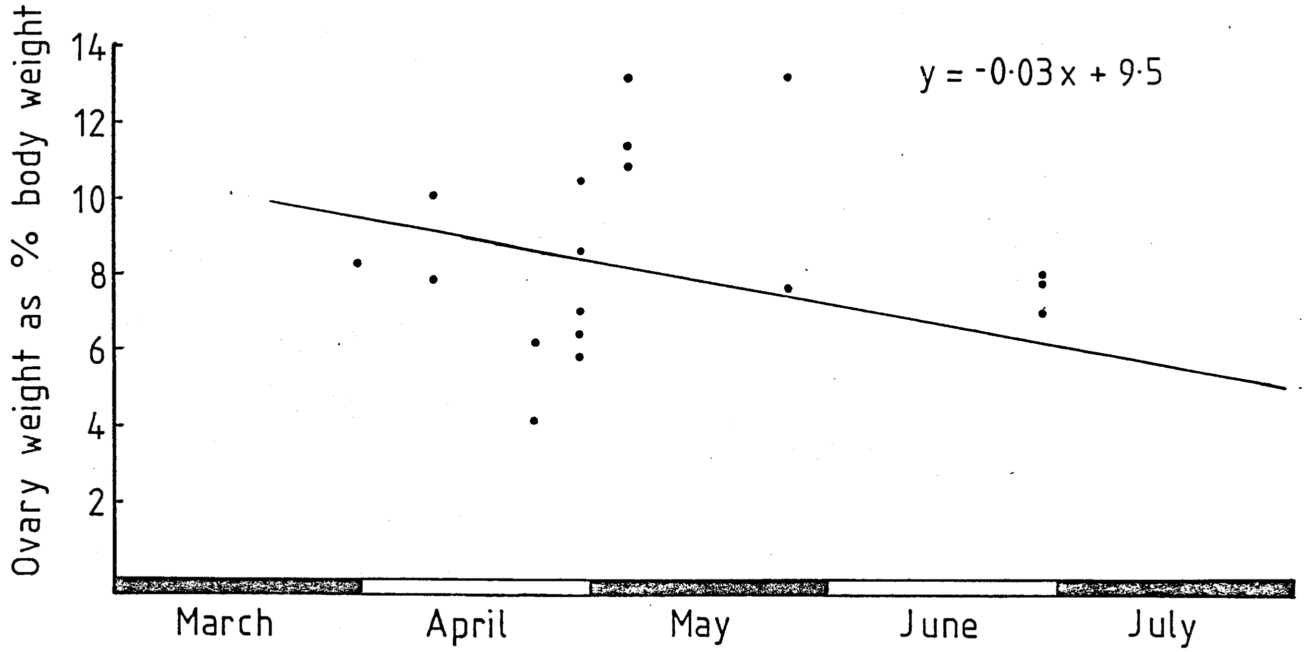


Figure 49: The relationship between normalized ovary weight and date of capture in female _T. cristatus_ at Milton Bryan.

The relationship between ovary weight and the date of capture is shown in Figure 49. Although the correlation here is non-significant ($r = -0.21$, $N = 19$, $p > 0.05$, Pearson), there is a negative trend which suggests that ovary weight decreases over the breeding season. This is consistent with what one would expect from egg deposition. However, it is not reflected in Figure 50 which shows the number of oocytes per individual plotted against the date of capture. This is very close to a random scatter ($r = -0.01$, $N = 19$, $p > 0.05$, Pearson). It is possible that this latter effect is due to females laying their largest oocytes only, in which case one would expect to find individuals with some yolked oocytes remaining at the end of the season. This is discussed further in chapter 4.

Six of the females were found to contain eggs in their oviducts i.e. they were ovulating. These animals were caught on April 10th & 29th, May 29th and June 29th. Verrell (in press) has found female smooth newts ovulating at any time from early April to June. This was for dissected specimens. Data from belly-pressing live animals in the field shows ovulation occurring from May to early July (see Verrell, 1984, for belly-pressing technique).

There was found to be a significant relationship between the number of oocytes in an ovary and the weight of that ovary ($r = 0.84$, $N = 19$, $p < 0.05$, Pearson; see Figure 51).

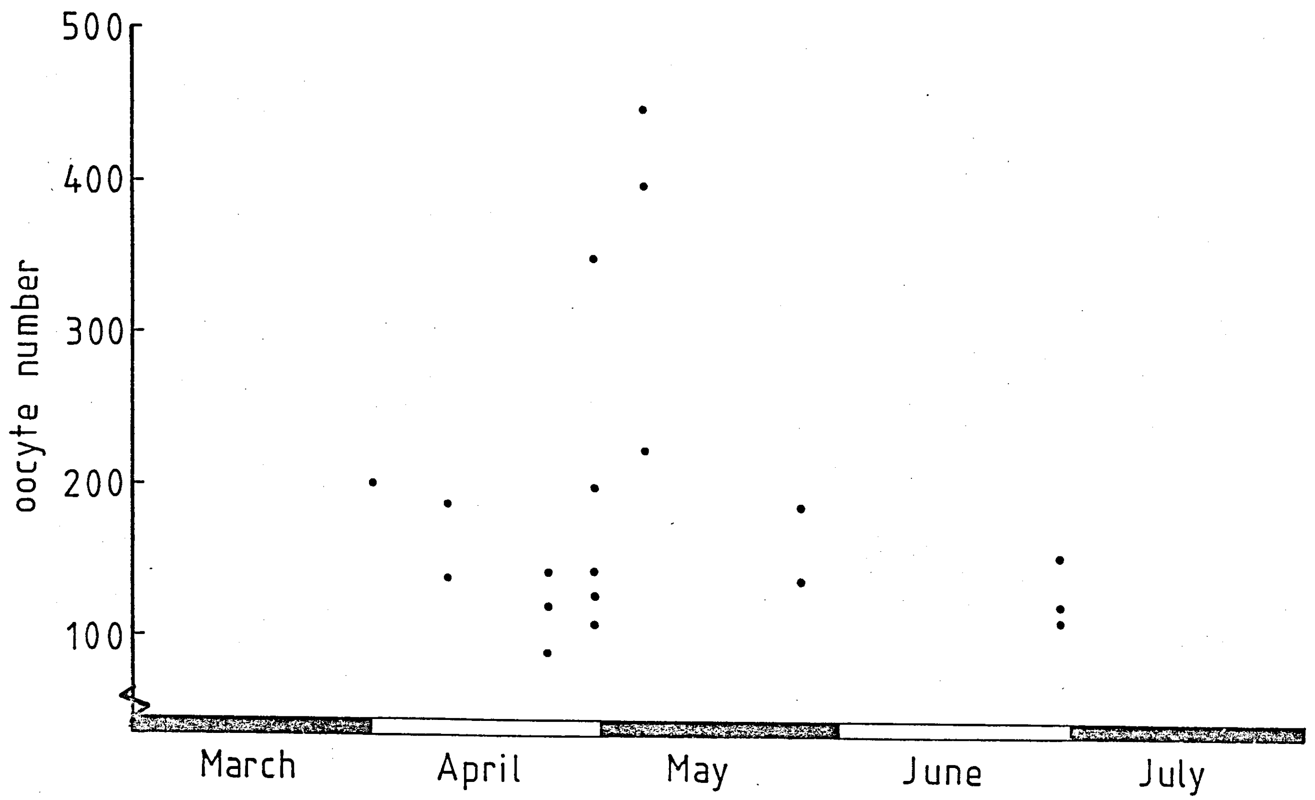


Figure 50: The relationship between the number of yolked oocytes in the ovaries of female <u>T. cristatus</u> and the date of capture of females at Milton Bryan.

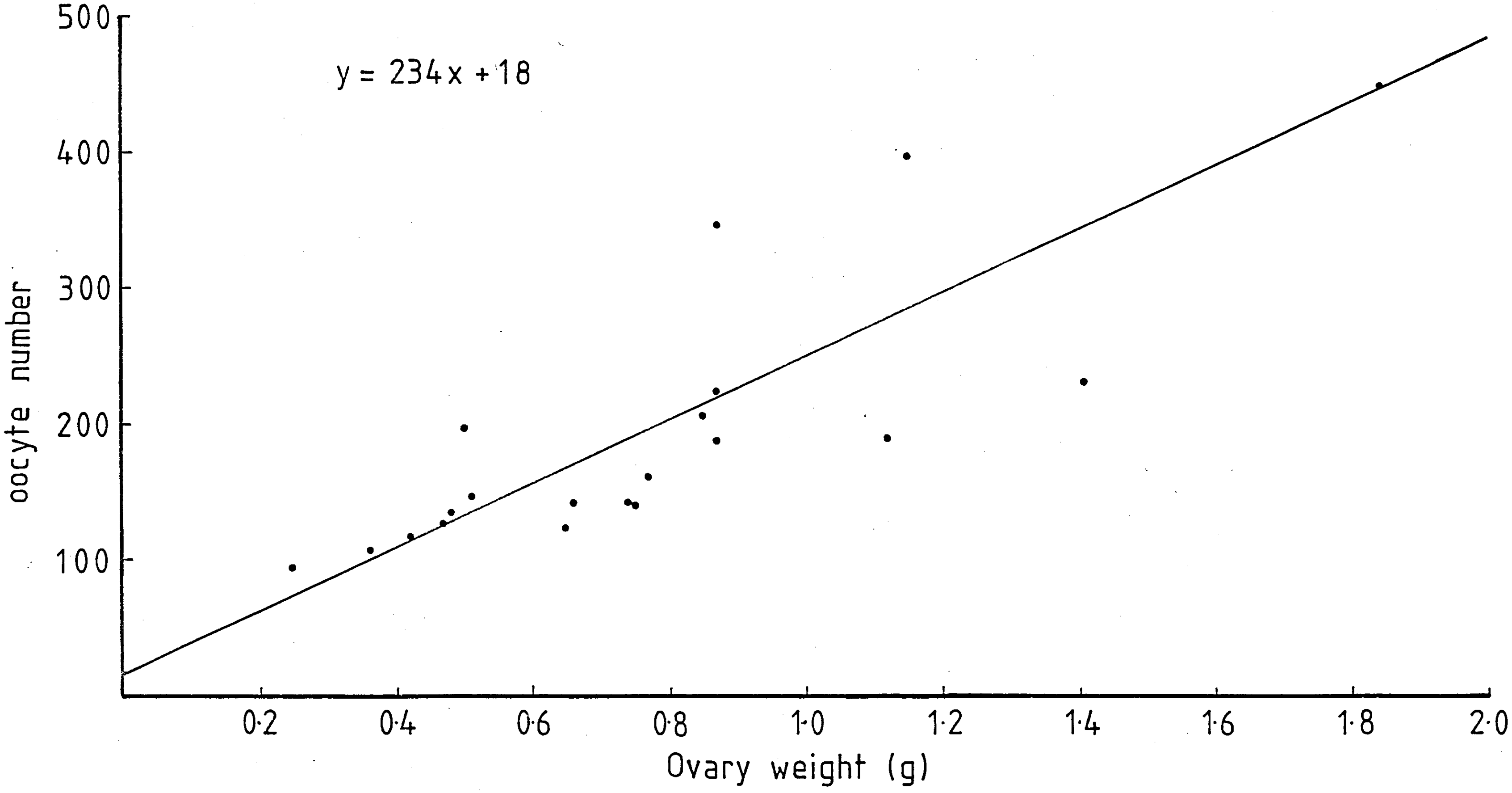


Figure 51: The relationship between the number of yolked oocytes per female and ovary weight in female _T. cristatus_ at Milton Bryan.

Furthermore, the heavier (i.e. larger) ovaries also contained larger oocytes on average than the smaller ones ($r = 0.64$, $N = 19$, $p < 0.05$, Pearson; see Figure 52). A similar result is obtained from plotting oocyte number against total body weight and SVL (see Figures 53 and 54). Significant results are gained for each ($r = 0.67$ & 0.65 respectively, $p < 0.05$, Pearson). Finally, there does not appear to be any relationship between the mean size of oocytes and the date of capture of an individual, as shown in Figure 55.

As with the testes there were found to be differences in the weights of the ovaries in some individuals (18 of those studied). In all cases bar two there were differences in the numbers of oocytes in each pair of ovaries which would account for these. There is no evidence however, that oocytes from one ovary are being laid first or whether alternation occurs.

3.5.3 Testes analysis for T. vulgaris.

Nineteen male smooth newts were measured and dissected. They were treated in the same way as the crested newts with the exception that crest height was not analysed. This was because measuring to the nearest mm. did not produce much variation and I did not feel justified in measuring to any greater accuracy. The relationships between these variables are shown in Figures 56 to 58.

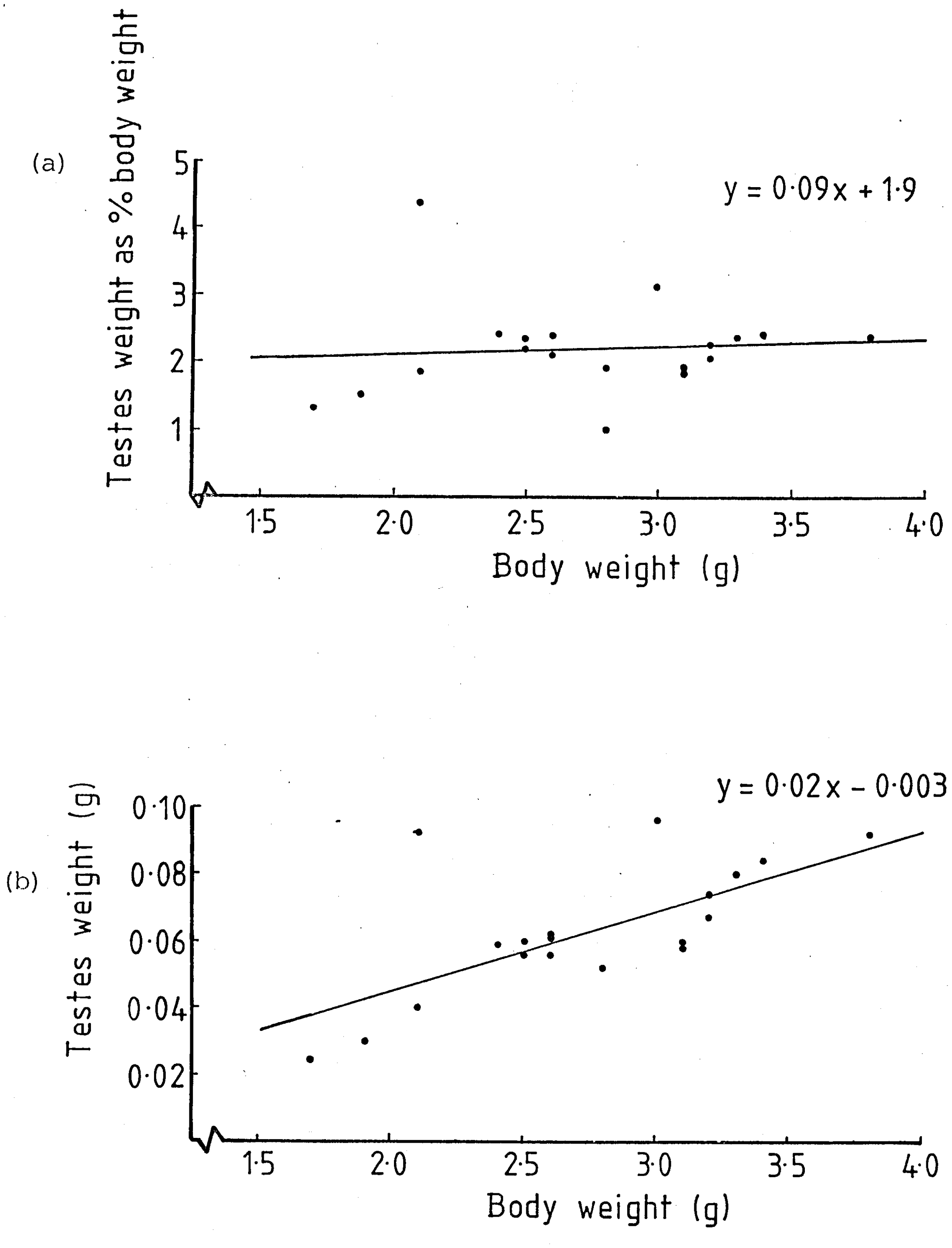


Figure 56: The relationships between (a) normalized testes weight and body weight and (b) non-normalized testes weight and body weight in male T. vulgaris at Milton Bryan.

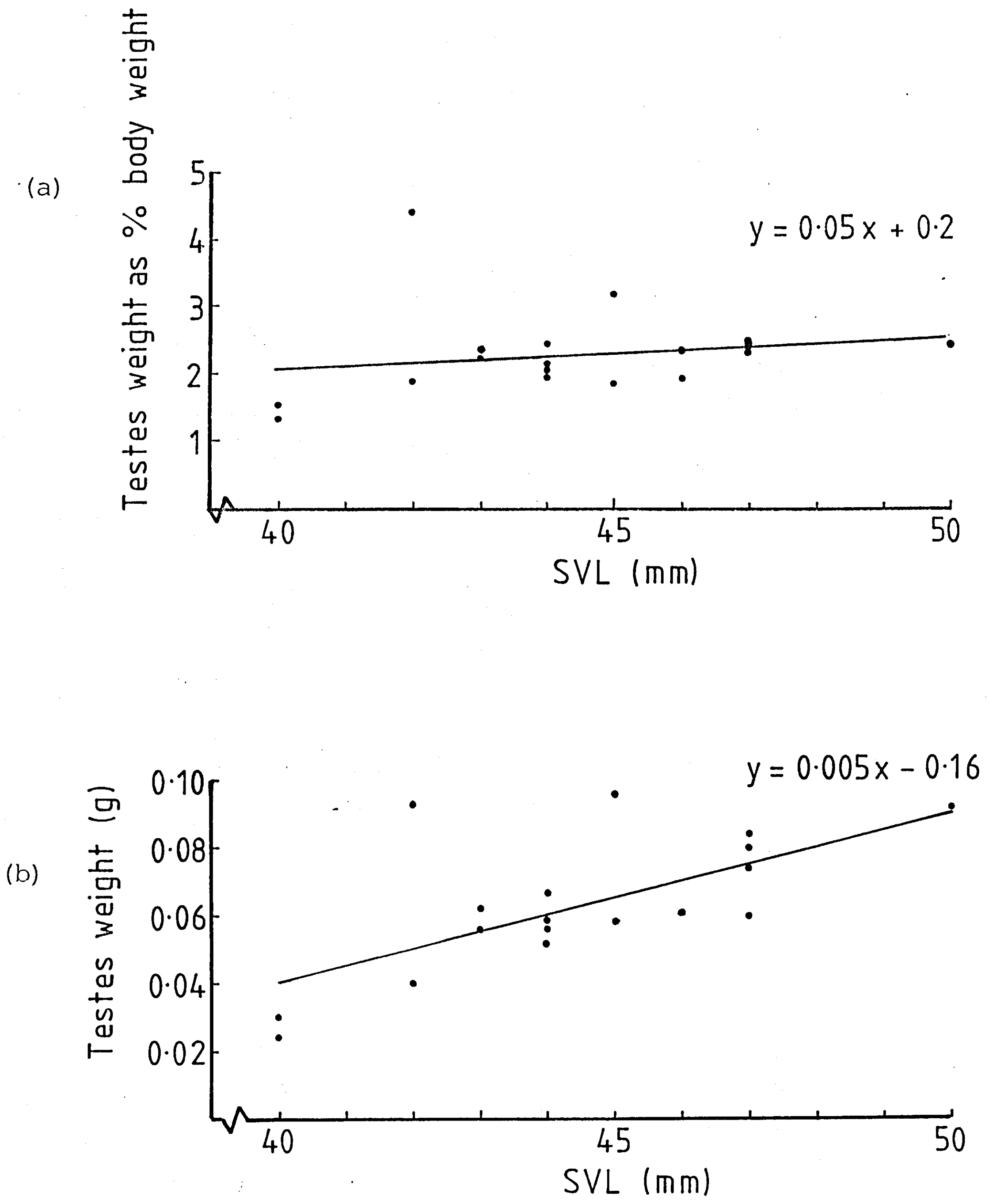


Figure 57: The relationships between (a) normalized testes weight and SVL and (b) non-normalized testes weight and SVL in male *T. vulgaris* at Milton Bryan.

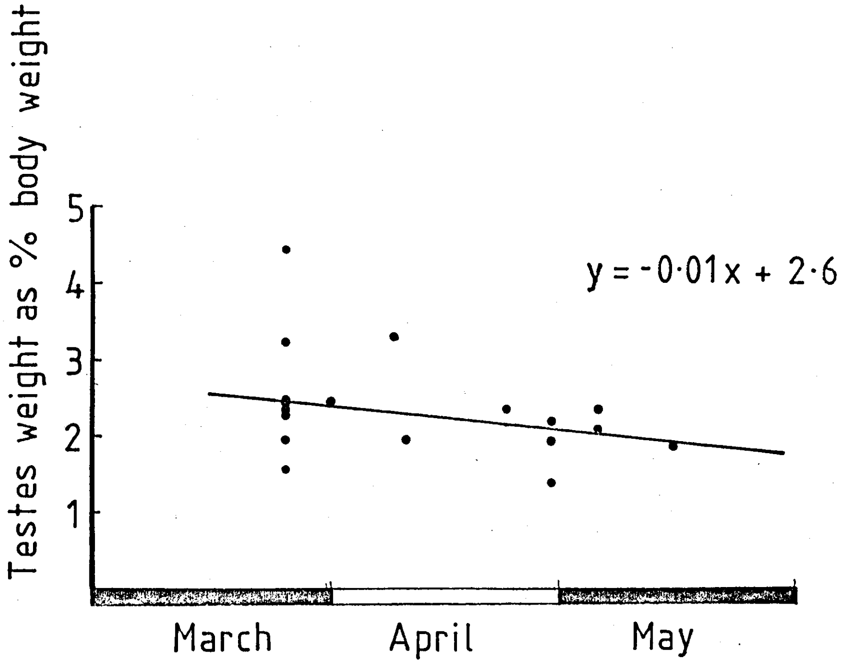


Figure 58: The relationship between normalized testes weight and the date of capture for male T. vulgaris at Milton Bryan.

These results are very similar to those obtained for the crested newt. There are non-significant correlations between normalized testes weight and SVL and body weight($r = 0.07$ & 0.17, $N = 19$ respectively, $p > 0.05$, Pearson). Again, if non-normalized data are used for these correlations then significant results are obtained ($r = 0.68$ & 0.66 respectively, $p < 0.05$, Pearson). The correlations between testes weight and date of capture and testis weight and lobe number are non-significant ($r = -0.38$ & 0.42 respectively, $p > 0.05$, Pearson).

The majority of the animals dissected had paired testes of equal weight. Only one pair showed a difference, this being one of 0.01g

3.5.4 Ovary analysis for T. vulgaris.

Very few female smooth newts were captured during 1981 so in order to avoid over-depletion of the population only 5 were killed for dissection. Therefore, little confidence can be put in the results that follow. Again, these animals were treated in the same way as the female crested newts. The results are shown in Figures 59 to 61. Non-significant correlations were obtained for normalized ovary weights plotted against body weight and SVL ($r = 0.48$, & 0.51 respectively, $N = 4$, $p > 0.05$, Pearson), but non-normalized data produced significant results ($r = 0.98$ for both measures,

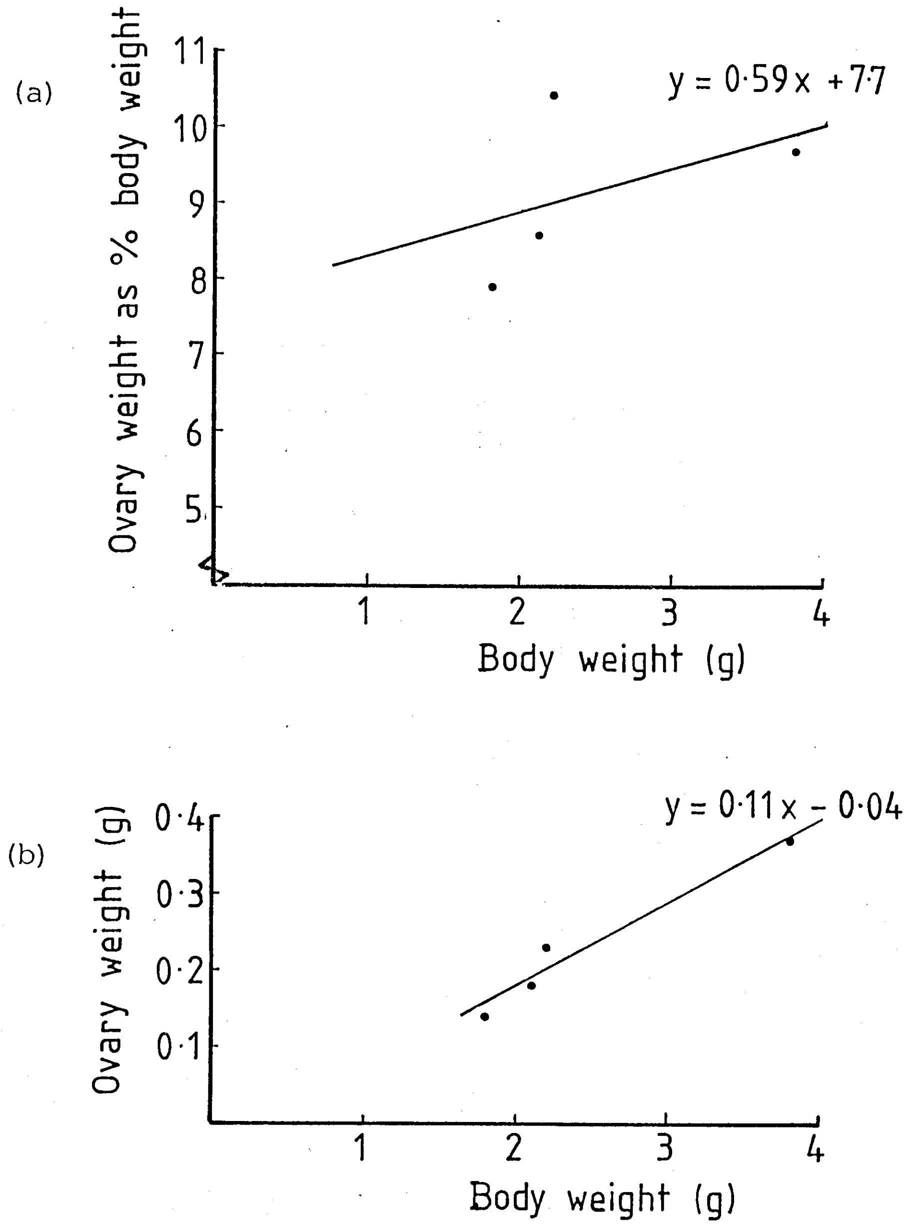


Figure 59: The relationships between (a) normalized ovary weight and body weight and (b) non-normalized ovary weight and body weight in female T. vulgaris at Milton Bryan.

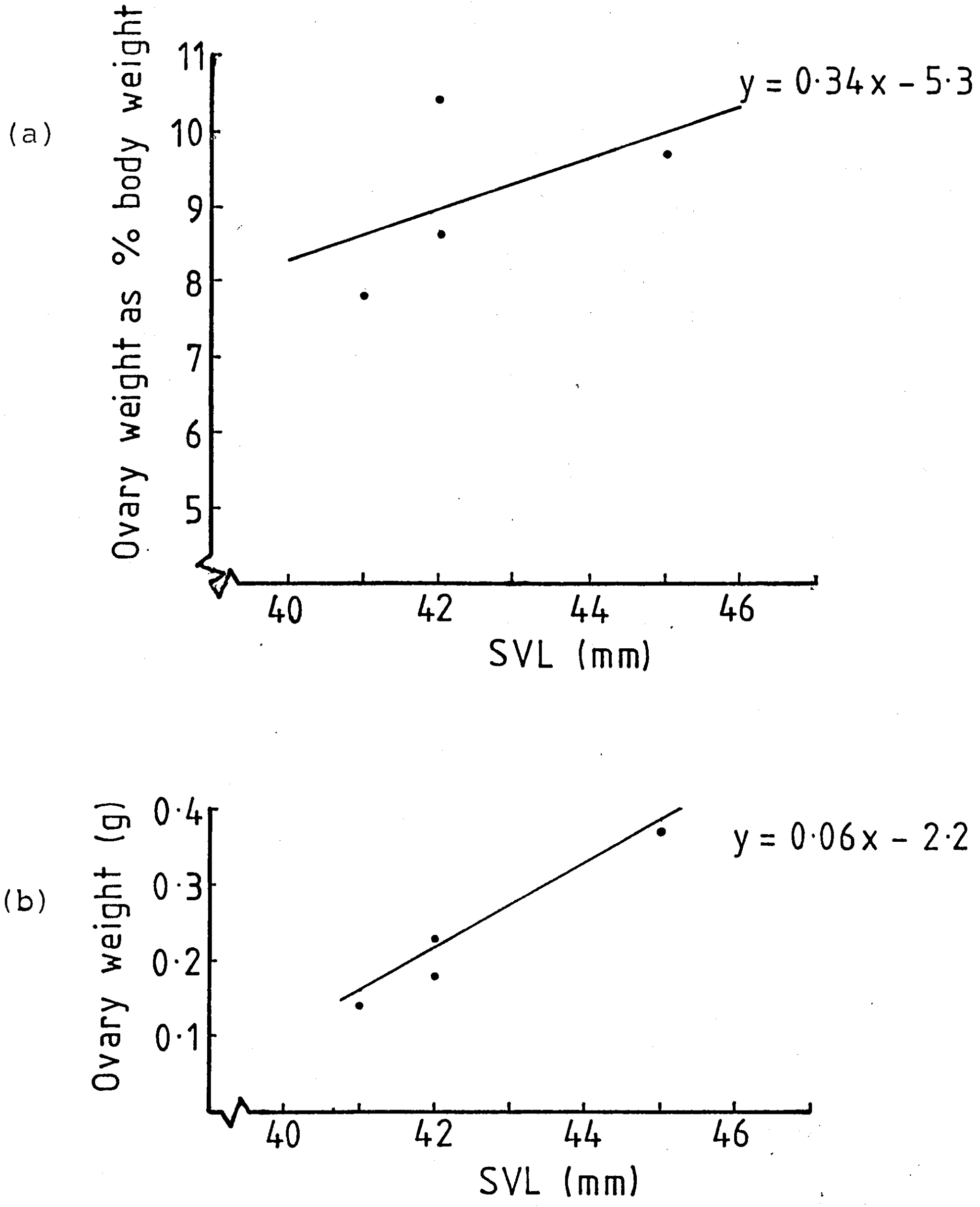


Figure 60: The relationships between (a) normalized ovary weight and (b) non-normalized ovary weight in female <u>T. vulgaris</u> at Milton Bryan.

$N = 4$, $p < 0.05$, Pearson).

The ovaries were found to comprise between 7.8% and 10.4% of body weight, with an average of 9.1%, a value close to that for the crested newt. Out of the four pairs of ovaries two were found to contain ovaries of unequal weight; this was due to differences in the number of oocytes.

3.5.5 Discussion.

There are few studies available in the literature which are directly comparable with the results of the testes analysis presented here for *T. cristatus* and *T. vulgaris*. M^{c}Curdy (1931) described the development of the testes in *Taricha torosa*, but did not relate this to body length or weight of individuals, although the existence of a multiple-lobed testis is mentioned. Miller & Robbins (1954) carried out a more detailed analysis of the reproductive cycle in this species. They found that each testis lobe was itself comprised of two distinguishable lobules; that containing mature spermatozoa was opaque white, whilst the other, containing spermatocytes and spermatids was pale grey. Their analysis was carried out on freshly killed specimens, rather than preserved animals. In this study, using preserved material, no such colour difference could be detected in the testes of either species in this study, their appearence being creamy-white.

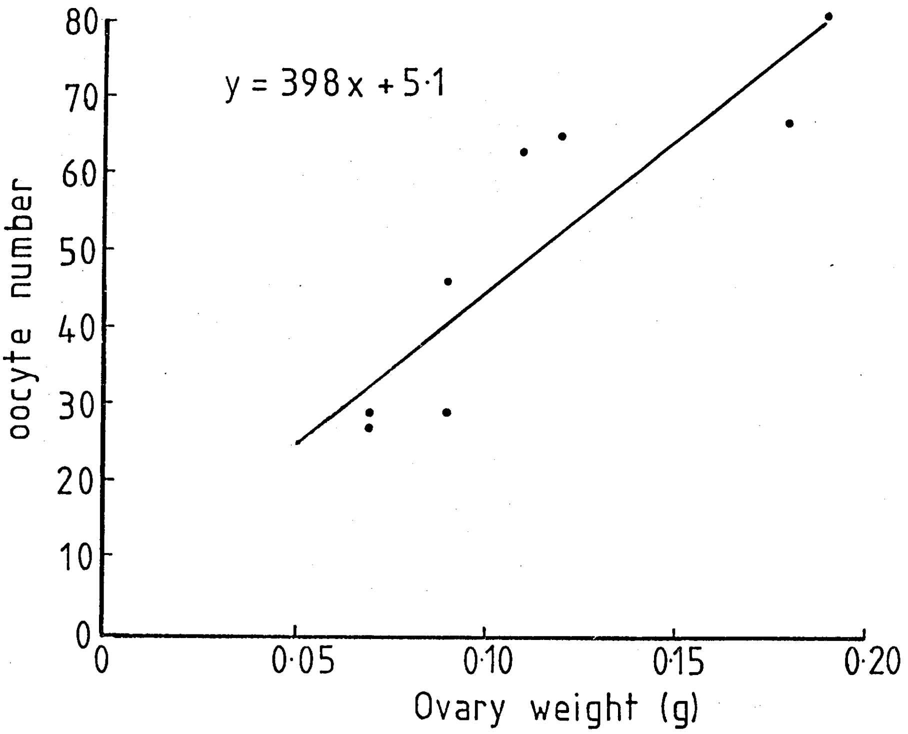


Figure 61: The relationship between the number of yolked oocytes per female and ovary weight in female T. vulgaris at Milton Bryan.

The breeding cycle of _Taricha torosa_ is different to that of _T. cristatus_ in that migration to the breeding site occurs in the winter months, with animals breeding during January to March. There is a terrestrial foraging phase after breeding, followed by a period of aestivation. This cycle is obviously a response to the climatic conditions prevalent in California where the species occurs. Given this difference one can still make some general comparisons between the two species, however.

Miller & Robbins (1954) found that there was a steady decrease in testes weight during the breeding season, with minimum weight occurring at the onset of migration away from the breeding site. The testes became active again during the foraging phase; this was evident as an increase in weight. I did not find a significant relationship between testes weight and date of capture, but the data did show a negative trend, indicating a general decrease in testes weight over the breeding season. The point at which testes weight was at a minimum in the Milton Bryan population was not detectable because no captures were made after the end of June for reasons which are not fully apparent. It appears to be a general feature of newt populations that very few captures are made at this time, although animals are still within the pond since this has also been noticed by Verrell & Halliday (pers comm.). It is likely that minimum testes weight occurs during June and July as appears to be the case for _T. vulgaris_

(Verrell unpublished data). During this time, before emigration, animals are presumed to be actively feeding and possibly regenerating sperm stores to some extent. Verrell (unpublished data) has data supporting this. This period would appear to coincide in function with the foraging phase of *Taricha*.

Average maximum testes weight in *Taricha* was found to be 1.0% of body weight (Miller & Robbins 1954). For *T. cristatus* testes weight is a little higher at 1.9% of body weight and for *T. vulgaris* higher still at 2.3%. No other comment was made by Miller & Robbins on the relationship between testes size and body size, but they did find that larger animals had a greater number of testicular lobes. Bennett (1970) has shown a positive correlation between SVL and testis lobe-number in *N. viridescens*, as did Adams (1940) who also reported that larger individuals possess heavier testes. Miller & Robbins (1954) reported that the right testis of *Taricha torosa* was larger than that on the left and cited a similar situation in *Hemidactylum scutatum*, after the work of Blanchard (1936). Adams (1940) also remarked on this inequality for *N. viridescens*.

The differences in correlation between non-normalized and normalized testes weight and body size in *T. cristatus* and *T. vulgaris* lead one to the conclusion that, although larger animals have heavier testes, the size of the testes are proportionally the same in large and small individuals. This suggests that may be a lack of allometric testis growth in these species. However, I am unclear as to the significance of this if true.

As mentioned at the beginning of this section the number of testis lobes present in individuals has been used as an ageing criterion for urodeles. However, this relationship is still under some debate, particularly in relation to the length of time lobes take to develop and what the maximum possible lobe number is for a given species. Organ (1961), for example, thought that in species of *Desmognathus* two lobes (one lobe per testis) were added every two years; hence, a four-lobed individual would be three or four years old (i.e. an animal with a total of four lobes, not four lobes per testis). Dolmen (1982) found a similar situation in *T. cristatus* and *T. vulgaris*. He reported that a new lobe was added per testis every second year after maturation of an individual. Thus, knowing the age at maturity of his population he was able to age animals with an error of one year. However, he found the number of lobes possible in both of these species to be 3 or 4, so that application of this ageing method for older animals is less reliable. I found no animals of either species with more than four lobes per testis; only five (out of 26) crested newts had three or four lobes and only one (out of 19) smooth newt had three lobes. The remainder had either one or two lobes per testis. Verrell (pers comm.) reports that there may be problems with the interpretation of this type of data since in smooth newts the lobes may only be apparent if the testes are sectioned i.e. testes may be functionally lobed with respect to sperm production, but this may not be apparent externally. If individuals from a population having the same number of lobes are of the same age, then it is clear that there was a wide spread of SVLs amongst animals of the same age in the Milton Bryan population during 1981 when the testes analysis was carried out. Verrell (pers. comm.) informs me that this is also true with regard to numbers of bone rings.

As with the testes analysis, there were few data available for comparison with the ovary analysis presented here. Most of these are in agreement with my findings. Hagström (1980a) dissected smooth and crested newts and found no significant difference between the species with regard to the number of yolked oocytes (100 - 200). In the smooth newt these were between 0.67 & 1.34mm in diameter and in crested newts somewhat larger at between 0.75 & 1.92mm. I found between 56 and 148 yolked oocytes in smooth newts and between 100 and 400 in crested newts, ranging in size from 0.44mm to 1.58mm and 0.35mm to 2.10mm respectively. Verrell found some individual virgin female smooth newts to have as many as 500 yolked oocytes in his population.

A more thorough study on smooth newt ovaries was done by Bell (1973). He dissected 90 females which had been collected during March and April 1972. Four types of oocyte were identified, small and large yolked and small and large unyolked. These were continuously distributed with respect to size. A similar finding was made for yolked and unyolked oocytes in females from the Milton Bryan population. I have not, however, drawn any distinction between large and small yolked oocytes, except to say that the largest oocytes are nearest in size to the ova found in the oviducts and that these are likely to be the first to be deposited during oviposition. There was no colour gradation detectable in yolked oocytes in this study, purely a change from white to yellow between unyolked and yolked oocytes. Bell estimated the total annual fecundity of females of a given age as being the total number of yolked oocytes. He was calculating age from his size-frequency distributions, however, which I have already argued is a dubious technique. Therefore, I would be inclined to interpret his findings with caution and substitute females of a given age with females of a given size. The large and small yolked oocytes, he suggested, would be used in two separate oviposition periods, but gives no evidence for this supposition. Hagström (1980a) does not report any such occurrence, whilst Miller & Robbins (1954) found that the total complement of ova in individual females of <u>Taricha torosa</u> were deposited within 24-48 hours. In addition, they found that ovary weight in this species was only some 5% of body weight. In *T. cristatus* and *T. vulgaris* this figure has an average value of 10%. Bell (1977) also records that immigrating and emigrating females had fewer yolked oocytes than expected; from this he suggests that some time is required in the water before a full complement of mature oocytes is obtained, although recent work by Verrell (unpublished data) refutes this. The number of mature oocytes was shown to increase with age (as calculated from his size-frequency analysis). My data agree with Bell's in so far as I find increasing oocyte size with increasing body size. However, I am not prepared to interpret this as age-specific fecundity as he has done. By hatching eggs from two females of different sizes he found that those from the larger female hatched first and gave rise to larger larvae. This may have consequences for the survival of larvae.

Egg production is correlated with body size in a number of other amphibians. Tilley (1974) demonstrated this in *Desmognathus ochrophaeus*, as did Hurlbert (1970) for *N. viridescens*. In the latter case, however, a linear relationship only existed in terrestrial animals; upon reaching water no correlation was found. The implications of variation in the size of ovaries and oocytes with body size are discussed more fully in the next chapter.

3.6.1 Migration of T. cristatus at Walton Hall.

The drift-fence/pitfall trap system at the Walton Hall pond was erected in order to gain information on the timing of immigration and emigration of crested newts at the site. The system proved to be rather ineffective, but the results obtained are shown in Figures 62 to 67. Approximately 80% of the data for 1981 were obtained by visiting the pond in the evening and picking animals up before they reached the pond.

From Figure 62 it may be seen that males started to enter the pond in 1980 several days before the females. There was an initial movement in February of 12 males and three females entering at the same time. A fairly long gap then followed until late March with no movement, after which immigration started again. This difference in the timing of entry between males and females is significant ($p < 0.05$, Kolmogorov-Smirnov two-sample test).

The entry of animals ceased in April (at least, no animals were caught) and no further immigration occurred until early August. At this time a very few animals entered, of both sexes, along with four juveniles of indeterminate sex. These latter individuals were between 52 and 55mm SVL. Emigration of animals also started at this time. Unfortunately, no data are available after August 13th because of the previously mentioned damage to the fence (see chapter 2).

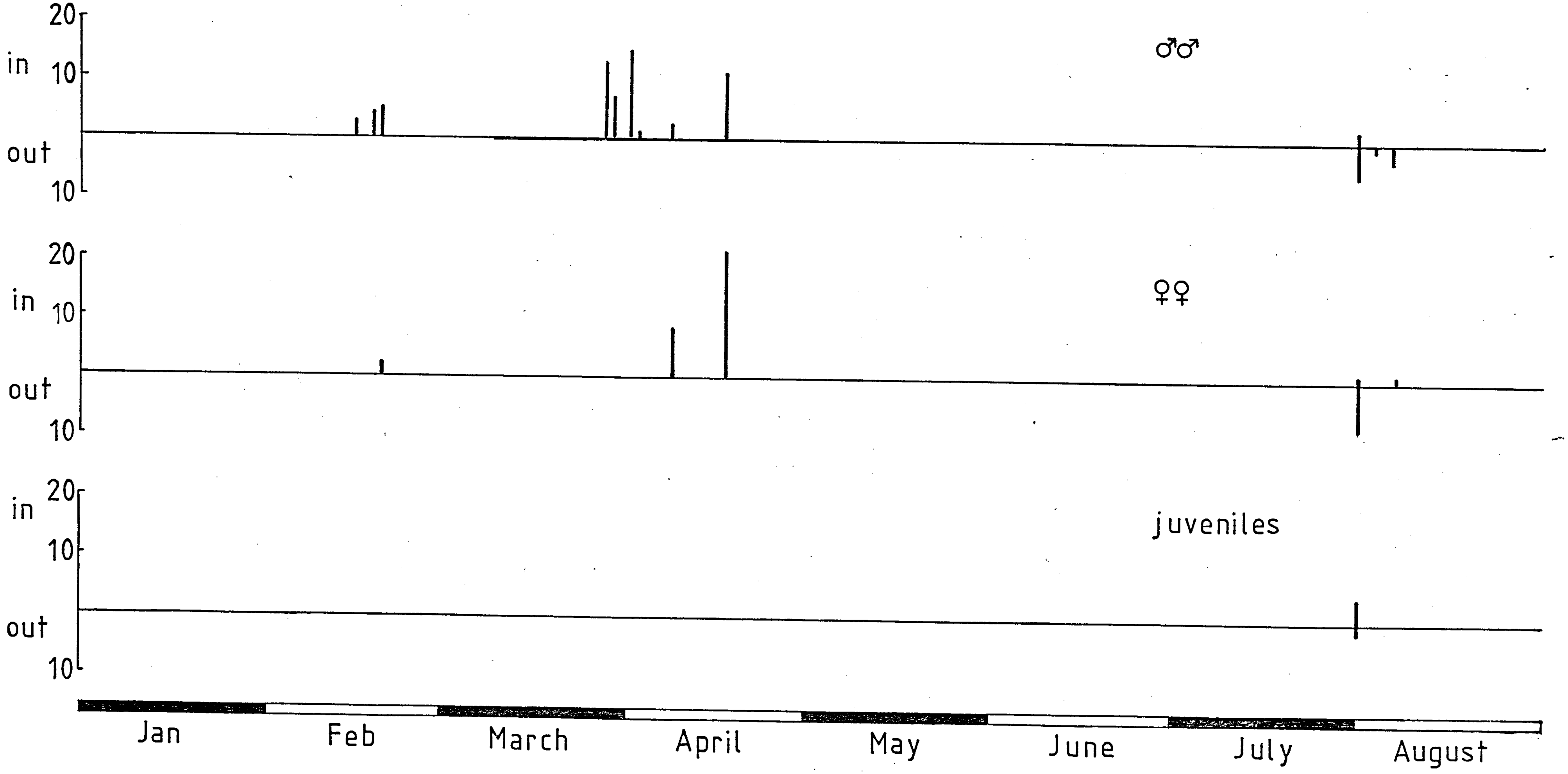


Figure 62: The timing of entry and exit of T. cristatus at the Walton Hall pond during 1980.

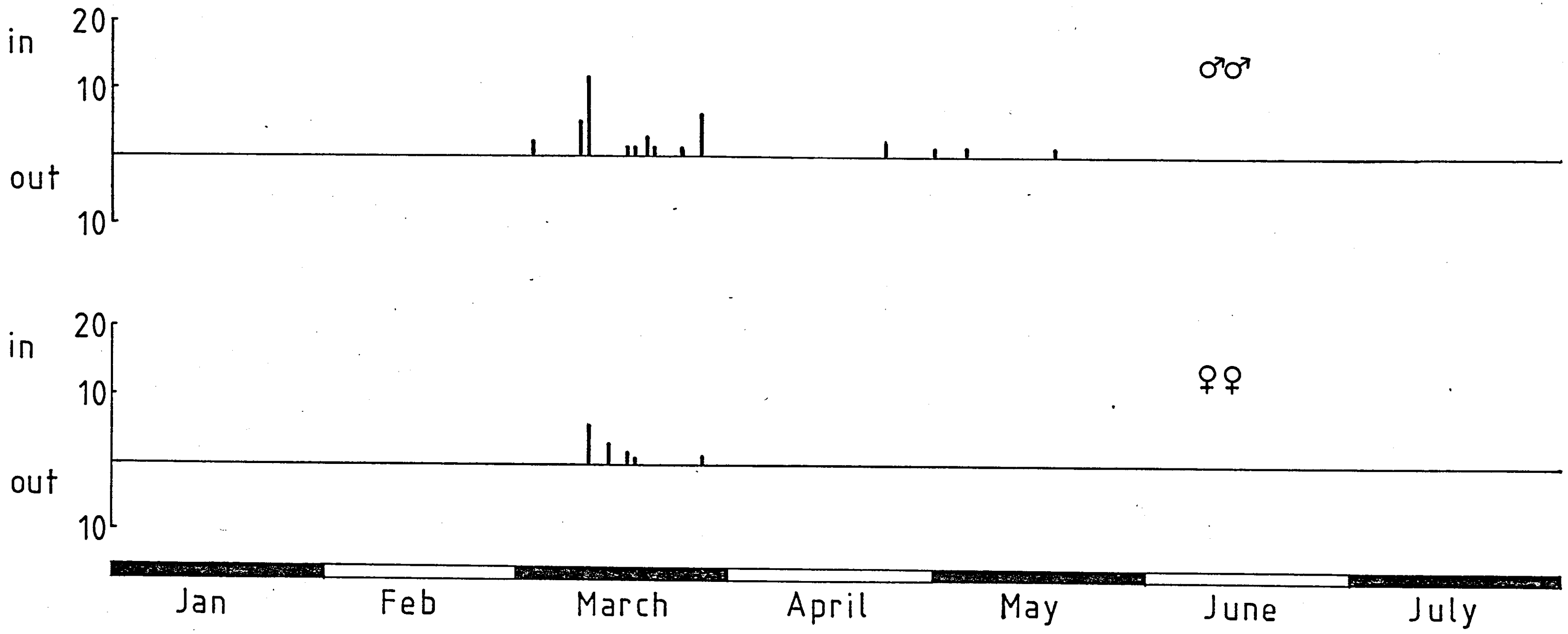


Figure 63: The timing of entry and exit of <u>T. cristatus</u> at the Walton Hall pond during 1981.

Use of the pitfall traps made it possible to identify the direction from which newts were migrating in order to reach the pond. Visiting the site in the evening also provided similar information. During 1980 85% of the animals entering the pond were captured in traps O5, O4 and O3 (see Figure 5). These are the traps closest to the road, suggesting that animals were moving to the pond from the south. This was also found in 1981 when animals were picked up from the car park in the evenings. Animals leaving the pond were found in the corresponding inner traps i.e. I3, I4 and I5 and also in I2. It is probable that indivivuals are seeking winter refugia in the hedgerow to the south of the car park and in the churchyard to the south-west of the pond. Searches were made under logs and other possible refuges in these areas, but no overwintering animals were found.

Data on daily rainfall and temperature for the Walton Hall area were obtained from the Meteorological Office in Bracknell, Berkshire. Figure 64 shows these data plotted against the number of animals caught during 1980. There is a non-significant correlation between entry into the pond and rainfall ($r = -0.10$, $N = 15$, $p > 0.05$, Pearson). However, there is a significant relationship with air temperature ($r = 0.69$, $N = 15$, $p < 0.05$, Pearson).

The equivalent data for 1981 are seen in Figure 65. Again, there looks to be a correlation between immigration and temperature. Analysis shows this to be non-significant, however ($r = 0.38$, $N = 10$, $p > 0.05$, Pearson). The relationship with rainfall is also non-significant ($r = 0.49$, $N = 10$, $p > 0.05$, Pearson). It should be noted, though, that both figures are approaching significance.

Animals began immigration later in 1981 than in 1980. If movement is related to temperature then this delay may be attributable to the very cold weather experienced during February 1981. As in 1980, males moved into the pond significantly earlier than the females ($p < 0.05$, Kolmogorov-Smirnov two-sample test).

Figures 66 and 67 show the SVLs of individuals entering the pond and the date of entry. There is no correlation between the two for either year if the sexes are treated separately. However, if the data for both males and females are combined, then a significant correlation is obtained for 1980 ($r = 0.27$, $N = 76$, $p < 0.05$, Pearson). In this particular year, then, smaller animals entered the pond earlier than the larger individuals. The reason for this is not clear, but it may be that the larger individuals require higher ambient temperatures for migration than the smaller individuals. This is discussed further in chapter 4.

Although these data are rather scanty they are in broad agreement with the findings of other workers. Verrell & Halliday (in press a) showed that male crested newts arrived

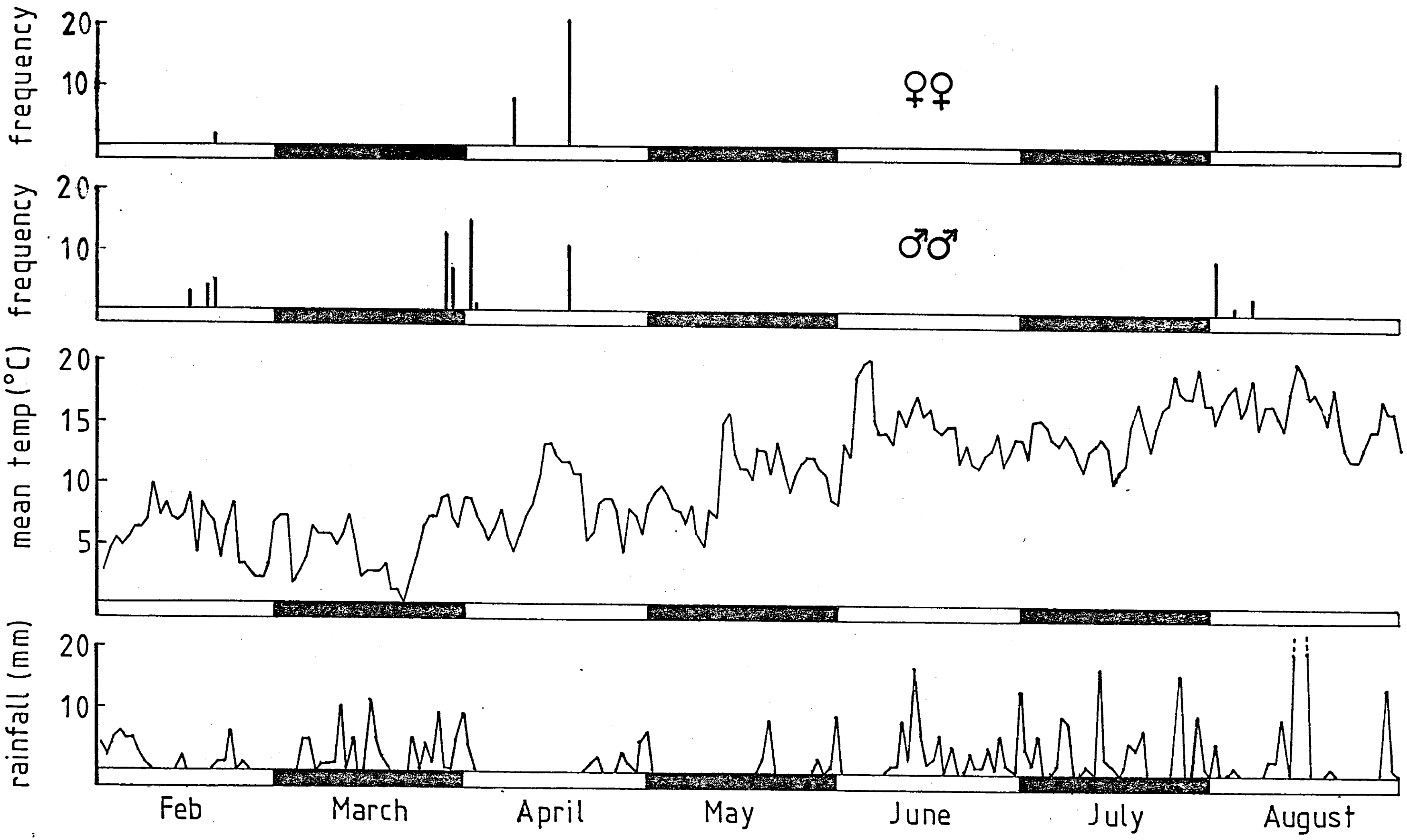


Figure 64: The immigration of T. cristatus at the Walton Hall pond related to mean daily temperature and daily rainfall.

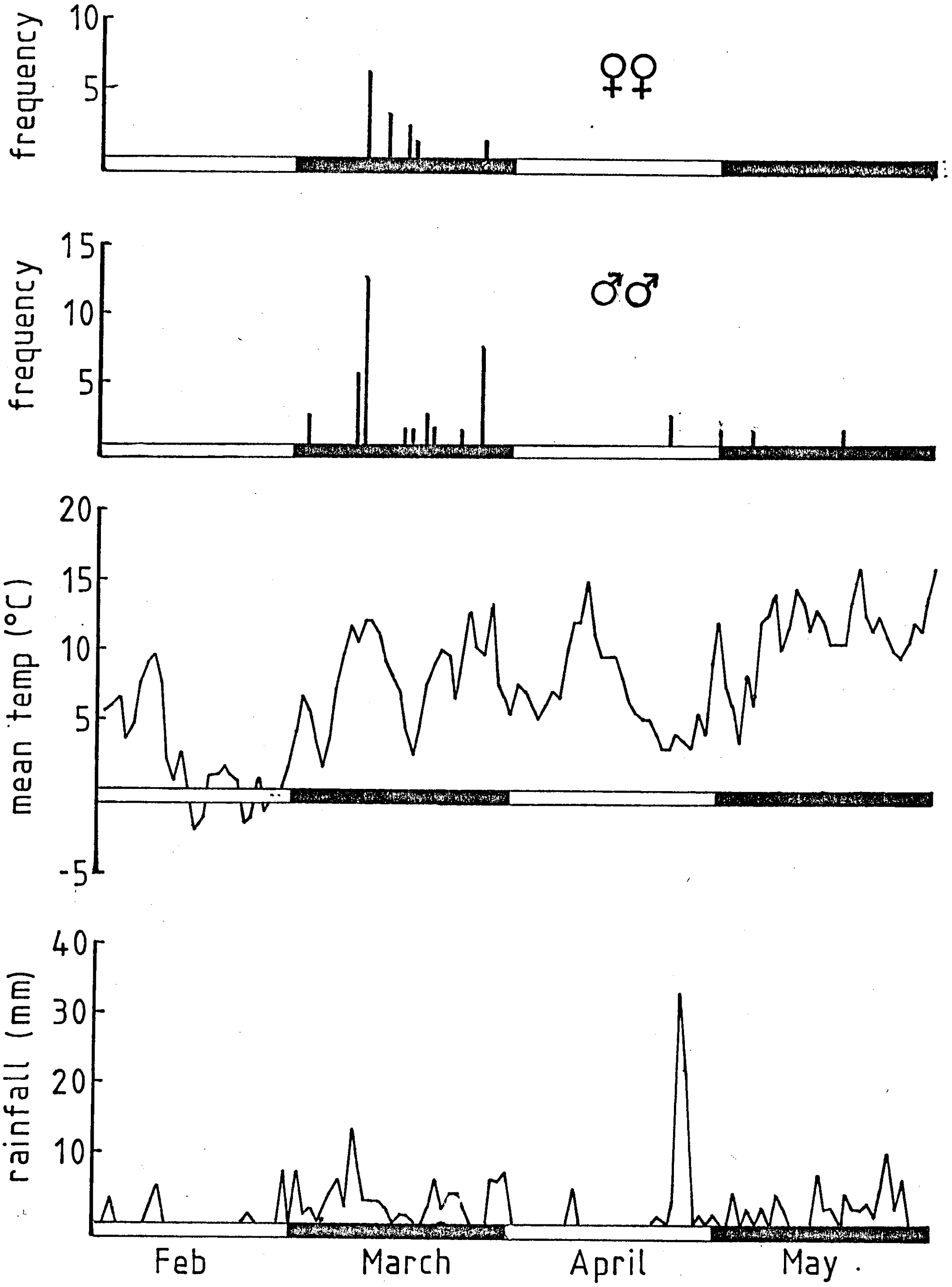


Figure 65: The immigration of T. cristatus at the Walton Hall pond in relation to mean daily temperature and daily rainfall.

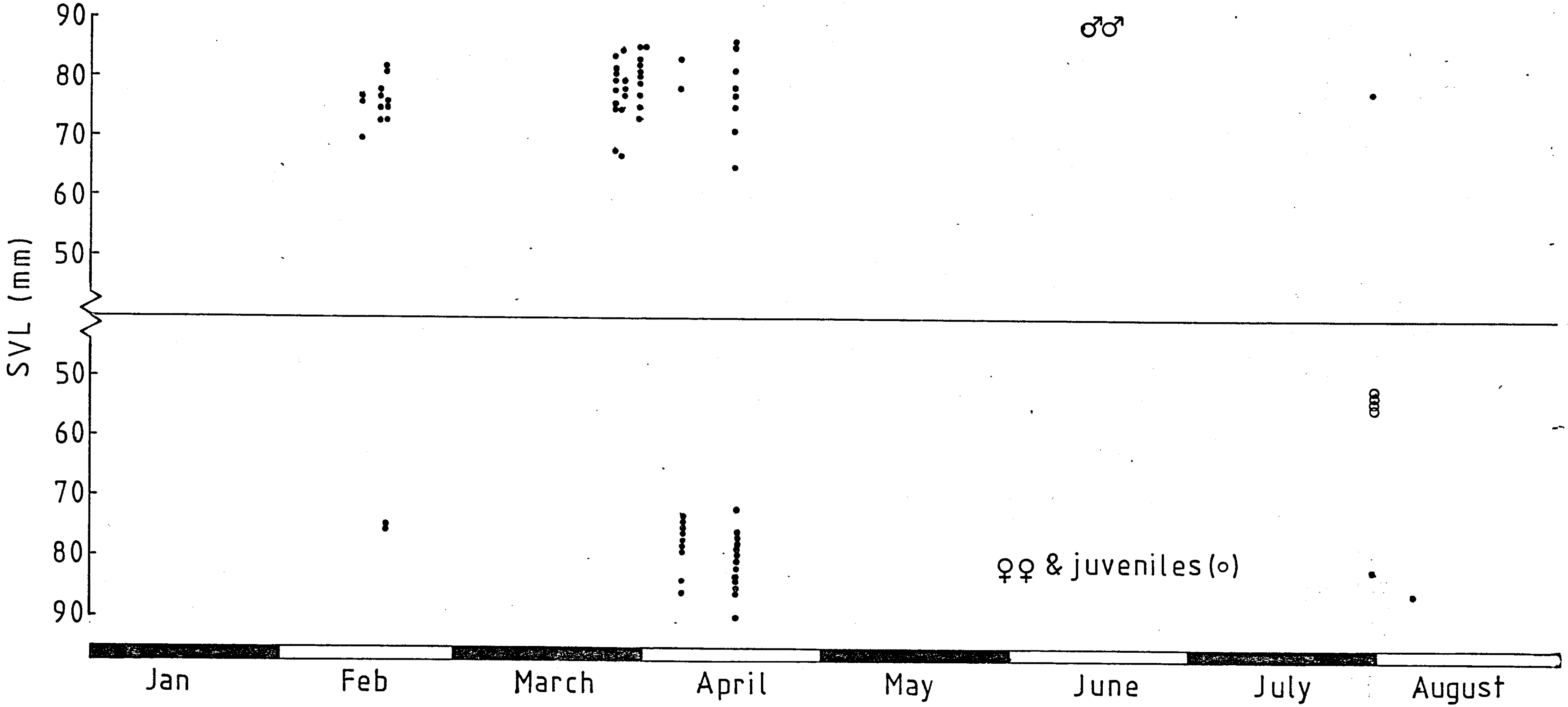


Figure 66: The sizes of individual _T. cristatus_ entering the Walton Hall pond during 1980.

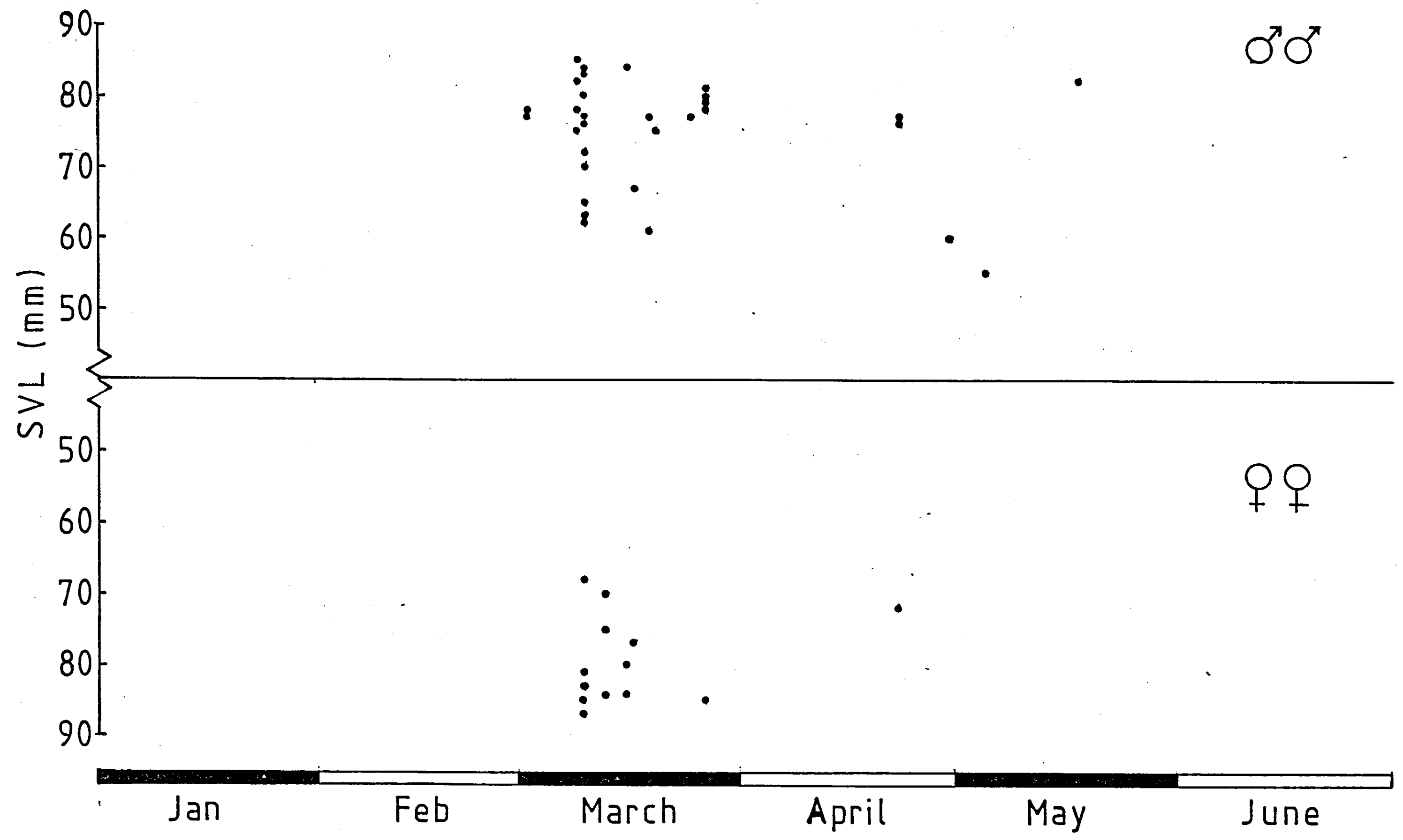


Figure 67: The sizes of individual T. cristatus entering the Walton Hall pond during 1981.

earlier at a breeding pond than females and migration was correlated with minimum daily temperature, (a critical temperature of 5^{o}C was quoted). Daily rainfall was not thought to have any influence. Griffiths (1984) obtained a similar result for smooth newts. In mid-Wales male palmate and smooth newts entered ponds at the same time and significantly ahead of their respective females (Harrison et al 1983). This is suggested as a mechanism whereby males may set up individual territories before the arrival of the females (following Dolmen's (1981) observation that smooth newts may be territorial). In this instance, rainfall was a significant factor as well as temperature.

Other species of newt exhibit the same migratory behaviour; c.f. work on *N. viridescens* by Hurlbert (1969 1970) and Healy (1975), on *Taricha rivularis* by Licht & Brown (1967) and Packer (1960) and on *Taricha torosa* by Pimentel (1960). Similarly, climatic influence upon the activity of other urodeles and also anurans during the breeding season has been demonstrated by Jaeger (1980) for *Plethodon cinereus*, by Semlitsch & West (1983) for *P. websteri* by Degani & Warburg (1978) for *Salamandra salamandra* and by Gittins et al (1980) and Gittins (1983) for *Bufo bufo*.

3.7 Analysis of stomach contents.

The stomachs of those animals used in the study of the reproductive organs were dissected and their contents examined. The results of this analysis are shown in Table 16. This gives the total number of each food item found in both species, with the number of individuals these items were found in given in brackets.

It is apparent that a variety of prey items are taken and that there is considerable dietary overlap between the two species. There is no indication, however, as to whether the two are exploiting different size ranges of prey where such overlap occurs. Dipteran larvae (mostly chironomids) were found in more stomachs than any other food item, whilst gastropods were numerically the most important prey. However, it should be noted that 38 snails were found in one individual female crested newt; without this figure they would constitute a less important item.

Hemiptera (mainly corixids), oligochaetes and small crustacea, such as Daphnia, comprised the remaining major prey items. Other species eaten only occurred in one or two individuals or in very low numbers.

It would appear that gastropods and oligochaetes were more important in the diet of crested newts at this site than they were for smooth newts.

FOOD ITEM	MICROHABITAT	TOTAL NUMBERS PER SPECIES *T. cristatus* males	 females	 *T. vulgaris* males	 females
Insecta:					
Ephemeroptera nymph	bottom	3 (3)		4 (4)	
Ephemeroptera adult	surface		1 (1)	1 (1)	
Odonata nymph	bottom		1 (1)		
Trichoptera nymph	bottom			3 (1)	1 (1)
Hemiptera	free swimming	4 (4)	5 (5)	3 (3)	
Coleoptera larvae	bottom	5 (4)	2 (2)		
Diptera larvae	free swimming	21 (7)	20 (7)	20 (9)	6 (3)
Crustacea:					
Asellus	bottom			1 (1)	
planktonic	free swimming		22 (6)	19 (4)	9 (3)
Oligochaeta	substrate	10 (3)	4 (4)	1 (1)	
Mollusca:					
Gastropoda	bottom	17 (5)	77 (10)	1 (1)	2 (2)
Lammellibranchia	bottom	4 (2)			
newt eggs	vegetation	2 (2)			
plant material		1 (1)			
empty		15	7	6	1

Table 16: Analysis of stomach contents of preserved *T. cristatus* and *T. vulgaris*. Figures in brackets indicate the number of individual stomachs which prey items occurred in.

Table 16 also lists the microhabitats occupied by the various prey species. There is evidence here to suggest that crested newts are predominately feeding on those species found at the bottom of the pond, whilst smooth newts are taking more of the free swimming species.

Individual items appear at various times of the season; there does not seem to be specialization on any one group in any one month and no evidence of a switch of diet at any point for either species, as has been suggested for T. vulgaris by Verrell (in press a)

These data are in accordance with the results of other workers. Avery (1968) observed that the three British species of Triturus, T. vulgaris, T. cristatus and T. helveticus displayed dietary overlap where they occurred together. Most available prey were taken, but not necessarily in the proportions in which they occurred; for instance, corixids and odonate nymphs were abundant but, rarely eaten. This is true for Milton Bryan where odonate and coleopteran larvae were found in large numbers but, only appear in 8 stomachs. Dolmen and Koksvik (1983) report that T. vulgaris preferentially took planktonic crustacea, whereas T. cristatus took mainly benthic species and those associated with the bottom of the pond. Crested newts were also shown to take larger prey items.

In America, Wood & Goodwin (1954) showed that Notophthalmus viridescens preyed on a variety of organisms. The same species is regarded by Burton (1977) and Attar & Maly (1980) as an opportunistic feeder, changing prey items as the abundance of each varies.

It is conceivable that trapping may have had an affect on the results observed here. It is unclear how much time is required for newts to digest the different prey items that they take; this will obviously depend on the size and type of prey. Therefore, certain items identified from stomach remains may have been eaten before animals entered the traps or after entry to the traps. Prey items were always available in the traps, having entered in the same way as the newts, so interpretation of these data must be treated with some caution.

CHAPTER 4. DISCUSSION.

Fluctuations in population size are well documented for a variety of vertebrate species, examples being voles (Krebs 1966), tits (Lack 1966) and the grey heron *Ardea cinerea* (Stafford 1969, Reynolds 1974). However, very little work has been carried out on long-term population changes in newts and other amphibians. In particular, there has been little discussion on the underlying reasons for population changes in these animals.

Predation would appear to be a prime factor in the control of *Triturus* populations. However, the evidence for this is primarily of an indirect nature and reports of predation on newts, either from direct observations or the presence of remains in the stomach contents of birds, fish, etc. are scarce in the literature. For example, Beebee (1979) reported that no newts were found in park and garden ponds which contained fish, although he does not state whether newts had been present before the introduction of the fish. Similarly, a number of newt populations in Swedish lakes are increasing because of the disappearence of fish through acidification of the water (Hagström, 1980c). In each of these cases it is not clear whether the effects were due to predation by fish or to competition with fish for food resources. United States, Gill (1978a) found leeches to be the major cause of mortality in some populations of *N. viridescens*.

However, no fish were found at the Milton Bryan site and there were no obvious predators of the adults of either newt species present, although Hagström (1971) reported that crested newts were important predators of adult smooth newts in his populations. However, I found no evidence of this in the specimens which I dissected. Adult crested newts are unlikely to suffer heavy predation due to the presence of a toxin in their skin. The precise chemical nature of this is unknown, but the substance was generally described by Ormerod (1872, cited by Frazer 1983). It is a whitish exudate and causes strong salivation and local muscle spasm; it also has an irritating effect on the mucous membranes of humans (personal observation). Furthermore, juvenile crested newts also have this protection and so may be less vulnerable to attack than juvenile smooth newts. In this feature they are similar to the red eft, the terrestrial stage of *N. viridescens*. The colouration of this phase is regarded as being aposomatic and Beebee (1979) suggests the belly colouration in crested newts may serve the same function when being appraoched from below.

The most likely sources of predation on smooth and crested newts at Milton Bryan are probably from the larvae and adults of aquatic coleopterans, such as *Dytiscus marginalis*, and the larvae of dragonflies, all of which occur in large numbers at the site. These probably account for the death of a great many tadpoles which, along with the egg stage, is the most vulnerable period in the life cycle of a newt. Bell and Lawton (1975) calculated the survival of smooth newt larvae to be 0.09 from hatching to metamorphosis. They also report a wide variety of predators on both stages. Verrell (in press b) estimated survival to metamorphosis to be 0.0023 for *T. vulgaris*, which is extremely low. This was based on one season's data, however, and it may be that the year in question was a particularly poor one for this species at his study site.

Macgregor & Horner (1980) reported that *T. cristatus carnifex* suffers 50% mortality during larval development due to a chromosomal irregularity. Chromosome I in these species shows a heteromorphic C-banding pattern and they found that larvae which did not exhibit this heteromorphism failed to develop beyond the tailbud stage. This phenomenon has since been described as occurring in *T. c. cristatus* also (Wallace, 1984). Such a high innate mortality is extraordinary and means that survival to metamorphosis is likely to be very low and possibly comparable with the aforementioned data for *T. vulgaris*. Although no work was carried out on the eggs and larvae of either species at Milton Bryan it was noticeable that very few larvae of either species were caught in the traps, particularly when considering the size of the adult population, and this is consistent with high mortality at this stage.

I have shown that the daily survival rate of adult crested newts during the breeding season is high, but that the yearly rate is somewhat lower. Adults must, therefore, be subject to their greatest mortality during the terrestrial phase. A major factor at this time may be the weather conditions. Most adults spend the winter in refugia, such as under logs, and at different depths from the surface (Smith 1951). Animals occupying shallow locations are unlikely to have much protection from low temperatures. Smith (1951) recorded 50% mortality of smooth newts wintering under timber during the severe winter of 1946/47. He also found that young animals survived this freeze better than adults. I presume from this he means smaller animals. A similar finding was made by Harris (1980); adults of Ambystoma maculatum which survived a pond freeze were smaller than those which perished. Newts are able to breathe through the skin as well as through the lungs. At the very low temperatures encountered during hibernation, metabolic activity is such that only a small amount of oxygen is required to keep an animal alive. However, if temperatures are extremely low, the higher surface to volume ratios of smaller individuals may enable them to maintain adequate oxygen levels whilst larger animals cannot.

From the size-frequency distributions (see chapter 3, section 3) it is clear that there was no great change in the mean size of male or female crested newts at Milton Bryan in years following a severe winter. Therefore, the above observation would appear not to apply to this population. Furthermore, the low population numbers in such years are primarily due to the absence of females. Since the mortalities of both sexes appear to be the same, as shown in chapter 3, section 2, it is unlikely that females are being affected by low temperatures to a greater extent than the males, unless the sexes are subject to different causes of mortality. Alternatively, females may be inhibited from migrating during cold weather to a greater extent than males, due to being larger and heavier on average. This may also occur in Bufo bufo (Halliday, pers comm.). Healy (1975) found that female red-spotted newts entered breeding ponds later than males of this species and he suggested that this was because females were egg-laden and so unable to move as quickly as males. He also discussed whether females might not be further from a breeding site than males at the onset of migration, although he had no direct evidence for this. If females do move more slowly as a result of carrying eggs then they may be more susceptible to sudden drops in temperature than males and may suffer greater mortality as a result.

Harris (1980) recorded two separate phases of migration in A. maculatum such that there were early breeders and late breeders. Early breeders were able to allow enough time for their offspring to metamorphose before desiccation of the pond, but the adults were liable to freezing. If a similar situation exists in crested newts then possibly those individuals migrating early to a breeding site are suffering greater mortality than those which delay the onset of migration. There does not appear to be any evidence of this in the literature, however.

A third explanation might be that some females are not breeding every year. This has been recorded by Hagström (1979) who found some adult crested newts to be completely terrestrial in some years, without resort to water at any time. He also found very few aquatic females in some years. There is no evidence that females were skipping breeding seasons at Milton Bryan; the apparent absence of some individuals may simply have been due to my not capturing them that season rather than to any genuine absence. However, this lack of direct evidence does not preclude the possibility of biennial breeding in some individuals.

The population structure in any one year is likely to be a reflection of the reproductive successes of previous seasons. Bell (1973) estimated that smooth newts achieve maturity after three to seven years. From data on bone rings, Verrell (unpublished data) has calculated that males mature after a minimum of two years and females after three years in this species. Hagström (1979) tentatively suggested five years as an average time for crested newts to reach maturity in Scandinavia. Therefore, the reproductive output in any one year will not be apparent as a return of breeding adults for at least three years. In the case of crested newts an indication of breeding success may well be first manifested as the numbers of juveniles returning to the pond. This figure is highly variable, as I have shown for Milton Bryan and as Bell (1979) found in his populations. For example, in 1980 and 1982 the numbers of juveniles caught at Milton Bryan were very low (3 and 0 respectively), whilst in 1981 and 1983 they were much higher (19 and 14 respectively).

This resort to water by juvenile crested newts before they reach maturity appears to be a general feature of the life-history of this species and one which is not shared by the smooth newt. Bell (1977) and Verrell & Halliday (in press a) both reported this difference and Hagström (1972) has recorded overwintering in the water by metamorphosed young and juveniles of the crested newt in Scandinavia. Bell (1979) remarked that juveniles may be returning to the water if feeding rates, and thus growth rates, are greater in this environment than on land, a factor which may have an important effect on the future fecundity of these individuals. There is no direct evidence for this suggestion from either the work at Milton Bryan or that of Verrell & Halliday (in press a), although the latter found an increase in the weight of emigrating juvenile animals, compared with their weight when immigrating. There is, however, direct support from a study by Healy (1973). He found that aquatic juvenile red-spotted newts had faster growth rates than the terrestrial efts and, in addition, that they matured earlier. He attributed this to environmental conditions having an influence on the amount of time available for efts to forage. These two traits were shown by markedly different populations however, the aquatic individuals occurring in a harsh coastal habitat and the terrestrial animals coming from a typical inland habitat. The omission of the eft stage is thought to be a response to the harsher coastal environment (Healy 1974). It is not known whether all or only a proportion of juvenile crested newts return to the water for a period during their development.

As mentioned in chapter 3, section 2, Bell (1979) regarded all individuals of less than 60mm SVL as juvenile, whilst at Milton Bryan it was possible to distinguish the sexes at 55mm SVL and occasionally less (as with the two males of 53mm SVL). This suggests that the population at Milton Bryan matures at a smaller size than Bell's population. Verrell & Halliday (in press a) found juvenile individuals at their pond to be between 40 and 51mm in length and also captured mature animals of less than 60mm SVL. Clearly, there is considerable variation between populations in the size of crested newts at maturity. Despite the difficulty of relating age to length in urodeles, it is tempting to suggest that the populations at

Milton Bryan and Yrrell are maturing earlier than Bell's Oxford population. Healy (1974) considered early maturity to be an adaptation to a harsh environment. The main study pond at Milton Bryan would appear to be rather stable, in that it does not become completely dry, even in the hottest summers. However, if temporary ponds are to be exploited as potential breeding sites, then it may be advantageous for animals to mature earlier and to disperse in order to colonize such ponds. If my study area contained fewer potential breeding sites than Bell's area then there may be more pressure on animals to reach maturity and colonize in my area than Bell's so accounting for this difference in size at maturity. Alternatively, there may be more food available at one site than another and hence animals may be able to forage at greater rates in these ponds.

On the whole the numbers of juveniles appearing at Milton Bryan are rather low, the highest number encountered being nineteen. Allowing for those individuals which may be colonizing new ponds, and so do not appear at the site of their birth, it is apparent that the annual recruitment of new adults into the Milton Bryan population is rather low. In some years, such as 1982, it would appear to be zero. A similar situation was reported by Semlitsch (1983) who found productivity to be zero in populations of <u>Ambystoma tigrinum</u> in some years.

There is a need for more work to be carried out on the juvenile stage of the life-cycle in Triturus, particularly on the fate of individuals upon leaving the breeding site after metamorphosis and on the precise role of this stage in the different species. Gill (1978a), for example, proposed that the eft stage of the red-spotted newt is a specific adaptation for the colonization of new, but temporary ponds. The primary role in crested and smooth newts may also be that of colonizers. Cooke et al (1980), for example, found large numbers of immature crested newts in ponds at Woodwalton Fen which had previously lacked the species. It is apparent, however, that different tactics are being shown by smooth and crested newt juveniles during dispersal from the observation mentioned above that immature crested newts resort to water whilst those of the smooth newt do not. This requires further investigation.

Salthe (1969) identified 3 modes of reproduction in urodeles. Crested newts and most salamandrids belong to the Type I mode; this is where females lay large numbers of eggs (100+) of a relatively small size, in still waters and without any parental care. Kaplan & Salthe (1979) discussed these modes in relation to the life-histories of a number of species of salamander. They showed that within any one mode, both ovum size and egg number increased with increasing body size. This fits with the differences observed between smooth and crested newts. The larger species develops larger ova and is able to produce more of them. They also found body size to be a significant constraint on total reproductive output at any given time. Thus, there is an expectation of a trade-off between the components of reproductive output; i.e. the size of ova cannot be increased without a decrease in egg number (assuming body size to be constant). Therefore, one would surmise that in order to produce more, larger ova a female must increase in overall body size. However, there is likely to be a cost in this. If resources are to be used in growth, then there will be a corresponding decrease in the amount of energy available for oogenesis. This conflict may be partially solved by having a rapid growth phase after the breeding season, assuming that this is possible.

Bell (1977) has shown that the fecundity of female smooth newts in any one year is equivalent to the total number of yolked oocytes contained in the ovaries. The remaining, unyolked oocytes are presumably for use in future breeding seasons. The time taken for these unyolked oocytes to mature is unknown. Verrell has found emigrating female smooth newts containing fully yolked oocytes and suggests that these may have matured after the female had completed laying for the season, rather than being unused ova from the main oviposition period. He is of the opinion that unused ova are, in fact, resorbed by females. In contrast, Hagström (1980) found that in his populations females rarely laid their full complement of yolked oocytes. He suggested that this may be a consequence of unfavourable conditions in the breeding pond, but he was unsure as to the fate of the unlaid ova. This failure of some females to mature and lay the largest possible clutch within the constraints of body size is discussed by Fraser (1980) who studied the environmental contol of oocyte maturation in *Plethodon cinereus*. He demonstrated that the size of oocytes was related to the condition or stoutness (his terminology) of the female, but the number of oocytes was not. This animal is somewhat different to *Triturus* in that it is a terrestrial salamander and shows Mode III reproduction, but the general result may hold for newts as well. If the size of oocytes is related to condition in crested newts it is conceivable that some females are required to skip a breeding season in order to build up sufficient energy reserves to develop enough ova to make breeding worthwhile.

These various related factors of ovum size, clutch size and offspring fitness are discussed by Kaplan (1980) for three species of *Ambystoma*. All three species show the Mode 1 reproductive pattern. He demonstrated that ovum size was correlated with the time taken for larvae to reach the feeding stage; this was the point at which larvae were able to actively take live prey. In addition, there was an increased advantage to larvae from larger ova after this stage had been achieved. Although there was this advantage to the females producing the larger ova, he pointed out that females producing more, smaller ova may achieve equal success if environmental conditions are primarily size-independent relative to larvae. Thus, he suggests that different females may adopt different strategies in any one breeding season and that they may vary strategies from year to year to suit environmental conditions.

Wilbur & Collins (1973) discussed the ecology of amphibian metamorphosis in a variety of anuran and urodele species. They argued that the variation in larval period and body size at metamorphosis for any given species could not be directly explained by differences in the date of hatching or ovum size. They suggested the existence of a non-normal distribution of competitive ability amongst tadpoles arising from mechanisms such as the production of growth inhibitors and size-selective feeding behaviour; such variation would lead to a relative advantage to the larger larvae in a cohort. The degree of skewing of body sizes in the cohort is density dependent and thus, size at metamorphosis is also density dependent. This argument is somewhat different to that of Kaplan outlined above. I feel that a fuller discussion of larval development is outside the scope of this thesis, since this area of the life-cycle has not been dealt with but clearly, there is a need for more work to be carried out on larval development in amphibians particularly in relation to ovum size, population density and possible competitive interactions between larvae and adult newts.

In chapter 3 section 2, I showed that overall sex ratios in the crested newt population at Milton Bryan varied from season to season from an excess of males in some years to equal numbers of both sexes in others. When the ratio is biased towards an excess of males then there will be greater competition between males for females, leading to greater variance in the mating success of the males (Trivers, 1976). In urodeles this increased competition may be manifest in a number of ways. First, there may be an increase in the incidence of sexual interference. This term was first used by Arnold (1976, 1977) who demonstrated its existence in a number of ambystomatids and plethodontids and in a variety of forms. In *Triturus* it may take the form of interruption of courting males by other males, or possibly female mimicry by males. This latter phenomenon has been demonstrated in *T. vulgaris* by Verrell (1984d). In this behaviour a male will mimic the behaviour of a female during a particular phase of courtship, thus enabling the mimicking male to 'steal' the female being courted. Such specific competitive behaviour has not been demonstrated in *T. cristatus*, but interruption of courting males is likely to be a common occurrence in some populations. I have made casual observations of male-male interactions in a number of populations, involving males displaying to one another, nudging one another and similar behaviour. In a study in Sweden, Grønlund & Sæterberg (unpublished data) observed that this type of behaviour was widespread in their population and also reported male-male encounters which were interpreted as aggressive and territorial. Males were observed defending stones or bare patches of substrate against other males by vigourous displaying and pushing. Such behaviour was generally temporary, however, and defending males would frequently swim away after a few moments. Gauss (1961) also reported that male crested newts were territorial from observing that individuals would scent-mark areas by rubbing their cloaca on the substrate. This has not been observed by any other workers, however, and Halliday (1977) is doubtful as to the existence of this more permanent territoriality in Triturus. The data from recaptured males at Milton Bryan showed considerable movement of individuals around the pond, which also indicates little territorial behaviour, although the temporary territoriality suggested by Grönlund & Säterberg would not be apparent from such recapture data. It may be, therefore, that under conditions of increased competition the incidence of territorial behaviour increases.

However, Warner & Hoffman (1980) suggested that the opposite may be true in some cases. They found that in populations of bluehead wrasse, Thalassoma bifasciatum (a coral reef fish) the mating success of territorial males decreased with increasing population density. Thus, at higher densities increased male-male competition produced a decrease in the incidence of territorial behaviour. They suggest that at high densities territories are simply not economically defendable.

Increased male-male competition may also lead to males arriving at breeding ponds before females and remaining within a pond for longer periods in some years than in others. This has been demonstrated by Douglas (1979) for *Ambystoma jeffersonianum*, although he only compared data from two breeding seasons. At Milton Bryan I have shown that there were significant differences between the mean recapture intervals for 1980, 1981 and 1982, when the male:female ratios were 2.5:1, 1:1.2 and 3.1:1, respectively. Thus, it would appear that males were in the pond for longer in 1980 and 1982 when the sex ratio was male biased than in 1981 when it was near equality. This is in agreement with Douglas. However, it should be pointed out that no difference was found in recapture intervals between 1982 and 1983 despite a change in sex ratio from 3.1:1 to 1:1.1. This may be due to the fact that many more animals were present in 1983 than in other years and so competition may have been high even though the sex ratio was close to equality. That is to say, population density and the sex ratio have a dual effect on the level of competition in any year.

The presence of males in breeding ponds for longer periods than females appears to be a general phenomenon amongst urodeles and has been reported for a number of species, e.g.

A. jeffersonium (Douglas, 1979), A. maculatum (Husting, 1965), Taricha rivularis (Hedgecock, 1978) and N. viridescens (Bellis, 1968, Gill, 1978 and Healy, 1974). However, the situation with regard to T. cristatus and T. vulgaris appears to be more variable, as discussed in chapter 3, section 4. In some populations there is no difference in the time the sexes spend in the water, whilst in others there is. Possibly environmental factors are having an effect. The general phenomenon of variation of the aquatic period of males is discussed with reference to possible sperm competition by Halliday & Verrell (1984)

Douglas suggested that intense male-male competition in A. jeffersonianum has lead to increased selection pressure for males to arrive at breeding ponds before the females. In this way, a male is able to maximise the number of females available to it for mating and so increase its potential reproductive success. Using a similar argument, Douglas goes on to suggest that entry of females into the pond should be delayed until the probability of their reproductive success is also at a maximum. The data for Triturus from this study do not disagree with this notion but clearly, there is a need for more work to be undertaken on this species in order to ascertain more fully how selection pressures may be acting to determine breeding strategies in any given year. It is apparent from comparing studies (e.g. Hagström, 1979 and Bell, 1977) of the species from different areas that whatever these pressures are, they are producing a variety of effects within and between populations.

Gadgil & Bossert (1970) produced an important theoretical paper on the life-historical consequences of natural selection which was, in part, a development of a previous paper by Cole (1954) on life-history strategies. They used models to simulate a variety of stategies which were equivalent to either 'big bang' (semelparous) reproduction or repeated (iteroparous) reproduction (the 'r' and 'K' selection of MacArthur & Wilson, 1967). Their predictions of life-history tactics for repeated reproducers are in broad agreement with what is observed in crested newt populations. In particular, they predicted that growth should continue up to the point where the reproductive potential reaches a maximum and that growth should continue beyond maturity. The latter is certainly true for T. cristatus. Whether or not the first part of their prediction holds is more a matter of conjecture. Growth does slow in crested newts after maturity and appears to cease at some point. The reason for this is not fully clear, but the size at which this happens varies between individuals. Under Gadgil & Bossert's analysis this implies that crested newts are reaching their maximum reproductive potential at a range of sizes within a given population. Again, this points to a high degree of plasticity shown in the breeding ecology of the species, a point which is generally stressed by Kaplan (1980) in relation to female reproductive strategies.

Gadgil & Bossert also predicted that fecundity is determined by the age of an individual. This follows conventional demographic theory. I have previously discussed the problems appertaining to relating fecundity with age in newts due to the variability in growth of animals. This problem was recently considered by Kirkpatrick (1984) who presented two theoretical models whereby size rather than age was the determining factor in the birth and death characteristics of individuals of species with indeterminate growth. These were referred to as the 'assignment at birth' and the 'variable' growth models. In the first of these, as its name implies, the growth of individuals varies due to differences determined at birth, whilst in the second, growth is variable through the lifetime of an individual. It is this latter model which would appear to be the more applicable to *T. cristatus* populations. The model states that individuals of the same age share the same expected growth rate but the realized growth rate is the sum of this expected rate plus a random increment that varies at each moment in time. This would produce the variation in size of individuals of the same age which is apparent within populations of *T. cristatus* and other urodeles. The model also allows individuals to grow smaller on occasion which is also a feature of *T. cristatus*, as I have demonstrated.

The application of Kirkpatrick's models to data from real populations of urodeles may well lead to a better understanding of the demography of such species than was previously possible using age-based analyses.

In conclusion, I wish to say a little about the status of the crested newt in the Milton Keynes area. In 1984 the Milton Keynes Development Corporation contracted members of the biology department of the Open University to survey a number of ponds in the designated city area. Ponds were initially identified from aerial photographs and thenceforth visited on the ground in order to determine whether a full faunal and floral survey was justified. Following this first phase survey a total of 94 ponds were finally investigated.

The principal aims of the survey were to obtain information on the relative abundances of the various amphibian species in the area and to identify those ponds most at risk from future urban development. Thirty-one ponds were found to contain at least one species of amphibian, but only five contained crested newts; a further survey in 1985 of another 25 sites revealed two more sites supporting populations of this species.

It was found that these seven ponds in which crested newts occured were all heavily vegetated. However, the percentage of open water varied from pond to pond, with three of the smaller sites having no open water to speak of at all. In addition, the sizes of these ponds were variable, both in surface area and depth. All had terrestrial vegetation in close proximity, generally no further than 50 yards away, so ample cover was available for animals upon leaving the ponds. A great many of the ponds investigated were located in arable fields and none of these contained crested newts. This is consistent with Beebee's (1977) finding in Sussex that both smooth and crested newts were absent from such potential breeding sites. The reasons for this are not fully apparent but would appear to involve a lack of terrestrial refugia; leaching of agrochemicals may also have a detrimental effect, although the nature of the chemicals used in the city are unknown. The sites also largely conform to the requirements set out by Cooke & Frazer (1976) as the ideal for crested newt breeding sites. However, it was suggested by these authors that crested newts prefer larger, open sites, which is in contrast to some of the ponds in Milton Keynes. The reason for this may be that suitable sites in the city have become so reduced in number that less suitable sites are being occupied. However, against this is the observation that some suitable areas have been found not to contain the species.

Clearly, the situation as regards crested newts in the city is an interesting one which would warrant further investigation. It is unfortunate that archival material on the status of the species in the vicinity of Milton Keynes is virtually non-existent and, where it does exist, is largely anecdotal. It may be that crested newts have always been scarce in this area, leading to low productivity and thus, low colonization rates of suitable ponds. Alternatively, the upheaval caused by the construction of the new city may have decimated the newt population to such an extent that recovery is unlikely or very slow. This is supported to some extent by the observation that since the start of development of the city it appears that somewhere in the region of 100 ponds have disappeared in the area; this is evident from Ordnance Suvey maps of the area prior to development. Such a decrease in potential breeding sites cannot have had anything but a detrimental effect on the species. In addition, of those ponds still extant, approximately one-third had dried up by May. Thus, suitable sites are again found to be at a premium. From an optimistic viewpoint, a number of new ponds have been created in the city, but as yet these have not been colonized by crested newts. The previous destruction of potential breeding sites may mean that the overall population in the area is so low, and annual productivity such that this process may take some considerable time. It may be, therefore, that judicious introduction of adults or juveniles into suitable sites is advisable, but only using animals from ponds which are themselves in jeopardy.

It is important, however, that wherever there is the possibility of creating new habitats for this or any other species of amphibian in Milton Keynes that care is taken to cater for all aspects of the life-cycle. Thus, the terrestrial habitat must be considered as well as the aquatic; surrounding land-use must be advised on in order to provide suitable refugia. The stocking of ponds must be at an adequate enough level for the population to maintain itself and, ideally, to increase and possibly colonize more sites. In addition, efforts should be made to increase public awareness where crested newts are concerned as has been successfully done in the case of frogs and toads, with the 'Frog Watch' and 'Help a Toad Across the Road' campaigns. With such initiatives it is to be hoped that the crested newt will become substantially more widespread than at present.

At the beginning of this thesis I outlined the areas I wished to investigate and some of the questions I wished to answer. I feel that I have acheived my aims to a large extent, but a number of questions still remain to be answered satisfactorally. The work at Milton Bryan provides a more detailed population study of the crested newt than was previously available for the species in the British Isles, with information gained, in particular, on sex ratios, annual survival and growth of adults and the variation in yearly population size and size-distribution within the population. The data from preserved animals has led to further knowledge about the fecundity of females and the relationship between fecundity and body size. In addition, data from Walton Hall relates migration with climatic factors and shows males to enter breeding sites before females. However, I feel that there is need for more work to be carried out on animals in the period between metamorphosis and first-breeding. This is the least understood phase of the life cycle and yet it is arguably the most crucial. Unfortunately, it is likely to also be the most difficult to study in the field. Possibly the development of microtransmitters will facilitate work in this area. The relationship between size at metamorphosis and size at maturity is also of prime importance as is that between ovum size and offspring fitness. Bell's work on the latter should be repeated here but under more rigourous conditions than he used.

Further work is required on the effect of varying population densities on male reproductive success and male-male competition. In line with this, it would be valuable to identify the various breeding strategies available to males and females and whether switching from one tactic to another occurs in individuals from year to year.

Finally, the question of the age-structure of populations needs to be cleared up if conventional demographic theory is to be successfully applied to this and other species of newt, although this may not be necessary following the introduction of Kirkpatrick's size-related models of demography.

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APPENDIX 1. PLANTS AND ANIMALS FOUND AT MILTON BRYAN AND WALTON HALL.

SUBMERGED/FLOATING
Potamogeton crispus

Nymphaea alba
P. crispus
Lemna trisulca
Ceratophyllum demersum

EMERGENT
Alisma plantago-aquatica
Carex riparia
Sparganium erectum
Epilobium hirsutum
Juncus effusus
J. inflexus
Mentha aquatica
Lycopus europaeus
Rumex sp.

FRINGING
J. inflexus

M. aquatica
L. europaeus
Glyceria sp.
Rumex sp.
Ranunculus repens
R. bulbosus
R. acris
Heracleum sphondylum
Plantago lanceolata
Galium aparine
Anthriscus sylvestris

The main plant species occurring at Walton Hall pond.

INVERTEBRATES
Insecta:
Ephemeroptera sp.
Dixella sp.
Corixa sp.
Ranatra linearlis
Limnophora sp.
Dytiscus marginalis
Enallagma cyathigerum
Coleoptera spp.
Gerris sp.
Chironomid spp.
Crustacea:
Asellus
Cladocera
Copepoda
Mollusca:
Limnaea stagnalis
L. pereger
Planorbis corneus
Oligochaeta
Platyhelminthes

VERTEBRATES
Amphibia:
Triturus cristatus
T. vulgaris
Bufo bufo
Pisces:
Gasterosteus aculeatus
Avies:
Gallinula chloropus
Ardea cinerea
Corvus frugilegus
C. corone
Pica pica
Mammalia:
Microtus agrestis

Invertebrate & vertebrate species observed at Walton Hall pond.

SUBMERGED/FLOATING
Myriophyllum spicatum
Potamogeton natans
excelsior
Ranunculus peltatus

EMERGENT
Equisetum fluviatile
Juncus effusus

Mentha aquatica
Veronica beccabunga

FRINGING
Salix alba
Fraxinus

Picea albies
Galium aparine
Urtica dioeca
Mercurialis perennis
Primula veris
P. vulgaris
Lychnis flos-cuculi
Rosa canina
Crataegus monogyna/
J. effusus
M. aquatica
V. beccabunga

Plant species occurring at Pond 1, Milton Bryan.

INVERTEBRATE
Insecta:
Ischnura elegans
Pyrrosoma nymphula
Lestes spousa
Sympetrum striolatum
Aeshna cyanea
Dytiscus marginalis
Coleoptera spp.
Gerris sp.
Notonecta sp.
Corixa sp.
Chironomid spp.
Trichoptera sp.
Ephemeroptera sp.
Crustacea:
Cladocera spp.
Copepoda spp.
Asellus
Platyhelminth spp.
Oligochaeta spp.
Mollusca:
Planorbis corneus
Pisidium sp.

VERTEBRATE
Amphibia:
Rana temporaria
Bufo bufo
Triturus cristatus
T. vulgaris
Avies:
Anas platyrhynchos
A. crecca
Aix galericulata
Gallinula chloropus
Fulica atra
Falco tinninculus
Strix aluco
Tyto alba
Mammalia:
Oryctolagus cuniculus
Lepus capensis
Sciurus carolinensis
Mustela ermina
Cervus elaphus
Muntiacus reevesi
Bos domesticus

Invertebrate and vertebrate species observed at Milton Bryan study site.

APPENDIX 2. TEST FOR RANDOM CAPTURES USING THE METHOD OF ORIANS AND LESLIE (1958)

The following tests were carried out on three groups of animals caught initially on 14th, 18th and 21st of March 1983 respectively. The full procedure is given by Orians & Leslie (1958).

Symbols used are as follows:

n = numbers recaptured on each occasion
x = number of times each individual recaptured
σ = theoretical variance

Group 1: Initially captured on 14th March 1983

Date	n_i	n_i^2
18 Mar	2	4
21 Mar	1	1
24 Mar	2	4
26 Mar	1	1
28 Mar	1	1
30 Mar	1	1
4 Apr	1	1
8 Apr	3	9
14 Apr	1	1
18 Apr	1	1
22 Apr	1	1
25 Apr	1	1
27 Apr	2	4
7 Jun	1	1
Totals	19	31

x	f(x)	xf(x)	$x^2f(x)$
0	12	0	0
1	8	8	7
2	4	8	16
3	1	3	9
4	0	0	0
Totals	25	19	32

$$\mu = \frac{\sum n_i}{N} = 0.76$$

$$\bar{x} = \frac{\sum xf(x)}{N} = 0.76$$

$$\sum (x - \bar{x})^2 = \sum x^2f(x) - \frac{(\sum xf(x))^2}{N}$$

$$= 17.6$$

$$\sigma^2 = \sum p_i q_i = \mu - \frac{\sum n_i^2}{N^2}$$

$$= 0.71$$

$$\chi^2 = \frac{17.6}{0.71} = 24.79$$ degrees of freedom = 19

$P > 0.1$

Therefore animals are being captured randomly.

Group 2: Initially captured on 18 March 1983

Date	n_i	n_i^2
24 Mar	2	4
26 Mar	1	1
5 Apr	3	9
8 Apr	1	1
11 Apr	1	1
14 Apr	2	4
22 Apr	1	1
27 Apr	1	1
29 Apr	1	1
4 May	1	1
12 May	1	1
3 Jun	1	1
7 Jun	1	1
13 Jun	1	1
Totals	18	28

x	f(x)	xf(x)	$x^2f(x)$
0	23	0	0
1	5	5	5
2	5	10	20
3	1	3	9
Totals	34	18	34

$$\mu = \frac{\sum n_i}{N} = 0.529$$

$$\bar{x} = \frac{\sum xf(x)}{N} = 0.529$$

$$\sum (x - \bar{x})^2 = \sum x^2 f(x) - \frac{(\sum xf(x))^2}{N}$$

$$= 24.47$$

$$\sigma^2 = \mu - \frac{\sum n_i^2}{N^2} = 0.505$$

$$\chi^2 = \frac{24.47}{0.505} = 48.45 \qquad \text{degrees of freedom} = 18$$

$P < 0.001$

Therefore, in this case, animals are not being caught randomly.

Group 3: Initially captured on 21st March 1983

Date	n_i	n_i^2	Date	n_i	n_i^2
26 Mar	3	9	25 Apr	4	16
28 Mar	3	9	27 Apr	1	1
5 Apr	2	4	29 Apr	1	1
8 Apr	4	16	2 May	2	4
14 Apr	5	25	4 May	1	1
18 Apr	5	25	6 May	1	1
20 Apr	1	1	15 Jun	1	1
			Totals	34	78

x	f(x)	xf(x)	$x^2f(x)$
0	21	0	0
1	14	14	14
2	7	14	28
3	2	6	18
4	0	0	0
Totals	44	34	60

$$\mu = \frac{\sum n_i}{N} = 0.773$$

$$\bar{x} = \frac{\sum xf(x)}{N} = 0.773$$

$$\sum (x - \bar{x})^2 = \sum x^2 f(x) - \frac{(\sum xf(x))^2}{N}$$

$$= 33.73$$

$$\sigma^2 = \mu - \frac{\sum n_i^{\,2}}{N^2} = 0.733$$

$$\chi^2 = \frac{33.73}{0.733} = 46.02 \quad \text{degrees of freedom} = 34$$

$P > 0.05$

Therefore, animals are being caught randomly.

APPENDIX 3

Calculation of crested newt survival using Jolly´s method.

For an explanation of the equations used in these calculations see the texts previously referred to in Chapter 3 section 2.

Calculation of male crested newt survival:

Arrangement of the raw capture data for male crested newts for 1980 to 1983 as a Jolly trellis produces the table shown below.

YEAR	CAPTURES (n_i)	RELEASES (r_i)	TIME OF RELEASE OF MARKS (j) 1	2	3	4
			recaptured marks (m_{ij})			
1	134	134	-	-	-	-
2	264	264	8	-	-	-
3	165	165	3	33	-	-
4	445	445	2	15	41	-

Using Jolly´s method this may be rearranged as:

YEAR	r	m	y	z
1	134	-	13	-
2	264	8	48	5
3	165	36	41	17
4	445	58	-	-

It is now possible to calculate the number of marks at risk in the population on any particular sampling occasion using the following equation:

$$\hat{M}_i = m_i + \frac{z_i \times r_i}{y_i}$$

Substituting from the above table we obtain:

$\hat{M}_2 = 35.5$ and $\hat{M}_3 = 104.4$

It is now possible to calculate the survival of these marks from one sampling occasion to the next using the following equation:

$$\hat{\theta}_i = \frac{\hat{M}_{i+1} + 1}{\hat{M}_i - m_i + r_i}$$

Thus we obtain:

$\hat{\theta}_2 = 0.36$

which means that between 1980 and 1981 animals had a survival rate of 0.36.

The error measurement for the survival rate is obtained from the equation:

$$SE_{\hat{\theta}_i} = \hat{\theta}_i \left\{ \frac{(M_{i+1} - m_{i+1})(M_{i+1} - m_{i+1} + r_{i+1})}{M_{i+1}} \left(\frac{1}{y_{i+1}} - \frac{1}{r_{i+1}} \right) \right.$$
$$\left. \frac{M_i - m_i}{M_i - m_i + r_i} \left(\frac{1}{y_i} - \frac{1}{r_i} \right) \right\}^{1/2}$$

from which we may calculate:

$SE_{\hat{\theta}_2} = 0.06$

Calculation of female crested newt survival:

Using the above argument for females we obtain the following:

YEAR	CAPTURES	RELEASES	TIME OF RELEASE OF MARKS (j)			
	(n_i)	(r_i)	1	2	3	4
			recaptured marks (m_{ij})			
1	43	43	-	-	-	-
2	227	227	4	-	-	-
3	63	63	1	19	-	-
4	394	394	4	23	19	-

This rearranges to:

YEAR	r	m	y	z
1	43	-	9	-
2	227	4	42	5
3	63	20	19	27
4	394	46	-	-

We may then calculate that:

$\hat{M}_2 = 27.1$ and $\hat{M}_3 = 90.6$

from which we obtain:

$\hat{\theta}_2 = 0.36$ and $SE_{\hat{\theta}_2} = 0.076$

$\hat{M}_i$ = no. of marked animals at risk in population in year i.

m_i = no. of marked animals caught in year i.

r_i = no. of marked animals released in year i.

y_i = no. of animals marked (and released) in year i and caught again subsequently.

z_i = no. of animals marked before year i, not caught in year i, but caught again subsequently.

$\hat{\theta}_i$ = proportion of year i population surviving until year i+1.