The migrations and terrestrial habitat utilisation of a population of great crested newts, triturus cristatus. at little wittenham wood, Oxfordshire

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The Migrations And Terrestrial Habitat Utilisation Of A Population Of Great Crested Newts, *Triturus cristatus*, At Little Wittenham Wood, Oxfordshire

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SUMMARY

The aims of this study were to evaluate the population size of *Triturus cristatus*, and investigate the density and distribution of the species during the terrestrial phase, at a lowland woodland site in Oxfordshire.

Barrier fencing lined with pitfall traps at intervals were used to capture newts migrating to and from a breeding pond and to sample migating individuals 122m from the pond. In addition, barrier fence enclosures 1450m^2 in area were set in grassland, deciduous woodland, and conifer plantation areas at distances of 100, 200, and 300m from the breeding pond, inorder to sample the over-wintering density. Captured animals were "marked"(photo of the ventral spot pattern).

The population using the breeding site was large (in excess of 1100 males and females), stable, and successfully produced a large cohort of post-metamorphic young in 1988. There were significantly more males than females. A shift in the population size structure was observed between the autunm emigrating population in 1988 and the spring immigrating population in 1989. Prefered routes of arrival and departure from the pond area were indicated.

It was found the population utilised a large area of surrounding habitats during the terrestrial phase. It was estimated 41% of the Top pond population migrated a distance of more than 122m in the autumn 1988. 1989 data, indicated 54% of

the population over-wintered over 122m from the pond. During dispersal,prefered routes of migration were indicated. 10.4% of marked individuals captured at outer fences during dispersal in 1988 were subsequently recaptured at the same location in the winter/spring of 1989.

Arable farmland was not used for over-wintering. There was however, an apparent preference shown for deciduous woodland blocks. These areas, on comparable soil types, supported higher numbers of over-wintering *T. cristatus* relative to conifer blocks and rank grassland/open areas. The abundance of surface lying dead wood was related the number of *T. cristatus* sampled in terrestrial areas.

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Introduction

Triturus cristatus is one of six amphibian species native to Britain. It is of the order Urodela and a member of the *Triturus* genus, which are widely distributed in North America and Europe (Smith, 1969). *Triturus cristatus* is the largest of all European species of newt and returns to the water at the end of winter to breed. *T. cristatus* is distributed over most of Europe but does not occur in southern and south west France, Iberia, South Greece, Ireland and the Mediterranean Islands (Arnold & Burton, 1978). Within the United Kingdom *T. cristatus* is present throughout most of England, where it is local and rather uncommon. It is absent and or rare in Cornwall and Devon and most of Wales and Northern Scotland (Cooke & Scorgie, 1983; Nicholson 1986).

The status of *T. cristatus* is classified as vulnerable (Nature Conservancy Council, 1989) in the U.K.. It is considered sufficiently endangered in Europe to warrant inclusion as a strictly protected species in Appendix 2 of the Berne Convention (1979). As a result of the U.K. ratifying this convention *T. cristatus* was included as a fully protected species in Schedule 5 of the Wildlife and Countryside Act (1981).

Since the war all British amphibians have probably declined in abundance (Nicholson, 1986; Beebee, 1973; Prestt, Cooke, and Corbett; Cooke and Scorgie, 1983). Beebee (1975) estimated that during the preceding decade there was a 50% loss of *T. cristatus* breeding ponds nationally. Agricultural intensification was highlighted as the main threat. By the 1980's, although agricultual and urban development were still the main cause of the breeding site destruction, the intensity of the decline was at a much reduced level, 2% a year. Moreover, the main percieved threat was from neglect of ponds and natural hydroseral succession (Nicholson, 1986).

Oxfordshire appears to have a higher than average occurrence of T. cristatus. Post-1970, there are 56 known records of T. cristatus sites in Oxfordshire (Coldrey & Campbell, 1983; Bell, 1979; D.Walker personal communication [pers. comm.]). In a systematic survey of 55 ponds, T. cristatus was present at 25% of sites in 1989 (D. Walker, pers.comm). A study of the ecology of Trituris vulgaris near Abingdon between 1971-73, found T. cristatus present in 65% of the 35 ponds surveyed (Bell, 1979). By comparison, 15% of 811 surveyed sites harboured T. cristatus in a national survey based on questionaires sent to correspondents (R. Oldham & M. Swann, pers. comm.).

Most research on amphibia has emphasised the importance of the breeding site, but they also require suitable terrestrial habitat. T. cristatus spend much of their annual time budget on land, and there is a urgent need to understand there specialised habitat requirements if, the quality of conservation advice is to be improved (Oldham, 1989). Little is known of the ecology, behaviour and dispersive abilities of T. cristatus in the terrestrial phase. Much of the information available derives, from incidental observation rather than quantitative studies (Fraser, 1983) with a few exceptions (Cooke 1986; Nicholson, 1986; Amtkjaer, 1981). The princeple reason for this is the difficulty of studying widely dispersed, nocturnally active populations.

This study sets out to examine the dispersive abilities and habitat preferences of a single population in detail. The study site lies within a large nature reserve and the aims were to aquire baseline information to allow the site to be enhanced or at least managed without detriment to the *T. cristatus* population. Specific objectives were to investigate the population size and status, and the extent to which the population was able to utilise contrasting habitat types surrounding the site.

T. cristatus's relatively low mobility and the congregation at the breeding site means the population size is best assessed in the aquatic phase. There are 4 main methods of censusing newts during the aquatic period, survey by torchlight count (e.g. Cooke, 1986; Nicholson, 1986), capture by underwater funnel trap (e.g. Griffiths, 1985; Nicholson, 1986), capture by pond net (e.g. Hagstrom, 1979). The practical advantages and disadvantages are listed in a British Herptelogical Society guide (1987). The fundamental disadvantage of the above methods is their reliability. Their efficiency may vary according to the particular biotic, climatic, physical, and chemical characteristics of the water body aswell as with the behaviour pattern of *T. cristatus*.

Surrounding the perimeter of a breeding site with barrier fencing, and lining it at intervals with pitfall traps, is a widely used alternative method in amphibian ecology (Phillips & Sexton, 1989; Robinson, 1977; Twitty, 1967; Reading, 1989; Jackson & Tyning, 1989; Nicholson, 1986; Podloucky 1989; Verell & Halliday, 1985; and Amtkjaer, 1981) and overcomes the deficiencies of the above methods. An absolute population estimate may be achieved by counting individuals leaving and entering. Trapping also, provides information on population dynamics. The practical constraint of this technique is that, it is time consuming and requires relatively expensive fencing materials.

The subject of habitat utilisation by amphibians has been approached using several techniques; radio tracking ; mechanical tracking (Sinsch, 1989), the enclosure of selected habitats (Oldham, pers. comm.); pitfall traps (Strijbosch, 1980; Cooke, 1986) and drift fencing with pitfall traps (Nicholson 1986; Bell 1979). T. cristatus has not been successfully radio-tracked despite recent attempts using 1.5g transmitters (Nicholson, 1986) due to the animals low mean weight of around 7-9 g. The maximum recommended ratio of transmitter weight to animal weight is 10% (Hutchison, 1987).

The terrestrial phase of adult T. cristatus may be separated into a sequence of 4 periods: 1) dispersal from the breeding site in the late summer, 2) foraging 3) hibernation overwinter, 4) migration to the pond. In this study, pitfall traps with drift fences are used to investigate periods 1,2,3,and 4. Enclosures of selected habitats have been adopted to provide information on 3.

To follow the ranging of individuals on land and to prevent recapture data from distorting estimates of population parameters, "marking" has also been undertaken. Several marking techniques used on other vertebrates are not applicable, for long and medium term studies of amphibians. The efficiency of recognition of clipped toes diminishes after 10 weeks because of the ability of Urodela to rejuvenate limbs (Nicholson, 1986; Robinson, 1977). Tagging and ringing is also unsuitable as a consequence of the flexible skeleton and regular shedding of skin. Other techniques, include dye marking (Hutchinson, 1987) suturing glass beads to the tail (Phillips et al, 1989) and the grafting of coloured skin from the belly to the dorsal area (Plytycz & Bigaj, 1984; Zuiderwijk & Sparreboom, 1986).

In this study recognition of individuals is based upon photorecords of their unique belly spot pattern (Hagstrom, 1973; Robinson, 1977; Nicholson, 1986; Amtkjaer, 1981). This method is relatively reliable, involves a simple precedure and does not require phyical deformity of the animal, nor act as a potential predator attractant.

STUDY AREA

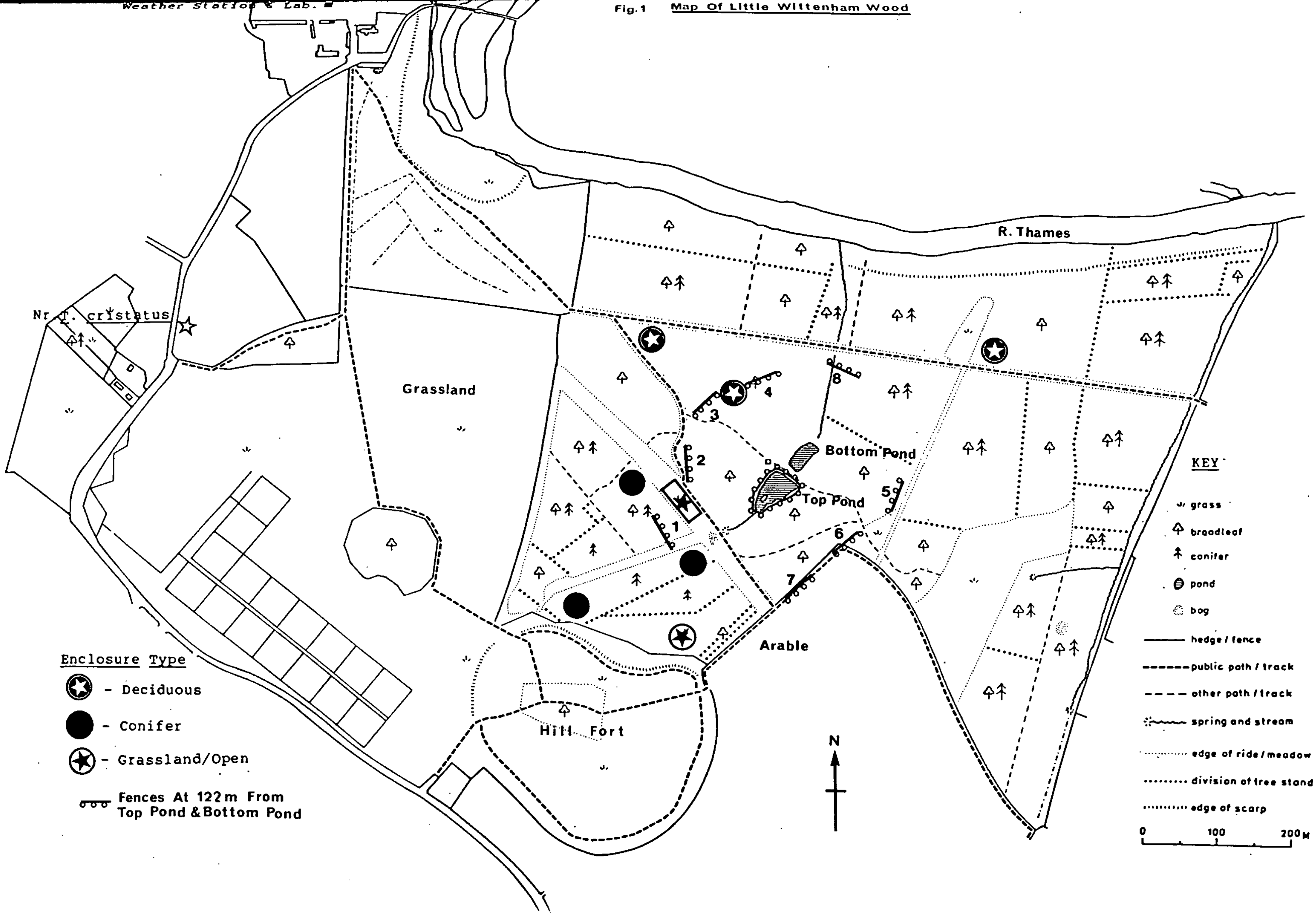
The study area (Fig 1) consists of two adjacent *Triturus cristatus* breeding ponds, the "Top" and "Bottom" Pond and surrounding land up to a distance of 350m. Nearly, the whole area lies within Little Wittenham Wood which is part of Little Wittenham Nature Reserve and owned by the Northmoor Trust. A portion of the study area to the east belongs to the neighbouring farm.

Little Wittenham Wood is 55 hectares (ha) and is situated 3 miles northwest of Wallingford and 12 miles south of Oxford (Ordenance Survey, O.S., grid reference, G.R., SU 573927). The wood is borderded by arable land on the east, permanent grassland on the west and the River Thames to the north. The south end of the wood borders an iron age hillfort with rank grassland on the ramparts and a haymeadow on the central plateau.

FEATURES OF LITTLE WITTENHAM WOOD

Typography:	North slope of the Sinodun Hills
Aspect:	NNE
Slope:	General gentle slope of about 1:22
Altitude:	Ranges from 48m in the N.E. corner and 105m in the S.E. corner.
Climate:	Wallingford (W), mean rainfall 664mm and Didcot, 680mm (Smith, 1976; Jarvis, 1973)
Wettest Months:	August and September (W)
Driest Months:	Febuary and March (W)

Fig.1 Map Of Little Wittenham Wood



Maximum Mean : Monthly Temp.	16^{o}c June (W)
Minimum Mean : Monthly Temp.	3^{o}c January (W)
Geology:	See Fig 2
Soils:	See Fig 3
Soils pH:	See Fig 4
Stand Types:	See Fig 5

HISTORY OF THE WOODLAND

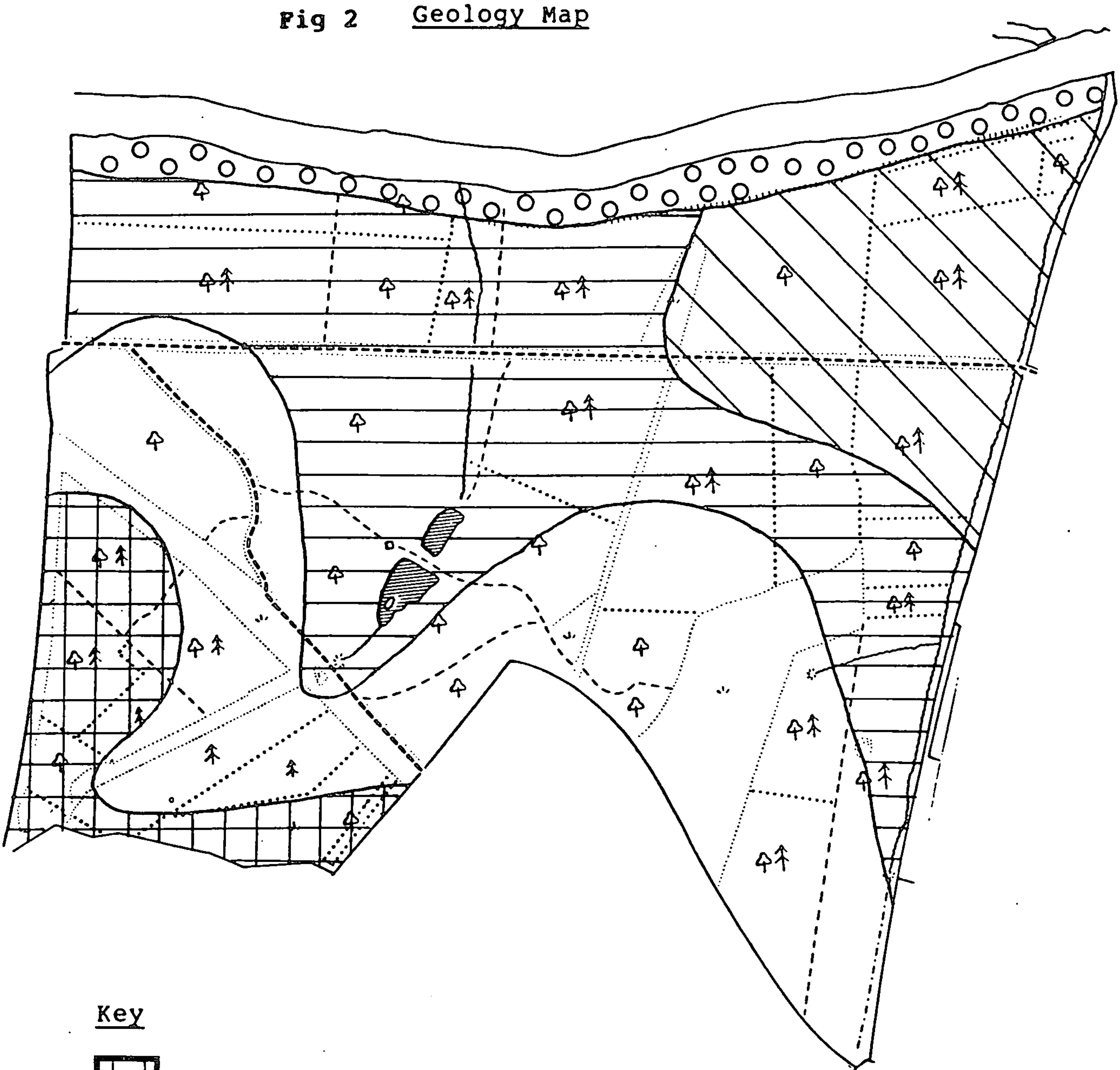
The exact age of the wood is uncertain. The first records certifying its existence are dated 1761. Parts of the site were previously cultivated and these were probably planted in the 17th or 18th century. Other parts of the wood may be much older either primary or ancient secondary woodland (Sandels, 1983).

The wood was managed as coppice with standards til about 1920, and as a sporting and timber woodland afterwards. Plantations of conifers and mixed stands with conifers were established in about half the woodland during the 1950´s and 1960´s (Sandels, 1983).

THE BREEDING SITE

The *T. cristatus* breeding sites the study is focused upon, consist of two large stable ponds 10m from each other, sharing the same water source. Their present use is as a wildlife conservation feature and in keeping with this function, minimal management is undertaken. Based upon the macro-invertebrate assemblage, the Top Pond and Bottom pond have been classified as

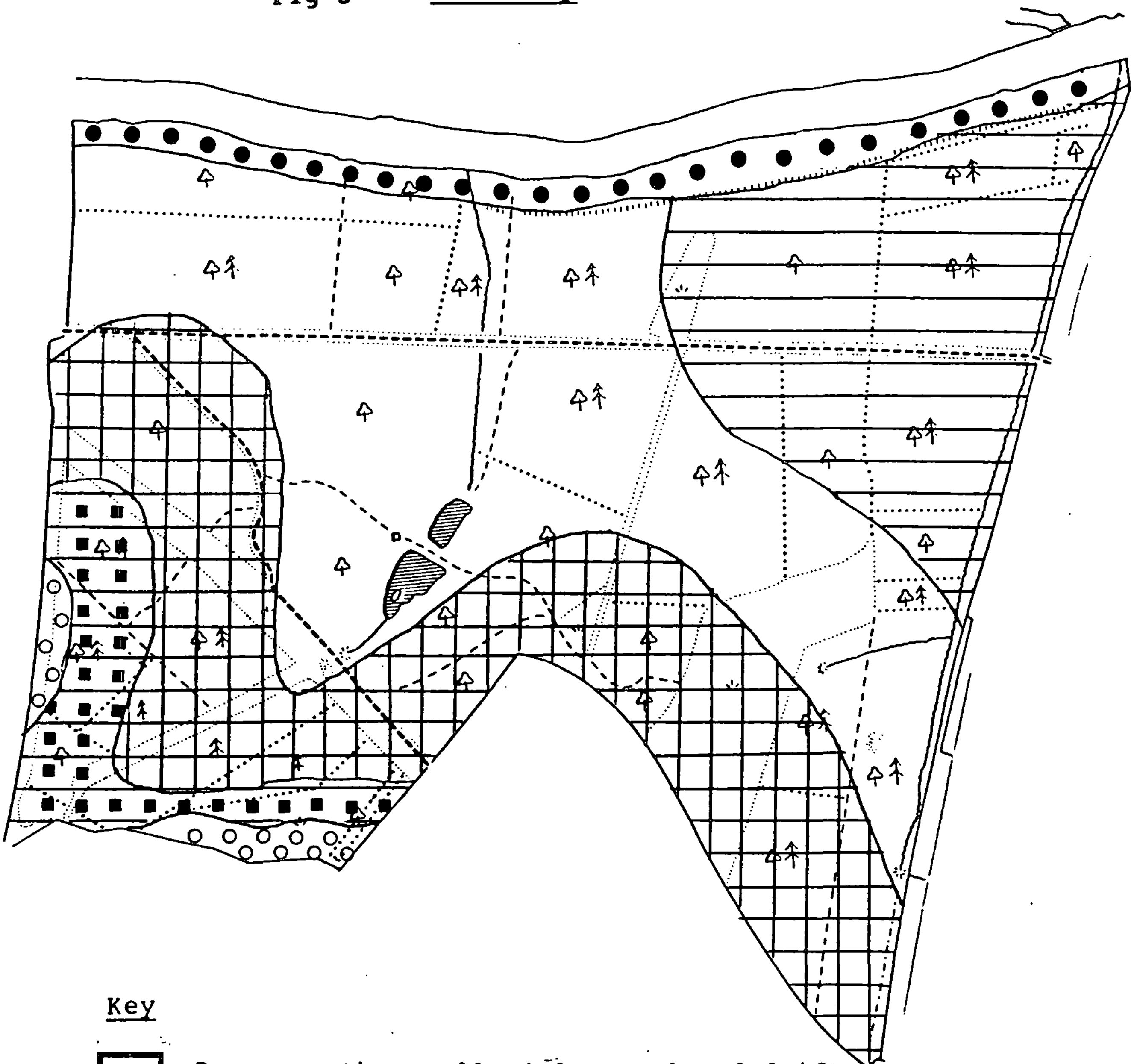
Fig 2 Geology Map



Key

- Lower Chalk
- Gault Clay
- Valley Gravel
- Alluvium
- Upper Greensand

Fig 3 Soils Map



Key

Brown earth on alluvial gravel and drift

Brown earth

Brown calcareous soil (< 40cm deep)

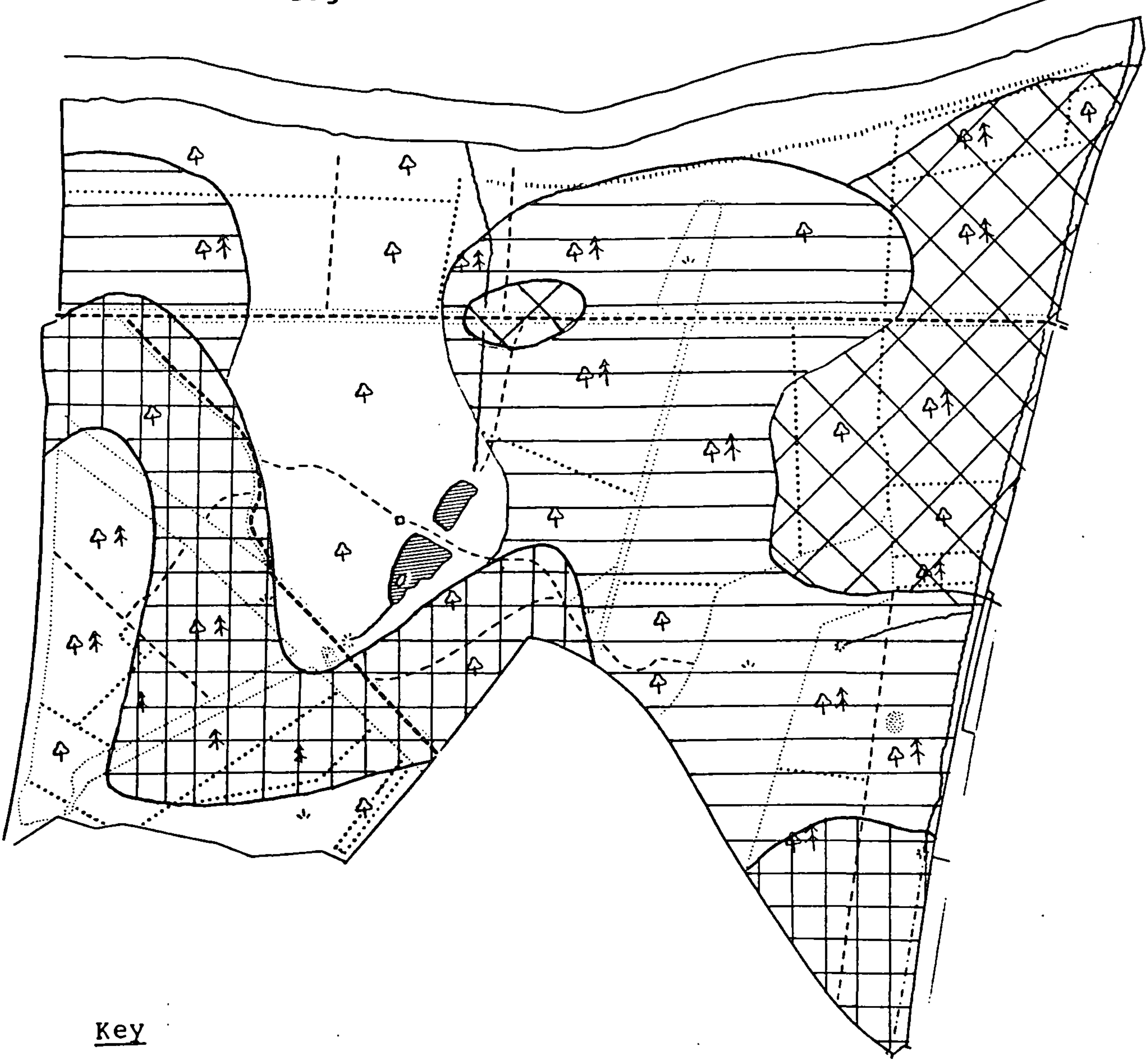
Brown calcareous soil (> 40cm deep)

Gleyed brown earth : surface water gley

Alluvial soil

Ref. Sandel,1983

Fig 4 Soil ph Map



Key

- ph 6 - 7
- pH 5.3 - 6
- pH < 5.5
- pH > 7

Ref. Sandel,1983

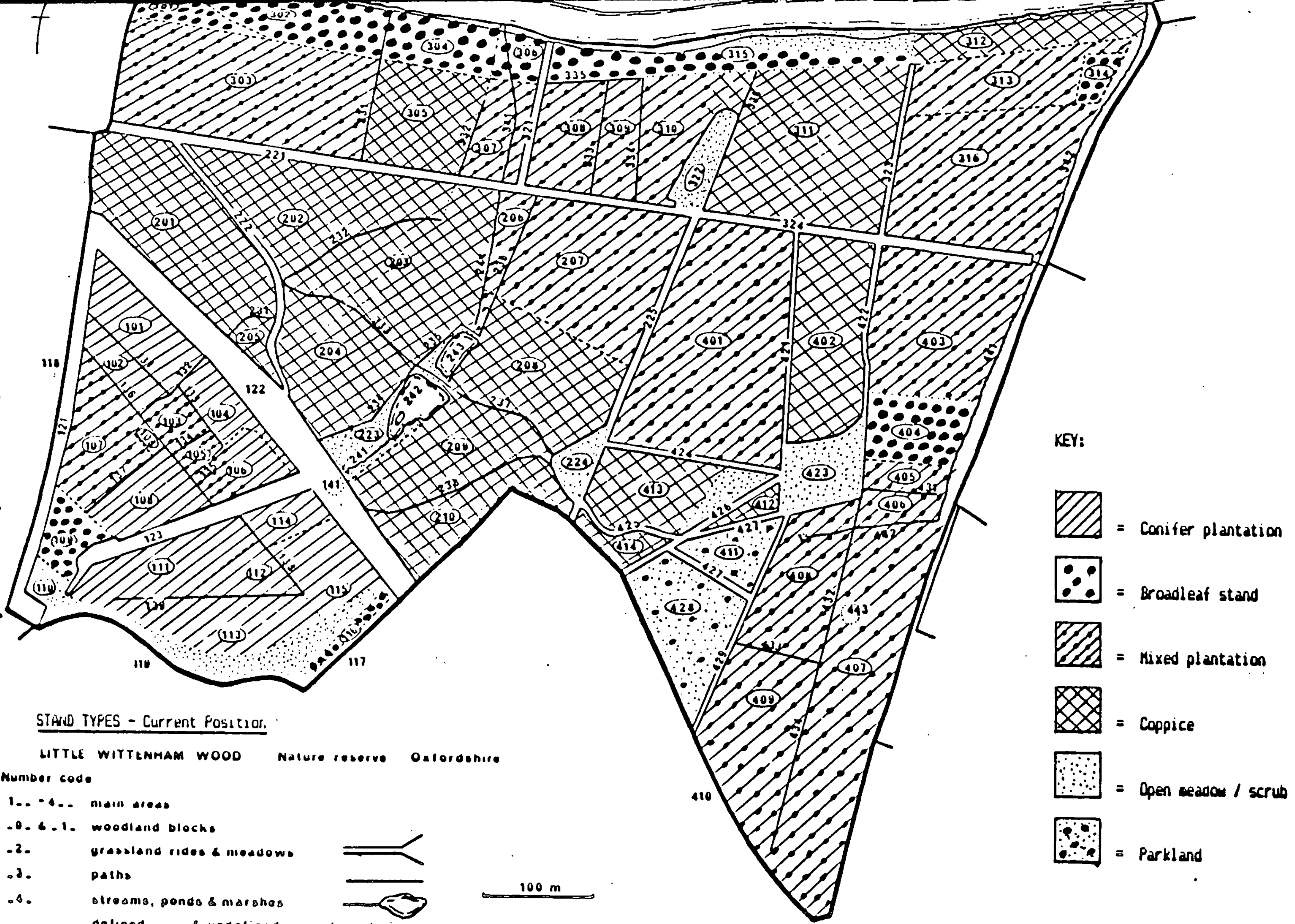


Fig 5 STAND TYPES - Current Position

LITTLE WITTENHAM WOOD Nature reserve Oxfordshire

Number code

1.. - 4.. main areas

.0. & .1. woodland blocks

.2. grassland rides & meadows

.3. paths

.4. streams, ponds & marshes

defined ---- & undefined .... boundaries of intermediate and low conservation value, respectively, in relation to a large sample of Oxfordshire ponds (D. Walker, pers. comm.).

Physical, chemical and biological features are listed below.

PHYSICAL FEATURES

	TOP POND	BOTTOM POND
LOCATION (Grid Ref.)	SU573927	SU573938
GEOLOGY	Gault Clay	Gault Clay
MAIN WATER SOURCE	VIA STREAM FROM A SPRING	OVERFLOW PIPE FROM TOP POND
PERIMETER (m)	180	120
ESTIMATED (EST.) SURFACE AREA (m^2)	1550	1010
MAXIMUM DEPTH (m)	1.5	1.8
MEAN DEPTH OF SEDIMENT (cm) RANGE	14.3 (1-62)	7.3 (2-29)
EST. FLUCTUATION OF WATER LEVEL (m)	0.5	0.4
SHADE FROM OVERHANGING TREES	See Fig 7	

CHEMICAL FEATURES

	TOP POND	BOTTOM POND
pH	7.58	7.14
DISSOLVED OXYGEN (%) RANGE OVER 48hr	35-100*	8-30*
ALKALINITY (m eq/l)	2.30	3.67
FREE CO2 (mM/l)	0.14	0.64
CONDUCTIVITY (micro siemens/cm)	376	464
SULPHATE (mg/l)	16.3	12.5
CALCIUM (mg/l)	48.2	68.0
MAGNESIUM (mg/l)	2.90	3.48
SODIUM (mg/l)	11.6	12.6
SULPHUR (mg/l)	12.5	10.1
SILICON (mg/l)	14.6	9.80
POTASSIUM (mg/l)	3.32	4.01
PHOSPHORUS (mg/l)	0.04	0.17
IRON (mg/l)	0.05	0.06

* O_2 RECORDED TOP POND 1-2 JULY 1989
  BOTTOM POND 3-4 JULY 1989

WATER SAMPLES FOR CHEMICAL ANALYSIS WERE COLLECTED ON 7 JULY 1988 BY "POND ACTION".

BIOLOGICAL FEATURES

	TOP POND	BOTTOM POND
VERTEBRATES		
BIRDS		
Tachybaptus ruficollis	+*	+*
Aythya fuligula	+*	+*
Anas platyrhynchos	+*	+*
Gallinula chloropus	+*	+*
Ardea cinerea	+	
Alcedo atthis	+	
MAMMALS		
Neomys fodiens	+	
Rattus norvegicus	+	+
Mustela vison	+	+
REPTILES		
Natrix natrix	+	+
FISH		
Carassius auratus	+	
(C. auratus x C. carassius)	+	
AMPHIBIA		
Bufo bufo (Est. No.)	1000-2000	2000-4000
Rana temporaria (Est. No.)	>100	>100
Triturus cristatus	+	+
Triturus vulgaris (Est. No.)	100-500	100-500

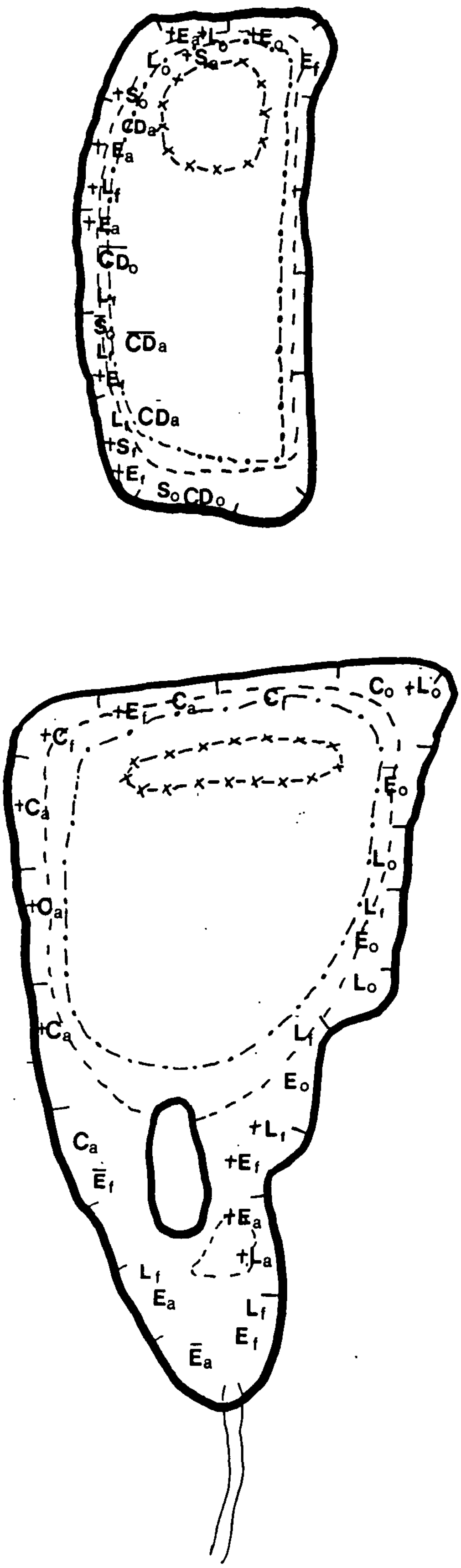
MACRO-INVERTEBRATES See Appendix 1

VEGETATION

	TOP POND	BOTTOM POND
MARGINAL AND EMERGENT	See Fig 6	
AQUATIC		
Lemna trisulca	+	+
Lemna minor	+	+
Potamegeton pectinatus	+	
Elodea canadensis	+	
Stratiotes aloides	+	
Charaphyta spp.	+	

+ Species/group present
+* Bird species which nest and feed

Fig 6 **Marginal And Emergent Vegetation Of The Wittenham Wood Ponds**



Key

Water Depth

0.5 - 1.0m
1.0 - 1.5m
1.5 - 2.0m

10m Suvey Unit

"DAFOR" Index Of Abundance For ssp. Per Survey Unit

a - abundant
f - frequent
o - occassional

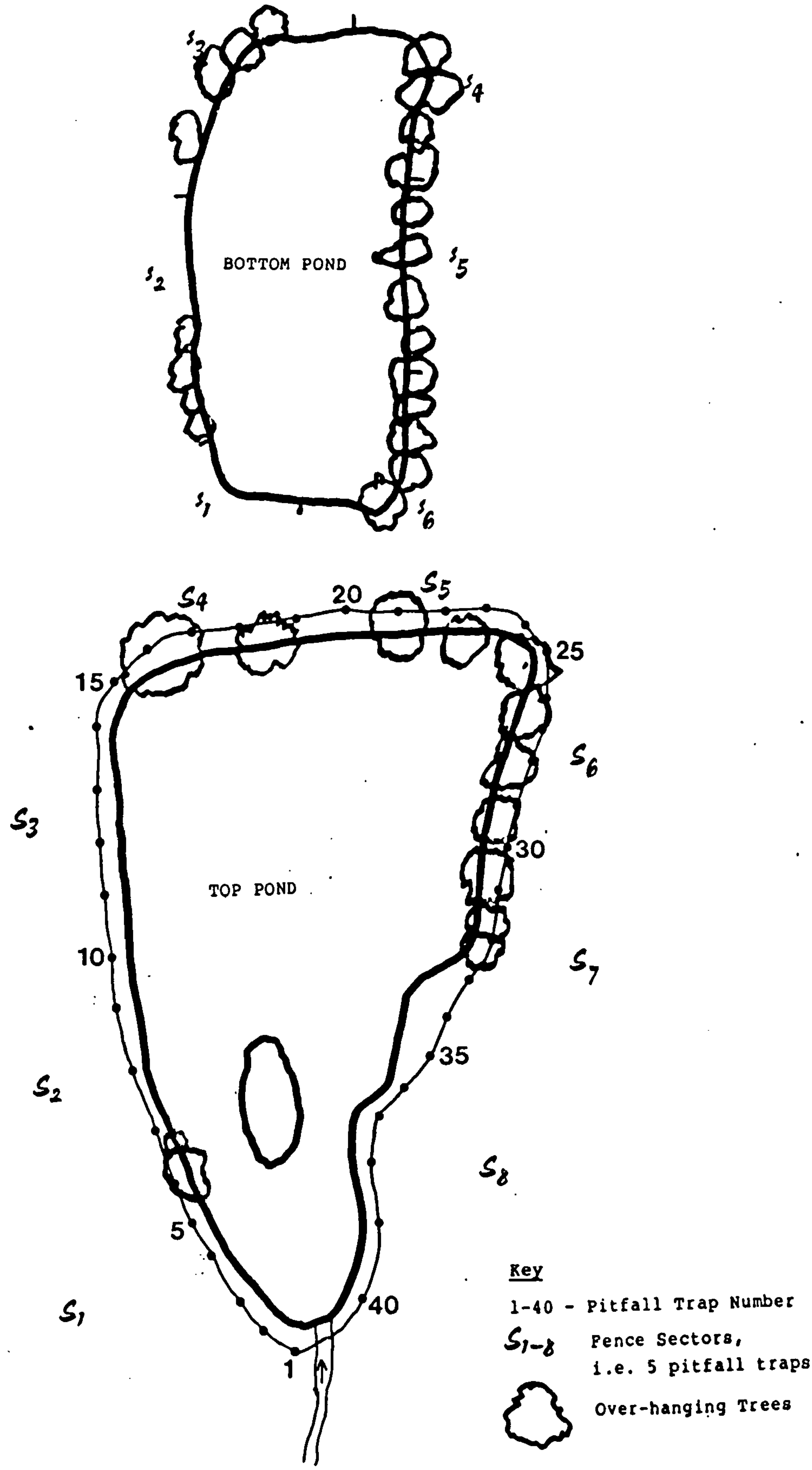
Status

Ē - Marginal
+E - Emergent And Marginal
E - Emergent

Species Per Survey Unit

E - *Epilobium* spp.
C - *Carex riparia*
L - *Lycopus europeaus*
CD - *Carex distans*
S - *Solanum dulcamara*

Fig 7 Postion Of Pitfall Traps And Over-hanging Trees



History of the Ponds

The ponds first appear in records on a 1842 map (Table 1). The shape of the ponds on map suggests the north side of the Top pond was dammed, indicating that the ponds were probably either man-made or, natural and then extensively modified. The precise function of the ponds is unknown. During the remainder of the century, the ponds reverted to marshland and woodland. Tree stumps present in the ponds today, confirm this fact. By 1933 the area was completely wooded over. However the pond area has a stream running through it and it is possible, pools of water too minor to include on Ordenance Survey (O.S.) maps survived when the woodland encroached. The ponds were recreated into their present form in 1969/70.

Table 1

Historical records of the Top and Bottom Ponds

DATE	STATUS	SOURCE
1842	2 LARGE PONDS WITH CAUSEWAY EVIDENT	TITHE AWARD MAP
1877	WETLAND/MARSH	O.S. 1ST EDITION OXON XLVI 25 INCH
1899	WETLAND/MARSH	O.S. 2ND EDITION OXON XLVI 25 INCH
1933	WOODLAND	O.S. 3RD EDITION OXON XLIXI 25 INC
1969	WOODLAND	AERIAL PICTURE
1970	2 PONDS WITH CAUSEWAY IN BETWEEN	AERIAL PICTURE
1982	NORTHMOOR TRUST AQUIRES THE WOOD	

Triturus cristatus Population

Records of the breeding population in the woodland ponds date back only to 1983. There are 22 terrestrial records for the species between 1983-1987, most originating from an invertebrate trapping programme. Juvenile and adult specimens have been recorded upto 500m from the breeding ponds, in the hillfort area.

In spring 1987 a maximum torchlight count of 197 animals was obtained for both ponds. However, only 1/3 of the perimeter was accessible for counting (R.D. Buxton, pers. comm.)

The nearest existing breeding site lies northwest, 0.9 km from the Top Pond (O.S G.R.565930). The population size is unknown, however, the pond is speculated to be several centuries old. It is plausible that far ranging individuals from this pond may have colonised the the woodland ponds after they were recreated in 1970. Alternatively, a relict population could have existed in the woodland in an unmapped small pool, that disappeared with the construction of the present ponds.

METHOD

FENCE MATERIALS

Lengths of low drift fencing (Oldham,1989) in conjunction with with pitfall traps were used to capture *T. cristatus* rangeing on land. The fencing acts as a barrier, interrupting the passage of the newt. In seeking to make progress in the forward direction, the newt will usually follow the inside of the fence looking for a gap and thus, be guided into a pitfall trap arranged at intervals inside the fence.

The fence arrangement was designed to capture newts on only one side. The drift fencing had a width of 25cm and was constructed of plastic netlon greenhouse shading with a 3mm diamond mesh and a width of 25cm. To prevent access under or over the fence, it was dug into the soil to a depth of approximately 3 - 5 cm and a 2 cm overhang was incorporated. The overhang was held in place by 7 cm lenghts of plastic coated wire weaved through the netlon mesh at close intervals. The fence was supported by wooden stakes at intervals of about a one metre.

The effectiveness of the fencing as a barrier was tested. A small square trial enclosure (0.7m x 0.7m) was erected out of the material. In three trials beginning on the 10 June 1988, 10 adults captured in funnel traps (Griffiths, 1985) were placed in the enclosure in the morning. After 24 hours, the enclosure was inspected and no adult *T. cristatus* escaped in the 3 trials.

Five similar trials were undertaken between 13-29 September each with, instead, a sample of 10 recently metamorphosed newtlets captured emerging from the Top pond.

Table 2

% Of Newtlets Retained In Small Trial Enclosure

TRIAL	DATE	NO.	% RETAINED
1	13/9	10	70
2	16/9	10	50
3	21/9	10	80
4	27/9	6	33
5	28/9	10	80
			63

The results (Table 2) show the mean percentage of newtlets retained for 24 hours was 63 %. As a result of these trials, it was concluded the drift fencing acted differentially as a barrier to newtlets and to adults. The difference was mainly attributable to the size difference, and its affect on climbing ability and gap penetration. In calculations later it is assumed the fence is 100% and 65% effective at retaining adult and juveniles repectively.

PITFALL TRAPS

Metal pitfall traps of 14.5cm diameter and 15cm depth were located at intervals along the side of the fence recieving the expected migration movement. Each trap was numbered and emplaced such that the rim of the top was level with the ground surface.

No bate was required. Traps were visited each morning.

Trials were undertaken to evaluate the effectiveness of the traps at retaining individuals and also the degree to which *T. cristatus* was prone to predation whilst in pitfall traps. On the 30 March 1989, 20 adults had their belly pattern recorded and were placed individually in traps surrounding the study pond overnight. By comparison with the belly pattern records the loss by escape and predation was determined the next morning. Similar trials were repeated on the 2 and 17 April 1989 with 10 and 8 adults, respectively.

In the 3 trials no losses were recorded by either escape or predation and no injury was observed. In this study, it is assumed that losses of adults between the time of capture in pitfall traps and their collection in the morning were negligible. However, it is noted that in general, for some predators the pattern of hunting changes with factors such as food availability over the seasons. Also, being poikiotherms, newt activity was observed to be higher in late summer/early autumn in response to the ambient temperature and generally improved condition. Together, these factors may affect the amount of predation and the rate of escape during the late summer emmigration and trials during this period would have been conclusive.

ASSUMPTIONS RELATING TO THE SAMPLING TECHNIQUE

Below is a list of the main assumptions relating to the use of drift fencing and pitfall traps.

1) Adult _T. cristatus_ arriving at a drift fence are guided into the nearest pitfall traps.

2) Individuals pitfall trapped were attempting to cross to the far side of the fence and travel away from it. Hence, _T. cristatus_ were released 1 - 2m from the place of capture on the far-side of the fence to allow them to continue in the direction of travel they were taking before capture.

3) The affects on the behaviour, reproduction, and survival of individuals, of interception by the fencing, capture in pitfall traps and the precedures of weighing, measuring and recording the belly pattern, are unknown and difficult to assess. In this study they are assumed to be negligible.

4) Drift fencing on the side with the overhang is 100% efficient as a barrier to adults and only 65% efficent to newtlets.

5) The occurrences of escape from pitfall traps are insignificant.

LOCATION AND DURATION OF TRAPPING

Pond Area

Monitoring of _T. cristatus_ in the aquatic phase in May 1988 by torchlight counts and funnel traps (Duff, 1989) suggested both Top and Bottom ponds held sizeable populations. Top pond was selected for encirclement by dift fencing because of its location closer to a variety of terrestrial habitats, namely arable farmland, the main conifer area, and rough grassland areas. Encirclement began on the 22 June and was complete by the 17 July. The fence was set between 1-2.5 m from the pond edge and was arranged to sample individuals emmigating from the pond area with the pitfall traps positioned inside the fence at 5 m intervals. The 40 pitfall traps that surrounded the pond were labelled 1-40 (Fig 7). The traps were lifted in December and the fence overhang removed following the last movements from the pond.

In Febuary 1989 the fence was adjusted to capture T. cristatus returning to the pond from surrounding terrestrial hibernation sites. Pitfall traps and the overhang were positioned on the opposite side of the fence to that used in the autumn trapping period. Pitfall trapping was ended on 6 May 1989.

Line Fences 122 m From The Ponds

In the autumn of 1988, 5 drift fences were spaced at intervals around the ponds to form an incomplete ring at a mean distance of 122 m from the pond (Fig 1). A shortage of time prevented the full plannned complement of 8 fences, labelled F1 - F8, from being completed until the spring. Natural and man-made obstacles, plus the difficulty of making the precise measurement of long distances in dense woodland resulted in pond-fence distances varying by up to 10m.

Table 3

Date 35m long sample fences became operational

Fence	Date of Erection	Trapping Periods	
F1	6.8.88	A/S	A = Autumn
F2	9.8.88	A/S	S = Spring
F3	11.8.88	A/S	
F4	1.9.88	A/S	
F5	20.9.88	A/S	
F6	17.2.89	S	
F7	24.2.89	S	
F8	24.2.89	S	

Figure 1 shows the location of the fences. Each fence was 35.5m long and lined with 8 pitfall traps at regular intervals. The fences were postioned at right angles to a straight line drawn between the mid-point of the fence and the nearest point of the pond. In the autumn the fences were arranged to intercept *T. cristatus* dispersing from the study ponds and in spring they were arranged to catch individuals moving in the opposite direction.

Terrestrial Enclosures

Large circular terrestrial enclosures were constructed out of dift fencing in January and Febuary, inorder to evaluate the number newts per unit area overwintering in different habitat types. It was planned to erect 3 enclosures in each of the 3 habitat types deciduous woodland, conifer plantation, and open/grassland areas. Within each habitat type an enclosure was located at a distance of 100m, 200m and 300m from the breeding ponds (Fig 1). However, early emergence from hibernation excluded the construction of an enclosure at 300m in a open/grassland area.

Enclosures were labelled according to the distance in metres from the ponds (i.e. 100, 200, and 300) and the habitat types. The latter were abbreviated to G, C, and D for grassland/open, conifer and deciduous woodland areas, respectively.

Each enclosure had a radius of 21.5m giving a perimeter of 142m and an area of approximately 1450 m^2. The size of the enclosure was determined in relation to the results of other studies. In the 4 sites considered by Nicholson (1986), the estimated densities of T .cristatus occupying the zone within 250 m of the breeding ponds was 1 newt per 200 m^2, 1 per 80m^2, 1 per 500m^2, and 1 per 500m^2. Moreover, large size circular enclosures were selected inorder to sample a representative area of habitat whilst optimising the geometric relationship between area and the amount of perimeter fencing required.

The location of the enclosures was determined by a number of criteria and and practical considerations. The areas chosen were relatively homogeneous, representative of the habitat type and excluded unusual features like streams (Note, enclosure 100G followed a square shape inorder to fit in the area of grassland). Obviously, the sampling distances of 100m, 200m, and 300m from the ponds had to be taken into account. Practical considerations, included the avoidance of public footpaths and tracks. Areas inpenetrable without the aid of machinery because of fallen wood or close spacing between trees were also avoided.

With the overhang of the fence fixed inwards pitfall traps were positioned at approximately 8 m intervals. With this arrangement individuals emerging from hibernation and situated within the enclosures could be sampled as they migrated out of area en route to the breeding ponds or some other area.

Preventing outlying T. cristatus en route to the ponds from entering the enclosures was attempted by adding an additional overhang facing outwards. It consisted of a strip of netlon about 4 cm wide stapled to the top of the overhang facing inwards. As a result of early emergence the additional overhang was only attached to the half of each enclosure fence furthest away from the ponds. Consequently, along half the enclosure perimeter newts could enter by climbing over the fence. Enclosures were operational between 18 Febuary and 17 April.

VARIABLES RECORDED FOR INDIVIDUALS OF T. cristatus TRAPPED

The features considered below were recorded, where possible, for each individual trapped, unless otherwise specified. Individuals were collected from the pitfall traps each day and processed at the Reserve Laboratory. They were then released near the site of capture.

Trap Location And Date

Pitfall trap location where practicable, and fence or enclosure position were noted, as was the date of capture.

Weather

Minimum/maximum temperatures and precipitation values were recorded daily at the Reserve Offices, 0.8 km from the study pond. Temperatures were measured behind a screen at a height of 1m.

Length

Length from the snout to tail end was measured to an accurracy of 1 mm using a ruler. Carefully handled, adults remain stationary and may be straightened to facilitate measurement.

The amount of variation during measurement was evaluated. Ignoring the plus or minus signs, the difference between individuals re-measured when recaptured within 10 days had a mean value and standard error (s.e.) of 1.71+/-0.10mm 1988 and 1989 data combined (sample size, n = 175). Moreover, when the plus or minus signs were considered, the new mean difference value was not significantly different from zero.

Mass

Mass was taken using a Pezola balance during the autumn migration and using a electronic balance accurate to 0.1 g over the spring migration. Mass measurements were omitted on a number of dates and they are listed in the appendix 2.

The differences in mass between re-weighing values was not used to assess the amount of variation because unlike length, the mass of an animal fluctuates over very short periods (Robinson, 1977).

Life-stage

Individuals were cateorgised as either adult, sub-adult, juvenile, or newtlet. These groups are defined below.

Adult

Adults are individuals which have reached sexual maturity. However, the relationship between sexual maturity, age, and size is complex (Hagstrom, 1977) and arbitary size devisions have been used. Following Nicholson 1986 adults are classed as individuals >109 mm.

Sub-adults

Sub-adults are individuals that have some sexual chacteristics but have not reached maturity. Sub-adult males are marked by the beginnings of visible secondary sexual chacteristics (rudimentary crest, white tail stripe, and swollen cloaca). The smallest male showing these features had a length of 92 mm.

Sub-adult females show no easily visible features distinguishing them from juveniles. Therefore, the lower size devision for all sub-adults is based upon the smallest male encountered. The sub-adult size limit was set at 90 mm.

Juveniles

These individuals are <90 mm and are developed from a previous years crop of larvea.

Newtlets

A product of the current years egg laying, these are post metamorphic individuals. They feature gill stubbs on emergence from the ponds.

Sex

Sex was determined by visual examination of secondary sexual characteristics, in particular for males; rudimentary crest, bright white tail stripe and swollen cloaca. Females and immatures retain a yellow tail underside.

"Marking"

Every adult has a unique belly pattern (Hagstrom, 1973). By making a record of the belly pattern for each animal captured the movements of individuals could be followed. Several approachs to logging belly patterns have been used by other workers. Hagstrom (1973), and Nicholson (1986), took photographs using a camera, however this is expensive, time consuming and there is a time lag between developing the film. Robinson (1977) drew the spot patterns manually onto pre-printed outlines but it is laborious and more liable to mistakes in re-identification. R.A. Griffiths (pers. comm.) tested logging belly patterns using a photocopying machine.

The latter method has a number of advantages and was adopted in this study, as a result of a photocopier being available close to the study site (0.8 km) at the Reserve Laboratory. The advantages are, photocopies are relatively inexpensive, newts can be handled quickly and a clear photo-record is produced instantly.

The photo record was made by placing the newt in a petra dish and photocopying the newts underside. The area of the dish where the head resided was blackened to reduce the glare experienced by the animal.

For the spring migration, only adults had their belly patterns recorded because Hagstrom (1973) found in T. cristatus less than 3 years old the pattern was still developing. However, for the spring migration sub-adults also had their patterns recorded because experience showed within the same season their patterns could be re-identified. Robinson´s (1977) findings support this assertion.

Recaptures

By visual comparison of belly pattern photo-records, individuals recaptured once or more could be identified. The method used to compare belly patterns involved sorting them on basis of the animals sex and length into bands of 5 mm. Then each pattern was manually compared with the photo-record of individuals of the same sex which occurred in the same or the adjacent length band. This precedure proved very laborious and because of the large numbers of belly patterns accumulated and lack of time only selected categories of patterns were compared.

The development of time efficent methods for compareing patterns used in identifiction of individuals when dealing with a large population is a general problem in studies like this one. Because of problems indicated above other workers using visual patterns to recognise individuals in a populations have developed time-efficent methods based on computer technology. Two examples include finger print recognition by the police and seal head spot recognition (R. Hibby, pers. comm.). A primitive system to compare T. cristatus belly pattern is under devolopment at Leicester Polytechnic (R. Oldham, pers. comm.)

Note:

Only a small proportion of newtlets were weighed and measured. This was carried out in the field because, their belly patterns were not yet developed and therefore, they did not need to be photocopied in the Laboratory.

Deadwood And Vegetation Survey

In order that the relationship between the number newts captured and the occurrence of surface lying deadwood could be investigated a survey was undertaken.

A transect was set up between the mid-point of each outlying fence F1-8 and (a) a point 100m beyond that, and (b) the nearest point of contact with a woodland pond. At 10m intervals, a 1m x 1m quadrat was laid out and the % coverage of the two most abundant ground layer plant species were estimated, aswell as the % of bare ground. A record was made of the sward height and habitat type.

The length of the transect was then slowly walked and each deadwood item (>2cm wide) lying on the ground surface crossing the transect string had its width and length measured (to the nearest 1 cm and 20cm, respectively). At each 10m interval along the transect, a line on the right hand side, 13 paces long (approximately 10m), perpindicular to the transect, was traversed and a record made of the deadwood as described above. The same precedure was repeated on the left hand side. The area of deadwood along a transect was totaled and used as an index value.

An absolute value for surface lying deadwood in the enclosures was gained by deviding them up into 4 quadrants and then systematically traversing each quadrant. Inaddition, light intensity levels were recorded by a Lux meter at 15 regular intervals around each enclosure´s perimeter. Ground layer plant species were also recorded as above.

Bottom Pond Monitoring

Between the 18 Febuary and 16 March 1989, the Bottom pond was enclosed with fencing and pitfall traps were placed at intervals. Newts captured in the traps were counted and released such that a population estimate could be derived and the distribution of immigration could be viewed.

RESULTS

Top Pond

Number Captured

The large number of captures at the Top pond in 1988 and 1989 confirms the presence of a very large breeding population of *T. cristatus* (Table 4). The abundance of newtlets caught emerging from the pond in 1988 indicates healthy egg hatching and larval survival.

The low representation of juvenile and sub-adult lifestages in the pond population is very marked, even when the lower probablity of capture of juveniles is taken into account.

This may reflect a low survival rate of newtlets in the previous 2 or 3 years, however in other populations studied these life-stages are primarily land dwelling, remaining resident in terrestrial habitats until sub-adult/adulthood (Nicholson 1986; Amtkjaer, 1981; Robinson, 1977).

Table 4

Total number of captures in pitfall traps 1-40 encircling the Top pond in 1988 and 1989

	LIFESTAGE					
	NEWTLETS	JUVENILES	SUB-ADULTS*		ADULTS*	
PERIOD			M	F	M	F
Summer/Autumn emigration (5.7.88-20.12.88)	1572	20	24	27	713	445
Winter/Spring Immigration (18.2.89-6.5.89)	-	28	73	61	574	433

* subsequent recaptures of same individual are excluded.

Migration Periods

The emergence from the Top pond was episodic with a high proportion adults and sub-adults emerging during a few nights in late August and early September,(Fig 8). Newtlet emergence with time showed an approximate normal distribution (Fig 9). This occurred later peaking in mid-September. The emergence of newtlets and of adults/sub-adults share little overlap temporally suggesting the two events are determined by different factors.

The number of adults and sub-adults departing per day was significantly ($P<0.01$) associated with rainfall but not temperature. Newtlet emergence, however, was not significantly related to either of these climate variables.

Winter/spring immigration was also episodic (10). There was no

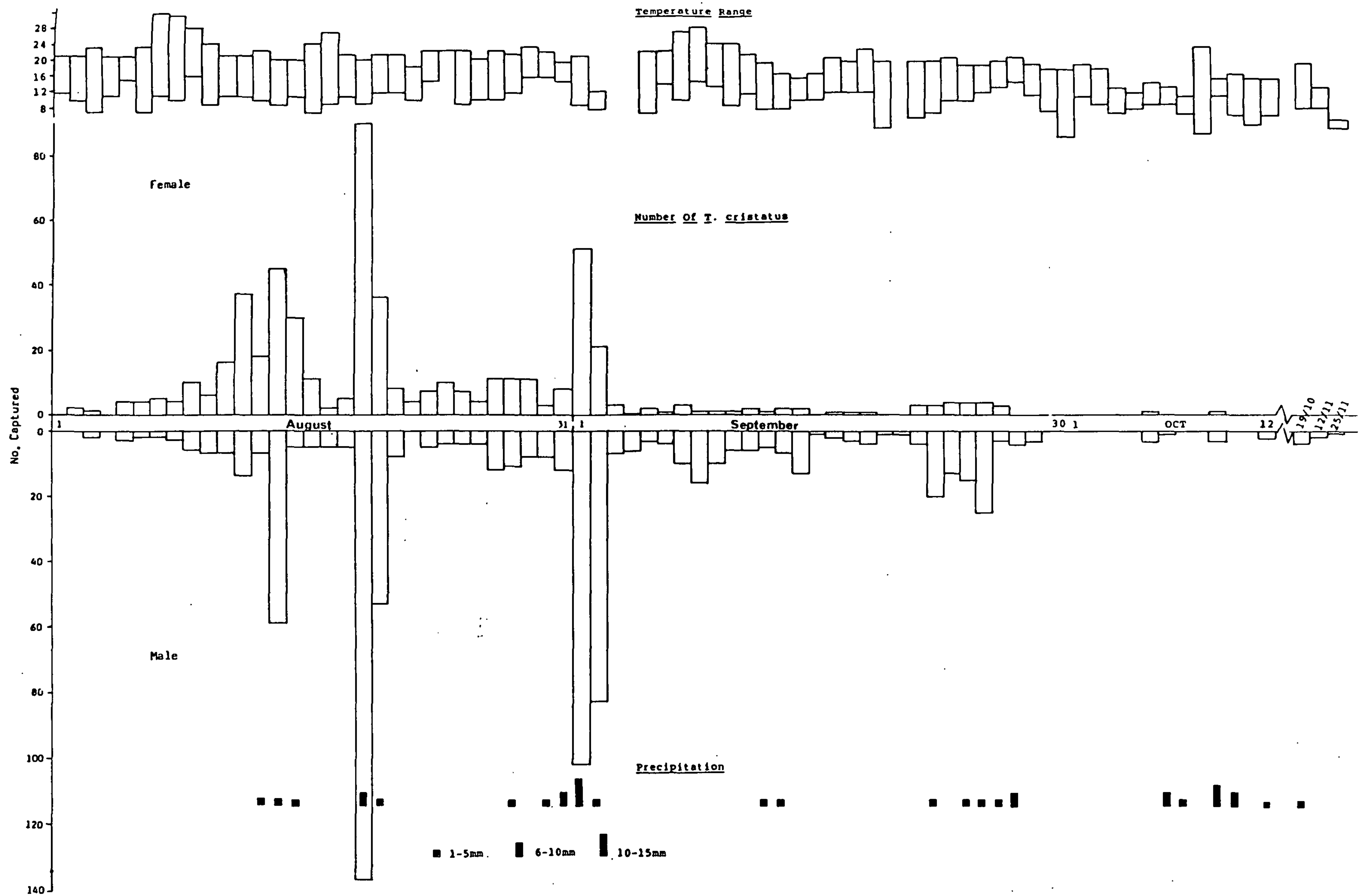

Temperature Range
28
24
20
16
12
8
80
Female
60
Number Of T. cristatus
40
20
0
1
August
31
1
September
30
1
OCT
12
19/10
12/11
25/11
0
No. Captured
20
40
60
Male
80
100
Precipitation
120
1-5mm
6-10mm
10-15mm
140

Fig 9 Emmigration of newtlets from the Top Pond

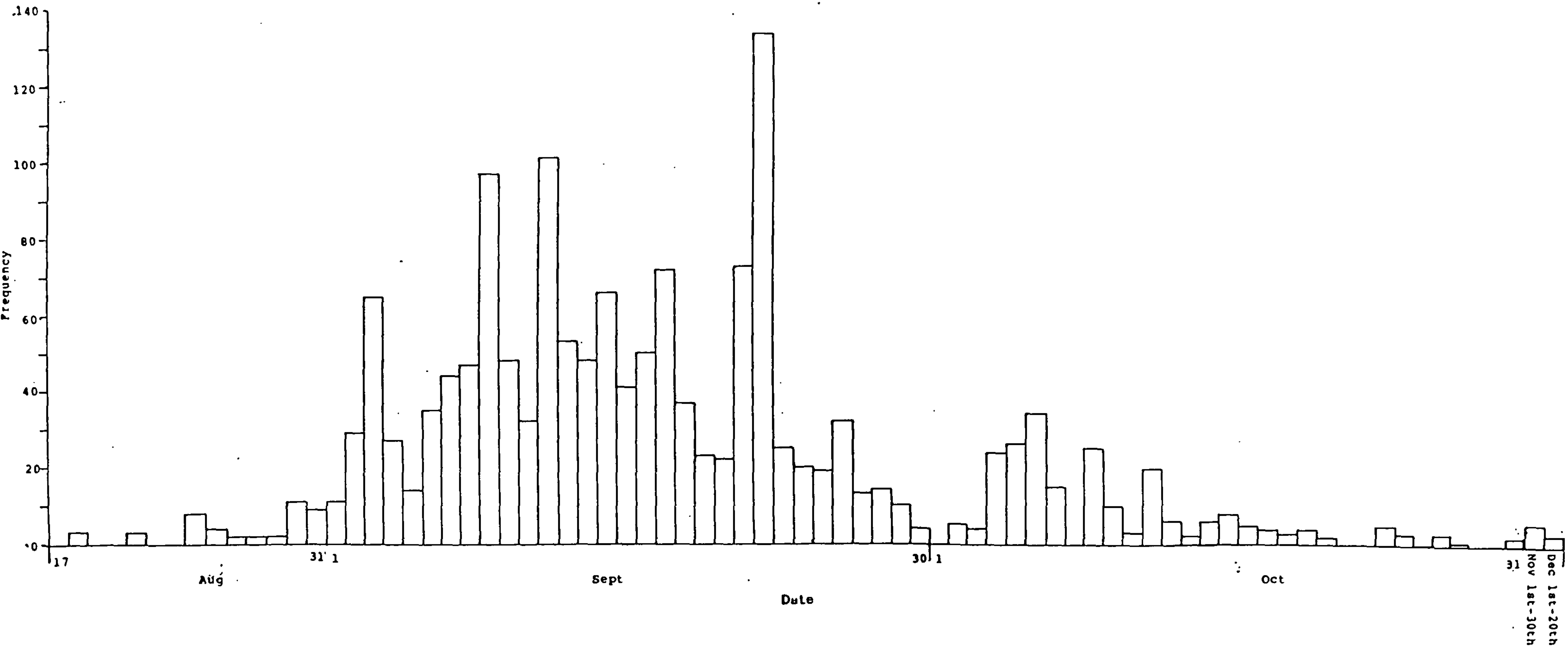
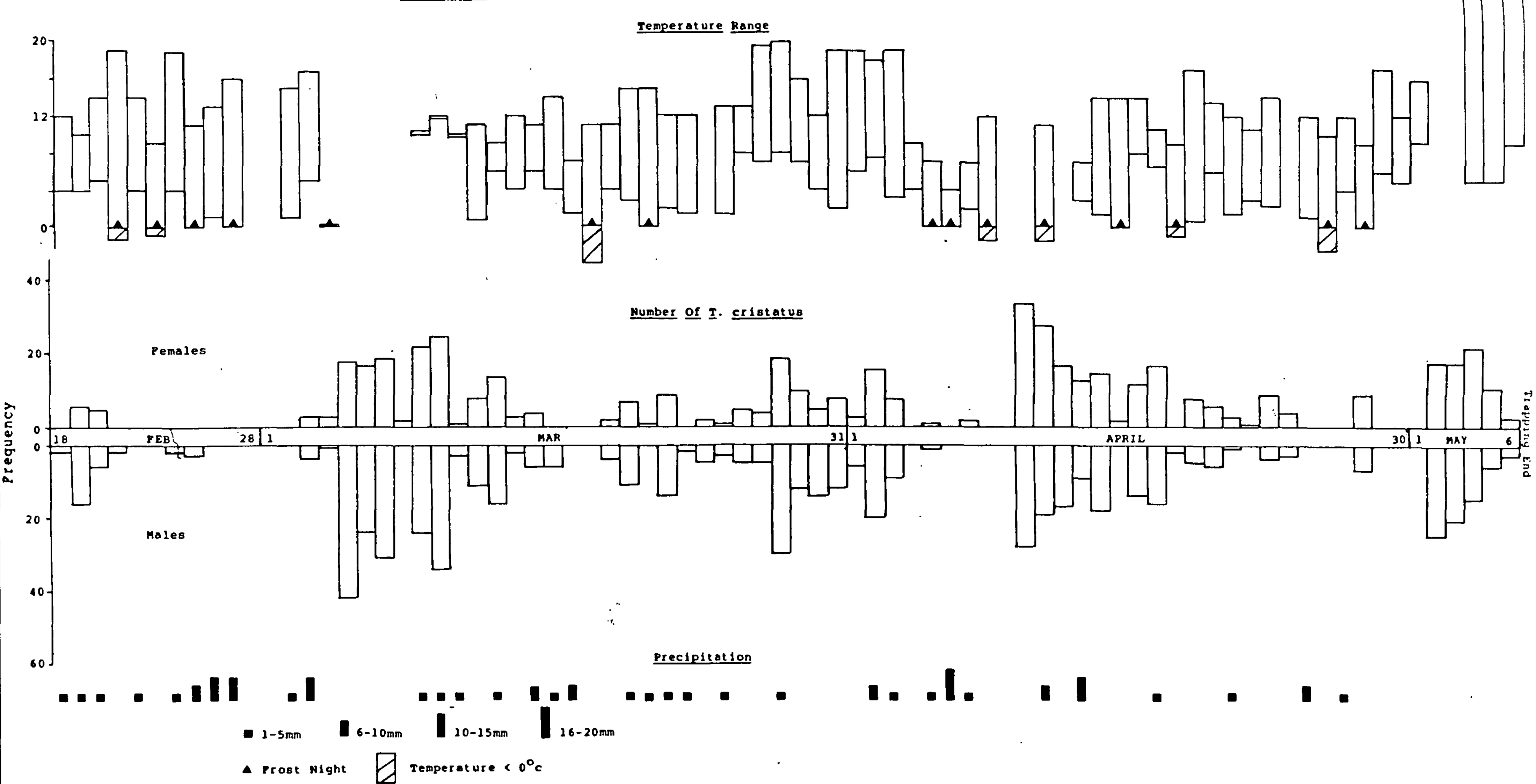


Fig 10 Immigration of adults and sub-adults into the Top Pond in 1989. Daily precipitation (mm) and minimum and maximum temperature (°c) are shown.



association between the number trapped and precipitation, nor daily maximum temperature. However, immigration over the period 18 Febuary to 31 March was significantly ($P<0.01$) associated with minimum temperature (Table 5).

Table 5

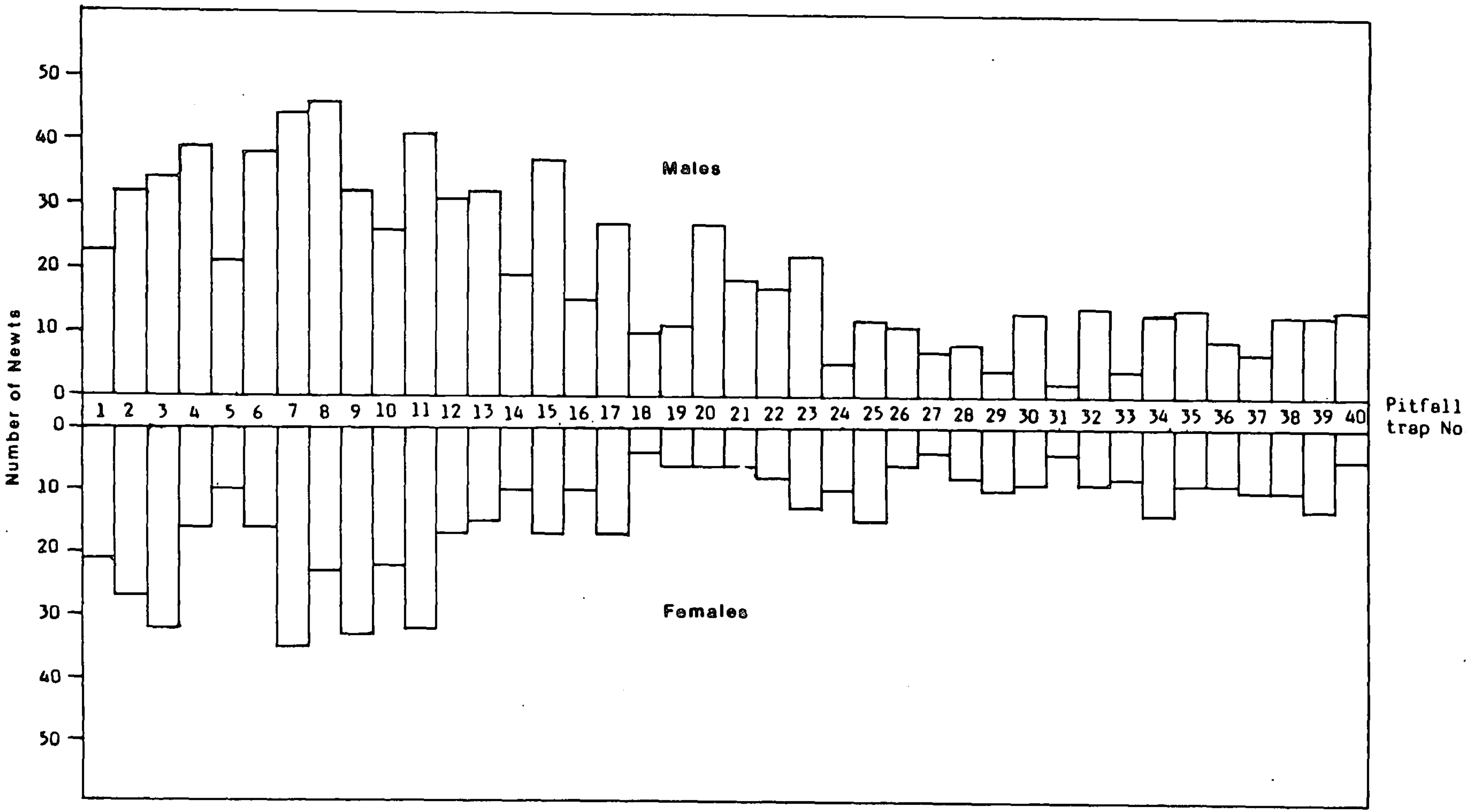
Regression Co-efficients, R, and Standard Errors, S.E., of the daily climate values and number captured around the Top Pond per day during the emigration and immigration.

	Emigration 17 July-30 Sept	**Immigration 18 Feb-5 May**
	R+/-S.E.	R+/-S.E.
Precipitation	+2.271+/-0.793 **	+0.000+/-0.438
Max Temp	-1.365+/-1.260	+0.032+/-0.356
Min Temp	-1.091+/-0.893	+0.009+/-0.514
Min Temp (18 Feb-31 Mar)		+2.701+/-0.554 **
Min Temp (1 April-6 May)		+0.911+/-0.753

* R significant at 5% level
** R significant at 1% level

Location Of Captures

The location of departure from, and arrival of each individual to the pond, was recorded interms of the pitfall trap number. Figs 11, 12 and 13 are bar-charts showing the numbers of captures per pitfall trap, during the adult/sub-adult emigration, *Fig 11* Location of capture of adults and sub-adults dispersing from the Top pond in 1988



... of capture of newtlets dispersing from the Top pond

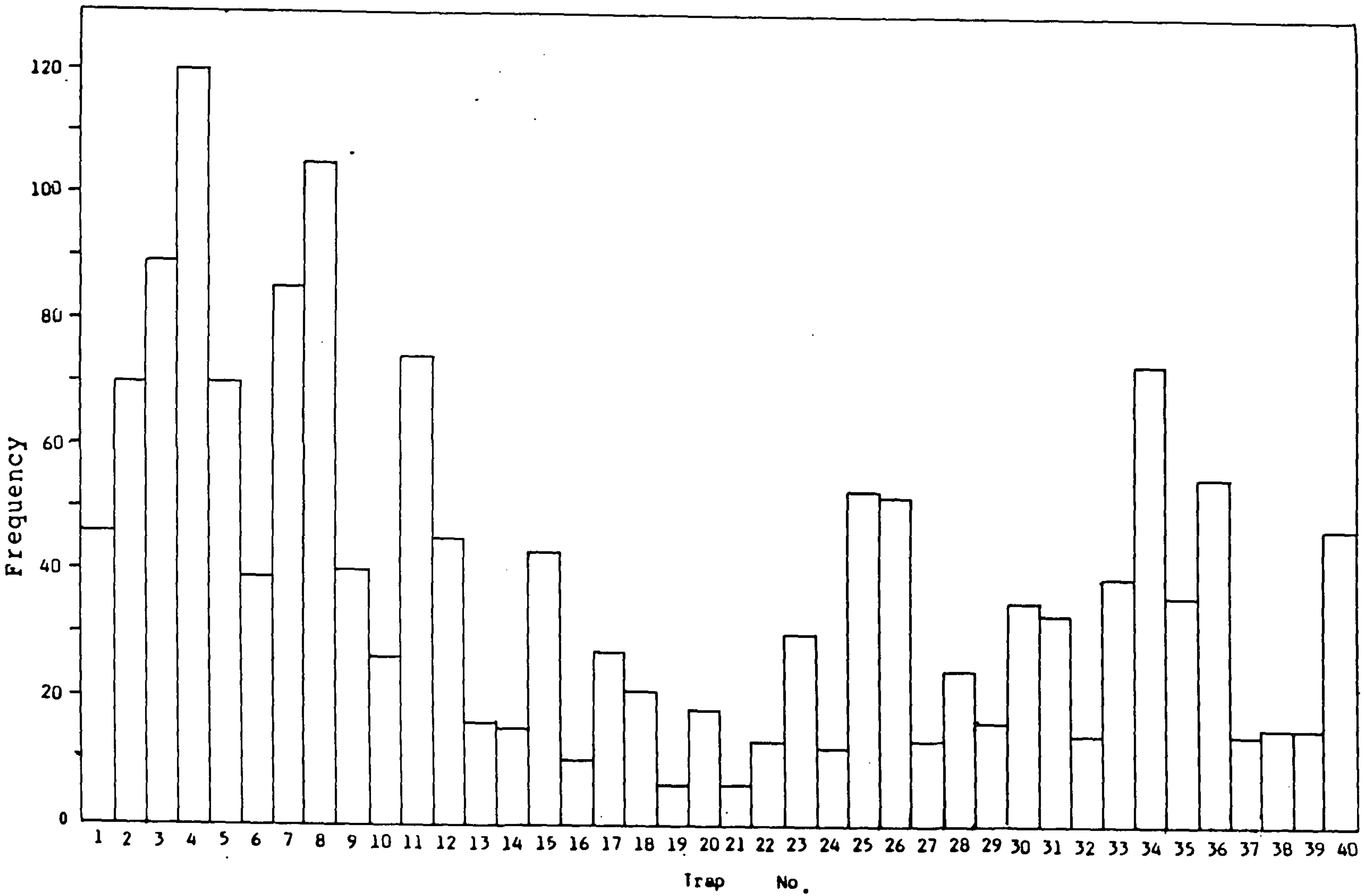
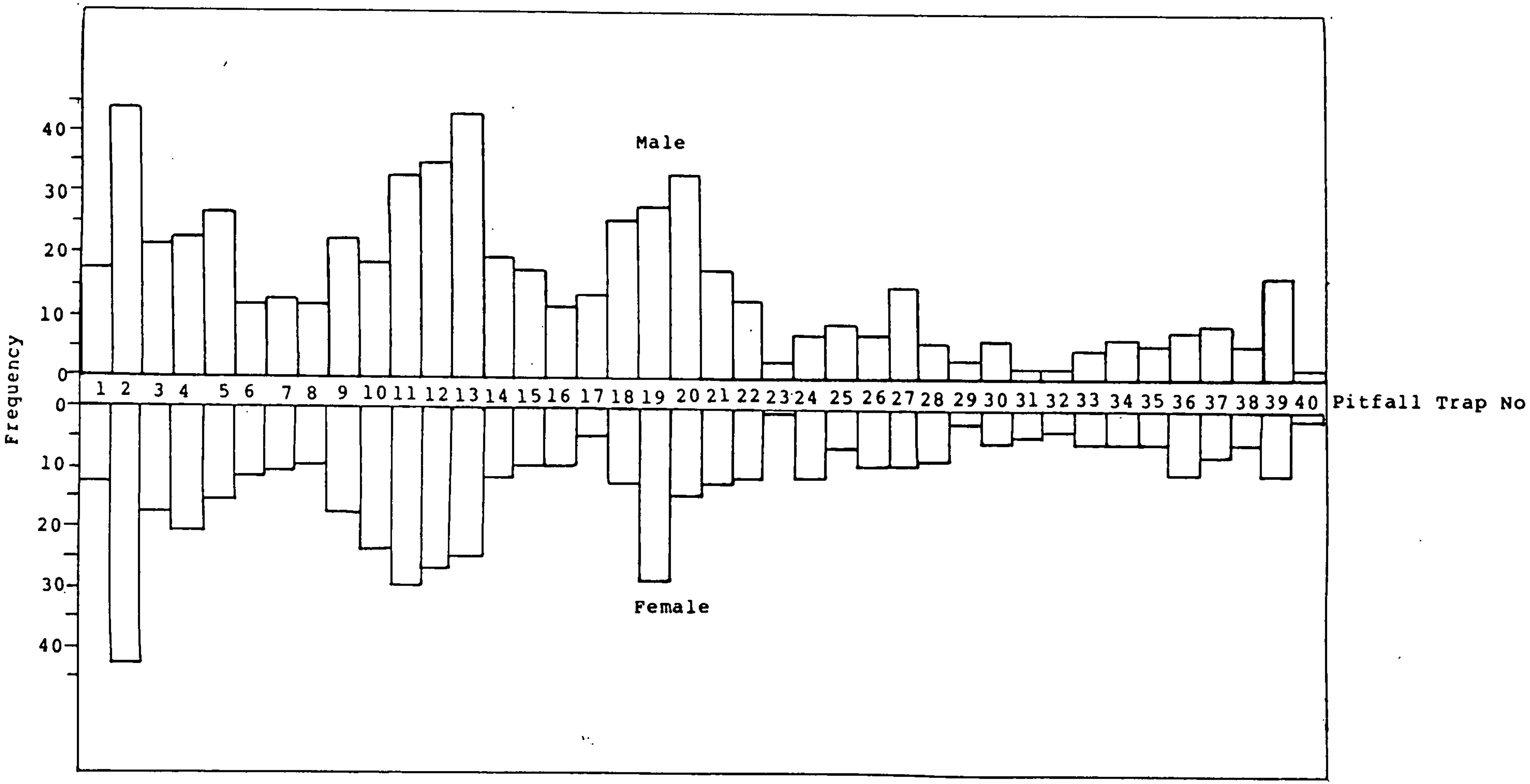


Fig 13 Location of capture of adults and sub-adults arriving at the Top pond in 1989



the newtlet emigration and the adult/sub-adult immigration. There is a large amount of variation between numbers caught in adjacent pitfall traps,and hence pitfall captures have been pooled into 8 sectors. The variation may indicate adjacent traps had differing catch success.

The departure point of newtlets was significantly related (P<0.01) to the departure point of adults and sub-adults in the summer/autumn migration (R=0.91,S.E.=0.18). Sex Ratio is also listed.

Table 6

1988 and 1989 pitfall trap captures surrounding the Top Pond, pooled into sectors

		SUMMER/AUTUMN 1988				WINTER/SPRING 1989		
s	pf	N	M	F	M:F	M	F	M:F
1	1-5	397	122	84	1.5:1	134	111	1.2:1
2	6-10	298	175	109	1.6:1	81	75	1.1:1
3	11-15	195	153	84	1.8:1	149	104	1.4:1
4	16-20	83	82	27	3.0:1**	113	72	1.6:1
5	21-25	117	64	51	1.3:1	50	45	1.1:1
6	26-30	141	42	34	1.2:1	36	38	1.0:1
7	31-35	195	46	44	1.1:1	22	27	0.8:1
8	36-40	146	53	39	1.4:1	40	38	1.1:1

s = sector pf = pitfall trap number N = newtlets
M = male F = female
** Significantly different from the population sex ratio 1988 (P<0.01)

The sectors were not used equally as departure routes from the pond by either males (chi^2 = 201.1, df=7) or females (chi^2=110.9, df=7) in 1988. The favoured routes for departing the pond corresponded to Sectors 1,2,and 3. These sectors were used by 61% of males and 59% of females.

In 1989, again, sectors were not used equally during the migration to the pond by either males (chi^2=211.7, df=7) or females (chi2=103.2, df=7). The highest number of captures were recorded in sectors 1,3 and 4; 63% of males and 56% of females were trapped in these sectors.

Captures in sector 2 were noteably lower in 1989 compared to 1988. However, overall for the population there was no significant change in the sectors used for during the arrival to the pond 1989 and departure in 1988 (Paired t-test, males: t=1.08, df=7 females; t=0.56, df=7).

122m Outer Fences

Numbers

The line fences were very effective at sampling newts away from the pond (Table 7). The fences F1-F5 were not used equally as routes for migration in 1988 (chi^2=41.13, df=4) or in 1989 (males: chi^2=169.38, d.f=5 females: chi^2=125.85, df=5). In 1988, F3 and F1 recorded the highest numbers, whereas in 1989, F4 and F3 captured the highest number of individuals. However, comparison of captures at F1-F5, during 1988 and 1989 showed no significant difference existed in captures between seasons (paired t-test,t=-0.91, df=4; see Fig 18).

Table 7

captures in 1988 of newtlets and individual adults and sub-adults ,n, at outer fences set at 122m

FENCE	F1	F2	F3	F4	F5
DATE FENCE OPERATIVE	6.8.88	9.8.88	11.8.88	1.9.88	20.9.88
n	72	37	86	35 (42)+	20 (33)+
MALE M	39	10	53	23	12
FEMALE F	33	27	33	12	8
M:F	1.2:1	0.4:1**	1.6:1	1.9:1	1.5:1
NEWTLETS	107	17	27	27	9

+; Estimated number newts which would have been captured had the fence been operational from 11.8.88. Basis of calculation is that for F1-F3, 17% of captures occurred before 1.9.88 and, 39% before 20.9.88.

**; Significantly different from the Top pond population sex ratio 1988 (P<0.01)

In 1989, F6,F7,and F8 completed the ring of fences, the results are appear in Table 8.

The distribution of newtlets captured at 122m fences was, also irregular. 57% of the total number of newtlets for F1-F5 were captured at F1.

Overall, there was no evidence that a higher proportion of the newtlet population dispersed further than adults and sub-adults during the summer/autumn. A total of 187 newtlets were captured at F1-F5 but when a trap efficiency is taken account of the estimated number reaching the fences was 297. What proportion of these emerged from the Bottom Pond was unknown. An estimated 270 adults and sub-adults were trapped at F1-F5.

Table 8

Captures in 1989 of individual adults and sub-adults, n, at outer fences set at 122m

FENCE	F1	F2	F3	F4	F5	F6	F7	F8
n	54	37	100	174	39	9	5	84
MALE M	33	17	50	94	16	4	2	38
FEMALE F	21	20	52	80	23	5	3	46
M:F	1.6:1	0.9:1	1.0:1	1.2:1	0.7:1	0.8:1	0.7:1	0.8:1*

* Significantly different from the Top pond population sex ratio (P<0.05)

Sex Ratio

The sex ratio of males to females for the population captured in pitfall traps departing the pond in 1988 was 1.50:1. It was significantly (P<0.01) different from 1:1,(Using normal approximation to the binomial distribution, d=6.42)The equivalent sex ratio in 1989 was 1.31:1 and also differed significantly (P<0.01) from 1:1 (d=4.31). The proportion of males observed arriving at the pond in 1989 was not significantly different to that observed leaving in 1988 (d=-1.85).

Variation Of The Sex Ratio During The Migations

Table 9

Variation of the sex ratio through the summer/spring migration and the degree difference from the population sex ratio of 1.5:1.

Days from 5.7.88	M	F	M:F	d
1-10	4	5	0.8:1	} pooled
				} n<30
11-20	12	15	0.8:1	}- -2.89**
				}
21-30	5	10	0.5:1	}
31-40	53	104	0.5:1	-6.98**
41-50	209	152	1.4:1	-1.20
51-60	250	137	1.8:1	+1.47
61-70	70	13	5.4:1	+4.36**
71-80	66	11	6.0:1	+4.45**
81-90	63	16	3.9:1	+3.41**
91-100	9	3	3.0:1	} pooled
				}- 0.996
>100	7	6	1.1:1	}

** significant to P<0.01

Results presented in Table 9, indicate that during July and early August, i.e. day 1-40, there was a higher tendency for females to leave the ponds. This finding contrasts, with the period from day 61 to day 90 when males showed a higher tendency to leave the pond.

In 1989, the situation was reversed (Table 10). The early part of the immigration, day 1-30 was marked by a predominace of male. However, between day 51-70, females arrived in greater numbers than did the males.

Table 10

Variation of the sex ratio through the winter/spring migration and the degree of difference from the population sex ratio 1.3:1

Days from 18.2.89	M	F	M:F	d
1-10	32	11	2.9:1	+2.38*
11-20	159	94	1.7:1	+1.92
21-30	80	55	1.5:1	+2.89**
31-40	85	53	1.6:1	-1.14
41-50	63	41	1.5:1	-0.86
51-60	125	133	0.9:1	+2.59**
61-70	26	37	0.7:1	+2.42*
71-80	69	70	1.0:1	+1.61

* significant P<0.05
** significant P<0.01

Variation of the Sex Ratio Around The Pond Perimeter

In 1988 the sex ratio for each sector did not differ significantly from the population sex ratio, except at sector 4 (d=3.39, P<0.01). Sector 4 had a prevalence of males and is adjacent to the bottom Pond. Similarly, during the immigration in 1989, the sex ratio did not vary significantly from the population ratio.

Sex Ratio At The Line Fences

In general the evidence suggested, the pattern and distance of dispersal from the pond was unrelated to sex. In 1988 (Table 7), the ratio of males to females captured at each fence did not differ significantly from that of population captured at the Top Pond, except at F2 (Binomial Approx. To The Normal Distr. d=-3.96) where a preponderance of females were captured.

Similarly, in 1989 (Table 8), no significant differences were obtained except at F8 (d=2.06, P<0.05)). At F8 a greater number of females were trapped.

Length

The snout to tail end length is a feature of T. cristatus, that exhibits sexual dimorphism (e.g. Nicholson, 1986: Verell & Halliday,1986). Sexual dimorphism was apparent in the length data presented. Females were on average larger than males. In fact one female measured 164mm, a length greater than the longest British specimen (163mm) reported in the literature (Boulenger, 1894).

Over the emigration period from the pond, the mean length of males and females departing the pond was 126.07+/-0.43mm (n=711) and 131.91+/-0.68mm (442), repectively. During the immigration in 1989, the mean length of males and females was 122.09+/-0.43 (n=639) and 124.81+/-0.62 (494). Males and females measured over the immigration were on average significantly smaller than males and females observed during the emigration (d=5.65 for males and

=6.56 for females, P<0.01).

The shift in population size structure between 1988 and 1989 may be examined by considering size class-frequency bar-charts in Fig 14 and 15. For females in 1989 there was an increase in the numbers occurring in the size class 110-114 and 115-120, and a sharp decrease in the occurence of larger females notably in size class 130-134mm and 135-140mm.

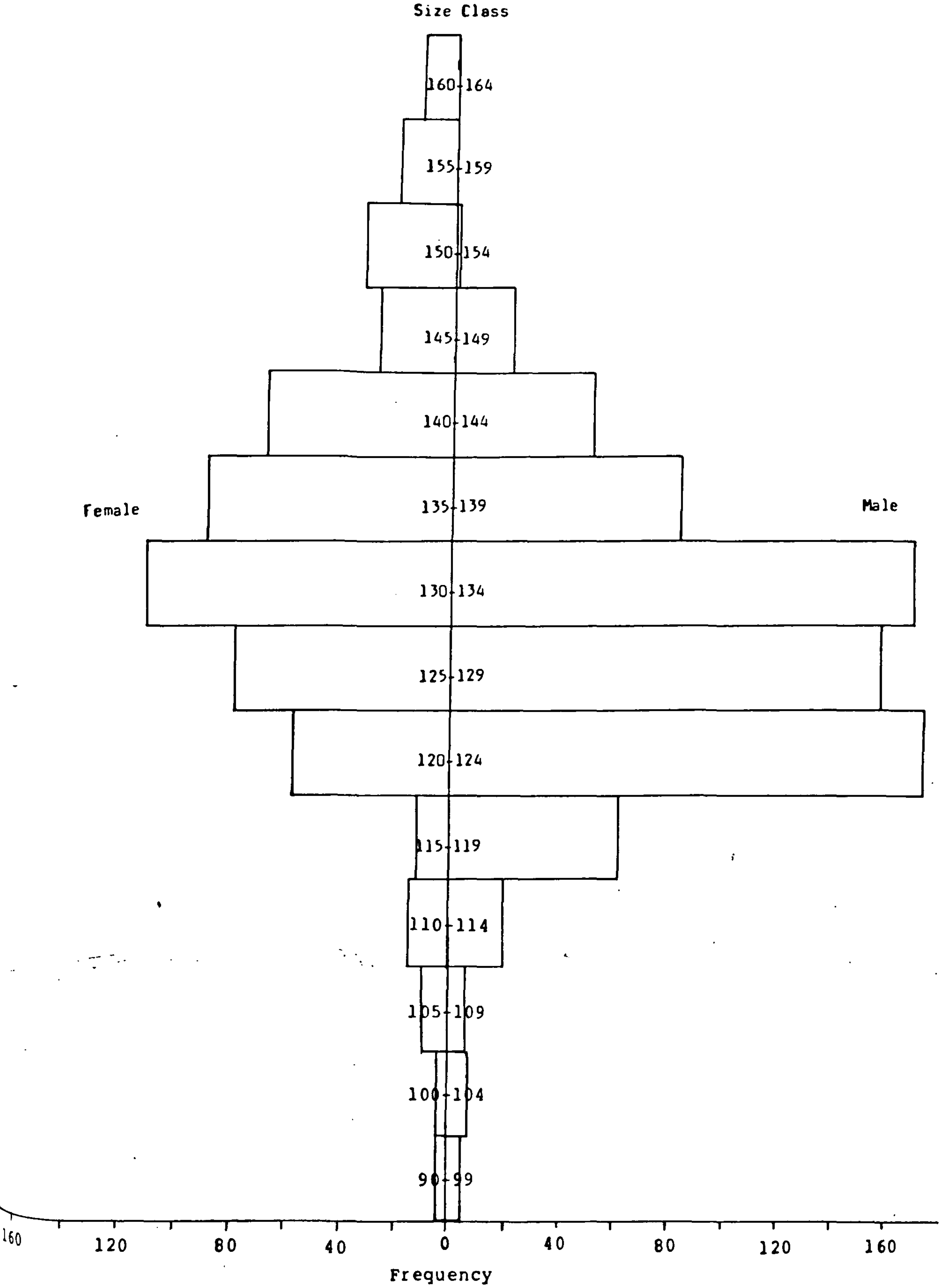
Comparison of the male size class-frequency distribution in 1988 and 1989 shows similar trends. There is a marked increase in numbers in the size class 119-115 and 110 -114 and decreases in the frequency oberved in size classes 125-129, 131-134,135-139 and 140-144.

A sample of newtlets were measured leaving the pond area between 18 August and 9 September. The mean length on emergence was 74.10 +/-0.19mm (n=379).

Variation Of Size In Different Sectors of the Pond

One Factor Analysis of variance, ANOVAR, indicated the mean size of females per sector in 1988 to be significantly different for females ($F=2.99$ $v_1=7$ $v_2=434$, $P<0.01$). Sector 3 was characterised by large females and sector 4 and 5 by unusually small females. The mean size of males per sector showed no significant variation($F=0.00$ $v_1=7$ $v_2=676$)

In 1989 there was significant variation between sectors in the mean length of males ($F=2.49$, $v_1=7$ $v_2=566$, $P<0.05$). Sectors 4, 5 and 2 registered high means. Mean length of females showed no marked variation (F=1.53, v1=7 v2=447).



14 Size-frequency barchart of the total length (mm) of emergent adults and Sub-adults in 1988

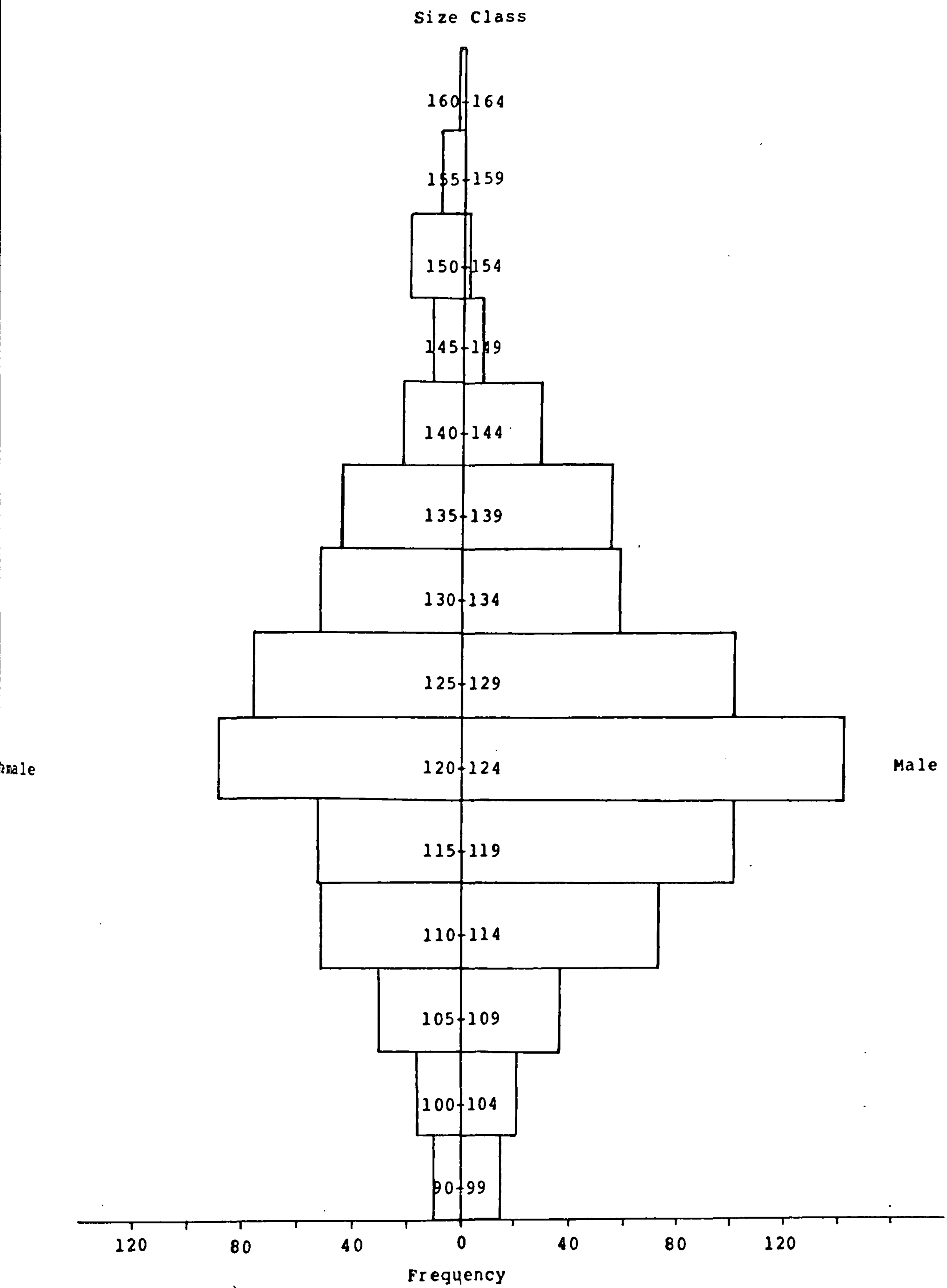


Fig 15 **Size-frequency barchart of the total length (mm) of immigrating adults and sub-adults in 1989**

Table 11

Mean length (mm) and standard error (S.E.) of males And females at each sector (S) surrounding the Top pond in 1988 And 1989

		1988 Emigration				1989 Immigration			
S	pf	M	+/-S.E.	F	+/-S.E.	M	+/-S.E.	F	+/-S.E.
1	1-5	126.51	0.73	130.94	1.01	120.69	0.89	125.202	1.38
2	6-10	126.97	0.72	132.03	1.22	123.78	1.10	125.03	1.71
3	11-15	128.03	0.77	136.78	1.56	121.55	1.04	127.63	1.59
4	16-20	126.79	1.29	127.11	2.79	124.56	1.16	124.42	1.80
5	21-25	128.25	1.37	127.68	2.85	123.75	1.53	126.51	2.01
6	26-30	124.03	1.87	130.21	2.08	119.52	1.67	123.16	1.64
7	31-35	124.4	1.60	131.46	1.83	117.57	2.15	122.10	3.58
8	36-40	126.18	1.28	132.85	1.91	119.80	1.37	119.49	2.37

Variation Of Size Through The Migation Periods

The length of individuals that departed the pond in 1988, 10 days after pitfall trapping began, were significantly smaller (P<0.01) than the pond population (Table 12). The period corresponds to the first half of July and refects activity amongst sub-adults. Between day 11 and 100 there was little evidence that females of different sizes departed the pond at different times. However, a preponderance of males larger than average left the pond area between day 51-60, day 70-80 and day 81-90 i.e the middle and latter half of the emigration.

Table 12

Variation of the mean length of males and females through the summer/autumn migration and the degree of difference from the population mean

Days from 7.7.88 D	M	S.E.	d/t	d.f.	F	S.E.	d/t	d.f.
1-10	104.50	2.14	-10.10**	3	104.00	5.46	-5.11**	4
11-20	120.83	3.71	-1.41	11	127.73	3.93	-1.06	14
21-30	117.40	3.49	-2.48	4	119.40	4.81	-2.60*	9
31-40	125.80	1.15	-0.23		133.30	0.99	+1.40	
41-50	126.39	0.64	+0.50		132.71	0.97	+0.83	
51-60	127.50	0.52	-2.74**		133.85	1.07	+1.81	
61-70	125.79	1.07	-0.26		135.31	4.06	+0.84	12
71-80	130.39	1.43	-3.03		134.09	4.11	+0.53	10
81-90	129.73	1.57	+2.33		123.25	4.84	+0.84	15
91-100	124.00	4.15	-0.50	8	138.33	14.43	+0.44	2
>100	116.14	3.89	-5.55	6	106.20	4.37	-5.89**	4

t Student´s t distribution
d Normal distribution

* P<0.05
** P<0.01

In 1989 the mean size of males arranged into groups of 10 days, showed no significant variation from the pond population mean through the duration of the immigration (Table 13). Female size showed a similar pattern with one exception. Between, day 31-40, the mean length of females was significantly larger than the population mean (P<0.05)

Table 13

Variation of the mean length of males and females through the winter/spring migration and the degree of difference from the population mean

Days from 18.2.89 D	M	S.E.	d/t	d.f.	F	S.E.	d/t	d.f.
1-10	121.78	2.07	-0.16		117.54	2.96	-1.75	10
11-20	123.33	0.87	-1.46		124.00	1.24	-0.57	
21-30	120.11	1.15	-1.64		123.21	1.79	-0.85	
31-40	123.64	1.10	+1.33		129.13	2.08	+2.26	
41-50	122.89	1.31	+0.59		124.88	2.36	+0.03	
51-60	120.96	0.98	-1.17		123.27	1.13	-1.29	
61-70	124.92	1.98	+1.35	25	126.81	2.34	+0.88	
71-80	120.01	1.33	-1.60		127.56	1.82	+1.66	

t Student´s t distribution
d Normal distribution
* P<0.05
** P<0.01

Variation Of Size At the Outer fences

The males trapped at F3 during the summer/autumn migration were significantly (P<0.01) smaller on average than males leaving the Top Pond in 1988. The other fences showed no differences.

The mean length of females at each of the outer fences was less than the Top Pond population mean. Females at F1,F2 and F3 were signicantly smaller. This may of arose if small individuals on average tended to migrate further and/or if the mean size of females in the Bottom Pond was small relative to the Top Pond. It was estimated 24% of individuals captured at F1-5 migrated from the Top Pond (See Table 16).

Interestingly, over the winter/spring migration no difference in mean length from that of Top Pond was apparent for either males or females at F1-F8, except at F1. Males at F1 were significantly smaller ($P<0.05$).

There was no apparent difference, when compared to the Top pond mean value, in the mean length of either males or female at F1-F8, except at F1. Males at F1 were significantly smaller ($P<0.05$).

Length And Mass For Adults & Subadults

Length and mass are strongly associated ($P<0.01$) in males and females. The relationships are described in Table 14 and are plotted in Fig 16.

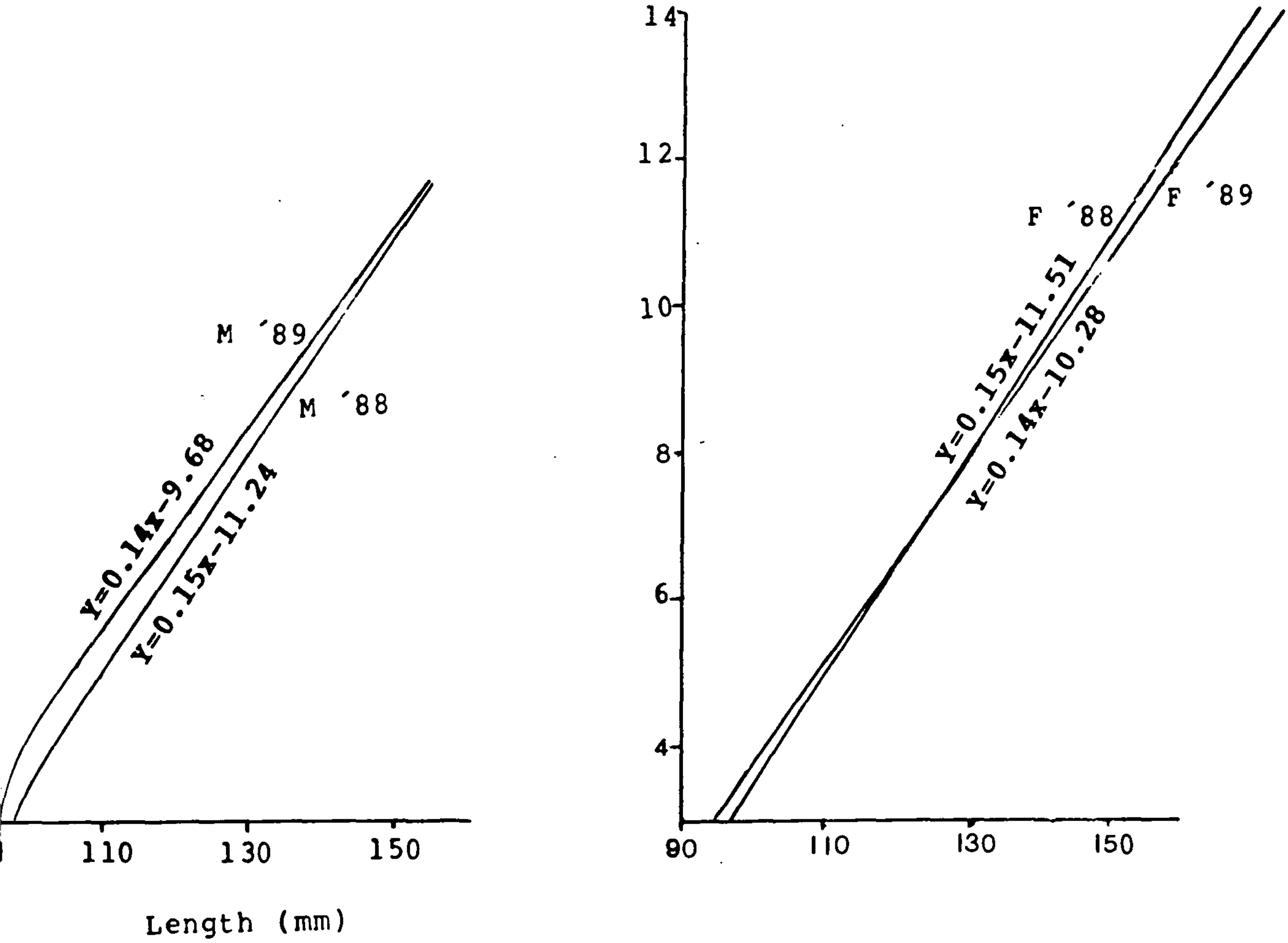
Table 14

Regression Line Equations describing the relationship between Mass (y) And Total Length (x).

	1988 EMIGRATION	1989 IMMIGRATION
MALES	**y = 0.15x - 11.24**	**y = 0.14x - 9.68**
	n=538 S.E.	n=414
	S.E=0.003	S.E.=0.004
FEMALES	**y = 0.15x - 11.51**	**y = 0.14x - 10.28**
	n=326	n=351
	S.E.=0.004	S.E= 0.003

S.E.= standard error of the regression coefficient

Comparison of the regression co-efficients obtained for males, 16 Linear regression lines describing the relationship between total length (mm) and mass (gm) in 1988 and 1989 for males and females



showed a significant difference (d=2.09, P>0.05). According to the equations obtained, males in the population were of greater mass per unit length in 1989 than in 1988. Female regression co-efficients were not significantly different (d=1.54).

Individual Movements

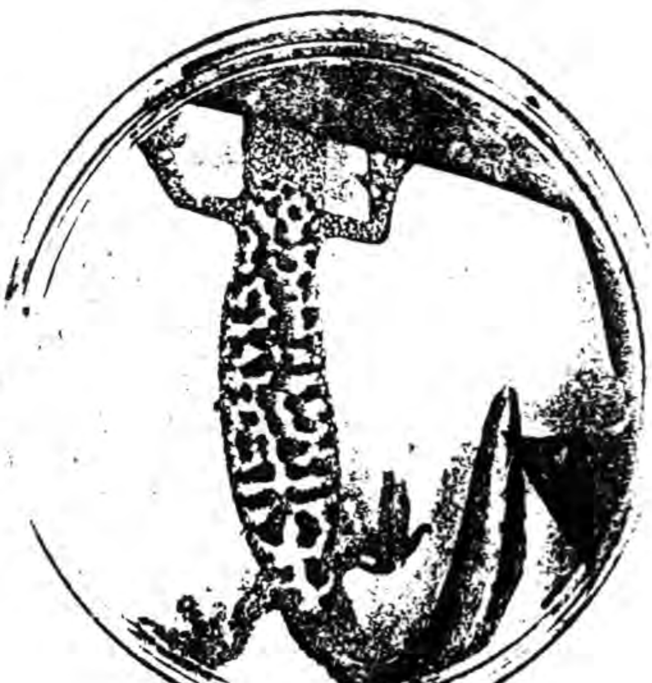
The photocopies of belly patterns worked adequately as a method of following the progress of individuals, however, with over 3000+ photo-records accumulated there was insufficient time to sift and match all the belly patterns. Fig 17 shows two individuals that were recaptured and re-identified.

7 Examples of photo-records of individuals captured in 1988 and subsequently recaptured

11 April 1989
F2, M, L. 140mm

22 Sept.1988
F2, M, L. 140mm

7 March 1989
F3, M, L. 131mm



14 Sept. 1988
F3, M, L. 133mm

Recaptures Along The Same Fence In the Same year

Table 15

Number, n, and % of recaptures of males and females within the same season at the Top pond and outer fences; the mean (+/- S.E.) number of days between recapture; and the mean (+/-S.E.) number of pitfall traps, PF, between 1st and 2nd capture.

RECAPTURES		n	%	Mean Days	S.E.	Mean PF	S.E.
POND-POND							
1988	males	26	4	14.7	2.9	4.9	1.0
	females	14	3	8.4	3.0	6.5	1.7
POND-POND							
1989	males						
	females	26	6	14.1	2.9	5.1	1.0
FENCE-FENCE							
122m	males	6	4	4.2	0.8		
1988	females	7	6	7.2	2.2		
FENCE-FENCE							
122m	males	28	11	16.8	2.6		
1989	females	14	6	15.6	3.7		

%: % of the total number ofindividuals sampled at a fence that were recaptured again at the same fence during the same season.

The number of individuals captured more than once at the same fence was small, ranging from 3-11% of the total number individuals captured. The results indicate that over the whole time the Top pond area was enclosed, a small element of the population was leaving the pond and then entering again and vice versa. The number of days between recapture varied greatly, but the means ranged from 11.2 - 18.3 days, a relatively long interval. This suggests, in most cases dis-orientation by the field methods was unimportant. The location of recapture relative to the initial capture site was on average between 4.9 and 6.5 pitfall traps away, equivalent to 25-32.5m in distance.

Pond - Fence Movements : Summer/Autumn

Table 16

The relationship between individuals place of departure from the pond and subsequent recapture at F1-F8 set 122m away. Also the proportion of individuals captured at both the fence and pond is expressed as a % of total fence captures.

POND SECTOR, s	**F1**	**F2**	**F3**	**F4**	**F5**	
1	7	2	2			
2	7	7	8			
3	2	2	6	5		
4	1		3	2		
5				2	2	
6					1	
7	1					
8						**F1-F5**
TOTALS	18	11	19	9	3	:60
CAPTURES PER FENCE	72	37	86	35	20	:250
	25%	30%	22%	25%	15%	:24%

TOP POND POPULATION WITH A PHOTORECORD= 779 60/779 = 7.70%

In general, the location of emergence from the the pond was related to the direction of the subsequent terrestrial migration, e.g. most newts emerging from the south of the pond migrated in a southern direction. Thus, numbers emerging per sector was a guide to numbers likely to migrate in a particular direction.

The bar-chart in Fig 19 shows the distribution of days between capture at the pond and capture at a fence. Two groups of individuals may be discerned each, showing different types of behaviour. There is firstly the 47% of individuals that data is available on, which arrived at the fence in under 6 days (or 6 nights); in fact 7 individuals covered the distance in 1 night. These fast moving individuals, mainly males, were possibly en route to distant habitats. Secondly there was a group characterised by a long gap between recapture. This group was made up individuals which appeared to spend a lengthy period in the habitats between the fence and the pond, possibly foraging.

Table 17

Days between departure from the pond and recapture at F1-F5 and the calculated rate of terrestrial migration.

	n	Mean days +/- S.E.	Mean Rate of travel per day m +/- S.E.	Range of travel per day values
MALES	40	13.6 +/-15.4	9.0 +/- 7.9	2 - 122
FEMALES	20	19.1 +/-16.2	6.4 +/- 7.5	2 - 122

Of the captures at F1-5 in 1988 only 24% were identified as having come from the Top Pond. This low figure was a consequence of two factors. Firstly, many newts captured at the fences migrated from the adjacent Bottom pond. Secondly, of the 1209 individuals captured at the top Pond, only 779 had their belly

Fig 18

Comparison of the outer fence captures in 1988 and 1989

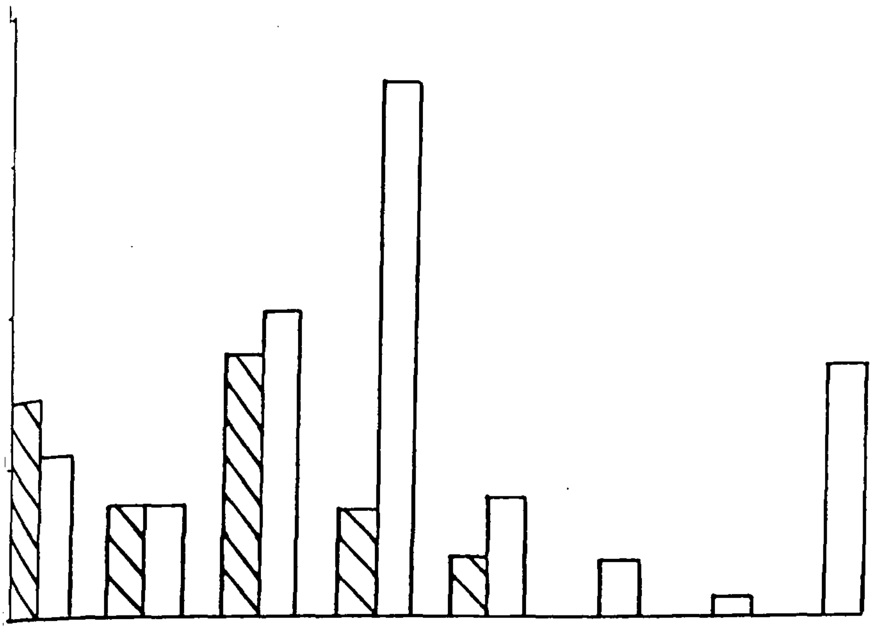
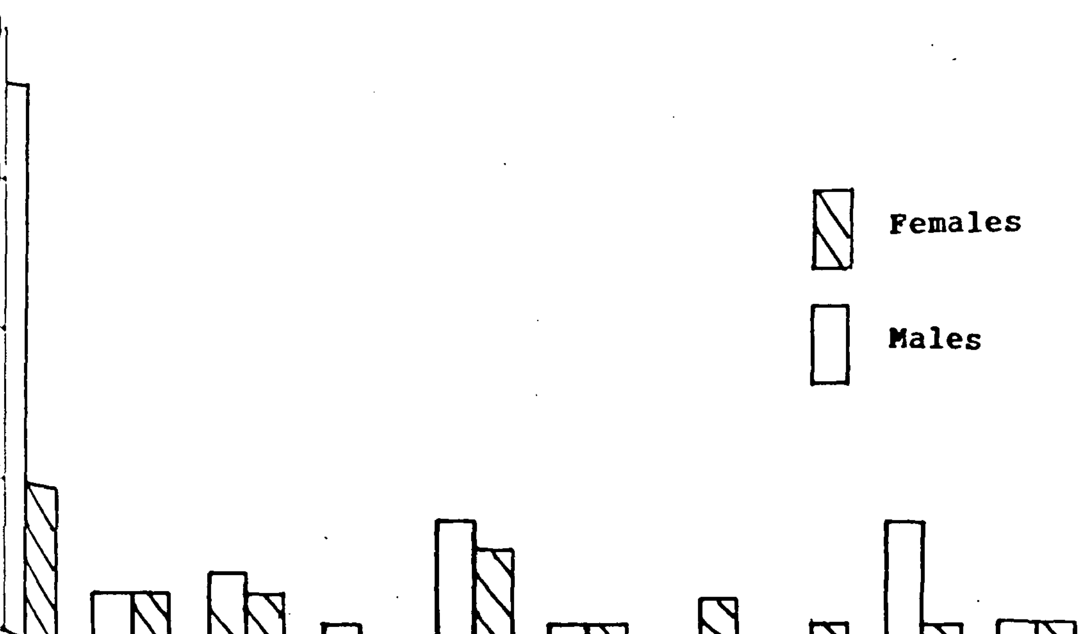


Fig 19

Distribution of days taken by adults and sub-adults to migrate a distance of 122m after departing the Top pond



patterns recorded in 1988.

The estimated percentage of the Top pond population of adults and sub-aduluts captured at the fences 1-5 pond was 7.70%. The fences each sampled 3.6% of the perimeter at 122m, and on this basis it calculated that 40.85 % of the Top pond population migrated 122m and beyond. No data was available on fence-pond movements in 1989.

Length of Hibernation

The number of days between last capture in the summer/autumn and first capture an individual in the winter/spring was taken to represent the length of over-wintering inactivity, and has been called the hibernation period. Data is available on 21 male and 4 female hibernation periods. The mean hibernation period for males was 180.0 +/- 4.75 days and 197.8 +/- 15.1 days for females.

Table 18

The number of individuals captured in the summer/autumn at an outer fence and subsequently, re-identified at the same fence in the winter/spring after hibernation.

	F1	**F2**	**F3**	**F4**	**F5**	
MALES	8	1	10	2	1	
FEMALES	1	1	2	0	0	F1-F5
TOTAL	9	2	12	2	1	26
% OF 1988 FENCE CAPTURE	12.5	5.4	14.0	5.7	5.0	10.4

Only 10.4% of individuals captured at F1-F5 in 1988 during dispersal phase were recaptured at the same fence during the winter/spring of 1989. This low value may have resulted from two possibilities or a combination of both. Firstly, a large proportion of the population may not of migrated towards the pond during the winter/spring period either because of high mortality, or because not all adults nor sub-adults return to the breeding site in successive years.

Secondly, newts may have ranged widely and not used the same route to travel towards the pond in the summer/spring. Data on the survival rate would aid the understanding of this subject but it is unavailable.

The sample of individuals measured in the summer/autumn and then re-measured in the winter/spring of 1989 showed anomalous results. Over this period the mean length of individuals significantly shortened (Student's t test, $t=2.13$ d.f.$=25$ $P<0.05$). Physical reduction in length over winter seems unlikely, and imprecision in the measurement of lengths may be important.

Over-wintering Habitat Preferences

Terrestrial Enclosures

In the 8 terrestrial enclosures set up 640 individuals were sampled between 18 Febuary and 16 April (Table 19 and Fig 22). The enclosures were not completely secure against newts from outside, therefore the numbers should be treated comparatively and not as absolute values.

Table 19

Abundance, sex ratio, mean length, and density of adults and sub-adults captured at each enclosure in the winter/spring.

ENCLOS. NO.	TOTAL NO.	NO. M	NO. F	SEX RATIO M:F	MEAN LENGTH (STANDARD DEV.) M	MEAN LENGTH (STANDARD DEV.) F	Density Area with one newt (m^2)
100C	100	61	39	1.9:1	122.90 (11.14)	121.75 (14.59)	14.5
100D	166	100	66	1.5:1	120.00* (10.36)	122.14* (10.37)	8.8
100G	76	40	36	1.1:1	124.98 (11.29)	124.19 (13.46)	19.1
200C	36	27	9	3.0:1*	119.88* (9.03)	123.8 (5.27)	40.3
200D	195	98	97	1.0:1	119.04** (9.32)	123.81 (12.70)	7.4
200G	57	29	28	1.0:1	122.51 (13.51)	117.85 (19.02)	25.5
300D	0	0					0.0
300C	10	1	9	0.1:1	136	121.45 (6.71)	145.2

* sign difference from 1989 Top Pond population value at $P<0.05$
** sign difference from 1989 Top Pond population value at $P<0.01$

All 3 habitats were utilised for over-wintering by substantial numbers of newts. Moreover, the number of animals sampled in 3 enclosures set at 100m was greater than for 3 enclosures set at 200m but only by a small margin .

Deciduous woodland enclosure supported very high numbers at both 100m and 200m. The deciduous enclosure at 300m supported no newts.

Conifer enclosures supported substantial numbers, and there was a decreasing order of abundance the further away the enclosures were from the breeding site.

The enclosures at 100m and 200m situated in grassland/open areas sampled numbers similar to equivalent conifer areas.

Males captured in 100D, 100C and 200D and females captured at 100D were significantly smaller in length than the Top Pond population, perhaps indicating the presence of a high proportion of younger individuals. The sex ratio of males to females captured in each enclosure was not significantly different, except at 200C, from the sex ratio encountered at the Top pond population in 1989.

Distribution Of Over-wintering *T. cristatus* Around The Breeding Ponds

With the 8 sample fences spaced at regular intervals to form a ring around the breeding sites it was possible to gauge the spatial pattern of migration for males and females. To estimate the number of newts over-wintering beyond 122m, the circumference of a complete circle encompasing all the fences has been divided into 8 sections, each including one fence. Then by applying the equation below, sector estimates were derived based on the numbers captured at the closest sample fence.

Fig 20 shows a schematic diagram with plots of the section values.

$$\left(\frac{Z}{Fs} \times S\right) - \frac{(Tp + Bp)}{C} = \text{Section Estimate of the number over-wintering beyond 122m}$$

Z = Number of T. cristatus captured per fence
Fs= Sample fence length, i.e 35.5m
S = Section length, estimated to be 130.4m
C = Number of sections
Tp= Estimated adult and sub-adult Population of the Top Pond in the Winter/spring 1989 i.e. 1141
Bp= Estimated adult and sub-adult Population of the Bottom . Pond in the winter/spring 1989 i.e. 2300 .This estimate is based on data presented in table 22.

The % of adults and sub-adults overwintering a distance of 122m or less from the breeding site was 46.18% The area within the circle with a radius extending 122m from the pond was calculated to be 83835 m^2, taking care to deduct $3320m^2$, the area of the two ponds. Thus, the density of adults and sub-adults over-wintering within 122m was estimated to be 1 individual per $52.7m^2$.

Table 20

Estimates of the breeding population of the Top pond and Bottom pond over-wintering 122m and beyond per sector

Section Estimate- Newts Beyond 122m	Nearest Fence	% OF BREEDING PONDS POPULATION
198.4	F1	5.76
135.9	F2	3.95
374.7	F3	10.89
639.1	F4	18.58
143.3	F5	4.17
33.1	F6	0.96
18.4	F7	0.53
308.5	F8	8.97
1851.4	F1-F8	53.82

Dead Wood and Ground Vegetation Surveys

The area of dead wood per enclosure showed considerable variation and was highest in deciduous areas and lowest in 100G (Table 21). 200G had a high score because, although the area is now open, the area formerly featured a sparse covering of larch trees which are now decaying. Vegetation characteristics and light levels are also found in Table 21.

Dead wood index for transects through the ring of fences F1-F8 are represented Fig 20.

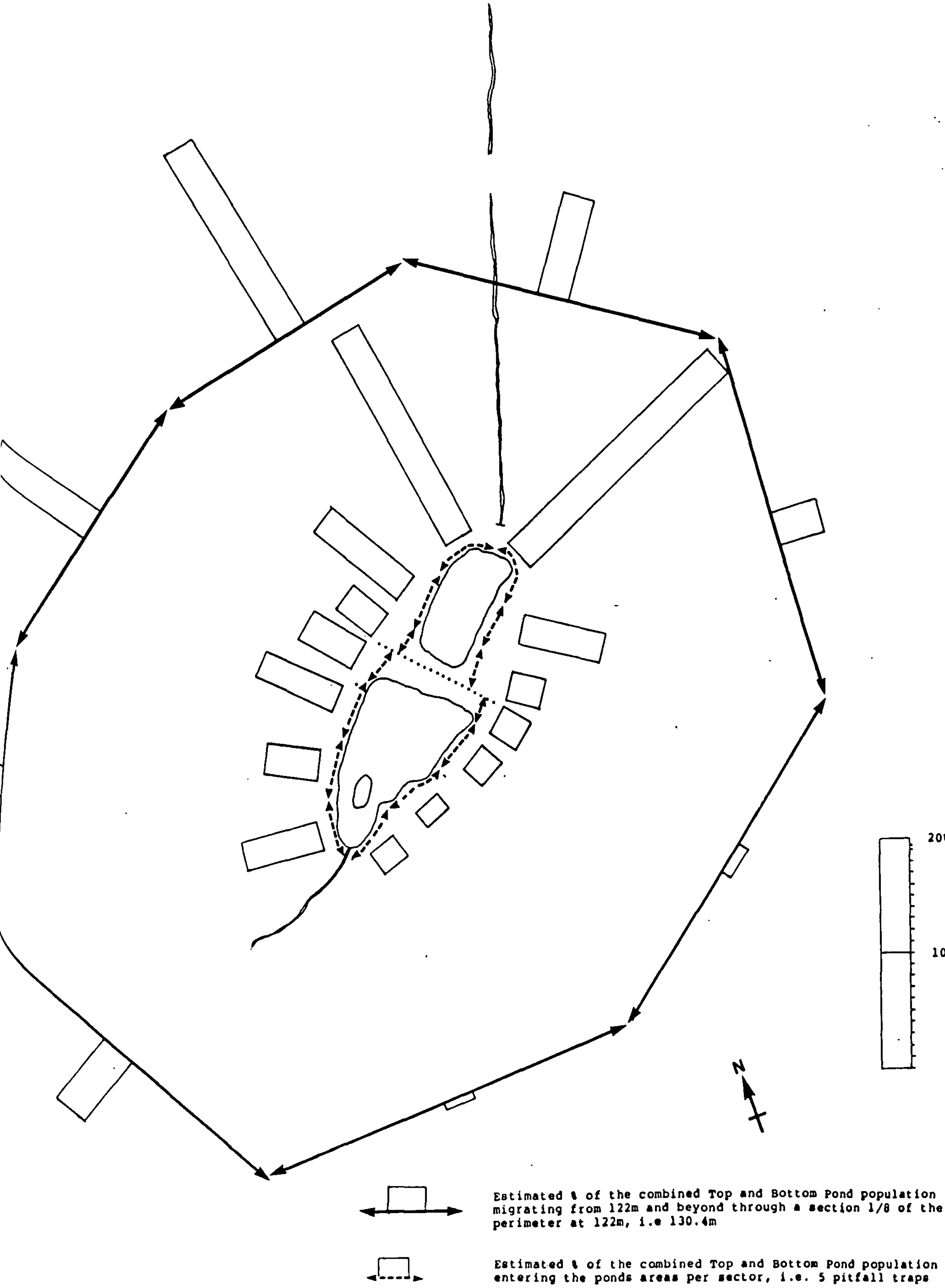
A significant regression co-efficent was obtained between the number of T. cristatus captured per enclosure and the area of dead wood ($t=2.56$, d.f.=6, $P<0.05$). A scatter plot and the estimated regression line are shown in Fig 24.

Similarly, the number of newts caught at fence F1-F8 in 1989 was related to the index value of dead wood in a corridor 100m beyond each fence ($R=0.114$, $t=4.53$ d.f.=6, $P<0.01$). See Fig 23 for a plot of the estimated regression line. The number of dispersing newts captured in 1988 at F1-F5 was unrelated to the index values of dead wood.

Bottom Pond Monitoring

Between 18 Febuary and 16 march 1989, 800 captures were recorded at the Bottom pond perimeter. By comparison over the same period 382 individuals were recorded at the Top pond. Hence the population using the Bottom pond during the 1989 breeding season was estimated to be twice that of the Top pond. In Table 22 is a breakdown of the location of captures expressed in terms of

Fig 20 Migration pattern of adults and sub-adults from the terrestrial over-wintering sites to the spring breeding ponds



Estimated % of the combined Top and Bottom Pond population migrating from 122m and beyond through a section 1/8 of the perimeter at 122m, i.e 130.4m

Estimated % of the combined Top and Bottom Pond population entering the ponds areas per sector, i.e. 5 pitfall traps

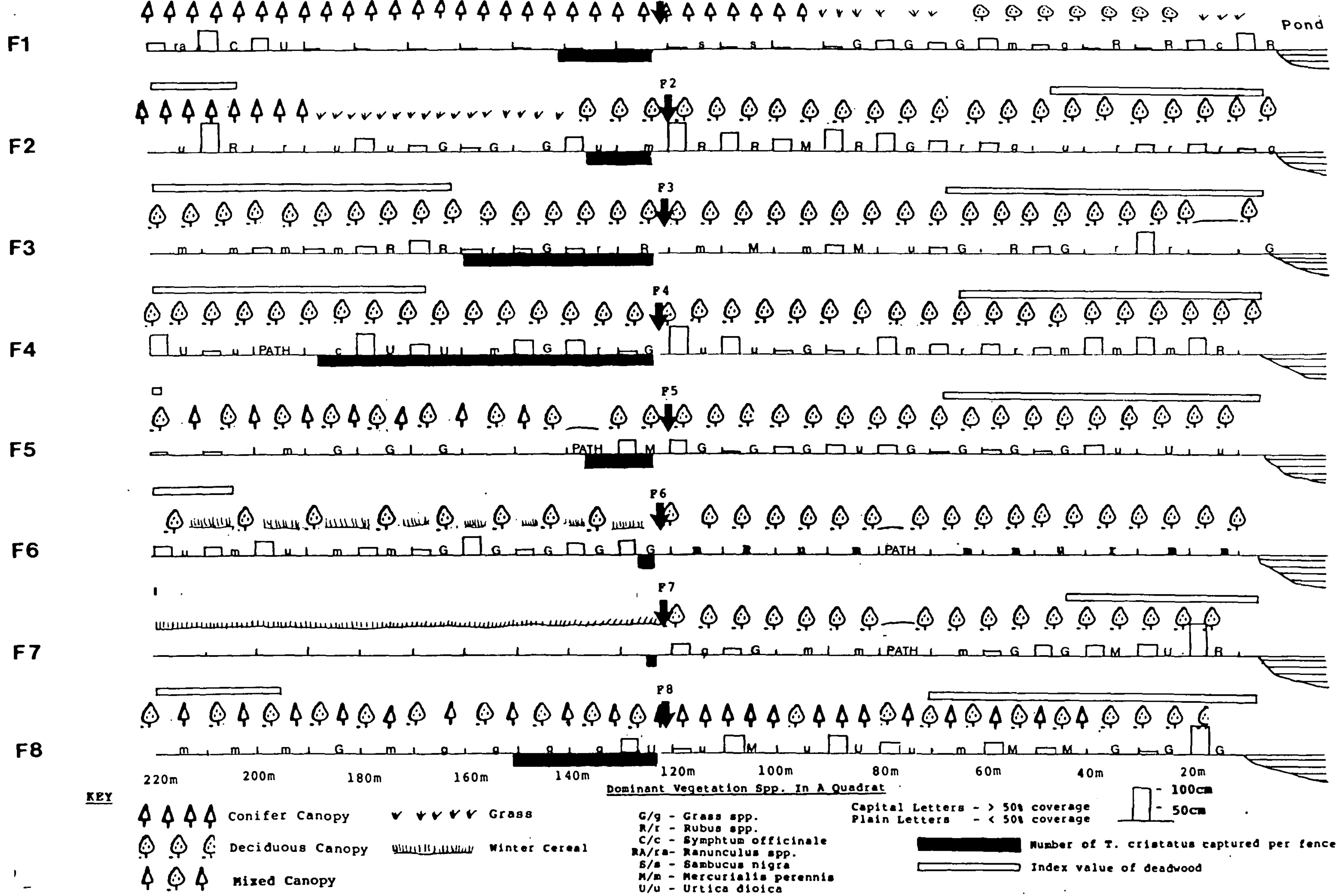
Table 21 Number Of T.cristatus Captured Per Enclosure And Enclosure Characteristics

ENCLOSURE	100D	100C	100G	200D	200C	200G	300D	300C
NO. T.cristatus	166	100	76	195	36	57	0	10
HABITAT TYPE	DECIDUOUS WOOD	CONIFER WOOD	GRASS RIDE	DECIDUOUS WOOD	CONIFER WOOD	GRASS RIDE	DECIDUOUS WOOD	CONIFE WOOD
DOMINANT VEGETATION	G,M,U, R	NONE PINE NEEDLES	G	M,R,G	NONE PINE NEEDLES	U,G,Ga	G,U,M, R	NONE PINE NEEDLE
MEAN HEIGHT VEGETATION cms (S.D.)	19 (14)	0 (0)	20 (12)	21 (19)	0 (70)	70 (21)	26 (26)	0 (0)
% BARE GROUND	20	100	5	60	1	0	39	100
AREA OF SURFACE DEADWOOD m2	30.5	7.7	0.0	26.5	1.2	15.4	14.2	6.4
SOIL * TYPE	BROWN EARTH	GLEYED BROWN EARTH	BROWN EARTH	BROWN EARTH	BROWN EARTH	BROWN CALCAR.	BROWN EARTH ON ALLUVIAL GRAVEL	BROWN CALCAR
SOIL pH *	>7	5.3-6	5.3-6	5.3-7	5.3-6	>7	6-7	>7
COMPARATIVE MEAN LIGHT LEVEL (S.E.) Lux #	490 (94)	1468 (246)	>1500 OFF SCALE	573 (144)	485 (67)	>1500 OFF SCALE	684 (162)	1051 (205
RECENT MANAGEMENT	NONE	NONE	1/2 MOWN ANNUALY	NONE	NONE	NONE	NONE	NONE

* taken from Sandel (1983)

readings taken on 11.7.89 between 10 & 13.00 hours

G - Gramineae
M - Mercurialis perennis
R - Rubus spp.
U - Urtica dioica
Ga - Galium aparine



F1
F2
F3
F4
F5
F6
F7
F8
Pond
P2
P3
P4
P5
P6
P7
P8
PATH
220m
200m
180m
160m
140m
120m
100m
80m
60m
40m
20m
KEY
Conifer Canopy
Deciduous Canopy
Mixed Canopy
Grass
Winter Cereal
Dominant Vegetation Spp. In A Quadrat
G/g - Grass spp.
R/r - Rubus spp.
C/c - Symphtum officinale
RA/ra- Ranunculus spp.
S/s - Sambucus nigra
M/m - Mercurialis perennis
U/u - Urtica dioica
Capital Letters - > 50% coverage
Plain Letters - < 50% coverage
- 100cm
- 50cm
Number of T. cristatus captured per fence
Index value of deadwood

22 Number of adults and sub-adults captured per enclosure between 18 Febuary and 16 April 1989

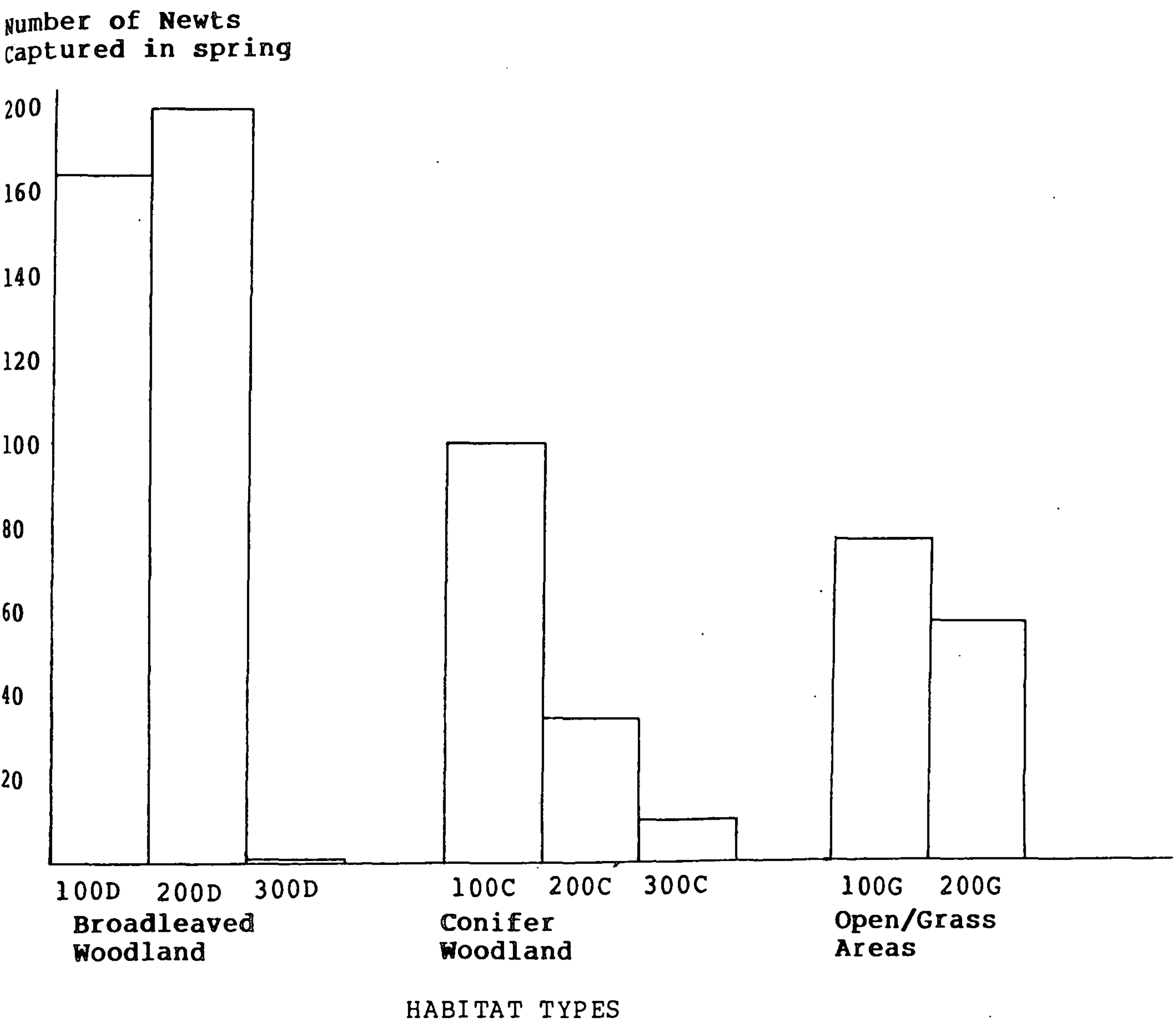
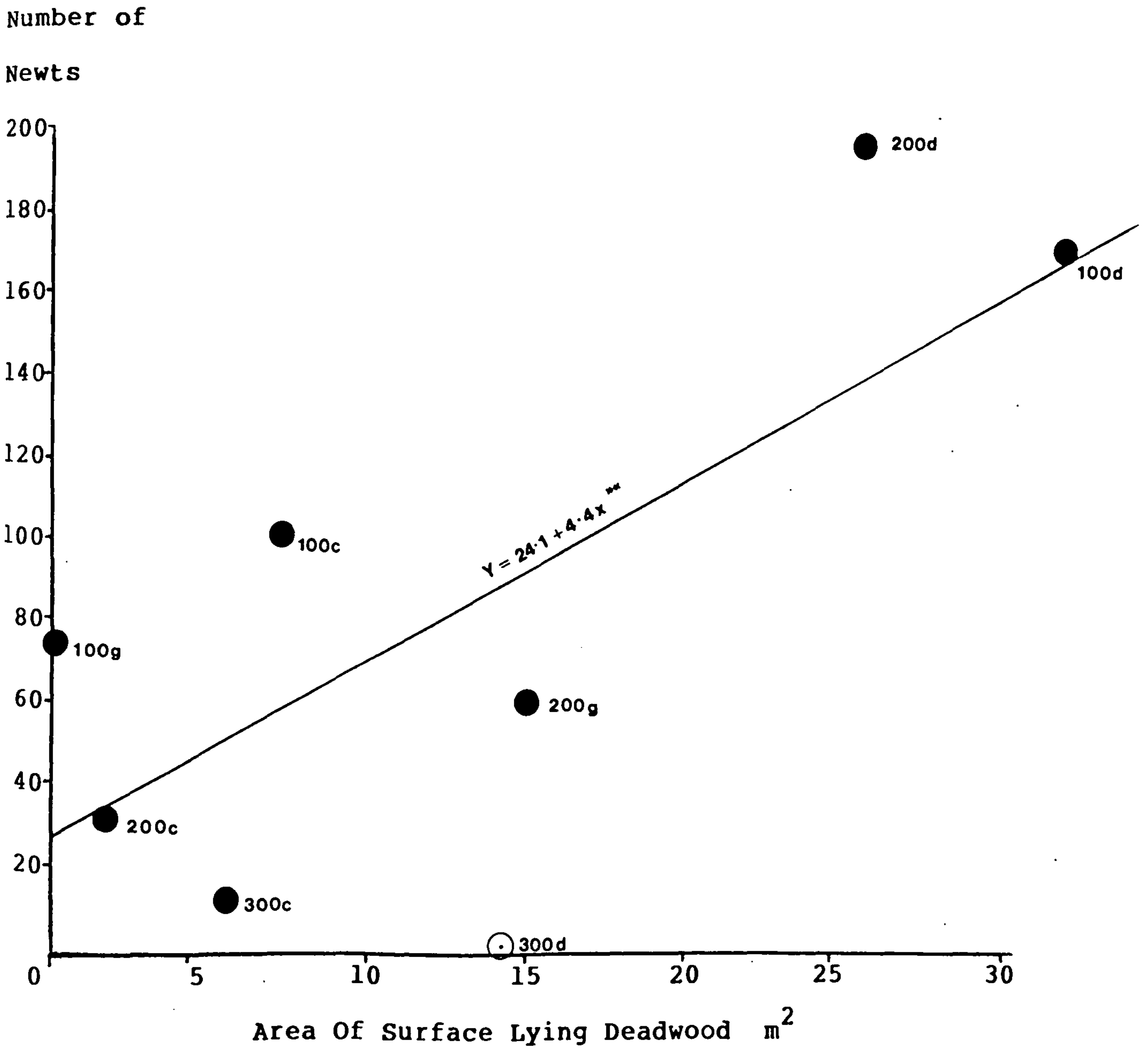


Fig 24

Relationship Between The Number Of Adults And Sub-adults Captured In Enclosures And The Area Of Surface Lying Deadwood



** – t = 2·6 P<0·05

sectors surrounding the pond.

Table 22

Number of T. cristatus captures around the Bottom pond between the 18 Febuary - 16 March 1989 (includes recaptures)

Sector	1	2	3	4	5	6
Number	41	109	233	298	84	35

DISCUSSION

T. cristatus exhibits a number of traits which are characteristic of k selected animals (MacArthur and Wilson, 1967). Within the genus, *T. cristatus* is large and long lived. Individuals regularly attain an age of 15-16 years in the wild (Francillon-viellot, Arntzen & Geraudie, in press; Hagstrom 1977). Delayed maturity and iteroparity are also Known traits. For amphibians the reproductive allocation is relatively low, *T. cristatus* females produce 60-300 eggs a year (Hagstrom,1980a) compared to 1300 and 600-2600 eggs in *Rana temporaria* and *Bufo bufo* respectively (Fraser, 1983). In addition, the careful ovipositing of single eggs in a protective leaf fold (Green,1980) may be interpreted as a relative form of parental care.

A feature of k strategists is a relatively stable population. At the Top pond there was no marked fluctuations in the number of adults caught departing the leaving the pond in 1988 and entering in 1989. Bell (1979) suggests long generation time and the occupation of several distinct niches, i.e. the aquatic and terrestrial phase, may moderate fluctuations in the population size since a disaster in one niche in one year will not cause extinction.

Larval production was successful in the Top Pond in 1988. The ratio breeding adults:emergent newtlets was estimated to be 1:2.2. This compares with 1:3.3 and 1:2.5 recorded by Amtkjaer (1981) at two ponds in Denmark. The terrestrial survival rate of metamorphosed newtlets is unknown, however Bell (1977) estimated an annual survival rate of 0.8 for *T. vulgaris*. If newtlet survival is the same as proposed for *T. vulgaris* then successful recruitment in the future may be anticapated.

The Top pond supports a very large population of *T. cristatus*. There are 21 detailed population estimates based either on mark and recapture or direct counts of the population (Nicholson, 1986; Halliday & Verrel, 1985; Amtkjaer, 1981; Zuiderwijk & Sparreboom, 1986; Hedlund & Robertson, 1989) Populations of less than 500 are recorded at 20 sites; only at Coleorton in Leistershire was the population estimated to be 1000. Although a small sample, it appears many sites were studied because they were home to "good" populations. Thus, the size of the Top pond population puts it in at least the top 5% of sites, and when the Bottom population is considered in conjunction, the placement increases still further.

When compared, the population size structure of males and females emigrating in 1988 from the pond was markedly different from that of the immigrating population in 1989. Immigrating population featured a higher proportion of smaller adults and sub-adults and a lower proportion of large adults. These results are consistent with the recruitement of young adults and the failure of larger males to return to the pond in the winter/spring.

Much of the influx of small sized animals may have represented mature individuals returning to the pond for the first time. While noting an individuals length is poorly related to age (Hagstrom, 1977; Francillon-vieillot, Arntzen and Geraudie, in press) it is assumed for large samples that a shift to smaller mean size reflects the arrival of younger animals. Estimates of the age of maturity range from 2-5 years (Smith,1969; Steward 1969; Frazer,1983; Hagstrom,1980).

The reduction in the proportion of larger males and females may have been partially caused by mortality during the terrestrial phase. The low numbers recaptured between years at the same fence F1-F5 lend some support to this proposition. Mortality values obtained at other sites vary considerably. Robinson (1977) estimated a mortality rate of 0.84 and 0.86 for males and females over a 2 year period. An annual mortality rate of 0.58 is quoted by Frazer (1983) without providing his source, while Hagstrom (1979) found the value to lie between 0.3 and 0.2 in his Swedish poulation.

A further possibility not to be excluded is, that in some years a proportion of adults remain terrestrial during the breeding season. In a 4 year study based on netting Hagstrom (1979) observed that some individuals were not recorded in the pond every year.

A clear predominance of males in the population was observed. Sex ratios in the literature show variation around the expected 1:1. However, some sampling techniques are sexually biast, e.g. funnel traps and torchlight counts (Nicholson, 1986; Griffiths, 1985). 10 out of 12 studied ponds with populations over 100 showed a male dominance. No explanation for the bias has been offered. Phillips et al (1989) discusses the male bias in the much studied Ambystomid genus. The lekking mating system of T.

cristatus described by Hedlund et al (1989), and Zuiderwijk et al (1986), in which there is always an operational sex ratio may be relevant.

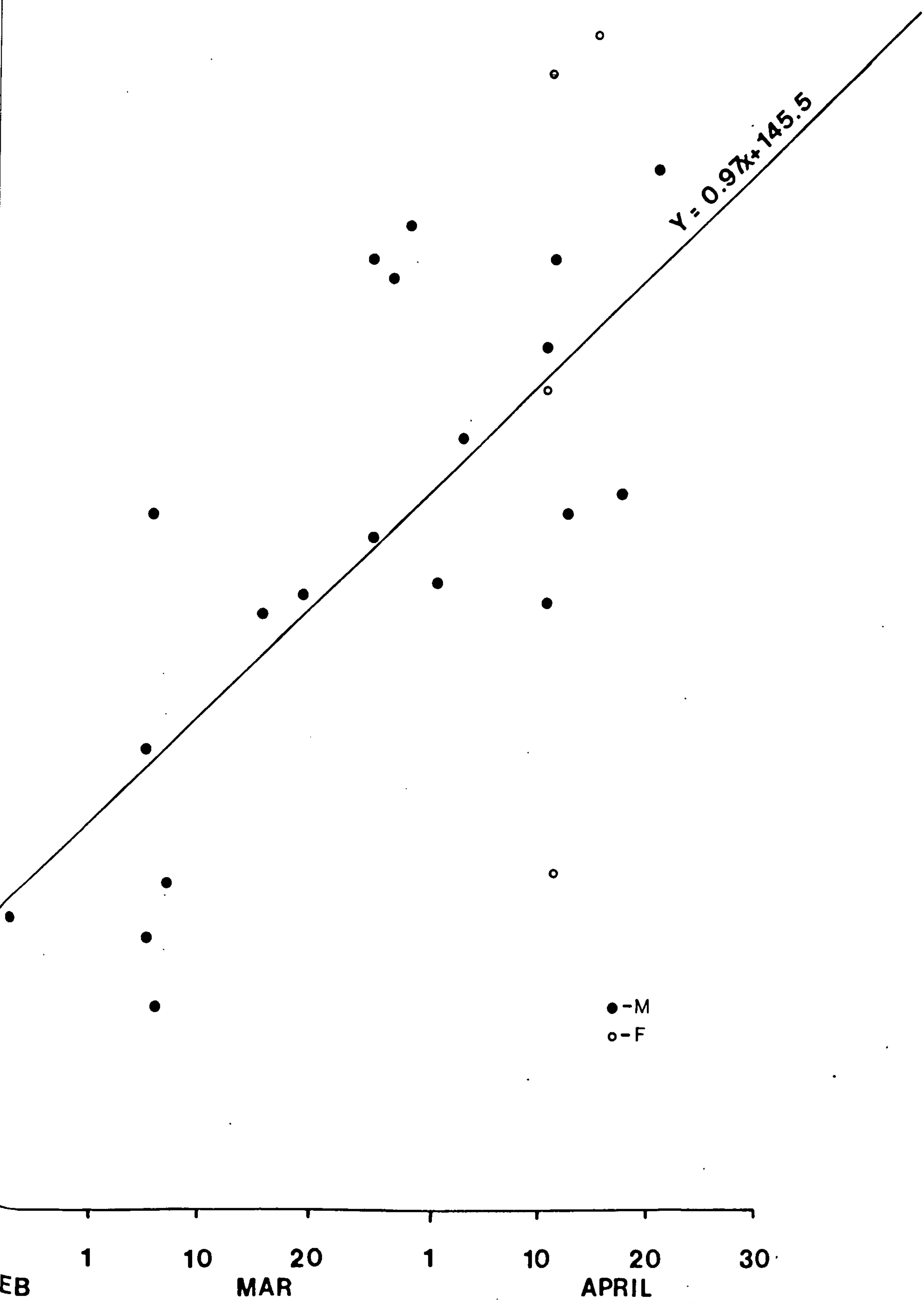
Examination of the dates of migration to and from the pond implied males arrived earlier in the breeding season and departed the pond later in late summer/autumn than females. The implication that females have a shorter aquatic phase is supported by estimates that females on average have a longer hibernation period (Note however the sample size was only 4 females). Robinson´s (1977), and Verell´s & Halliday´s (1985) data conforms with this conclusion. Hagstrom (1979) noted equal aquatic periods and Amtkjaer´s (1981) data indicated the median length of the aquatic period was longer in females.

Amongst individuals of the same sex the length of the hibernation showed a high amount of variation. Fig 25 is a plot of the hibernation length against the date of first recorded activity and shows males with a short hibernation period tended to be active early in the winter/spring. Males that arrived early at the pond in the breeding season were not generally the males that departed the pond early in the previous summer/autumn. Amtkjaer, (1981) recorded similar trends in Denmark.

Habitat Utilisation

The data indicates that *T. cristatus* was adaptable in it´s habitat requirements and was able to survive in a variety of areas. However, the results provide support that adults use

25 <u>Relationship between the length of hibernation (days) and the date of immigration in 1989</u>



habitats differentially. In deciduous woodland stands the highest numbers of fence captures and the highest densities of overwintering newts were logged. Stands 201, 202, 203, 204, and 305 would appear to offer prime habitat conditons (see Fig 5).

The mixed stands (207, 206, 307, 308, 309, 310) to the north-west appear to have been utilised by high numbers however, the importance of these areas may be over-emphasised if the outlet stream from the Bottom pond was used as a prefered migration corridor. The importance of the distant riverside Poplar stands 301, 302,304,306, 335, and 315 is difficult to evaluate without sampling the area.

Generally, areas to the east of the ponds were relatively under occupied and least prefered. T. cristatus did not over-winter in arable areas, though Cooke(1986) proposed that at the end of summer arable land was used preferentially as a feeding ground. Captures at F6 and F5 indicated a relatively small proportion migrated to stands 428/411 of scrub and open meadow. Nicholson (1986) and Robinson (1977) at other sites, found this habitatto be prefered. Further, there was no tendency to use the arable/wood boundry (hedgerow) leading to F6 as a migratory route.

Conifer blocks, despite a uniformly bare ground layer supported substantial numbers. Further, 1988 data provides evidence that newtlets were using the grass-ride/conifer block interface as a prefered migratory corridor. The importance of the stream into and out of the pond was difficult to assess since it was uncertain whether it was the habitats nearby or the presence of the water channels that lead to captures at F1 and F8.

If the pattern of land-use is to be understood, consideration needs to be given to the mechanisms causing individuals to take up residence in a particular area.

It is helpful to group those factors determining land-use into those that are intrinsic and those that are extrinsic. Intrinsic factors includes inate behaviour and motivation during the terrestrial phase. Extrinsic factors operating during this period which affect the landuse by newts include the edaphic, physical, and biological chacteristics of the habitat.

Dispersal from the breeding site is one of the main intrinsic factors. In this study evidence of preferred routes of emigration from the pond were found and the direction of exit from the pond was related to the subsequent direction of terrestrial dispersal. Hence, the key question that needs to be addressed is what determined the departure point from the pond,- was it environmental cues within and around the pond or was it previous experience of distant habitats aquired in other seasons?.

The literature though scant on the subject suggests adults may have a terrestrial home-range which they inhabit in consecuative years. Robinson (1977), found that individuals moved in the same direction in successive years. Nicholson (1976), corroborated this. Dolmen (1981), observed _T. vulgaris_ returning to the same refuge annually. Joly (1963,1968) reported that _Salamandra salamandra_ in France exhibited home ranges. Further, several studies have demonstrated that ambystomatid salamanders use the same route when moving between their breeding pond and terrestrial habitat both within years and between years (Phillips et al, 1989). This ability is termed migratory orientation. Moreover, in the genus Ambystoma summer home ranges are common (Semlitsch, 1981; Douglas and Monroe,1981). Smells emmitted by certain water plants or humidity gradients may represent guiding factors in newt orientation (See Dolmen 1981). Work by Phillips suggests Notophalmus viridescens have the ability to orient and navigate themselves using the earths magnetic field (Phillips, and Adler, 1978).

Studies over a series of years are needed to finally prove the existence of home ranges in adult and sub-adult T. cristatus. Evidence in this study is inconclusive. Firstly, the direction of exit from the pond was related to the subsequent direction of migration. However, only 10% of individuals captured at outer fences migating away from the pond in 1988, were recaptured at the same fence in the spring of 1989, this may however, reflect high mortality.

The dispersion of pattern of newtlets may have a strong bearing on the terrestrial distribution of the whole population and also requires further investigation. Newtlets with no prior experience of the surrounding terrestrial areas would be expected to depart the pond perimeter randomly. This was not the case in 1988, high numbers emerged from sector 1, 2, 3 and 7. The cue determining the point of exit is not uderstood. However, empirical observations indicate that the sectors recording high emergence featured unshaded margins; a high proportion of available marginal and emergent vegetation; and shallow water.

The shores where egg-laying in spring was observed to be the most abundant also coincided with areas of high emergence. Further, the departure per sector of newtlets was significantly related to the numbers of adults and sub-adults leaving the pond per sector.

Turning to surface lying deadwood, this may be classified as an extrinsic factor. Variation in the number of newts captured was positively related to the amount of dead wood, and it is presumed that dead wood functions as a shelter from the elements and from predators. Whilst, more work is required to evaluate the relationship, the finding has obvious implications in conservation management. The presence of dead wood in an area may enhance the availability and quality of shelter, allowing a higher number of newts to reside in an area.

Incidental observations often cite deadwood as a place of shelter (Buxton pers. comm; Fraser, 1983; Smith 1969). The feet of _T. cristatus_ are not equipped for active digging so they use natural shelters or burrows (Fraser, 1983). Moreover, micro-habitat preference experiments (Nicholson,1986) have indicated _T. cristatus_ prefer " micro-habitats incorporating, abundant easily penetrated cavities, particularly in materials with a high water retention capacity". This description fits a fallen log which has had time to "bed-down". Thermal qualities may be of importance to hibernating _T. cristatus_ (Frazer,1983)

Under most commercial woodland management, little dead wood is left on site when timber is extracted, however, in the 1970s at Wittenham Wood, Dutch Elm Disease (_Ceratocystis ulmi_) caused the death of a crop of Elm trees. The high abundance of dead wood in certain areas can be ascribed to the ravages of the disease.

Another component of the terrestrial environment considered to influence the survival rate during hibernation is soil type (Smith,1951). At enclosure 300D (deciduos woodland) no newts were captured in the spring of 1989. This result is anomolous with the general conclusion that deciduous areas with a relatively large area of deadwood supported the greatest numbers of newts. But the soil 300D occurs on is a Brown Earth on alluvial gravel. It is sandy, very freely drained and consists of about 30% stones (Sandel, 1983). It is proposed the thermal and hydrological chacteristics of this soil type are unfavourable to over-wintering newts.

Terrestrial Hinterland

53% of the population of the Top pond and Bottom pond appeared to over-winter beyond 122m. Evidence from enclosures indicate that high densities occur at 200m in favourable habitats but then decline with distance. Based on the values obtained in this study it is estimated that approximately 90-95% of the adult and sub-adult population over-wintered within a distance of 450m from the pond. These results corroborates Beebee´s (1977) assertion that the species requires a large terrestrial hinterland with preferably areas of scrub and open woodland. How representative these terrestrial requirements are of smaller populations is difficult to assess, as habitat quality is clearly an important factor. Observations at Shillow Hill lead Cooke (1986) to suggest the population of 500-2000 of T.cristatus remained more or less confined to a 2ha site.

Rates Of Migration

The fastest rate of migration previously recorded was 70m in a week (Nicholson, 1986). At Little Wittenham, it has been demonstrated that during the summer/spring migration individuals are capable of crossing in excess of 122m per night. This figure compares with the average speeds of 58-164m per hour obtained for Bufo bufo (Moore, 1954), which have hinterlands several kms in radius.

Nicholson proposed that on emergence newtlets disperse widly up to 500m and migrate greater distances than the adults before the onset of winter. From trap results in 1988, newtlets appeared to have a lower tendency to be captured at 122m in relation to adults. Note, late emergence of newtlets shortens time available for dispersion. However, the descrepancy with Nicholson's findings could be due to the quality of habitat availale in the vicinity of the pond.

REFERENCES

ARNOLD, E.N. AND BURTON, J.A. 1978. A field guide to the reptiles and amphibians of Britain and Europe. Collins, Glasgow.

AMTKJAER, J. 1981. An ecological study of newts in Denmark with the greatest importance attached to matters concerning Triturus cristatus. Specialerapport ved Zoologisk Laboratorium, Inst. f. zoologi og zoofysiologi, Arhus Universitet, unpublished.

BEEBEE, T.J.C. 1973. Observations concerning the decline of the British amphibia. Biol. Cons., 5:20-24.

BEEBEE, T.J.C. 1975. Changes in the status of the great crested newt, Triturus cristatus, in the British isles. Brit. J. Herp. 5: 481-490

BEEBEE, T.J.C. 1981. Habitats of the British amphibians (4): agricultural lowlands and a general discussion of requirements. Biol. Cons. 21:127-139

BELL, G. 1977. The life of the smooth newt (Triturus vulgaris) after metamorphosis, Ecological Monographs 47:279-299.

BELL, G. 1979. Populations of Crested newts, Triturus cristatus in Oxfordshire, England. Copeia, 1979 2:350-353.

BOULENGER, G.A. 1894. Size of British newts. Zoologist 52:145-147.

BRITISH HERPETOLOGICAL SOCIETY, 1986. Surveying for amphibians: a practical guide. B.H.S..

COLDREY, J. AND CAMPBELL, J.M. 1983. An atlas of Oxfordshire amphibians and reptiles, occasional paper No. 4. Oxfordshire County Council, Woodstock.

COOKE, A.S. 1986. Studies of the Crested newt at Shillow Hill, 1984-1986. Herpetofauna News 6:4-5.

COOKE, A.S. & SCORGIE, H.R.A. 1983. The status of the commoner amphibians and reptiles in Britain, No 3. Nature Conservancy Council.

DOLMEN, D. 1981. Local migration, rheotaxis, and philopatry by Triturus vulgaris within a locality in central Norway. Brit. J. Herp. 6:151-158.

DOUGLAS, M.E.AND MONROE, B.L. 1981. A comparative study of topographical orientation in Abystoma (Amphibia: Caudata). IBID 1981:460-463.

FRANCILLON-VIELLOT, H., ARNTZEN, J.W. AND GERAUDIE J. in press. Age, growth and longevity of sympatric T.cristatus, T. marmoratus and their hybrids (Amphibia, Urodela). A skeletochronological comparison. J. Herp.

FRASER, D. 1983. Reptiles and amphibians in Britain. Collins , London.

GREEN, D. 1984. A study of the Great Crested Newt (Triturus cristatus) in Durham and Tyne and Wear. Durham County Conservation Trust Ltd.

GRIFFITHS, R.A. 1985. A simple trap for studying newt populations and an evaluation of trap behaviour in smooth and palmate newts, Triturus vulgaris and T. helveticus. Herp. J. 1:5-10.

HAGSTROM, T. 1973. Identification of newt specimens by recording the belly pattern and a description of photographic equipment for such registrations. Br. J. Herpet. 4: 321-326.

HAGSTROM, T. 1977. Growth studies and ageing methods for adult Triturus vulgaris and T. cristatus Laurenti (Urodela, Salamandridae). Zool. Scripta 6:61-68.

HAGSTROM, T. 1979. Population ecology of Triturus cristatus and T. vulgaris (Urodela) in S.W. Sweden. Holactic Ecol. 2:108-114.

HAGSTROM, T. 1980. Growth of newts (Triturus cristatus and T. vulgaris) at various stages. Salamandra 16:248-251.

HAGSTROM, T. 1980a. Egg production of newts (Triturus cristätus and T. vulgaris) in South Western Sweden. Ass. St. Amp.& Rep. 1:1-8.

HEDLUND, L. ROBERTSON, J.G.M. 1989. Lekking behaviour in crested newts, Triturus cristatus. Ethology 80, 111-119.

HUTCHINSON, V.H. 1987. Guidelines for use of live amphibians and reptiles in field research. A.S.I.H., H.L., and S.S.A.R..

JACKSON, S.D. AND TYNING, T. 1989. Effectiveness of drift fences and tunnels for moving spotted salamanders, Ambystoma maculatum, under roads. Amphibians and roads - proceedings of the toad tunnel conference (Ed. T.E.S. Langton). ACO Polymer Products Ltd, Shefford.

JARVIS, J. 1973. Soils of the Wantage and Abingdon district. Soil Survey Of Great Britain, Harpenden.

JOLY, J. 1963. La sedentarite et le retour au gite chez la salamandre tachetee, Salamandra salamandra quadrivirgata. Comptes Rendus Hebdomadaires des Seances. Academie des Sciences, Paris 256:3510-3512.

JOLY, J. 1968. Donnees ecologiques sur la Salamandra salamandra. Annales des Sciences Naturelles, Zoologie, Paris. 10:301-366.

MACARTHUR, R.H. AND WILSON, E.O. 1967. The theory of island of biogeography. Princeton University Press, Princeton, New Jersey.

MOORE, H.J. 1954. Some observations on the migration of the Toad (Bufo bufo) Brit. J. Herp. 1:194-224.

NATURE CONSERVANCY COUNCIL, 1989. Guidelines for the selection of biological SSSI´s. Nature Conservancy Council, Peterborough.

NICHOLSON, M. 1986. Status and ecology of the Warty Newt (Triturus cristatus) - Final Report. Leicester Polytechnic under contract to the N.C.C.. Nature Conservancy Council, Peterborough.

OLDHAM, R. 1989. Potential tunnel systems at road developments in England. Amphibians and roads - proceedings of the toad tunnel conference (Ed. T.E.S. Langton). ACO Polymer Products Ltd, Shefford.

PHILLIPS, C.A. AND SEXTON, O.J. 1989. Orientation and sexual differences during breeding migrations of the spotted salamander Ambystoma maculatum. Copeia, 1989 1:17-22.

PHILLIPS, J.B. 1986. Two magnetoreception pathways in a migratory salamander. Science 233:765-767.

PLYTYCZ, B. AND BIGAJ, J. 1984. Preliminary studies on the growth and movements of the Yellow-bellied Toad, Bombina variegata (Anura: Discoglossidae). Amphibia-Reptilia 5:81-86.

PODLOUCKY, R. 1989. Protection of amphibians on roads - examples and experiences from Lower Saxony. Amphibians and roads - proceedings of the toad tunnel conference (Ed. T.E.S. Langton). ACO Polymer Products Ltd, Shefford.
Amphibians and roads,

PRESST, I., COOKE, A.S. AND CORBETT, K.F. 1974. British amphibians and reptiles. In Hawksworth, D.L. (Ed), The changing flora and fauna of Britain 6;229-254. Academ. Press.

ROBINSON, J. 1977. A study of a newt colony on Castor Hanglands National Nature Reserve. Nature Conservancy Council, unpublished

READING, C.J. 1989. Opportunistic predation of common toads Bufo bufo at a drift fence in southern England. Proceedings of the toad tunnel (Ed. T.E.S. Langton). ACO Polymer Products Ltd, Shefford.

SANDEL, A.J. 1983. Little Wittenham Wood, a working plan for the period 1984 to 1993. M.Sc. thesis, Oxford University.

SMITH, M.A. 1951. British amphibians and reptiles. Collins, London.

SMITH, L.P. 1976. The agricultural climate of England and wales: Aerial averages 1941-1970. H.M.S.O., London.

STENHOUSE, S.L. 1985. Migratory orientation and homing in Abystoma maculatum and Abystoma opacum. Copeia, 1985 1:631-637.

STEWARD, J.W. 1969. The tailed amphibians of Europe. David & Charles, Newton Abbot.

STRIJBOSCH, H. 1980. Habitat selection by amphibians during their terrestrial phase. Brit. J. Herp. 6:93-98.

TWITTY, V.C. GRANT, D. AND ANDERSON, O. 1967. Home range in relation to homing in the newt, Taricha rivularis. Copeia, 1967:649-653.

VERREL, P. AND HALLIDAY, T. 1985. The population dynamics of the Crested newt, Triturus cristatus, at a pond in southern England. Holarctic Ecology 8: 151-156.

ZUIDERWIJK, A. AND SPARREBOOM, M. 1986. Territorial behaviour in the crested newt, Triturus cristatus and marbled newt, T. marmoratus (Amphibia, Urodela). Bijdragen tot de Dierkunde, 56 2:205-213.

APPENDIX 1

MACRO-INVERTEBRATES	TOP POND	BOTTOM POND
HIRUDINEA		
Helobdella stagnalis	+	+
Theromyzon tessulatum	+	+
Glossiphonia complanata		+
MOLLUSCS		
Acroloxus laccustris	+	
Bithynia tentaculata	+	
Lymnea peregra	+	+
Lymnea stagnalis	+	
Planorbis albus	+	+
Planorbis crista		+
Planorbis planorbis	+	
Potammopyrgus jenkinsii	+	+
Valvata piscinalis	+	
CRUSTACEA/MALACOSTRACA		
Asellus aquaticus	+	+
Crangonyx pseudogracilis	+	+
Gammarus pulex	+	
ARANEAE		
Argyroneta aquatica	+	
MEGALPTERA		
Sialis Lutaria	+	+
EPHEMEROPTERA		
Caenis robusta	+	+
Cleoen dipterum	+	+
TRICHOPTERA		
Holocentropus dubius	+	
Holocentropus picicornis	+	
Anabolia nervosa	+	
Limnephilus lunatus	+	+
Athripsodes cinerea	+	
Mystacides longicornis	+	
Triaenodes bicolor	+	+
HETEROPTERA		
Cymatia bonsdorfii		+
Cymatia coleoptrata	+	+
Callicorixa praeusta		+
Sigara distincta	+	
Sigara dorsalis	+	
Sigara fossarum		+
Ilyocoris cimicoides		+

Nepa cinerea	+	
Gerris lacustris	+	
Gerris odontogaster		+
ZYGOPTERA		
Coenagrion puella	+	+
Enallagma cyathigerum	+	
ANISOPTERA		
Aeshna cynea	+	
Sympetrum striolatum	+	+
COLEOPTERA		
Noterus clavicornis	+	+
Haliplus confinis	+	
Haliplus Flavicollis	+	
Haliplus immaculatus	+	
Haliplus lineatocollis	+	
Haliplus ruficollis	+	
Agabus bipustulatus	+	+
Agabus sturmii	+	+
Dytiscus marginalis	+	
Hydroporus palustris	+	+
Hydroporus planus	+	+
Hygrotus inaequalis	+	+
Hyphydrus ovatus	+	+
Ilybius fenestratus	+	+
Ilybius fuliginosus	+	+
Ilybius quadriguttatus	+	+
Ilybius subaeneus	+	+
Ilybius ater	+	+
Anacaena globulus	+	
Anacaena limbata		+
Enochrus testaceus	+	
Graptodytes pictus	+	
Helophorus aquaticus		+
Helophorus brevipalpis	+	+
Hydrobius fuscipes		+
Laccobius bipunctatus	+	+
Oulimnius tuberculatus	+	
Hygrobia hermanii	+	+
Dryops. sp	+	

Addtional Taxa (Not all identified to species)

Oligochaetae		+
Larvea		
COLEOPTERA		
Dytiscidae	+	+

Hydroporinae	+	+
Hyphydrus ovatus	+	
Hydroplilidae		+
Haliplidae	+	
Helodidae		+
Hygrobia Hermanii		+
DIPTERA		
Choboridae	+	+
Culicidae		+
Chironomidae	+	+
Stratiomyidae		+
LEPIDOPTERA		
Nymphula sp	+	
HETEROPTERA	+	+
Notonecta sp.	+	+
Corixini		

Macro-invertebrates were sampled on 26.6.87 and 7.7.88 by"Pond Action". For macro-invertebrate sampling, a 3 minute period was divided equally between the different microhabitats observed. A standard pondnet of 1mm mesh was used.The precedure was repeated 3 times.

+ Species/group present

APPENDIX 2

Dates on which no mass and/or length measurements were taken. Also shown are dates when no photo-records were made.

Date	Mass	Length	Photo-record
7.8.89		*	*
19.8.89-28.8.89	*		*
20.2.89-14.3.89	*		

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U N I V E R S I T Y O F D U R H A M

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