

**SOME OBSERVATIONS ON *CERAGRION TENELLUM*  
(DE VILLERS) IN SOUTHERN ENGLAND  
(ZYGOPTERA: COENAGRIONIDAE)\***

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The coenagrionid *C. tenellum* was studied by capture-recapture and direct observation in several neighbouring areas along a small stream in the New Forest, Hampshire, England. The New Forest is important ecologically because it is probably the last remaining area of heathland in lowland Britain which is large enough to support many of the characteristic plants and animals. Notably, the Forest's bogs and nearby heathland provide habitats for *C. tenellum*, resulting in this species being commoner there than anywhere else in Britain. The imaginal *C. tenellum* was very selective in the areas of stream colonised: it was only common where the stream was wide and boggy with a dense growth of *Hypericum elodes*. Deeply incised and clear, gravelly parts of the stream were avoided. Most individuals in well established populations were highly static, but a high proportion of insects in sites away from the main population centres were wanderers. Most movement within an established colony was from the periphery inwards; relatively few individuals were observed to move from the centre outwards. Adult male *C. tenellum* show relatively little tendency to move far once they are associated with a colonial group. The population numbers declined consistently throughout the study periods (first three weeks of August, 1974 and 1975), and only five individuals out of 704 males seen were teneral. The mean length of the life for adult males in different populations varied between 8 and 17 days. Survivorship in males was nearly random with age for the major part of the life span. A detailed analysis of the capture-recapture data revealed only one occasion when marking had a deleterious effect on survival. The percentage of males ranged from 57 to 68 percent and the mean mating frequencies were 13 percent (males) and 35 percent (females). Frequent aerial fighting between males was not observed to lead directly to movement of any individuals away from the colony area. A few male-to-male interactions were definitely sexual. Mating

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occurred at water, in fine weather, and falls into the copulation type classified as 'long'.

## INTRODUCTION

*Ceriagrion tenellum* (de Villers) is a zygopteran which appears to have its centre of distribution in the Mediterranean region, extending northwards to Britain and Germany, and as far east as Syria (Longfield, in CORBET et al., 1960). In Britain, *C. tenellum* is only known to occur in a very few localities, mainly in southern England and Wales, where it is apparently at the extreme limits of its ecological tolerance in north-western Europe. Since it is considered to be a 'Mediterranean' species, *C. tenellum* is possibly under some ecological stress in Britain in that the habitats are sub-optimal for the species. In particular, the habitats occupied by this species in Britain are often very restricted in size, specialised and climatically limiting which may result in them being only marginally suitable, so that the observations recorded here may not be typical of *C. tenellum* populations elsewhere in Europe.

*Ceriagrion tenellum* is a coenagrionid of medium-small size, similar in size and build to the common *Ischnura elegans* (Vander L.). According to ROBERT (1958), it is the only species of *Ceriagrion* found in Europe. The genus *Ceriagrion* is mainly found in Africa and Asia where several species occur, especially in tropical areas. According to Longfield, (in CORBET et al., 1960), in Britain, *C. tenellum* breeds only in acid bogs and runnels in south and southwest England and Wales (including Anglesey).

As far as is known, no similar studies of this species have been carried out. Ecobehavioural studies of *C. tenellum* were made by MOORE (1964) in Dorset, southern England and CORBET (1957) studied the life history of this species in the New Forest of Hampshire, where the present work was done.

The observations were carried out on imaginal populations on Ober Heath during August in 1974 and 1975. This paper is mainly concerned with distribution and habitat selection, population numbers and survival rates, dispersal movements and reproductive behaviour, with reference to weather and other environmental factors.

## THE NEW FOREST HABITATS AND ODONATA FAUNA

The 'New' Forest was created about 1079 when King William I selected the area between the Solent and the sea for afforestation. The Forest lies in the broad and shallow Hampshire basin which is filled with a mixture of gravels, sands and clays laid down when the area was occupied by a large river estuary or shallow sea. The clays and sands were deposited first and the gravel was apparently spread by glacial action to form gravel cappings which have been eroded by streams to expose the underlying materials. The vegetation reflects three main topographical types. The gravel plateaux are essentially heathland with a natural growth of Scots pine (*Pinus sylvestris* L.) and birch (*Betula verrucosa* Ehrl.) together with gorse (*Ulex europaeus* L.), heather (*Calluna vulgaris* (L.)) and grasses. The richer areas separating the plateaux are chiefly loams supporting

oak (*Quercus robur* L.), beech (*Fagus sylvatica* L.), yew (*Taxus baccata* L.), holly (*Ilex aquifolium* L.) and hawthorn (*Crataegus monogyna* Jacq.). The marshy ground is colonised by heath (*Erica* spp.), bracken (*Pteridium aquilinum* (L.)), sedges (*Carex* spp.), bog moss (*Sphagnum* spp.), cotton grass (*Eriophorum latifolium* Hoppe), with some alder (*Alnus glutinosa* L.) and willow (*Salix* spp.) thickets (SMALL, 1975).

It is considered that the New Forest is ecologically important because it is probably the last remaining area of heathland and bog in lowland Britain which is large enough (34400 ha) to support indefinitely many of the characteristic animals and plants. The Forest's bogs are formed of saturated peat deposits filling hollows and valleys. They are usually base-enriched due to leaching of the more acid areas of their catchments. The bogs and nearby heathland are floristically and faunistically probably the richest habitats to be found in the Forest, some of the species being rare or very local. Into this category come the coenagrionid dragonflies *Ischnura pumilio* (Charp.) and *Ceriagrion tenellum*, both of which are probably commoner in the New Forest than anywhere else in Britain.

The *Ceriagrion tenellum* populations studied were associated with Ober Heath stream, which runs in a north-westerly direction along the northern edge of Ober Heath, near to Brockenhurst, Hampshire. The study area was ecologically diverse since young and mature *Pinus* forest, stream, bog and heathland were all in close association at this point (Fig. 1).

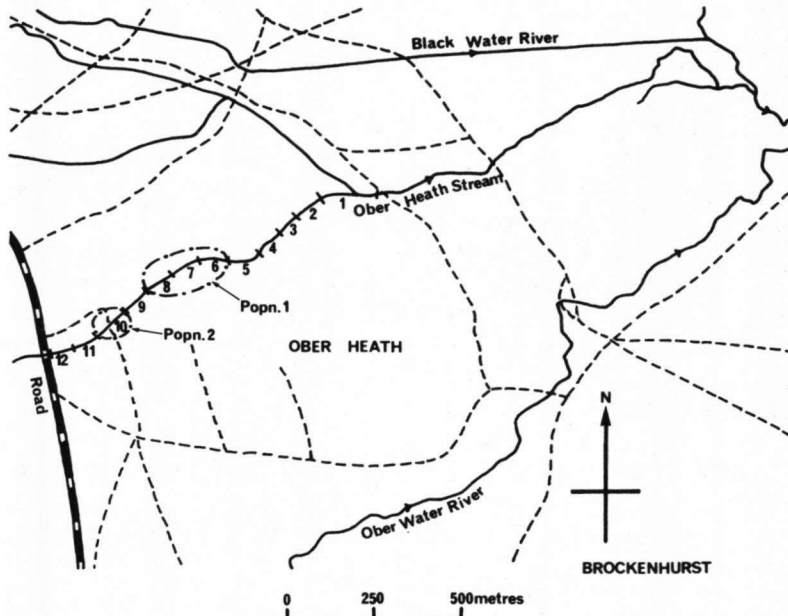
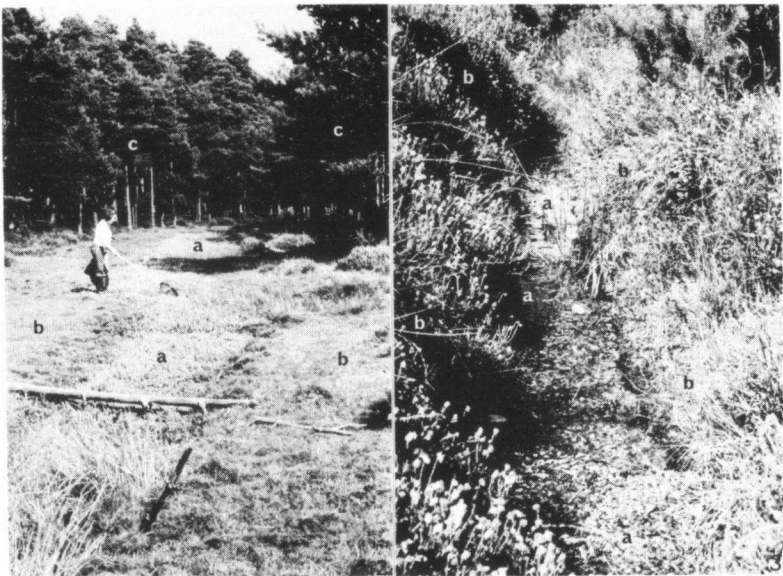


Fig. 1. Map showing Ober Heath area of the New Forest, 1974 and 1975: (1-12) Sampling sectors of Ober Heath stream; — (Popn. 1) Area occupied by *Ceriagrion tenellum* Population 1 (in sectors 6, 7 & 8); — (Popn. 2) Area occupied by Population 2 (in sector 10); - - - - -: Footpaths and tracks.

In July, 1974, Ober Heath stream was surveyed from its origin near the tarred road at Rhinefield Lodge (Map ref. SU 268 035) to its confluence with another small stream about one kilometre to the north east (Map ref. SU 277039). The stream varied considerably in character. In some parts the stream was between one and two metres wide; here it was shallow, muddy and boggy, often with a dense growth of water plants, especially *Hypericum elodes* L. In other areas the stream occupied a deeply incised channel (artificially deepened to improve drainage of the surrounding bog and heathland) which usually had a gravelly bed. The gravelly parts of the stream were freer of vegetation than the muddy sections (Figs. 2, 3). Some parts of the stream were more or less open, whereas others were shaded by small or large pine trees.

The Odonata fauna of the New Forest area is rich in that 33 species have been recorded there. Of these, the following 13 species were observed on Ober Heath in 1974 and 1975: *Lestes sponsa* (Hans.), *Calopteryx virgo* (L.), *Enallagma cyathigerum* (Charp.), *Ischnura elegans* (Vander L.), *Pyrrhosoma nymphula* (Sulz.), *Ceriagrion tenellum* (Vill.), *Cordulegaster boltoni* (Don.), *Aeshna juncea* (L.), *Ae. grandis* (L.), *Anax imperator* Leach, *Libellula depressa* (L.), *Orthetrum coerulescens* (Fb.), *Sympetrum striolatum* (Charp.). In addition, *Ischnura pumilio* (Charp.) and *Orthetrum cancellatum* (L.) have been recorded on Ober Heath in recent years (PARR, 1969), but



Figs. 2-3. Ober Heath stream: (2) Sectors 7 & 8, looking NE: (a) Dense growth of water plants, especially *Hypericum elodes*, covering water surface, — (b) Short turf, — (c) *Pinus* sp. plantation; — (3) Sector 9, looking SW: (a) Clear water flowing in incised channel over clean gravel stream bed, — (b) Steep stream banks with *Juncus* spp., *Calluna vulgaris* and *Erica* sp.

were not observed in July or August, 1974 or 1975, probably because the main flight period had ended.

The species known to breed in Ober Heath stream, apart from *Ceriagrion tenellum*, are *Pyrrhosoma nymphula*, *Cordulegaster boltoni* and *Orthetrum coerulescens*. *Ischnura pumilio* bred in the stream in 1968 and probably also in 1969. Single specimens of *Calopteryx virgo*, *Ischnura elegans* and *Enallagma cyathigerum* were seen at the study site in 1974 but there is no evidence that any of these species bred there.

## METHODS

The populations on Ober Heath in 1974 and 1975 were studied using the capture-recapture method and direct observation. The procedures and techniques utilised were essentially similar to those described in detail for *Ischnura elegans* by PARR (1965, 1973a, 1973b) and which were also used by PARR (1976) in a population study of *Enallagma cyathigerum*. The allocation of a unique number, which was applied to the wings with a coded series of paint spots, necessitated marking each individual only once. The capture-recapture data have been analysed using the methods of FISHER & FORD (1947), JOLLY (1965) and MANLY & PARR (1968).

The mean survival rates given for the Manly & Parr and Jolly methods are means of daily survival estimates. If sampling days were not consecutive, then the estimated rate raised to the relevant root was calculated to provide a daily rate. Thus, if sampling occurred on day 4, with an estimated survival rate of 0.8 and next occurred on day 6, the mean rate for this two day period is  $\sqrt{0.8}$ , or 0.8944. Similarly, with an estimated survival rate of 0.71 for a three day period, the daily rate applicable is  $\sqrt[3]{0.71}$ , or 0.8921. If the estimated survival rate for any sampling period exceeded 1.0, the value of 1.0 was taken as the daily survival rate for the purposes of estimating the mean rate.

In both August 1974 and August 1975, the populations of *C. tenellum* were studied for periods of about three weeks and attempts were made to sample each population every two days. Unfortunately, adverse weather conditions sometimes prevented the following of a completely regular sampling programme, although the time between successive samplings was never longer than three days.

In 1974 two relatively discrete and neighbouring subpopulations (called Population 1 and Population 2) were studied, but in 1975 only Population 2 was marked and observed in detail.

## DISTRIBUTION AND MOVEMENTS

Although *C. tenellum* has been described as a Mediterranean species by CORBET et al. (1960), it occurs in southern Britain, central France, northern

Spain and Switzerland. SCHMIDT (1977) reports it is on the verge of extinction in Western Germany. Since it also occurs in Morocco, Algeria, Sardinia and Sicily, the species clearly has a fairly wide range of ecological tolerance, especially in terms of climate. It seems likely that whilst it is intolerant of extreme cold, the primary factor limiting its generally wider distribution in Europe may be the lack of suitable habitats.

The distribution of *C. tenellum* in Britain is mainly restricted to areas adjacent to the southern seaboard, with other outposts in Norfolk, Surrey, Sussex, Hampshire, Gwent and coastal Wales. In these areas it is especially associated with small streams, runnels and pools in acid bogs. It is noticeably absent from the northern and central areas as well as from the whole of Ireland.

In 1974, Ober Heath stream and the immediate area surrounding it was divided into twelve sectors and each was assessed for relative abundance of imaginal *C. tenellum*. Figure 1 and Table I demonstrate that the distribution of *C. tenellum* was extremely uneven, some stretches being devoid of the species and in others it was abundant. In all the areas where *C. tenellum* was abundant the stream was wide and boggy, with a dense growth of *Hypericum elodes* (Fig. 2). The species was less common in the more heavily shaded sections and was almost totally absent from the deeply incised and gravelly parts of the stream (Fig. 3). This resulted in three well defined sub-colonies occupying the more favoured areas, with varying degrees of isolation from neighbouring populations.

The characteristics of the twelve sectors are summarised in Table I. The length of each sector was determined partly by well defined natural markers, such as prominent trees, and partly by the characteristics of the stream. An attempt was made to keep each sector very roughly the same length; in practice the lengths of the sectors ranged from 74 to 97 metres with a mean of about 85 metres, measured by pacing. That this method of estimating distance was accurate enough is demonstrated by the sum of the estimated lengths of all the twelve sectors being 1016 metres; the measured length of this part of Ober Heath stream on an Ordnance Survey map 1:25,000 scale, is almost exactly 1000 metres.

In 1974 the population at Sector 1 was found to be continuous with larger populations further down the stream and it was decided that this colony could not be marked satisfactorily because of the large numbers of individuals. It was noticeable that this large colony, partly in Sector 1, was associated with an open marshy length of stream dominated by *Hypericum elodes*. However, in 1975 this part was dry and the colony had disappeared. Sectors 2, 3 and 4 were also dry in 1975; in the previous year only very occasional individuals could be located in these shady and deeply incised sections, totalling about 266 metres. Sectors 5-12 contained some water in both 1974 and 1975 and supported two further colonies of *C. tenellum*. Sector 5 was heavily shaded by

young pines for all of its length; this single factor was almost certainly responsible for the relative lack of *C. tenellum* there. Sectors 6-8 were largely marshy with *H. elodes* as the main emergent vegetation. This section of approximately 250 metres had an effectively single population (Population 1) of *C. tenellum*, which was most dense in the more open areas of Sector 7 and sparse in the more shady parts of Sector 6. The stream in the upper part of Sector 8 and the whole of Sector 9 (Fig. 3) was deeply cut with the banks overhung with ling heather (*Erica* sp.), *Calluna vulgaris* and *Juncus* sp. and it had a clean gravelly bottom: *C. tenellum* was very rarely observed there. Sector 10 which was 96 metres in length supported Population 2 which was entirely restricted to a 51 metre central section where the stream varied from 0.7 to 2.5 metres wide and where it was marshy. The narrow and deeply cut ends of Sector 10 were devoid of *C. tenellum*. Population 2 also extended on to the boggy ground to the south of Sector 10. No *C. tenellum* were seen at 11 and 12 which were respectively a narrow deep channel containing flowing water and a mere seepage, being the origin of the stream.

Table 1

The characteristics of the Ober Heath stream (1016 m) and the distribution of *C. tenellum*

Sector	Length (m)	Nature of the stream	Status of <i>C. tenellum</i>	Notes
1	80	SM	C (1974 only)	Mostly open, joins another stream; dry 1975
2	83	IG	—	Shaded by pines; dry 1975
3	86	IG	—	Shaded by pines; dry 1975
4	97	IG	R	Shaded by pines; dry 1975
5	90	SM	R	Shaded by pines
6	78	SM	C	Partly shaded by pines
7	90	SM	C	Fairly open; joined by small runnel
8	82	SM/IG	C	Partly shaded by pines; deep and gravelly in upper section
9	82	IG	R	Deep channel
10	96	SM/IG	C	Mostly open, some pines; boggy ground near stream
11	78	IG	—	Deep channel
12	74	IG	—	Origin of stream, a mere seepage

The flow direction of the stream was from Sector 12 towards Sector 1. — Key to abbreviations: SM = shallow and marshy; — IG = incised and gravelly; — C = common - well defined colony present; — R = rare; — — = absent.

A record was kept of movements between the two main populations and between Sectors 6, 7 and 8 occupied by Population 1. During August 1974, 20 immigrants to the combined sites 6, 7 and 8 were recorded, of which 14 were males. A summary of these movements is presented in Table II. The

Table II  
Immigration to Sectors 6, 7 and 8 (Population 1) from other sectors — August 1974

	Sectors			
	4	5	9	10 (Popn 2)
Number of males marked in the relevant sector	2	10	1	131
Males moving to Popn 1	0	6	0	8
Number of females marked in the relevant sector	2	8	1	61
Females moving to Popn 1	1	3	1	1

immigrants originated from Sectors 4, 5, 9 and 10 and only in the last of these (Population 2) were the insects numerous. The low frequency of *C. tenellum* in Sectors 4, 5 and 9 suggested that stable resident populations did not exist there. Table II shows that of the 24 individuals marked in Sectors 4, 5 and 9, 11 (45.8 percent) were recaptured in Population 1, which supports the initial impression that the insects in those sectors were not resident. In contrast, Population 2 at Sector 10 appeared to be a stable, discrete colony and this would seem to agree with the small number (9/192; 4.7 percent) which were observed to move to Population 1.

In the same period of August 1974, no immigrants from other sectors were recorded at Sector 10 occupied by Population 2.

During 1975, Population 2 was the only one studied in detail. However, on 31 July, 1975, 39 males and 13 females were marked at Sector 6, but none of these was ever seen at Sector 10. Since virtually the whole of Population 2 was marked by the end of the study on 21 August, it is unlikely that many of those individuals coded at Sector 6 could have escaped detection had they moved to Sector 10. When Population 1 was sampled on 21 August, three specimens originally marked there on 31 July were recaptured, together with one male marked at Sector 10 on 2 August and recaptured there on 4 and 6 August. On 21 August, 22 unmarked individuals were also caught in Population 1.

The movement of individuals between Sectors 6, 7 and 8 (Population 1) in August 1974 was analysed (Tab. III). Totals of 257 males and 183 females were marked in these three sectors. Of the 160 males and females marked in Sector 6, 11 (6.9 percent) moved to Sector 7, and none went to Sector 8. Out of 204 of both sexes marked in Sector 7, only 10 (4.9 percent) moved to Sectors 6 and 8 (7 and 3 individuals respectively). In contrast, although only 76 were marked in Sector 8, 26 (34.2 percent) left to be recaptured in Sectors 7 and 6 (24 and 2 individuals respectively). The proportion of insects observed to leave Sector 8 was very significantly higher than the proportions leaving Sectors 6 and 7 ( $p < 0.001$  in both cases).

An analysis of the records of all individuals recaptured at least once in single sectors and combinations of sectors (Tables IV and V) demonstrates



Table III

Local movements within colony boundaries: movement of individuals between Sectors 6, 7 and 8 (Popn 1), 1974

Movements	♂	♀	Totals
<i>From sector 6 to Sector 7 or 8</i>			
Total individuals caught at Sector 6	107 (100)	67 (60)	174 (160)
Total observed to move from Sector 6 to Sector 7	7	4	11
Total observed to move from Sector 6 to Sector 8	0	0	0
<i>From Sector 7 to Sector 6 or 8</i>			
Total individuals caught at Sector 7	145 (113)	101 (91)	246 (204)
Total observed to move from Sector 7 to Sector 6	5	2	7
Total observed to move from Sector 7 to Sector 8	2	1	3
<i>From Sector 8 to Sector 6 or 7</i>			
Total individuals caught at Sector 8	46 (44)	33 (32)	79 (76)
Total observed to move from Sector 8 to Sector 6	0	2	2
Total observed to move from Sector 8 to Sector 7	20	4	24

Note: Numbers in parentheses indicate totals marked at a sector.

Table IV

Local movements within colony boundaries: analysis of records of all individuals recaptured at least once in single sectors and combinations of sectors. (The numbers in the body of the table are the numbers of individuals recaptured in the relevant sector or combination of sectors). Populations I, 1974

Sex	Sectors and combinations of sectors							Totals
	6	7	8	6 + 7	7 + 8	6 + 8	6 + 7 + 8	
♂	56	70	14	12	20	0	0	172
♀	17	34	8	5	5	2	0	71

Table V

Local movements within colony boundaries: percentages caught in single sectors and combinations of sectors. Population 1, 1974. Sample size: 172 ♂, 71 ♀. (Data from Tab. IV)

Movements	♂	♀
% always caught in same sector	81.4	83.1
% only moving to one adjacent sector	18.6	14.1
% caught in only two, but not adjacent sectors	0.0	2.8
	100.0	100.0

the mobility of individuals in a different way from that of Table III. Tables IV and V show that very similar proportions of males (140 out of 172, 81.4 percent) and females (59 out of 71, 83.1 percent) were always recaptured in the same sector. Only 18.6 percent of males and 16.9 percent of females were observed to change sectors and none was recorded as visiting all three Sectors 6, 7 and 8.

### POPULATION NUMBERS

The male population sizes were estimated for Population 1 (1974) and Population 2 (1974 and 1975). The methods of FISHER & FORD (1947), JOLLY (1965) and MANLY & PARR (1968) were used to analyse the capture-recapture data and the estimates are expressed as three-point moving averages to smooth the expected extremes of over and under estimation (MANLY, 1969) (Figs. 4, 5 and 6). The estimates of population size for Population 2 obtained by Jolly's and Manly & Parr's methods in 1974 and 1975 are so similar that they are expressed as single lines on Figures 4 and 5. Population estimates obtained by the capture-recapture technique tend to become more reliable as the proportion of marked specimens increases in the population and this is evident in the current set of results. In general, all the estimates reflect the expected population decline throughout the sampling periods. This observed decline in population sizes was almost certainly primarily due to a natural mortality operating on ageing populations. Few general specimens were seen throughout the sampling periods, since the main emergence is probably in June and July (CORBET, 1957; LONGFIELD, 1949). The number of unmarked individuals reduced rapidly in the course of the marking programmes, which also suggests that the populations were recruiting relatively few new insects during the study (Fig. 7).

Population 1  
(Sectors 6, 7 and 8),  
1974. Figure 4

The population estimates by the Jolly and Manly

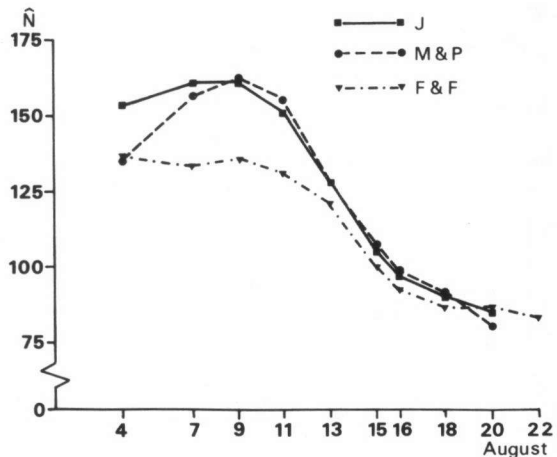
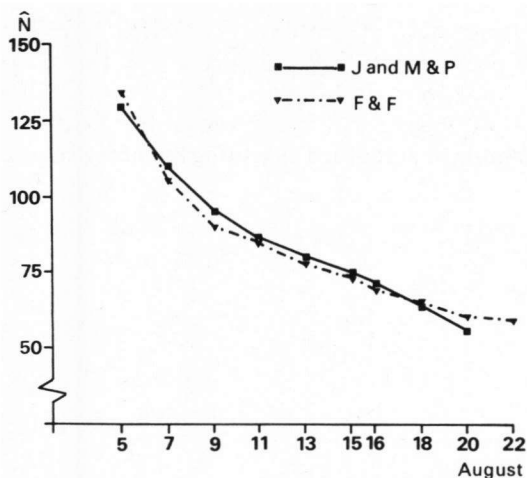
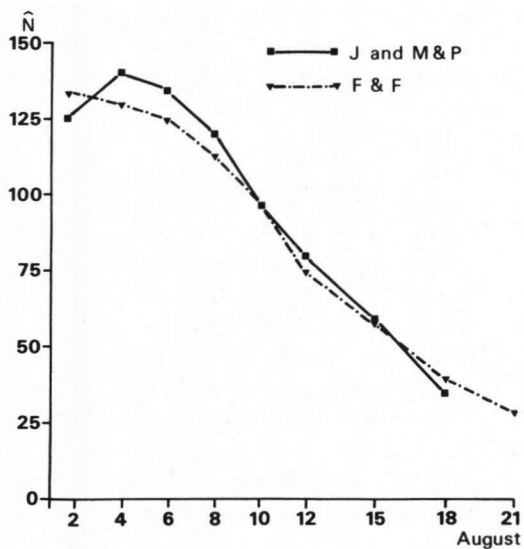


Fig. 4. Estimated numbers of males ( $\hat{N}$ ) in Population 1 (August, 1974); three-point moving average: M & P = MANLY & PARR (1968) method; — J = JOLLY (1965) method; — F & F = FISHER & FORD (1947) method.



(Fig. 5. Estimated numbers of males ( $\hat{N}$ ) in Population 2 (August, 1974); three-point moving average: M & P = MANLY & PARR (1968) method; — J = JOLLY (1965) method; — F & F = FISHER & FORD (1947) method.



(Fig. 6. Estimated numbers of males ( $\hat{N}$ ) in Population 2 (August, 1975); three-point moving average: M & P = MANLY & PARR (1968) method; — J = JOLLY (1965) method; — F & F = FISHER & FORD (1947) method.

& Parr methods agree well except for the first estimate when there is a difference of 26.6. In contrast, the Fisher & Ford estimates show large differences from the other two sets of data on the second, third and fourth sampling occasions and the estimate on the first sampling day is much lower than the corresponding Jolly estimate. After the fourth sampling occasion, the Fisher & Ford estimates follow the Jolly and Manly & Parr values, but are generally lower. The overall impression is that the male population was probably stable at about 150 individuals until approximately 11 August, and declined in numbers thereafter.

Population 2  
(Sector 10), 1974.  
Figure 5

The estimates of male population size obtained by the three methods are very similar to each other, especially those of Jolly and Manly & Parr which are represented by a single line. Figure 7 shows that although the proportion of unmarked males in the samples fell to around 10 percent or less by the fourth sampling occasion, there were always some unmarked

specimens caught. The estimated population curve indicates a consistently declining population throughout the sampling period, with the numbers falling from about 130 to 55.

### Population 2, 1975. Figure 6

The estimated population trends show a similar pattern to those for the same colony in 1974. Unlike 1974, the numbers of unmarked insects fell in a regular pattern, so that the ninth and tenth samples were all marked individuals (Fig. 7). This was probably because the average sampling intensity (MANLY & PARR, 1968) was higher in 1975 (0.78) than in 1974 (0.56) since only one population was sampled in 1975, whereas two were marked in the previous year. The estimates provided by the Jolly and Manly & Parr methods are virtually exactly similar to each other and the Fisher & Ford series show only minor differences from the other two methods. The population on 2 August was approximately 135 male individuals and it had declined to about 30 by 21 August.

## SURVIVAL RATES AND MARKING EFFECTS

### MALE SURVIVAL RATES, MORTALITY AND LONGEVITY

The estimation of survivorship was obtained in a similar manner to that adopted in the studies of *Ischnura elegans* (PARR, 1973b) and *Enallagma cyathigerum* (PARR, 1976); that is to say, from life table data and from the direct analysis of capture-recapture data. In fact, these two methods are not fully independent because the life tables were calculated from the raw capture-recapture data. Neither method is wholly satisfactory as utilised here because (1) the age at first capture was largely unknown as most of the damselflies were post-teneral and many were certainly sexually mature. Only five out of 704 male individuals seen in 1974 and 1975 were teneral. (2) The age at death is also generally unknown; only in those few individuals actually found dying (e.g. in spiders' webs) is the effective time of death known. (3) The sampling periods were shorter than the maximum life span, thus depressing the estimates of survival from the life tables. This factor has little or no effect on the estimates obtained by the Fisher & Ford method. The three populations studied showed surprising differences in their mean survival rates and in the form of their survivorship curves (Fig. 8).

### LIFE TABLES AND SURVIVORSHIP

Population 1 (1974) showed the lowest overall survival which was largely

due to the disappearance of 40.2 percent of the marked population between sampling occasions 1 and 2. Thereafter, the semi-logarithmic curve is distinctly convex, indicating a generally increasing mortality rate. The mean survival, as calculated from the life table data, is 5.7 days; however, those individuals surviving to day 2 had an expectation of survival of 7.2 days, and for days 3, 4, 5 and 6 the expectation of survival was also greater than the mean life time.

Population 2 (1974) had the highest overall survival with 9.4 days and only a 19.1 percent loss between days 1 and 2. The major part of the survival curve is nearly straight except for the extreme ends, indicating that mortality was close to being random with respect to age. The expectation of life between days 2 and 3, and between 3 and 4 was 10.5 and 9.6 days respectively, that is to say, slightly higher than the mean survival time.

The survivorship curve for Population 2 (1975) is intermediate between the curves for the same population in 1974 and Population 1, also in 1974. The loss rate between days 1 and 2 was 25.5 percent and after this period the curve is slightly convex, indicating that mortality only increased slowly throughout the life span. The mean length of life indicated by the life table was 7.2 days, although those individuals surviving to day 2 had an expectation of 7.9 days further life. The extremely marked cut off of the survivorship curve is artificial since the sampling period did not span the maximum possible survival time, which is probably in excess of 30 days.

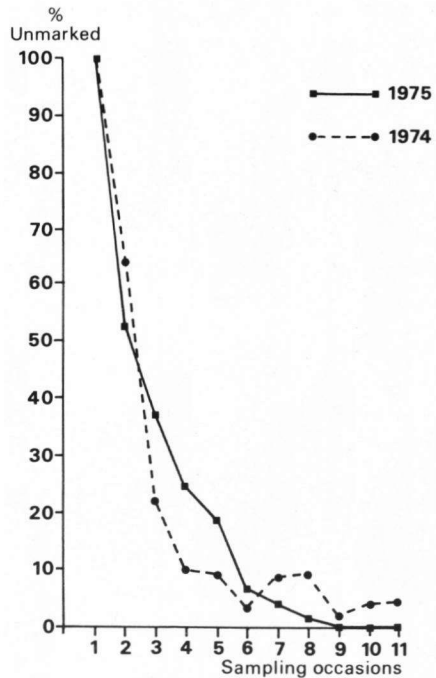


Fig. 7. Percentages of unmarked males in samples of Population 2 in 1974 and 1975.

SURVIVORSHIP ESTIMATED BY CAPTURE-RECAPTURE ANALYSIS

As would be expected, the survivorship calculated directly from the life tables is lower in all three cases than the equivalent rates obtained by the

Table VI

Males. Survival ( $\hat{s}$ ) and mean length of life ( $\bar{L}$ ) estimated from life table data and analysis of capture-recapture data. Maximum observed survival in days ( $L_m$ ) is also given

Population		Life table	Fisher & Ford	Jolly	Manly & Parr
1 (1974)	$\hat{s}$	0.8230	0.8932	0.8949	0.9335
	$\bar{L}$	5.7	8.8	9.0	14.5
	$L_m$	21.0*			
2 (1974)	$\hat{s}$	0.8931	0.9445	0.9431	0.9435
	$\bar{L}$	9.4	17.5	17.1	17.2
	$L_m$	20.0*			
2 (1975)	$\hat{s}$	0.8615	0.8849	0.8942	0.8901
	$\bar{L}$	7.2	8.2	8.9	8.6
	$L_m$	20.0*			

\* Maximum possible: spans the observation period.

standard methods of capture-recapture analysis (Tab. VI), since the latter techniques are not strongly affected by a sampling period much shorter than the maximum life span. However, MANLY (1970) showed, by means of computer simulations, that the Fisher & Ford method may produce biased estimates of population parameters if mortality rates are age dependent. It is, therefore, of some importance to attempt to assess the validity of the population size and survival estimates obtained by the method of Fisher & Ford by examining the specific population life table characteristics.

Unfortunately, the life table for Population 1 (1974) has no close parallel in the set analysed by MANLY (1970), although his tables J and L are closest in general form, having high infant mortality and then an ageing effect after a period of relatively high survival.

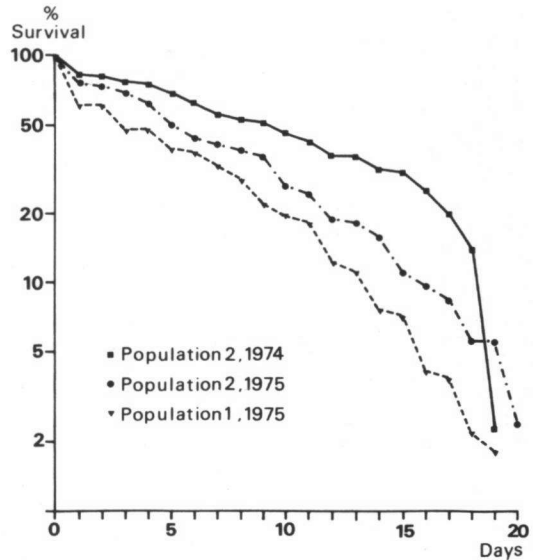


Fig. 8. Male survivorship curves from life tables derived from capture-recapture data.

Although Manly's results do not show any very definite pattern in the bias of estimates, some of his results (e.g. L2 and L7) do suggest that Fisher & Ford's method may underestimate population size with this type of life table. Other simulations carried out by Manly (e.g. L1, L4 and L5) give different results and it appears as though factors such as true population size, sample size, number of births and true survival rate affect the estimates obtained in ways not yet fully understood. In the population under consideration, the early mortality rates are rather higher than those in Manly's life table L, which may explain the generally lower population estimates of the FISHER & FORD (1947) method compared with those of the JOLLY (1965) and MANLY & PARR (1968) methods. It is, therefore, probable that the Fisher & Ford estimate of mean daily survival (0.8932), representing a mean length of life of 8.8 days is also too low, although the true value may have been lower than the MANLY & PARR (1968) estimate of 14.5 days. However, the mean daily survival rate for the Jolly method (0.8949) is virtually identical to that of Fisher & Ford.

The life table of Population 2 (1974) is not closely similar to any of Manly's, but is to some extent intermediate between his tables I and L. The main difference between Manly's tables I and L is that I has a constant mortality rate for the first half of the table, whereas table L has two periods of high mortality, at the beginning and at the end. The life table of Population 2 (1974) has only moderately increased early mortality and according to Manly's results we may expect very little bias for any of the methods used in the analysis of the data. The survival rates (Tab. VI) and the population estimates (Fig. 5) for the Fisher & Ford, Jolly and Manly & Parr methods agree very closely indeed. The mean length of life estimated from these techniques (about 17 days) is almost double that calculated from the life table (9.4 days).

The capture-recapture data for Population 2 (1975) give a life table which is similar to Manly's table L. Manly's simulation results do not show any clear pattern for life table L and the present population is closest to his populations coded L1 and L2. Manly's tables suggest that we might not expect very significant differences between the results obtained by any of the three methods of capture-recapture analysis employed, and indeed, the respective survival rates for FISHER & FORD (1947), JOLLY (1965) and MANLY & PARR (1968) are 8.2, 8.9 and 8.6 days. These values are likely to be more accurate than the figure of 7.2 days derived from the life table since the latter does not encompass the full potential life span of the insect.

#### THE MARKING EFFECT ON SURVIVORSHIP AND POPULATION NUMBERS

A method for testing a possible temporary marking effect in capture-recapture studies is described by MANLY (1971). In his method, Manly

assumes that specific animals are only marked once, for example at time  $t_1$ , and by the second occasion of sampling, time  $t_2$ , if they are still alive, they will have overcome this marking effect. MANLY (1971) and PARR (1976) discuss a capture-recapture programme involving a population of the zygoteran *Enallagma cyathigerum* (Charp.) in which there was slight evidence of a marking mortality.

Table VII  
Analysis of capture-recapture data to test for a marking effect (method of MANLY, 1971)

Date	Popn	Estimates		Estimated S.E.		g	p
		$\hat{\varphi}$	$\hat{\varphi}^*$	$\hat{\varphi}$	$\hat{\varphi}^*$		
4.VIII.74	1	0.9481	0.6858	0.1027	0.0651	0.8996	p > 0.1
7.VIII.74	1	1.0886	0.9063	0.1116	0.1222	1.3537	p > 0.1
9.VIII.74	1	0.6836	0.8478	0.1142	0.1305	-1.1505	p > 0.1
11.VIII.74	1	0.7897	0.8774	0.1212	0.1556	-0.5371	p > 0.1
5.VIII.74	2	0.9173	0.9512	0.0859	0.0624	-0.0905	p > 0.1
7.VIII.74	2	0.9698	1.0602	0.0795	0.0950	-0.1950	p > 0.1
2.VIII.75	2	1.0593	0.7917	0.0517	0.0798	2.8665	0.01 > p > 0.002
4.VIII.75	2	0.8507	0.7605	0.0717	0.0975	0.7995	p > 0.1
6.VIII.75	2	0.6689	0.7162	0.0611	0.0997	-0.4187	p > 0.1

Table VIII  
Parameters used in the calculation of Table VII (ref. MANLY, 1971)

Date	Popn	$r_1$	$r_2$	$z_1$	$z_2$	$u_1$	$m_1$	$m_2$	$l_1$
4.VIII.74	1	13	30	10	25	67	15	37	42
7.VIII.74	1	30	28	25	33	40	37	53	27
9.VIII.74	1	28	27	33	33	29	53	46	19
11.VIII.74	1	27	22	33	38	23	46	37	15
5.VIII.74	2	18	38	23	28	36	21	45	32
7.VIII.74	2	38	30	28	38	13	45	39	12
2.VIII.75	2	39	44	18	30	45	41	59	32
4.VIII.75	2	44	47	30	24	36	59	74	24
6.VIII.75	2	47	54	24	23	25	74	65	17

The data in the present study have been analysed using Manly's method, wherever sufficient information is available (Tab. VII). In effect, this analysis has been carried out whenever the parameters  $r_1$ ,  $r_2$ ,  $z_1$ ,  $z_2$ ,  $u_1$ ,  $m_1$ ,  $m_2$ , and  $l_1$ , as defined by MANLY (1971), are equal to, or greater than 10 (Tab. VIII). Since we cannot rule out the possibility that marking may result in an increased survival (mainly since predator response may be different) then we have to apply a two-sided test, in which the value of the statistic g will be significant at



the 5 percent level if it lies outside the range  $-1.96 < g < 1.96$ . If marking reduces the probability of survival then the  $g$  values will be positive, but if it increases the chance of survival then the  $g$  values will be negative. Table VII shows that five  $g$  values were negative and four were positive, although only one indicated a significant difference between  $\hat{\varphi}$  and  $\hat{\varphi}^*$  (for Population 2, 2 August 1975:  $g = 2.867$ ;  $0.01 > p > 0.002$ ). This result can be taken to represent strong evidence for a deleterious marking effect on 2 August 1975 which is associated with a rather low population estimate (Fig. 6). Other fairly high positive  $g$  values occur on 4 and 7 August 1974 (Population 1) and may represent genuine, but statistically non-significant, marking mortality since the Jolly and Manly & Parr population estimates for those days are otherwise unaccountably depressed (Fig. 4).

## SEX RATIOS AND MATING PATTERNS

### SEX RATIOS

In common with many Zygoptera species, males always heavily predominated at water. Counting all captures and recaptures (i.e. summed samples for each day), males accounted for between 68 and 81 percent of the populations studied. If only individuals are scored (not recaptures) then the observed male percentage ranges from 57 to 68 in the sampled populations. The overall variation in the sex ratios at different sites and between different years is considerable and rather puzzling since relatively large numbers are involved (Tab. IX). It is not certain whether the observed imaginal sex ratios reflect a true divergence from equality, since data are not available for larval or exuvial sex ratios.

Table IX  
Observed sex ratios\*

Date	Population	♂ Nos.	♀ Nos.	% ♂
1974	1	661 (271)	295 (189)	69.1 (58.9)
1974	2	494 (131)	119 (62)	80.6 (67.9)
1975	2	699 (204)	281 (152)	71.3 (57.3)
<i>Overall sex ratios</i>		1854 (606)	695 (403)	72.7 (60.1)

\* The numbers not in parentheses represent summed samples, i.e. an individual may be counted more than once. The numbers in parentheses only include individuals once. The totals include all insects, i.e. immatures and matures.

## MATING PATTERNS (MATING FREQUENCIES)

We define mating frequency as the number of matings observed divided by the total number of sexually mature insects of the relevant sex caught (including recaptures), expressed as a percentage. This definition is, in effect, the same as the one we used in our study of three other coenagrionid species (PARR & PALMER, 1971). We note again here that this definition differs from that used by BICK & BICK (1961).

The mating frequencies for *Ceriagrion tenellum* recorded at Ober Heath are presented in Table X. There is a clear tendency for male mating frequencies to be considerably lower than for females because the latter sex are always less likely to be seen at water than males. There are, however, inconsistencies in the data, in that apart from male/female comparisons, all the pairs of results tested in Table X show significant differences, except males (1974) in Populations 1 and 2, where  $\chi^2_{(1)} = 0.4343$ ;  $0.5 > p > 0.4$ . Sexual activities, as well as feeding flights are certainly strongly affected by weather conditions in *C. tenellum*. Sunshine, high temperatures and low wind speeds all contribute to activity levels being raised. The warmer and sunnier conditions prevalent during the 1975 sampling compared with 1974 provide an explanation for the generally higher mating frequencies in 1975. The high female mating frequency for Population 2, 1974, seems to be a reflection of the extreme imbalance in the sex ratio, females being relatively scarce at water (Tab. IX).

Table X  
Mating frequencies (sexually immature forms omitted)

Date	Population 1		Population 2	
	♂	♀	♂	♀
1974	52/618 (8.4%)	52/285 (18.2%)	35/489 (7.2%)	35/113 (30.9%)
1975	—	—	148/698 (21.2%)	148/281 (52.7%)

Means (both populations and both years): male 13.1%, female 34.6%. — Males, 1974, Popn 1/2 mating frequency:  $\chi^2_{(1)} = 0.4343$ ; — Males, Popn 2, 1974/75 mating frequency:  $\chi^2 = 31.9$ ; — Females, 1974, Popn 1/2 mating frequency:  $\chi^2_{(1)} = 4.7$  ( $0.05 > p > 0.02$ ); — Females, Popn 2, 1974/75 mating frequency:  $\chi^2_{(1)} = 6.0$  ( $0.02 > p > 0.01$ ).

## NOTES ON AGGRESSIVE AND SEXUAL BEHAVIOUR

Males of *C. tenellum* frequently perch within half a metre of each other on emergent stems and many apparently spontaneous non-feeding flights were witnessed. These flights often resulted in aerial fighting between two, three or

more neighbouring males. This behaviour of spontaneous flights leading to intra-specific aggression between males resulted in a general distribution within the colony area which is characteristically a pattern of over dispersion (KERSHAW, 1971). However, in the colonies observed on Ober Heath, fighting did not lead to the obvious withdrawal of any individuals from the waterside or colony area, since males always adjusted their position locally following overt aggression from neighbouring males. The results of MOORE (1964) with *C. tenellum* show that in his experiments, clashes between males resulted in some individuals leaving the water (small artificial ponds) so that only a certain maximum number of territorial males tended to remain. Presumably, the natural situation reported in the present studies merely underlines the fact that numbers of adult males are broadly stabilised or actually declining late in the flying season so that territorial clashes do not usually result in distant dispersal. The situation may be different earlier in the season when many new individuals are joining the flying population daily. No response to territorial males of *Orthetrum coerulescens* was noted although sometimes *O. coerulescens* males flew up to investigate fighting *C. tenellum*.

Although most attacks by males on other males appeared to us to be purely aggressive, some were clearly sexual in nature, and three instances were seen when the aggressor attempted to attain an in tandem or copulatory position. It is possible that populations of *C. tenellum* in which the all-red female form (f. *erythrogastrum* Selys) is common might show a lower rate of sexual recognition than we recorded for the Ober Heath colonies. We recorded only two f. *erythrogastrum* throughout our sampling periods in 1974 and 1975 on Ober Heath. All the other females were the all black f. *melanogastrum* Selys, or the common black and red form, or variants of these two main types.

Matings occurred by the water, usually on low plants such as *Juncus* and *Eleocharis* or small *Pinus* trees, and was seen at any time from 10.30 hrs until about 16.30 hrs. Whether or not copulations were seen on particular days and the time during the day when it occurred seemed to depend on the weather. Most sexual activity was observed in hot and sunny conditions and it was completely suppressed in cool and wet weather. Two complete copulations were seen during the work at Ober Heath in 1975: 14 August, 15.29-16.14 (45 minutes) and 16 August, 12.31-14.02 (91 minutes). These copulations proceeded according to the following timetables:

**14 August:**

- 15.29: Marked male and unmarked female (f. *melanogastrum*) assumed the wheel position having just arrived in tandem.
- 15.35: Male warded off another male which approached the pair by opening ('flicking') his wings.
- 15.38: Male and female making abdominal flexing movements while still in copula.
- 15.45: Copulation pair approached by two other males simultaneously. The mating male repeated wing flicking movements and the two intruding males withdrew.

- 15.46: Another male driven off by wing opening movements of the mating male.
- 15.59: A solitary male attempted to assume the in tandem position with the copulating male by grasping his head/prothorax for 20 seconds before finally flying away. The copulating pair appeared undisturbed by this event.
- 16.14: The wheel position was broken and the pair flew in tandem to two nearby perches in quick succession.
- 16.17: The pair flew off in tandem.
- 16.21: The pair were seen in tandem six metres from the copulation site, with the female ovipositing amongst *Hypericum elodes*.

Throughout these observations the weather was still with weak sunshine; the shade temperature was 23°C. and the relative humidity was 81 percent.

#### 16 August:

- 12.27: Marked male seized marked black and red form female immediately she appeared at the water. The pair flew to a small *Pinus* tree at the water's edge, but soon descended to the water, where the female perched at the tip of a broken-off *Juncus* stem, with the male held upright by his appendages attached to the female prothorax. The pair soon moved so that the male was perched and the female was supported only by the male's appendages. The male attempted to attain the wheel position, but the female did not bend her abdomen sufficiently for this to be achieved.
- 12.31: The pair moved to a nearby *Eleocharis* stem protruding from the water, and they immediately assumed the wheel position. The pair soon shifted their position to face into the wind.
- 12.50: Flew briefly and moved down to a grass stem.
- 13.04: Flew briefly again to another nearby grass stem, probably due to wind disturbance.
- 13.28: The pair fell off their grass stem perch but recovered immediately and assumed their previous position.
- 13.43: It was noticed that in varying sunny and dull periods, the pair were quite still when cloud obscured the sun, but they made abdominal movements when the sun appeared.
- 14.02: The copulation ended, and the pair, still in tandem, moved to a nearby *Juncus* stem. The female did not attempt oviposition, probably because the sky had become overcast. At this time there was no other *Ceriagrion* activity.

When the pair commenced copulation, the weather was sunny and breezy with a shade temperature of 21°C. and 72 percent relative humidity. By 13.43 it had become mostly cloudy and the shade temperature had fallen to 20°C. while the relative humidity remained stable at 72 percent.

The difference in the length of time spent in the wheel position in these two copulations may be related to the weather conditions, especially shade air temperature, but it is clear that *C. tenellum* falls into the copulation type classified as 'long' by CORBET (1962).

## DISCUSSION AND CONCLUSIONS

The analysis of relative mobility of male *C. tenellum* at water may be used to compare this species' movements with some other zygopterans. Similar analyses have been made for *Ischnura elegans* (PARR, 1973b) and *Enallagma*

*cyathigerum* (PARR, 1976). Allowing for differences in the size of sampling sectors, *C. tenellum* seems to be the most static of the three zygoptera mentioned here, whereas *E. cyathigerum* is certainly the most mobile. In the present study, 81.4 percent of male *C. tenellum* were always recaptured in the same sector, the mean length of which was 83 metres, whereas PARR (1973b) found that in sectors averaging about 100 metres long, 71.1 percent of male *I. elegans* were never observed to leave the sector in which they had been marked. In sectors averaging 44 metres long (PARR, 1973b, 1976) about 47 percent of male *I. elegans* always remained in the same sector, but only 23 percent of *E. cyathigerum* males did so (Fig. 9). Working with *E. cyathigerum* in California, United States, GARRISON (1978) presents data indicating that movement of males was on average much less evident in his population

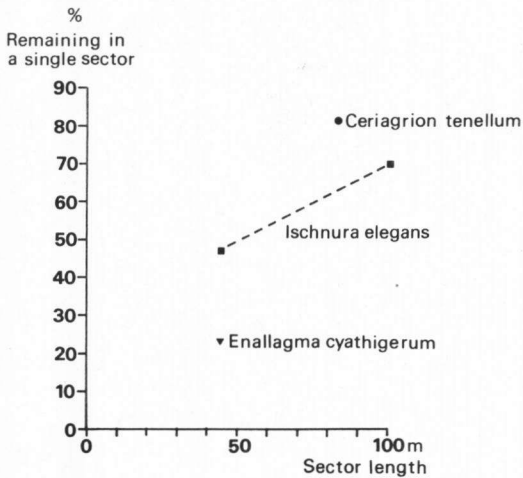


Fig. 9. Relative mobility of males of *Ischnura elegans*, *Enallagma cyathigerum* and *Ceriagrion tenellum*.

than in any of the English zygopteran populations mentioned here. However, as Garrison's study lasted only 10 days, it is possible that a more prolonged period of study might have demonstrated greater mobility. Similarly, because the present study of *C. tenellum* only lasted approximately three weeks in each of the years 1974 and 1975, there is a slight danger that these mobility figures are not fully comparable with the data presented for other species

and populations. The fact that in the present study, most movement within the area occupied by Population I was from the periphery inwards is interpreted as indicating that as the population density declined, individuals in marginal zones were more able to move inwards and establish themselves in more optimal microhabitats.

Marking insects such as Zygoptera does entail the need for considerable care and it is an operation in which one can expect to become more skilled with experience. In the absence of any other obvious factors, it is presumed that the marking process itself introduced an additional mortality factor to the normal mortality rate on 2 August, 1975. This was the only occasion when Manly's test for a marking effect indicated a significant difference (in either direction) between  $\hat{\varphi}$  and  $\hat{\varphi}^*$ . Nevertheless, such a result underlines the need

for constant care in handling and marking insect populations in order to eliminate undesirable and spurious factors. It is possible that the relatively low population estimates recorded for Population 1 on 4 and 7 August, 1974 (Fig. 3) and for Population 2 on 2 August, 1975 (Fig. 5), are a reflection of a marking effect although a significant  $g$  value is only recorded for the latter date.

Certain differences were noticed in the data for Population 2 in 1974 compared with 1975. It is probable that the considerable differences in weather conditions for the two sampling periods could have contributed to the observed differences in survival rates (and hence, population decline) and mating frequencies. The summer of 1975 in Hampshire was generally warmer, sunnier and drier than 1974; the first half of August 1975 was particularly hot and sunny, although the second half experienced more normal weather. During the period of 2-22 August, 1974 the maximum daily temperature ranged from 17-22.5°C. with a mean of 20.0°C.; the cloud cover (measured in 8ths and recorded while sampling was carried out) ranged from 0-8, with a mean of 4. The comparable figures for the period 1-21 August, 1975 were 18-30°C. (mean 23.8°C.) and cloud 0-7 (mean 3).

Contrary to expectations, survival was lower in 1975 than in 1974 at Population 2. Although *C. tenellum* has been considered to be a Mediterranean based species, the British populations may be best adapted to cooler weather characteristic of southern Britain. It is possible that the faster population decline and lower overall survival rate witnessed in 1975, compared with the previous summer, may be directly attributable to the unusually hot, sunny and dry conditions of that year. Presumably further south in Europe, *C. tenellum* is better adapted to withstand heat and drought in the imaginal state. Although survival seems to have been depressed by the high temperatures and drought of 1975, in contrast, activity levels in general were higher than in 1974, and in particular, mating frequencies were much higher in 1975. It would appear that the weather-determined survival rate may be balanced by a similarly controlled reproductive rate (mating frequency) in the imaginal population.

The populations in small bogs, runnels and pools in the New Forest are especially susceptible to dry conditions caused by heat and lack of rain, or by drainage schemes. Thus, numbers of *C. tenellum* may easily become very depleted or populations completely exterminated unless care is taken to conserve a number of key breeding sites. Since British populations seem to be well adapted to the cool conditions normally occurring in their habitats, climate does not appear to be a major factor limiting the species' southerly and westerly distribution in Britain. It is probable that habitat requirements are the primary reason for the species' very limited distribution in the British Isles. The extreme selectivity of the flying population for boggy stream areas with little open water was particularly evident in the Ober Heath populations,

with the water plant *Hypericum elodes* apparently acting as a key factor associated with the selection of oviposition sites.

In conclusion, *C. tenellum* is ecologically and behaviourally a typical zygopteran in Britain. The sexually immature imagines undergo their maturation away from water and females are seen at water far less frequently than males. It is highly selective about its breeding sites and its imaginal activities are strongly affected by weather conditions. An ovipositing female is usually attended by a male, pairs frequently fly in tandem, and females have a relatively high mating frequency. In most of these points *C. tenellum* behaves similarly to British populations of *Coenagrion puella* and *Enallagma cyathigerum*.

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#### REFERENCES

- BICK, G.H. & J.C. BICK, 1961. An adult population of *Lestes disjunctus australis* Walker (Odonata: Lestidae). *SWest. Nat.* 6: 111-137.
- CORBET, P.S., 1957. The life histories of two summer species of dragonfly (Odonata, Coenagrionidae). *Proc. zool. Soc. Lond.* 128: 403-418.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P.S., C. LONGFIELD & N.W. MOORE, 1960. *Dragonflies*. Collins, London.
- FISHER, R.A. & E.B. FORD, 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Heredity* 1: 143-174.
- GARRISON, R.W., 1978. A mark-recapture study of imaginal *Enallagma cyathigerum* (Charpentier) and *Argia vivida* Hagen (Zygoptera: Coenagrionidae). *Odonatologica* 7 (3): 223-236.
- JOLLY, G.M., 1965. Explicit estimates from capture-recapture data with both death and immigration - stochastic model. *Biometrika* 52 (1-2): 225-247.
- KERSHAW, K.A., 1971. *Quantitative and dynamic ecology*. Edward Arnold, London.
- LONGFIELD, C., 1949. *Dragonflies of the British Isles*. Warne, London & New York.
- MANLY, B.F.J., 1969. On a method of population estimation using capture-recapture data. *Entomologist* 102: 117-120.
- MANLY, B.F.J., 1970. A simulation study of animal population estimation using the capture-recapture method. *J. appl. Ecol.* 7: 13-39.
- MANLY, B.F.J., 1971. Estimates of a marking effect with capture-recapture sampling. *J. appl. Ecol.* 8: 181-189.
- MANLY, B.F.J. & M.J. PARR, 1968. A new method of estimating population size, survivorship and birth rate from capture-recapture data. *Trans. Soc. Brit. Ent.* 18: 81-89. Neuchâtel & Paris.
- MOORE, N.W., 1964. Intra- and interspecific competition among dragonflies (Odonata). *J. Anim. Ecol.* 33: 49-71.
- PARR, M.J., 1965. A population study of a colony of imaginal *Ischnura elegans* (van der

- Linden) (Odonata: Coenagriidae) at Dale, Pembrokeshire. *Fld Stud.* 2: 237-282.
- PARR, M.J., 1969. Comparative notes on the distribution, ecology and behaviour of some damselflies (Odonata: Coenagriidae). *Entomologist* 102: 151-161.
- PARR, M.J., 1973a. Ecological studies of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). I. Age groups, emergence patterns and numbers. *Odonatologica* 2 (3): 139-157.
- PARR, M.J., 1973b. Ecological studies of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). II. Survivorship, local movements and dispersal. *Odonatologica* 2 (3): 159-174.
- PARR, M.J., 1976. Some aspects of the population ecology of the damselfly *Enallagma cyathigerum* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* 5 (1): 45-57.
- PARR, M.J. & M. PALMER, 1971. The sex ratios, mating frequencies and mating expectancies of three coenagriids (Odonata: Zygoptera) in northern England. *Ent. scand.* 2: 191-204.
- ROBERT, P.A., 1958. *Les Libellules (Odonates)*. Delachaux & Niestlé S.A. Neuchâtel & Paris.
- SCHMIDT, E., 1977. Ausgestorbene und bedrohte Libellenarten in der Bundesrepublik Deutschland. *Odonatologica* 6 (2): 97-103.
- SMALL, D., 1975. *In: Explore the New Forest - Forestry Commission Guide*. H.M.S.O., London.