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SOME ASPECTS OF THE POPULATION ECOLOGY OF THE DAMSELFLY *ENALLAGMA CYATHIGERUM* (CHARPENTIER) (ZYGOPTERA: *COENAGRIONIDAE*)

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The main observations were carried out on imaginal populations of *E. cyathigerum* at Dunham Park, Cheshire. The capture-recapture method using unique marking was extensively employed, as well as direct observations. – Tenerals moved away from water during the maturation process. Most individuals marked had completed their maturation and had returned to water. Males at water were always cerulean blue with black markings, but females showed a great variation in ground colour. The form of the emergence and population curve and the long flying season strongly suggest that it is a summer species. Two population peaks, in June and July, were observed: the second peak was the larger of the two and was temporally dispersed suggesting that a large proportion of the larval population overwintered in the antepenultimate or younger instars. The *Enallagma* population at Pond 3 was almost extinct in June 1970, whereas a total estimated population of about 500 was present in the 1966 season. The highest steady density counts ranged from 16.8 to 47.8 insects per 100 metres of shore line at Dunham, but an exceptional value of 363 per 100 metres was recorded at Pen Ponds, Surrey, in 1967. It is suggested that physiological condition is more important in controlling numbers at water than male intra-specific interactions. Post-maturation mortality is probably nearly random with respect to age, but the marking process seemed to result in an abnormally high rate of egress in the first day after initial capture. The mean length of life for males at water was about 12 days and the maximum observed survival was 39 days. Most male individuals of *E. cyathigerum* show a greater mobility within the colony area than males of *Ischnura elegans*.

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INTRODUCTION

The zygopteran *Enallagma cyathigerum* has a circumboreal distribution and Longfield (*in* CORBET et al., 1960) has suggested it may be one of the most abundant dragonflies in the world. It occurs north of the Arctic Circle in Fennoscandia and Russia; almost up to the Arctic Circle in North America, and as far south as southern California, Florida* and southern Korea (Longfield, *in* CORBET et al., 1960).

With the exception of MACAN (1964, 1974) there seems to be little recorded work on the ecology of this species and it is, therefore, impossible to tell to what extent the results and observations recorded here are characteristic of many other populations. It is to be expected that populations of *E. cyathigerum* in colder or continental type climates and also in the most southerly parts of its range will behave differently from populations in northern Cheshire, where most of this work was carried out. The main populations studied were centred on two ponds (Fox Hole Pond or Pond 3 and Old Man Pond or Pond 1) in the private portion of Dunham Park, Altrincham, Cheshire. This habitat (Nat. Grid reference SJ 740 870) has been described in PARR & PALMER (1971). Some observations were also made in Richmond Park, Surrey, in southern England.

The imaginal population at Dunham was sampled for the entire flying season in 1966 and during June in 1970, using the capture-recapture method. This paper is primarily concerned with the emergence pattern, imaginal population numbers, survivorship, longevity and dispersal. The sex ratios, mating frequencies and mating expectancies of *E. cyathigerum* and other Zygoptera have been discussed in PARR & PALMER (1971).

METHODS

The populations at Dunham were studied by means of the capture-recapture method. The procedure and techniques utilised were essentially similar to those which have been described in detail for *Ischnura elegans* (Vander Linden) by PARR (1965, 1973a, 1973b). Each individual when first captured was allocated a unique number which was marked on the wings with a coded series of spots in quick drying cellulose or enamel paint. Individuals were, therefore, only marked once. The capture-recapture data have been analysed using the methods of JOLLY (1965) and MANLY & PARR (1968) (for population estimates) and FISHER & FORD (1947) (for survival rates). Most of the calculations involved in these estimates were carried out with the aid of a KDF9 Leo-Marconi computer at the University of Salford.

* Prof. M.J. WESTFALL, Jr. and Mrs. L. GLOYD (pers. comm.) have stated that *E. cyathigerum* almost certainly does not occur in Florida.

EMERGENCE PATTERNS AND POPULATION NUMBERS

In contrast to the coenagrionid *Ischnura elegans* which has also been studied in the habitats in Dunham Park (PARR, 1973a, 1973b), *Enallagma cyathigerum* shows an almost 100 percent movement away from water in the maiden flight of tenerals. Most of the teneral *E. cyathigerum* seen at water were very newly emerged and were virtually impossible to mark uniquely. The vast majority were marked when they were clearly post-teneral. Due to the difficulty of obtaining sufficient numbers of markable teneral insects it was not possible to estimate the length of the maturation period spent away from water.

The first individuals were taken at Pond 3 on 6 June, 1966 and 4 June, 1970. Three specimens (all males) were taken at Pond 1 on 1 June, 1970, the first day sampling was carried out. In 1965, the first five exuviae found during the season (2 male and 3 females) were collected on 19 May at Island Pond (Pond 2).

POND 3, 1966

Population estimates were obtained for males, but not for females as so few of the latter sex were caught. However, as there is good evidence (PARR & PALMER, 1971) from exuvial counts that the true sex ratio at emergence is 1:1 it is reasonable to assume that the numbers of females associated with any particular colony (but not necessarily at water) will be roughly similar to the number of males in the colony. Although sample sizes were small, the capture-recapture data for males seem relatively reliable and there is a substantial measure of agreement between the estimates obtained using the method of JOLLY (1965) and MANLY & PARR (1968), (Fig. 1). The population estimates are expressed as three-point moving averages and the seasonal population trends

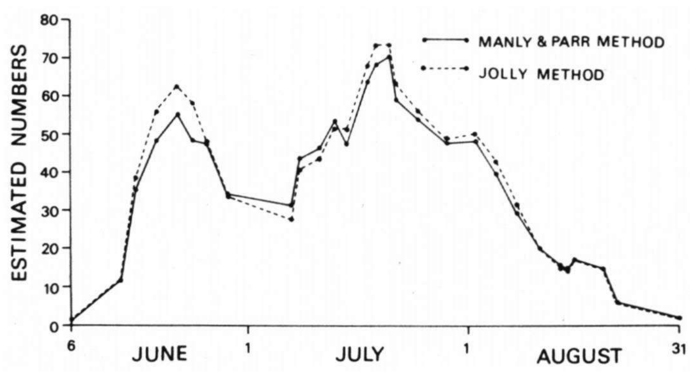

Fig. 1. *Enallagma cyathigerum*: estimated numbers of sexually mature male imagines at Pond 3, Dunham Park, Cheshire, 1966.

are clearly discernable. The population which began to emerge during the first days of June climbed to an early peak on 21 June and thereafter declined until about the 7th July. A second and larger peak in numbers was reached in the period 19-21 July. A steady decline in numbers occurred from this time until the end of August when the last individuals disappeared from the colony site.

The season's total population size was estimated using the method of SHEPPARD (1951), utilising a daily survival rate calculated from the FISHER & FORD method (1947) and daily population estimates from MANLY & PARR (1968). This has probably resulted in a slightly positively biassed estimate of total population size, due to the marking effect (see Discussion). The number of males at Pond 3 in 1966 was thus estimated as 258.4. As it was assumed that the sex ratio is unity and there may be a slight positive bias, the total population was probably about 500.

POND 3, 1970

The population of *E. cyathigerum* was sampled again in 1970, during the month of June. As the sampling period did not extend over the whole flying season it was not possible to obtain a picture of the seasonal emergence pattern for that year. It was, however, very noticeable that the population had virtually disappeared since it was last sampled in 1966, only twelve male specimens being seen during the whole of June. Four of these twelve insects were recaptured at least once, one of them recaptured four times in all. Only one of these males was captured while in copula. Only three female *E. cyathigerum* were seen at Pond 3 in 1970, all being taken in copula. Only one was paired with a male of its own species, the others being paired with a male *Ischnura elegans* and *Coenagrion puella*. Inter-generic pairings are by no means uncommon in these three species, but these examples seem to suggest that it occurs more frequently in cases when mates of the same species are difficult to locate.

POND 1, 1970

The population of *E. cyathigerum* was also sampled at Pond 1 during June 1970. Although simultaneous samplings of *I. elegans* and *C. puella* were also made, it did not seem that the total number of insects was so large as to make the relatively small samples unreliable. Analysis of the capture-recapture data for *I. elegans* and *C. puella* yielded meaningful results; however, the data relating to *E. cyathigerum* proved unreliable. Analysis by the methods of JOLLY (1965) and MANLY & PARR (1968) gave widely differing estimates of population size and both methods produced non-synchronised erratic oscillations which were almost certainly very poor reflections of the real numbers. These results are, therefore, not reported.

HIGHEST STEADY DENSITY

MOORE (1964) stated that "if a population of male dragonflies is observed continuously, it becomes obvious that there is a value of population density which is maintained for most of the time and is only momentarily exceeded". He called this value the Highest Steady Density (H.S.D.), and defined it as "the highest population density maintained for a consecutive minute or a longer time in any period of observation". MOORE studied the H.S.D.'s of 15 species of anisopteran and zygopteran dragonflies, including *E. cyathigerum*. He expressed the H.S.D. of each species as the number of males per 100 metres of pond edge, and this procedure is adopted here.

The perimeter of Pond 3 in Dunham Park was about 143 metres in 1966. The H.S.D.'s for this pond were calculated from the number of insects caught on specific sampling occasions. It is assumed that the numbers actually caught were a reasonable reflection of the numbers present on a particular day at the pond's edge. Other individuals were present flying over the water or resting on the emergent vegetation and dead tree branches projecting from the water: many of these could not be caught. Some individuals were almost certainly absent temporarily from the immediate vicinity of the water. It is clear, therefore, that the H.S.D. cannot be equated with actual population density in the colony as a whole, in this particular example. The H.S.D.'s recorded do, however, represent the linear distribution of male individuals around the pond margin.

The four highest H.S.D.'s recorded were 20.3 (15 June) and 16.8 (23 June) (representing the first population peak); and 27.4 (19 July) and 26.7 (21 July) (representing the second population peak). Three of the values recorded by MOORE (1964) – 60, 47 and 44 – are in excess of these values, but seven other H.S.D.'s mentioned by Moore for *E. cyathigerum* are close to or lower than the Dunham Park figures. The H.S.D. values recorded in Dunham Park and by Moore for the same species on the Arne peninsula, Dorset, in southern England, appear to represent the range of normal densities in these habitats.

However, several counts of males of *E. cyathigerum* were also made at Pen Ponds, Richmond Park, Surrey in southern England on 11 August, 1967. This was done because the species appeared to be present in vast numbers along the water's edge and over the open water, as well as inland some way from the pond shore. A very cursory glance suggested that the H.S.D. was almost certainly far in excess of any value recorded by MOORE (1964). The actual counts were carried out along the western shore of the large (south) pond (Nat. grid ref. TQ 197 727 - 198 730) in warm, still and mostly sunny weather. The western shore of the south Pen Pond is fringed partly by *Juncus* and partly by trees which grow right on the bank. Parts of the *Juncus* fringed areas are relatively straight and these were used to estimate the H.S.D. of *Enallagma*. All the shores of the ponds which were exposed to sunlight were crowded with high densities of the

Table I

Highest steady density counts made at Pen Ponds, Richmond, Surrey

(11 August, 1967)

Length of section of pond shore in yards		Numbers recorded and time of day		Mean
	Yards	*14.05 hrs*	*14.30 hrs*	
(i)	5	20	15	17.5
(ii)	6	26	24	25.0
(iii)	11	30	31	30.5
Totals	*22*	*76*	*70*	*73.0*

73/22 = 3.318 insects/yard; H.S.D. = 362.9/100 metres.

species: the selection of limited stretches of the pond shore for the counts was to ensure the maximum accuracy.

Three sections of *Juncus* fringed pond shore, in total length about 22 yards, had an average number of 73 males of *E. cyathigerum*, giving 3.318 damselflies per yard. When converted to H.S.D., 362.9 insects per 100 metres of pond shore were present (Tab. I). These counts recorded at Pen Ponds constitute a remarkable exception to the range of values recorded elsewhere. It must be emphasised that the three sections of the shore in which the counts were made were representative of most of the open parts of the water's edge, but were selected because they were straight and this facilitated accurate counting. Several members of the general public standing by the shore were heard to comment on the very numerous bright blue insects, which in itself, was indicative of their extraordinary abundance.

SURVIVORSHIP AND LONGEVITY

POND 3, 1966

The determination of survivorship and longevity of male *E. cyathigerum* was accomplished less satisfactorily than for *I. elegans* in the same habitat (PARR, 1973b). The primary reason for this is that these parameters were estimated from the capture-recapture data by noting the frequencies of time intervals between first capture and last capture: the age at first capture was always unknown as the insects were all post teneral and were probably all sexually mature. The individuals were likely to have been of a fairly constant age when first captured and marked, being those insects in the population which had recently completed their maturation process and returned to water for breeding.

Teneral males were only very rarely seen and females of any age were taken too infrequently to yield any information on survival.

The survivorship curve for male *E. cyathigerum* at Dunham is clearly divisible into two parts (Fig. 2). Out of the 202 individuals contributing to the life table from which the survivorship curve is derived, only 103 (51.0%) were ever seen again. However, if an insect was recaptured at all, its chances of being seen again were disproportionately high compared with its chances of survival from day 0 to day 1. Thus, although the semi-logarithmic survivorship curve from day 1 onwards indicates that death was practically random with respect to age (Type II of DEEVEY, 1974), the very high loss rate between days 0 and 1 results in a definite deviation from a constant mortality for all age groups and is equivalent to an overall survival rate of 86 percent. The survival rate (calculated from the life table) from day 0 to day 1 was 51 percent, whereas from day 1 onwards, the rate was almost constant at around 92 percent. Assuming the apparent high mortality from day 0 to day 1 was the result of a marking effect, a 92 percent survival rate would indicate a mean length of life of about 12.2 days for males attaining sexual maturity.

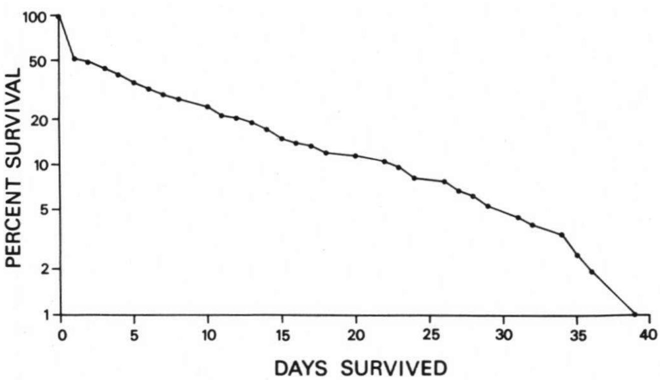

Fig. 2. *Enallagma cyathigerum*: Survivorship curve from the male sexually mature population at Pond 3, Dunham Park, Cheshire, 1966.

The mean observed survival of male *E. cyathigerum* as calculated from the life table data was 6.5 days, but this is clearly an underestimate of actual mean life span. As all individuals were apparently sexually mature when marked the mean survival period must have been appreciably in excess of 6.5 days. However, when the length of life was calculated from the capture-recapture data using the method of Fisher and Ford an overall mean value of 12.1 days was obtained for the greater part of the flying season (15 June - 15 August). This latter estimate is probably reasonably realistic, but it may be regarded as slightly positively biassed for the reasons given in MANLY (1969, 1970). Nevertheless, it accords very well with the value of 12.2 days obtained from the life table, if the 'marking effect' mortality from days 0 to 1 be ignored.

The maximum observed survival for males was 39 days, which is the same as that recorded for *Ischnura elegans* (PARR, 1973b), although the actual maximum life span must exceed this by some days if an allowance for the maturation period is made.

DISPERSAL AND LOCAL MOVEMENTS

(LOCAL MOVEMENTS WITHIN THE COLONY BOUNDARY, POND 1, 1970)

E. cyathigerum seems to be a typical zygopteran in that teneral individuals leave the neighbourhood of water and do not return until the maturation process has been completed. It is during the maturation stage that, presumably, many individuals disperse away from the parent colony never to return. Sexually immature individuals of *E. cyathigerum* were frequently seen in Dunham Park away from the vicinity of the ponds, but were generally absent from the waterside.

Local movements of adult male *E. cyathigerum* were studied at Pond 1 in 1970 using the same sampling sectors as described in the study of *Ischnura elegans* (PARR, 1973b). Each individual which was recaptured at least once was classified according to its recapture history at the sectors of the pond. These individuals were scored according to whether they remained in a particular sector for the whole of their recapture history, or moved to one or more different sectors subsequently. The results were used to place individuals into one of five classes (Tab. II). Whilst the sample sizes are rather small, only just over one fifth of the individuals remained in the sector in which they were

Table II

Local movements within the colony area at Pond 1, 1970: analysis of records of all male individuals recaptured at least once in single sectors and combinations of sectors

Mobility class numbers and description	Number of individuals	Percentage
1. Always caught in same sector	12	22.6
2. Only moving to one adjacent sector	22	41.5
3. Caught in only two but not adjacent sectors	16	30.2
4. Caught in three sectors	2	3.8
5. Caught in four sectors	1	1.9
Totals	*53*	*100.0*

originally caught. In contrast, nearly half (125/261) of the recaptured male *I. elegans* at Pond 1, 1970, did not change sectors (PARR, 1973b). Analysis of the numbers of male *E. cyathigerum* and male *I. elegans* recaptured in only one sector or two adjacent sectors (e.g. 1 and 2, or 2 and 3) of Pond 1 indicates that there was a real difference in the mobility of the two species, which seems to be correlated with the habit of *Enallagma* males to fly freely over the surface of the water, whereas males of *Ischnura* do not (Tab. III).

Table III

Comparison of numbers of male *E. cyathigerum* and male *I. elegans* recaptured in only one sector or two adjacent sectors of Pond 1, 1970

Species	Class numbers (cf. Tab. II) 1	2	Totals
E. cyathigerum	12	22	34
I. elegans (PARR, 1973b)	125	92	217
Totals	*137*	*114*	*251*

$\chi^2_{(1)} = 5.90;\ 0.02 > p > 0.01$

Further evidence of the much greater mobility of *E. cyathigerum* is that 30.2 percent of males recaptured were caught in two, but not adjacent sectors, e.g. sectors 1 and 3, or 2 and 4 (class 3 in Table II), whereas only 12.3 percent of *I. elegans* at the same pond were in this class.

DISCUSSION

The JOLLY (1965) and the MANLY & PARR (1968) methods of analysis of the capture-recapture data produce population estimates for males which agree well in their general trends (Fig. 1). A similar, bimodal, seasonal distribution in numbers has been reported for *Ischnura elegans* by HEWETSON & O'ROURKE (1960) and PARR (1973a). Whilst no other specific information seems to be available on the life history of *E. cyathigerum* in northern Cheshire, it is probable that it is a 'summer' species (CORBET et al., 1960) and is mainly univoltine in this area. As in the case of *I. elegans* (PARR, 1973a), it is postulated that the first individuals seen flying were semi-voltine and had passed their second winter as final instar larvae. The bulk of the first population peak were insects that had over-wintered in the penultimate instar and which were univoltine. The second peak would then have been formed by those individuals which over-wintered as antepenultimate or younger instars and which were also univoltine. These would be expected to take until mid-July to metamorphose, and as several young instars were involved, a dispersed emergence period would result. Under more extreme conditions of climate and nutrition MACAN (1964) has shown that *E. cyathigerum* often needs two or three years to complete its life cycle in the English Lake District, although some individuals may be univoltine each year. It is, of course, possible that with varying ecological factors such as weather, nutrition and altitude, the duration of the life history of this species may be equally flexible in Cheshire.

Examination of the estimated numbers (Fig. 1) shows that the Manly & Parr method tends to produce estimates which are lower than the estimates given by the Jolly method. This phenomenon has also been noticed in the study of *I. elegans* (PARR, 1973a). MANLY (1969, 1970) has shown that when mortality is dependent on age, and hence the assumptions necessary to justify the method of Jolly do not fully hold, this is often reflected in the positively biassed estimates obtained. The positive bias in the results obtained for *I. elegans* (PARR, 1973a) were interpreted as indicating that mortality of the teneral imagines was significantly higher than for older insects, especially as the life table data also supported this theory. However, this explanation cannot hold for the present study of *E. cyathigerum* as virtually all individuals were post-teneral when marked. It seems likely that this positive bias observed in the present Jolly estimates can be explained by a higher mortality affecting individuals in the first one or two days after marking. MANLY (1971) describes a method of testing for a temporary marking effect in capture-recapture studies. In an analysis of the present *E. cyathigerum* data he concludes that there is slight evidence of a marking mortality, at least on some days, thus supporting the conclusion reached by comparison of the estimates obtained by the two methods discussed here. It is, therefore, suggested that a marking effect may also be detected in capture-recapture studies by noting the positive bias, if any, produced by Jolly's method estimates of population size and survival rate over the estimates obtained by Manly & Parr's method. This will only be a valid comparison, of course, if one can be reasonably certain that age dependent mortality, (particularly high 'infant' mortality) is not occurring.

The nature of the apparent marking effect needs to be considered further. Two main possibilities seem to exist. The act of catching and marking the insects may result in a strong tendency for them to disperse immediately, so that many never find their way back to the parent colony. In this work, the insects were marked uniquely on first capture and therefore were only marked once; when recaptured subsequently only a very brief examination was necessary to determine the code number borne by the insect. Secondly, the handling necessary to apply the marks, or the carrying of the marks may result in lower viability. This could be caused by actual damage when the mark is applied or by making the insect more vulnerable to predators or simply less efficient in the air. It is considered probable that all of these possibilities contribute to the apparent high mortality rate of newly marked *E. cyathigerum*. It is clear that the marking effect, whatever its actual cause, is mainly temporary in the sense that there does not seem to be any evidence based on the survivorship curve that survival is other than random with advancing age.

The unsatisfactory population estimates obtained at Pond 1 in June 1970 may be related to the characteristic habit of male *E. cyathigerum* of flying for long periods over open water and perching on emergent vegetation away from the water's edge. At a pond the size of Pond 1 (about 60 x 30 metres), or larger, this habit makes the acquiring of a random sample exceedingly difficult. It is considered that this factor alone can explain the conflicting estimates provided by the two methods of analysis of the capture-recapture data. Pond 3 is much smaller (about 50 x 20 metres) than Pond 1, so that the insects were less well able to avoid the pond's margins, and hence, the samplers' nets, than at Pond 1.

Careful observation of the swarms of male *E. cyathigerum* seen at Pen Ponds, Surrey on 11 August, 1967, produced absolutely no evidence that individuals were caused to leave the water as a result of any direct interaction between individuals. The remarkably little aggressive behaviour, despite the high density, gave the very clear impression that dispersal to and within various parts of the habitat (water's edge, over open water or in open parkland away from water) could have been due to the physiological condition of the insects and not to direct competition such as fighting or threat display.

BUCHHOLZ (1951) and ZAHNER (1960) agree that territoriality and aggressive behaviour was stronger in sparse populations of *Calopteryx splendens* (Harris) than dense ones. Similarly, PAJUNEN (1962) considers that aggressive behaviour tends to become more pronounced as the numbers of *Leucorrhinia dubia* (Vander Linden), *L. rubicunda* (L.) and *L. caudalis* (Charp.) diminish during the season. Territorial behaviour was witnessed for *E. cyathigerum*, but not for *Ischnura elegans* or *Coenagrion puella* males in the Dunham populations. Suitable emergent vegetation or twigs would be occupied by adult males of *E. cyathigerum* during fine weather during the day, but each male would soon select a new perch, so that 'defence' of a particular territory was very short-lived. That is to say, males of this species would 'defend' a succession of small territories and perches during each day but encounters between rival males were never observed to result in a male leaving the water. BICK & BICK (1963) reached a similar conclusion for the North American *E. civile*.

The presence of both male and female damselflies at water may, at least in some species, be determined more by their physiological state than their age *per se* or density of population. Females of many species are unlikely to appear at water unless they are ripe for mating or oviposition. Males may withdraw from water after mating if that act results in a significant waning of the sex drive, although some males of both *E. cyathigerum* and *I. elegans* were recaptured at water the day after copulating. The situation is further complicated by the observation in July, 1975 of numerous pairs of *E. cyathigerum* flying in tandem at distances of up to 800 metres from the nearest breeding site in the Delamere Forest area of Cheshire. These mature pairs were flying on heathland, in woodland and along hedgerows in company with many single individuals in both mature and immature colouring. Further observations are required in order to fully investigate the movements of any zygopteran in relation to water.

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