

**ECOLOGICAL STUDIES OF *ISCHNURA ELEGANS* (VANDER LINDEN)
(ZYGOPTERA: COENAGRIONIDAE). I. AGE GROUPS,
EMERGENCE PATTERNS AND NUMBERS**

M. J. PARR

Department of Biology, University of Salford,
Salford M5 4WT, England

Received May 30, 1973

Imaginal populations of the damselfly *Ischnura elegans* were studied by means of capture-recapture methods in Cheshire and Pembrokeshire, U.K., from 1965-1970. Age grouping of both males and females was accomplished by noting characteristic colour changes associated with the ageing process. There is some indication that the distribution of immature imagines in the colonies at Dunham, Cheshire, was partly determined by the available vegetation shelter from wind. *Acorus* seems to afford greater protection than *Juncus*. By noting the age group composition of the colonies and studying the population estimates it was found that *I. elegans* had bimodal emergence curves with peaks in June and July/August. The population sizes at the Dunham Ponds bore a direct relationship to the size of the pond.

The total estimated season's sizes for Ponds 1 and 2 (1965) and Pond 3 (1966) were about 2000, 4700 and 450 respectively. The sexes were about equally represented in these estimates. The populations in June 1970 at Ponds 1 and 3 were between three and five times larger than for the corresponding months in 1965 (Pond 1) and 1966 (Pond 3). It was found that *I. elegans* is active under a wide range of weather conditions, only winds in excess of 20 knots, heavy rain, and a day temperature of less than 15°C (especially in combination) completely suppress flight.

INTRODUCTION

These studies continue a series on the biology and ecology of British populations of the damselfly *Ischnura elegans* (Vander Linden) (Odonata: Coenagrionidae) and other coenagrionids (PARR, 1965, 1969a, 1969b, 1970; PARR & PALMER, 1971; PARR & PARR, 1972). The only other detailed and quantitative studies of *I. elegans* in Britain have been made by MOORE (1954, 1964) and

LORD (1961). The present studies extend these pioneer efforts and are primarily concerned with seasonal emergence patterns and numbers of imagines.

METHODS AND HABITATS

The populations were studied by means of the capture-recapture method (MANLY & PARR, 1968; PARR, 1965 and PARR, GASKELL & GEORGE, 1968). The use of this method and the appropriate methods of analysis of the capture-recapture data allow the collection of much information which cannot be obtained in any other way. This is especially true when the insects are given unique marks and are teneral when first captured and marked.

The capture-recapture data were analysed using the methods of FISHER & FORD (1947), JOLLY (1965) and MANLY & PARR (1968). The method of Fisher and Ford makes the important assumption that the survival rate is constant throughout. This inherent disadvantage can be circumvented to a large extent by analysing the data in a series of overlapping blocks, as was done in this work, so that separate survival rates are obtained for different times of the season. Fisher & Ford's method also assumes that mortality is random with respect to age. This method's chief advantage lies in the fact that its averaging of the data allows it to be used relatively effectively when other methods fail to operate at all due to insufficient data. Jolly's method assumes that an animal has a probability of surviving over a specified time interval and it makes very efficient use of the data. However, Jolly's method also assumes that mortality is random with age. MANLY (1969, 1970) has shown that when mortality is dependent on age, and hence the assumptions necessary to justify the methods of Fisher & Ford and Jolly do not fully hold, this is often reflected in the distinctly biased estimates obtained. The method of MANLY & PARR (1968) makes fewer assumptions than the other main methods, but it may be considered as a special case of Jolly's method. In particular, it does not assume that death is random with respect to age, and when estimating population size, it is not necessary to assume that marking does not affect mortality. The relative advantages and disadvantages of these three methods are considered by MANLY (1969, 1970, 1971). In the present paper population numbers have been estimated by all three methods mentioned above. This has been done to allow, for the first time, a comparison of the three methods using field data.

Standard error estimates for the estimates of population size and survival have not been given. MANLY (1970) suggested that they are often not very useful since they are highly correlated with the estimate to which they relate. In a later paper, MANLY (1971) showed that for Jolly's method, underestimates of population size appear more accurate than they really are because of a positive correlation between estimates of population size and their estimated standard

errors. MANLY (1971) says "An estimate with a small estimated standard error can in these cases therefore arise either because the estimate is genuinely accurate or because it is a large underestimate. This means that standard error estimates cannot be relied upon to measure sampling error". Although Manly's comments refer specifically to JOLLY's (1965) method, he considers that they will also apply to all other formulae of a similar type that have been obtained for other methods of analysing capture-recapture data.

Most of the present studies were carried out at three ponds in the private portion of Dunham Park, near Altrincham in north Cheshire and these habitats are described in PARR & PALMER (1971). In the main, the work reported here was carried out in the summers of 1965 and 1966. The work was continued in 1970, primarily to compare survival rates of *I. elegans* in different colonies (PARR & PARR, 1972). Although the work in 1970 was restricted to the month of June, the results, where relevant, are included here.

AGE GROUPS, EMERGENCE PATTERNS AND NUMBERS

Imaginal colour phases and age

The work of LORD (1961) showed that the thoracic ground colour of male *I. elegans* was age determined. Most of Lord's data related to individuals kept in captivity in the laboratory: it, therefore, seemed important to study the phenomenon of colour change due to ageing under field conditions. The colours of *I. elegans* referred to in this work were matched against the Standard Colour Samples (SCS) in KORNERUP & WANSCHER (1967). The applicable SCS designation(s) is given in parenthesis immediately after a colour is first mentioned in the text.

Male *I. elegans*, which are monomorphic with respect to pattern, show a change in ground colour of the thorax from green (27A6) through blue-green (25A6) to turquoise-blue (24A6), which may be used to place them in approximately defined age groups. This is apparent when the recapture history of individuals first marked when teneral is examined. By the appropriate methods of analysis of these raw data the average time spent in each of the colour phases may be estimated with some degree of accuracy. The age group structure of the population may then be assessed at any time in the flying season by examination of the colour phases in each sample.

Tenerals only remain with imperfectly developed colouring for approximately one day after emergence and the next day they may be recognized as teneral-green, i.e. with a green thorax but with the glistening wings typical of the still teneral insect. Two methods have been used to determine the relationship between colour phases and age grouping in *I. elegans*. The first and intrinsically

most accurate method involves the use of each individual originally marked when teneral, teneral-green or green, and scoring these for colour phase when captured subsequently. Individuals which were post-teneral and green when first captured have only been included in this analysis if they were recaptured still green after an interval of at least three days. Examination of all the relevant data indicates that such insects had a high probability of being about 2-3 days old when first captured. Figure 1 shows the relationship between thoracic ground colour and age in male *I. elegans*. It is based on the recapture histories of 111 individuals at Ponds 1, 2 and 3 in the years 1965, 1966 and 1970. The differences in maturation rates between the populations at the three ponds and in different seasons were not very marked; the rates of colour change recorded are, therefore, averages and may be taken to represent the normal rates encountered in northern England. Figure 1 shows that up to about 5.5 days most individuals are green and that none is green after ten days. The most rapidly maturing individuals begin changing to blue-green thoracic colour on the second day, but only after six days are more than 60 percent blue-green. Virtually 100 percent are blue-green for the 9th-12th days of their existence. From the 12th day there is a steady fall in the number of blue-greens as they mature into their final blue thoracic colour. After about 18 days, however, most individuals are definitely blue and all individuals are blue by day 27. This latter phase lasts for the remainder of the insect's life. Examination of the data shows that the large overlap between green/blue-green and blue-green/blue phases is caused by individuals changing colour at different ages, not by slow colour changes. The actual colour changes were often observed to be accomplished in one or two days.

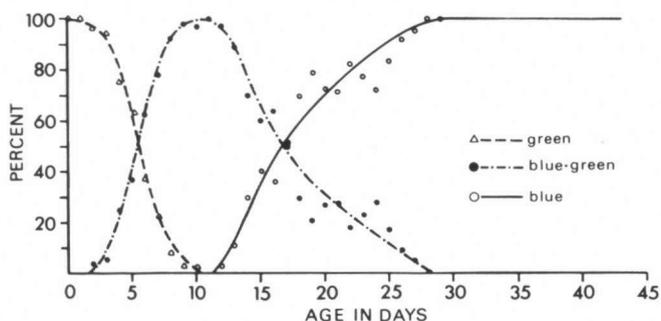


Fig. 1. Change of thoracic ground colour with age in male *I. elegans*. Based on recaptures of individuals marked when teneral, teneral green or green from Ponds 1, 2 and 3 for 1965, '66 and '70, utilising three-day moving averages; curves fitted by eye.

The second method which has been used to determine the relationship between colour phases and age grouping in male *I. elegans* is as follows. Examination of the raw recapture data allows the calculation of the mean observed survival times of teneral, teneral-green, green, blue-green and blue phases. Similarly, it is possible to calculate the mean observed time taken by a particular colour phase to change to another phase. All individuals which were recaptured at least once were used in these calculations. For example, the mean observed time spent in the green phase at Pond 1 (1965) was 1.8 days, and the observed mean time taken for green to change to blue-green was 5.3 days. It is clear that the observed survival time of any colour phase tends to be an underestimate, whereas the observed time taken by a certain phase to change to another colour tends to be an overestimate of the real time value. It may be argued that if the mean time taken for green to transform to the blue-green phase is observed to be, say, 5.3 days, then this time represents partly blue-green survival time; the green to blue-green change itself occurs fairly rapidly since classification of the colour phases was always quite easy. It is, therefore, possible to allocate this time of 5.3 days partly to the survival time of the green phase and partly to the blue-green phase in the same proportion as the observed times spent as green and blue-green. Hence (for Pond 1, 1965) as the green phase was observed to last 1.8 days and the blue-green phase 3.8 days on average, the green to blue-green transformation (5.3 days) may be estimated, on average, to represent 1.7 days as the green phase and 3.6 as the blue-green phase. Similarly, the 8.1 days taken for the transformation of the blue-green to blue may be split into 2.5 days for the blue-green phase and 5.6 days for the blue phase as this is the same proportion as the observed survival of 3.8 and 8.3 days for blue-green and blue respectively. These calculations allow the mean survival times of the colour phases at Pond 1 (1965) to be estimated as:

$$\begin{aligned}
 \text{Teneral + teneral-green} &= 2.0 \text{ days} \\
 \text{green} &= 1.8 + 1.7 = 3.5 \text{ days} \\
 \text{blue-green} &= 3.8 + 3.6 + 2.5 = 9.9 \text{ days} \\
 \text{blue} &= 8.3 + 5.6 = 13.9 \text{ days}
 \end{aligned}$$

Table I gives the adjusted mean survival times of the thoracic colour phases in days obtained by this technique. It is interesting to note that the time values obtained in this way correspond closely with the 50 percent time values for green, blue-green and blue in Figure 1.

The relationship between colour phases and age of female *I. elegans* is more difficult to define than for males. This is largely because females are recaptured less frequently than males and the existence of three colour morphs independent of age (LORD, 1961; PARR & PALMER, 1971) further dilutes the information. The relationship between female colour phases and age has been established by

Table I

Males. Adjusted mean survival times of colour phases (in days) obtained by utilising data from all individuals captured at least twice

	t + g	bg	b
Pond 1 1965	5.5	9.9	13.9
Pond 2 1965	5.8	9.7	10.8
Pond 3 1966	7.0	12.9	14.3
Pond 1 1970 (June)	7.0	11.4	8.0*
Pond 3 1970 (June)	5.8	10.8	10.5*
<i>Means</i>	6.2	10.9	11.5
Mean age at which colour changes occur	6.2	17.1	

* These values must be expected to be low as sampling was only carried out for one month (June).

the analysis of all recaptures.

The colour changes that occur during maturation of the female morphs may be accurately described by reference to the SCS used for males:

(1) *rufescens* → *infuscans-obsolata*

The reddish thoracic colour (SCS 10C4 to 13C4) of *rufescens* changes to brownish-grey (5C2) or greyish-yellow (4C5) in fully mature *infuscans-obsolata*. The brownish 8th abdominal segment of *infuscans-obsolata* varies between light brown (6D4) and brown (5E7). The time spent as *rufescens* was on average 8.1 days. One individual marked as a teneral was recaptured as *infuscans-obsolata* seven days later, and another also marked as a teneral was recaptured eleven days later in an intermediate state between *rufescens* and *infuscans-obsolata*.

(2) *violacea* → *infuscans*

The violet thoracic colour (15C4, 16C5, 17C5 and 21C5) of *violacea* changes to apple-green (29C7) in young *infuscans*. The *infuscans* phase passes through a series of thoracic changes, the principal ones being apple-green (29C7) → greyish-green (1D5) → olive-yellow (2C6) → also olive-yellow (2D6). Some individuals of *infuscans* assume a darker and browner thoracic colour with advancing age. The brownish 8th abdominal segment of *infuscans* is similar to that of *infuscans-obsolata* and varies between light brown (6D4) and brown (5E7). The mean age for transformation of *violacea* to the apple-green *infuscans* was 6.9 days. The most rapid observed maturation of a *violacea* individual to *infuscans* occurred after six days and one other individual was seen to change to *infuscans* after seven days.

(3) *violacea* → andromorph

The violet thoracic colour of individuals destined to become andromorphs appears to be indistinguishable from the colour of those destined to become *infuscans*. However, the green (27A6) of young andromorphs is different from the green of young *infuscans*. The successive green, blue-green and blue thoracic colours of andromorphic females are identical with the colour phases seen in males. The mean age for transformation of *violacea* to the green andromorph was 5.9 days, and the most rapid change to green andromorph occurred four days after emergence. Table II gives the adjusted mean survival times of the female colour phases in days.

Table II

Females. Adjusted mean survival times of colour phases (in days) obtained by utilising data from all individuals captured at least twice

	t + r →	i - o	t + v → (i)	i	t + v* → (a)	a
Pond 1 1965	8.4	10.6	5.5	15.4	2.8	17.4
Pond 2 1965	6.4	14.8	5.4	15.6	3.6	13.0
Pond 3 1966	7.4	20.1	7.0	22.4	6.0	24.9
Pond 1 1970 (June)	8.1	13.7	7.9	13.0	7.1	16.3
Pond 3 1970 (June)	10.3	13.6	8.7	11.7	- ‡	- ‡
<i>Means</i>	8.1	14.6	6.9	15.6	5.9	17.9
Mean age at which colour change occurs	8.1		6.9		5.9	
Mean survival	22.7		22.5		23.8	

* Data sparse ‡ Insufficient data for an estimate.

Table III

Males. Numbers of individuals of immatures (t + g) and adults (bg + b)

	Immatures		Adults		Totals
Pond 1 1965	131	(168.8)	228	(190.2)	359
Pond 2 1965	448	(417.1)	439	(469.9)	887
Pond 3 1966	84	(77.1)	80	(86.9)	164
<i>Totals</i>	663		747		1410

(Expected values in parentheses) $\chi^2 (2) = 21.44 ; p < 0.001.$

Table IV

Females. Numbers of individuals of immatures (t + v + r) and adults (a + i + i - o)

	Immatures	Adults	Totals
Pond 1 1965	92 (112.6)	99 (78.4)	191
Pond 2 1965	389 (357.4)	217 (248.6)	606
Pond 3 1966	81 (92.0)	75 (64.0)	156
<i>Totals</i>	562	391	953

(Expected values in parentheses) $\chi^2 (2) = 19.17$; $p < 0.001$.

Proportions of immature and adult age groups

Analysis of the numbers of different individuals (not recaptures) of immatures and adults recorded at the three Dunham ponds (Tabs III and IV) reveals considerable variation of the proportions of these age groups.

Relatively few immatures of either sex were recorded at Pond 1 compared with Ponds 2 and 3. It is possible that this is a reflection of the gross ecological differences of the sites. Pond 1 had little tall dense vegetation fringing the water-side and it is fully exposed to westerly winds. This may have resulted in the movement away of moderate numbers of teneral damselflies in their early flights. Pond 2 contrasted with Pond 1 in that it had a dense fringing growth of *Acorus calamus* L. and *Typha latifolia* L. for much of its perimeter. Hence, although parts of Pond 2 were exposed to westerly winds the immature imagines were afforded considerable protection by vegetation. Pond 3 had little dense fringing plant growth, but as it lies in a deep hollow, the position and the *Juncus* spp. edging the pond provided sufficient cover to have prevented excessive movement away of young imagines.

A study of the immature/adult composition at the two main vegetation types at Pond 2 supports these observations (Tabs V and VI). For both males and females there was a significant excess of immature forms in the combined Sectors 1, 2 and 3 in which the dominant waterside vegetation was *Acorus*. This was particularly striking for the latter sex. Also consistent with these observations is that, apparently, a larger number of *I. elegans* moved from Pond 1 to Pond 2 during the 1965 season, than the reverse, despite the fact that the population at Pond 2 was much larger than at the other pond.

Table V

Males. Numbers of immatures (t + g) and adults (bg + b) in relation to main vegetation types at Pond 2, 1965 (including recaptures)

Sectors of pond	Immatures	Adults	Totals
1, 2 & 3 combined: Acorus + some Typha	323 (305.2)	453 (470.8)	776
4 & 5 combined: Juncus + some Acorus	195 (212.8)	346 (328.2)	541
<i>Totals</i>	<i>518</i>	<i>799</i>	<i>1317</i>

(Expected values in parentheses) $\chi^2_{(1)} = 4.17$; $0.05 > p > 0.02$.

Table VI

Females. Numbers of immatures (t + v + r) and adults (a + i + i - o) in relation to main vegetation types at Pond 2, 1965 (including recaptures)

Sectors of pond	Immatures	Adults	Totals
1, 2 & 3 combined: (Acorus + some Typha)	259 (239.8)	179 (198.2)	438
4 & 5 combined: (Juncus + some Acorus)	184 (203.2)	187 (167.8)	371
<i>Totals</i>	<i>443</i>	<i>366</i>	<i>809</i>

(Expected values in parentheses) $\chi^2_{(1)} = 7.37$; $0.01 > p > 0.001$.

Seasonal emergence patterns

Ischnura elegans is known to have a long flying season in the British Isles and in most other parts of its range. It occurs regularly from mid-May to mid-September, and exceptionally from late April to October (LONGFIELD, 1949). By analysis of the data obtained at the Dunham Park colonies it has been possible to elucidate the seasonal emergence patterns for that area. As it was found that many individuals of the relatively immature imaginal stages tend to remain near to the water of the parent colony (unlike most other Odonata that have been studied), this fact has been used to study the age group structure of the colonies at Dunham. Each time sampling was carried out, all individuals of *I. elegans* were scored for thoracic colour, and were, therefore, easily classified into junior and senior age groups.

The period of emergence of imagines, and hence the flying season, was longest at Pond 2 (1965) and shortest at Pond 3 (1966). Although the male and female colour changes are not strictly comparable on a temporal basis, it was found convenient to index the age-state of the colonies by designating teneral and/or green males as immature; similarly, for females, teneral and/or *violacea* and *rufescens* as also immature. Blue-green or blue males and andromorphic, *infuscans* or *infuscans-obsolata* females were, therefore, termed mature. It should be noted, though, that green males and *violacea* and *rufescens* females were occasionally seen in copulation.

The emergence patterns at the three colonies have been represented by plotting the percentage of adult individuals captured (Fig. 2) and the numbers of immatures captured (Fig. 3) for the flying seasons of 1965 and 1966. Examination of these figures illustrating the age group structures for these seasons shows clearly the extended period of emergence for all three colonies. The data for Pond 2 indicate two main periods of emergence for both males and females: the first half of June and the first half of August. There seems little doubt that there was also a second main emergence at Pond 1, commencing soon after the middle of July, following the initial period of emergence in the first half of June. In contrast to Ponds 1 and 2, the data relating to the colony at Pond 3 in 1966 do not suggest a clearly defined bimodal emergence curve. The numbers of immature and mature individuals of both sexes captured at Pond 3 appear at first sight to indicate a single main emergence peak from early to late June. The numbers of immature imagines captured fell steadily from the end of June to the end of the emergence periods for both males and females, some immatures being captured until early August. However, a detailed study of the data for Pond 3 (Fig. 2) shows that after a steady increase in the percentage of adults from 21 June until 11 July, the complete senescence of the population is halted temporarily by a small emergence of new imagines from 11 July until 29 July.

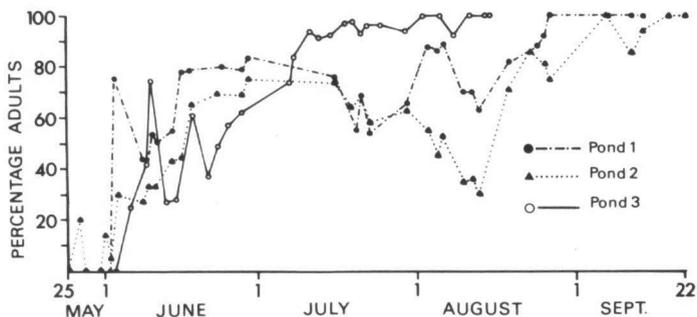


Fig. 2. The emergence patterns at Pond 1 (1965), Pond 2 (1965) and Pond 3 (1966) expressed as the percentage of adults (blue-green + blue males and andromorph + *infuscans* + *infuscans-obsolata* females) captured throughout the flying seasons; sexes combined.

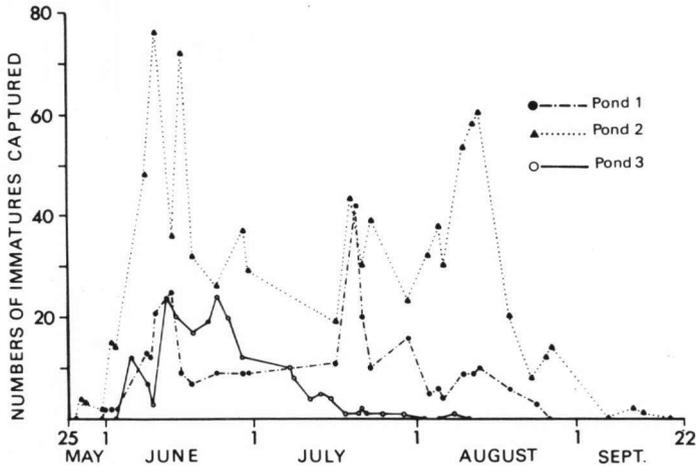


Fig. 3. The emergence patterns at Pond 1 (1965), Pond 2 (1965) and Pond 3 (1966) expressed as numbers of immatures (teneral + green males and *violacea* + *rufescens* females) captured throughout the flying seasons; sexes combined.

Imaginal population numbers

The population estimates may be criticised for a number of reasons. Perhaps the two most important criticisms of these estimates are that they are not as precise as one would have wished them to be, and that the time intervals between samplings were sometimes too long. The precision of the estimates is clearly partly linked with the length of time between successive samplings. A lengthy period between sampling occasions will greatly reduce the number of marked insects available for recapture and hence will tend to introduce a large variance. Theoretically, the most accurate results would probably be obtained if the population were sampled every day. This was not attempted in these studies owing to very variable weather conditions and other commitments which necessarily limited the amount of time available for field work. In fact, as the work progressed it became abundantly clear that a season-long study involving daily sampling would result in considerable disturbance and destruction of the habitat. The trampling effect on the waterside vegetation was becoming noticeable even in the short, preliminary study of *I. elegans* (PARR, 1965) and it was also very obvious at Pond 3 in 1966. That this was less noticeable at Ponds 1 and 2 was partly due to the large area to be covered in sampling these sites. Hence, there was probably less disturbance of the colonies at Ponds 1 and 2 in 1965 and the proportion of the population marked was less than at Pond 3 in 1966. The average sampling frequencies for the different populations are given in Table VII.

Table VII

Average sampling frequencies in days for the ponds in Dunham Park

Year	Ponds		
	1	2	3
1965 (whole season)	3.5	3.5	—
1966 (whole season)	—	—	2.6
1970 (June only)	2.0	—	2.1

Comparisons of the results indicate that the Manly & Parr method tends to produce estimates that are lower than the estimates produced by the other methods. This is almost certainly a reflection of the fact that mortality was not random with respect to age, and that the results in the methods of Jolly and Fisher & Ford gave positively biased estimates. It may be assumed that the Manly & Parr estimates are effectively unbiased (MANLY, 1970).

The estimates of population size are of interest from two main standpoints:

- (1) The variations in numbers and seasonal distribution of numbers in different colonies, and
- (2) The variations in numbers in different years in specific colonies.

Separate male and female population estimates were obtained by the three methods already mentioned. In no case did the estimates of population sizes suggest that either sex was clearly numerically dominant, nor was there any clear indication that the proportion of the sexes changed seasonally. The male and female estimates obtained by each method and relating to each specific sampling occasion were summed, and these results are shown in Figures 4, 5 and 6, expressed as three-point moving averages. This treatment of the results has to a large extent eliminated the extremes of over- or underestimation which are common, and to be expected in capture-recapture studies (PARR, 1965; MANLY, 1969), and yet allows the seasonal population patterns to be recognized.

(1) *Pond 2 (1965)* — Fig. 4.

The population estimates for Pond 2 obtained by the three methods agree fairly well except at the end of July and beginning of August when the values obtained by the Manly & Parr method are much lower than by the other two methods. As the percentages and numbers of immatures increased from mid-July until 13 August, indicating a second main emergence of imagines, it is likely that the Fisher & Ford and Jolly estimates for this period are more realistic than those obtained by Manly & Parr's method. Two definite population peaks are evident: the last three weeks in June and the first two weeks in August, when the daily population was about 600 imagines. The population commenced emergence in late May and continued flying until the last week in September.

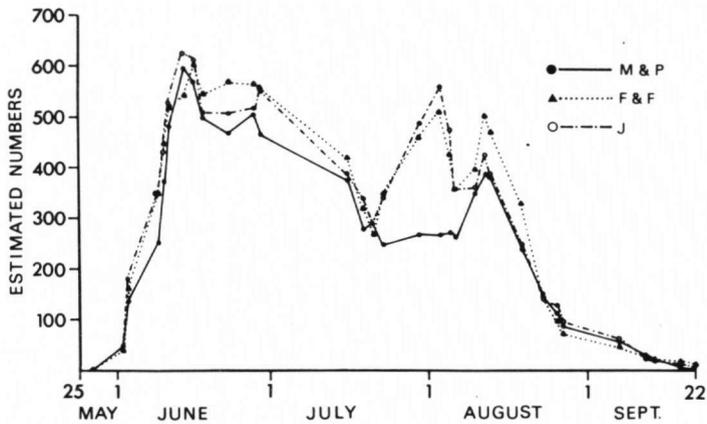


Fig. 4. Estimated numbers at Pond 2 (1965); three-point moving average, sexes combined. F & F = FISHER & FORD (1947) method; J = JOLLY (1965) method; M & P = MANLY & PARR (1968) method.

(2) Pond 1 (1965) – Fig. 5.

The estimates derived by the three methods agree in indicating population peaks in mid-May and mid-July, although the estimates obtained by Manly &

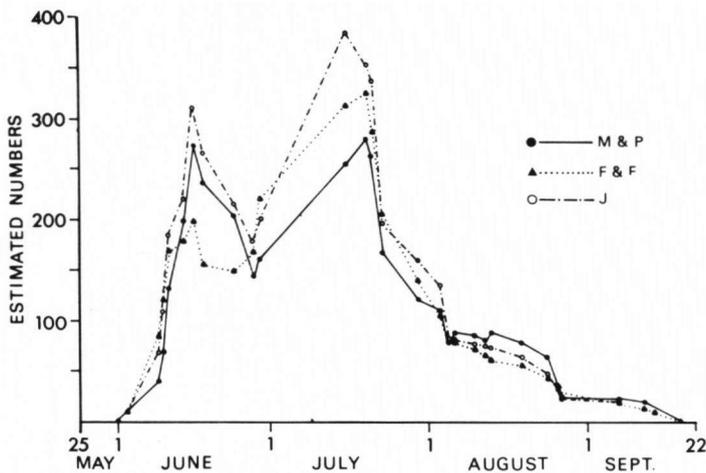


Fig. 5. Estimated numbers at Pond 1 (1965); three-point moving average, sexes combined. F & F = FISHER & FORD (1947) method; J = JOLLY (1965) method; M & P = MANLY & PARR (1968) method.

Parr's method for mid-July are much lower than those recorded for the other two methods. Both percentages and numbers of immatures were highest during these periods of maximum population size (Figs. 2 and 3). The imagines commenced emergence in late May and the last individuals were seen on 14 September. Maximum daily numbers were probably about 275-300 in mid-June and mid-July.

(3) *Pond 3 (1966)* – Fig. 6.

The population estimates for this pond in 1966 obtained by the methods of Jolly and Manly & Parr are remarkable in their high degree of correspondence. It can be seen that despite the smoothing due to the taking of three-point moving averages, two rather ill-defined peaks occur around 21-23 June and 7-8 July. It is evident from Figures 2 and 3 that new emergences continued until August. The estimates by Fisher & Ford show the first of these maxima in June, but the second is barely visible by this method. Maximum numbers were about 200 during these two periods of greatest abundance. The population commenced emergence early in June and the last individuals were seen on 16 August.

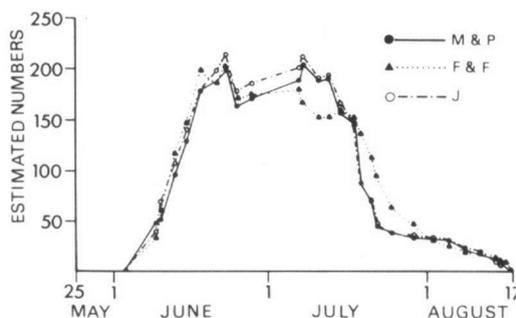


Fig. 6. Estimated numbers at Pond 3 (1966); three-point moving average, sexes combined. F & F = FISHER & FORD (1947) method; J = JOLLY (1965) method; M & P = MANLY & PARR (1968) method.

These three neighbouring populations differed from each other in a manner that was largely consistent with differences in the gross ecology of the sites. The largest pond (2) supported a population of *I. elegans* in 1965 which was the largest of the three colonies studied during 1965/66 and which had the longest flying season. Its two emergence peaks were widely separated temporally. The smallest pond (3) was associated with the smallest population which had the shortest period of imaginal activity and two poorly defined emergence peaks (1966). The population of *I. elegans* at Pond 1 (1965) was intermediate in these respects. There was no indication that the populations at Pond 1 and 2 were markedly different in size in 1966 compared with 1965.

It is likely that different temperature regimes in the three ponds have definite effects on the growth rates of *I. elegans* larvae living in the ponds. In southern France *I. elegans* is known to have three generations per year (AGUESSE, 1961), whereas in south Lancashire it is mainly univoltine (PARR, 1970) and it is semivoltine on the Outer Hebridean island of Benbecula (PARR, 1969b). These recorded differences in the length of the life history seem to be related particularly to temperature differences in the spring, summer and autumn months. The relatively large volume of water of Pond 2 might be expected to remain somewhat lower in summer and rather higher in winter than the water in Pond 3. The cooling in the autumn months would be quicker in the smaller pools than Pond 2. Thus it may be postulated that the longer periods for relatively slow growth of larvae at Pond 2 would result in less synchronisation in development and greater separation of the emergence peaks than at Pond 3, where the active period of growth would be shorter. CORBET (1957) proposed that a system of lower temperature thresholds operates to reduce temporal variation in the spring for some other Zygoptera. It seems unlikely that such a system operates in the case of *I. elegans* (PARR, 1970). The first imaginal peak at each of the populations was probably due to emergence of insects which overwintered in the penultimate instar, and the second peak was formed by those insects which overwintered as antepenultimate or younger instars. The few imagines which were seen flying in May in both 1965 and 1966 were almost certainly individuals which had overwintered in the final instar. The population of larval *I. elegans* studied by PARR (1970) was established at one end of a narrow linear lake in south Lancashire, which might be expected to cool rapidly in autumn and warm up quickly in spring. Significantly, this population showed little evidence of a bimodal emergence as there was rapid maturation of the bulk of the larvae during May and June. In their study of the dragonflies of the Gearagh, West Cork, Ireland, HEWETSON & O'ROURKE (1960) recorded a bimodal seasonal distribution in the numbers of *I. elegans*. Their collections showed well defined peaks at the end of June/beginning of July and in the first week of August, 1954. The Gearagh is an area of wet woodland on the river Lee near Macroom, Co. Cork. Hewetson & O'Rourke report that the river suffers frequent and violent flooding which adversely affects the larval habitats. It is, therefore, not surprising that this Irish population should show a temporally well despersed emergence curve.

The populations of *I. elegans* at Pond 1 and 3 were studied again in June, 1970, primarily in order to investigate the relationship between survival rates, colony size and predation of the imagines (PARR & PARR, 1972). At both Pond 1 and Pond 3 the population sizes in June, 1970 were very much larger than for the corresponding pond in June, 1965 or 1966 (Fig. 7). The June, 1970 population at Pond 3 was of the order of three times as large as the population in 1966. Similarly, the number of imagines in June, 1970 at Pond 1 was between

four and five times as large as in 1965. While no detailed study was undertaken of the population at Pond 2 in 1970, direct observations showed that the number of imagines greatly exceeded the numbers present in 1965 and 1966. It can be stated with certainty that a capture-recapture study of the population at Pond 2 in 1970 would have yielded little information owing to a very low recapture rate.

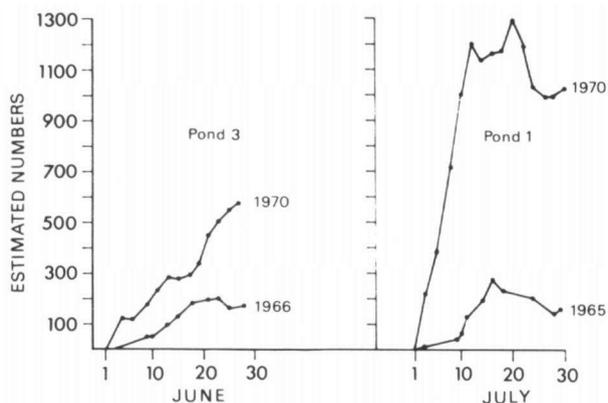


Fig. 7. Estimated numbers at Ponds 1 and 3 for June, 1970, compared with estimates obtained in earlier years; three-point moving average, sexes combined. Manly & Parr method.

Season's total population sizes

The estimates of the total numbers present at each colony are presented in Table VIII. There were, unfortunately, insufficient data to allow an estimate of total females at Pond 1. The method for obtaining these estimates is given in PARR & PALMER (1971). It may be noted that these results suggest that the imaginal sex ratio is nearly unity, and that the population sizes are directly related to the linear dimensions of the respective ponds.

Table VIII
Estimated total season's population sizes and pond sizes

	Pond 1 (1965) (55 x 24m)	Pond 2 (1965) (165 x 114m)	Pond 3 (1966) (45 x 21m)
Male	1018.3	2270.1	218.4
Female	—*	2440.0	226.4

* Insufficient data to allow estimate.

Sample sizes and weather factors.

The relationship between numbers of imagines available for capture and weather conditions is complex and difficult to analyse satisfactorily. The Manchester Meteorological Office supplied daily data relating to Manchester Airport, for the flying seasons of 1965 and 1966, on cloud cover, wind direction and velocity, barometric pressure, relative humidity, maximum and minimum temperature, rainfall and sunshine hours. Dunham Park is about eight kilometres from Manchester Airport Meteorological Station.

Examination of the numbers of *I. elegans* captured shows no obvious relationship with wind direction, barometric pressure, relative humidity or minimum (night) temperature. Wind speed is generally unimportant *per se* unless very high; this species, *Coenagrion puella* (L.) and *Enallagma cyathigerum* (Charp.) (common Zygoptera often found with *I. elegans* in England) are able to fly successfully in air speeds of 19-20 knots. Wind speeds in excess of this range are usually encountered only in association with other adverse factors which themselves inhibit activity.

Of the weather factors considered, those having the most obvious effects on zygopteran activity were light values, rain, wind velocity and daytime temperature. Light was considered indirectly as cloud cover (expressed in 8ths) and hours of sunshine. It was found that direct readings of light intensity using a light meter were too variable in different sites under identical sky conditions to yield any useful information. Figure 8 illustrates the range of certain weather factors (cloud cover when sampling, sunshine hours per day, maximum daytime temperature and maximum wind speed) which allow a high degree of activity of *I. elegans*, and hence, for a large sample to be obtained. For this purpose, the arbitrary number of one hundred imagines captured in a day's sampling was taken to represent a large sample. The maximum number taken in any one day was 172 on 29 June, 1965, when cloud cover was 1/8th, and there were 9.5 hours of sun; the maximum temperature was 21.7°C and the wind speed was 1 knot per hour. These are what might commonly be termed 'good' weather conditions for diurnal insect activity in England. However, 152 individuals were caught on 21 July, 1965, when there was total cloud cover for the whole day, the maximum temperature was 17.1°C and the wind speed was 5 knots. It is clear, therefore, that the absence of sunshine does not in itself inhibit flight activity in *I. elegans*. This species will also show considerable activity in very low maximum daytime temperatures providing the wind is not strong, even if there is little sun. For example, on 30 July, 1965, when the maximum temperature recorded was 14.4°C and there were only 3.3 hours of sun (mostly early morning, before sampling was carried out), 111 individuals were taken, presumably because there was complete calm. Rain, strong wind and a temperature below 14°C inhibit activity, especially in combination. Heavy and continuous rain

always prevents or stops flight activity (e.g. 21 June, 1965) even though temperature, wind, cloud and sunshine levels are within the ranges normally tolerated. Light drizzle, on the other hand, has little inhibitory effect (e.g. 21 July, 1965).

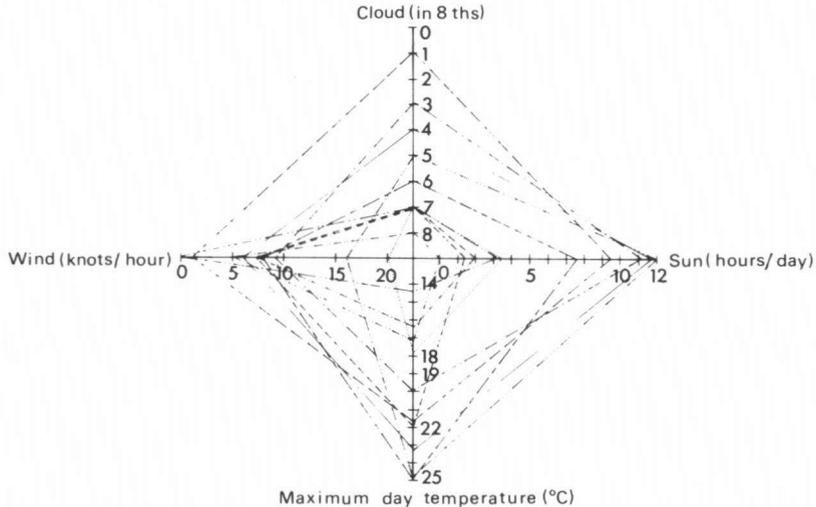


Fig. 8. Diagram illustrating the range of certain weather factors allowing a high degree of activity of *I. elegans*. The diagram represents the weather on 10 actual days in 1965 when more than 100 individuals were caught on each day.

In summary, it may be said that *I. elegans* is an exceedingly adaptable species in that flight, feeding and sexual behaviour may occur under a great range of weather conditions in the British Isles. Only extreme cold, very strong wind or continuous rain completely prevent this species carrying out the activities mentioned. Conditions commonly regarded as 'good' in human terms (sun, lack of wind and high temperatures) always allow much activity. However, dull and humid weather may prove equally suitable for this species. In contrast, *Coenagrion puella* and *Enallagma cyathigerum* are especially inhibited by lack of sun and low temperatures in the British Isles.

ACKNOWLEDGEMENTS

It is a pleasure to thank the Earl of Stamford for allowing me to work in the private portion of Dunham Park, Cheshire. I am grateful to my wife, MARION, who shared the field work in 1970 and who has read and criticised the text. Mr. B.F.J. MANLY was of great assistance on statistical and computational matters. My thanks are also due to Professor G.R. RAMAGE and Professor W.E. KERSHAW of the University of Salford, for providing facilities and financial support for this work.

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