

**ECOLOGICAL STUDIES OF *ISCHNURA ELEGANS* (VANDER LINDEN)  
(ZYGOPTERA: COENAGRIONIDAE). II. SURVIVORSHIP, LOCAL MOVE-  
MENTS AND DISPERSAL**

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Imaginal populations of *I. elegans* were studied by means of capture-recapture methods in Cheshire and Pembrokeshire, U.K., from 1965 to 1970. Although the survival rates did not alter with time, the populations had characteristic survival rates which differed from each other. This was probably due to differential predation by birds. Survival was shown to be heavily age dependent, the heaviest losses occurring at the teneral stage. Maximum survival was 42 days for males and 50 days for females. No evidence was obtained to indicate a general movement away from water by teneral insects: many individuals stayed at the water's edge during the maturation period. The maturation period may be as short as three days (males) or four days (females), although it is probably usually a little longer. Many individuals do not move more than 100 metres from their emergence site. A few individuals are wanderers over relatively great distances and are presumably important as founders of new colonies. In many respects (great general adaptability, activity in cool and dull weather, rapid maturation which is usually at water, persistence of females at water, and a very long copulation time) *I. elegans* does not conform to what seem more general zygopteran characteristics.

**INTRODUCTION AND METHODS**

The first paper in this series (PARR, 1973) dealt primarily with seasonal emergence patterns and numbers of imagines in British populations of *Ischnura elegans*. The present paper deals with survivorship, mortality, longevity, local movements and dispersal.

The methods employed were described in PARR (1965, 1973). Most of the observations were carried out at three ponds in Dunham Park, Altrincham, north Cheshire (PARR & PALMER, 1971). However, some observations on dispersal in *I. elegans* were made on populations on the Dale peninsula (south-west Pem-

brokeshire, Wales, United Kingdom). Standing water is scarce on the Dale peninsula and it occurs almost exclusively as irrigation ponds which have been constructed by damming streams in small steep valleys. The irrigation ponds at Dale support populations of *I. elegans* which are discrete and are particularly suitable for studies of dispersal in this species.

## SURVIVORSHIP, MORTALITY AND LONGEVITY

An estimate of imaginal mean longevity (average length of life) may be made from capture-recapture data by noting the frequency of time intervals between first and last captures (CORBET, 1952; PARR, 1965). This is, in effect, the life table method. Three major criticisms may be levelled at this technique as utilised by these authors:

- (1) The individuals were of unknown and, therefore, presumably of variable ages at the time of first capture.
- (2) Marked individuals which were never seen after first capture were not included in the calculation of average longevity.
- (3) The age at death was unknown because the age at first capture was often not known and the date of last capture was probably not the date when death occurred.

In these present studies of *I. elegans* an attempt has been made to assess male longevity more accurately. It was considered that the information available for females was insufficient to warrant detailed analysis. A method for age grouping males has been described in PARR (1973). Ideally, a study of longevity and survival should be made on individuals first captured when teneral or teneral green, as they would not be older than one day. In practice, it was found impossible to obtain sufficient of this primary age group which were subsequently recaptured and, therefore, all individuals which were teneral, teneral green or green were included for the construction of detailed life tables in accordance with the methods of DEEVEY (1947). The results of the study in age grouping suggest that the average age of the green colour phase was 2-3 days. Such individuals will provide a better approximation to the true longevity and survivorship than insects of random ages. However, if there is especially high mortality of freshly emerged damselflies the use of a large proportion of postteneral (green) insects will tend to obscure it, leading to a survival rate and longevity which are too high.

There is no valid reason why insects which were never seen again after initial capture should not be scored in assessing longevity and survivorship. If a certain proportion of these insects did die during the period between the first capture (day 0) and the next day, this was of great significance in relation to survival estimates.

A much more difficult problem with which to come to terms is the estima-

tion of the most probable time of death. An insect which was observed to survive from day 0 to (say) day 10, clearly has a certain probability of surviving for some time longer. Because of this fact it is obvious that, on average, the estimated longevity and survival of a population will be too low unless this factor is taken into account. It is also possible to obtain estimates of mean longevity and survival rate using the various methods which have been devised to analyse capture-recapture data. Of these methods, that of FISHER & FORD (1947) is perhaps the most useful in this connexion. Although MANLY (1970) has shown that this method gives positively biased estimates of survival if there is high 'infant' mortality, it is interesting to compare the estimates from the life tables and the method of Fisher & Ford, in the light of Manly's results. Unfortunately, Manly does not utilise any life tables which are very closely similar to those of the *I. elegans* populations studied. Manly's life tables which appear to be most applicable are the two he labels G and H. His artificial populations G/2, G/3 and G/4 (generated on an electronic computer) may be taken to approximate roughly to the populations under consideration here. Reference to Manly's results shows that the Fisher & Ford survival estimates are positively biased between 14 and 17 percent for the populations G/2, G/3 and G/4. Whilst it is virtually certain that the Fisher & Ford estimates of *I. elegans* survival are positively biased, if the estimates are adjusted to the extent suggested by Manly's results we obtain values that are lower than those given by the actual life tables. As the life tables would certainly seem to underestimate the survival rate and length of life because age at death is unknown, we may conclude that the true values lie inbetween those given by the two methods (Tab. I). The detailed life tables have been used to construct graphs of survivorship ( $l_x$ ), age-specific mortality ( $q_x$ ) and life expectancy ( $e_x$ ) for the three populations studied. (Figs. 1, 2 and 3).

Table I  
Males. Survival ( $\hat{s}$ ) and mean length of life ( $\hat{L}$ ) obtained from life table data and analysis of capture-recapture data using the method of FISHER & FORD (1947). Maximum observed survival in days ( $L_m$ ) is also given.

		Life Table	Fisher & Ford
Pond 1	1965 $\hat{s}$	0.8370	0.8958
	$\hat{L}$	5.6	9.1
	$L_m$	39	
Pond 2	1965 $\hat{s}$	0.7450	0.8724
	$\hat{L}$	3.3	7.3
	$L_m$	38	
Pond 3	1966 $\hat{s}$	0.9150	0.9234
	$\hat{L}$	11.0	12.4
	$L_m$	39	

## Survivorship curves

As age is expressed as percentage deviation from mean length of life in the survivorship curves (Fig. 1) it can be seen that the populations differ considerably in their mean life span, although the maximum observed survival is virtually the same in the three colonies (Tab. I). The three populations are all similar in that mortality of the youngest imagines is heavy (65.5 percent from day 0 to day 1 for the population at Pond 2). After the first day of life the curve for the Pond 2 population is relatively straight and diagonal, indicating that death is random with respect to age. The curve for the Pond 1 population is less obviously straight and if the early, and therefore, most reliable, part is considered it can be seen that it is definitely convex after the earliest period when survival is low. The population at Pond 3 also showed low survival for the first day, but this was less marked than for the other two populations. After day 1, survival at Pond 3 was high, and was always higher than the survival rates for the populations at Ponds 1 and 2. The survivorship curve is definitely convex although it is rather irregular owing to small numbers.

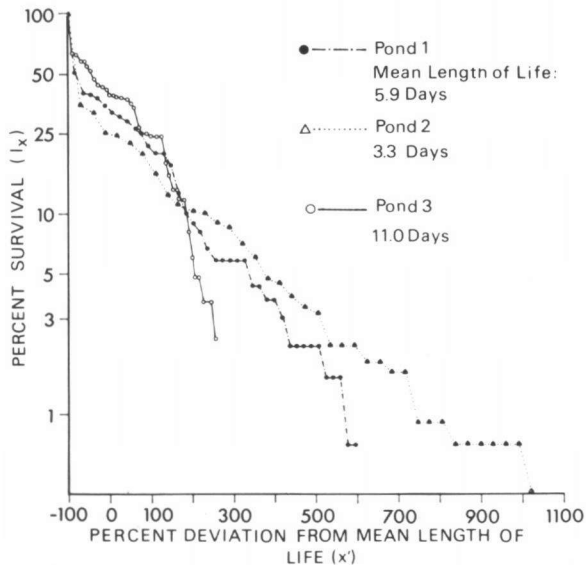


Fig. 1. Survivorship curves for three populations of male *I. elegans*, age being expressed as percent deviation from the mean length of life. From life tables derived from capture-recapture data.

## Age-specific mortality rates

Figure 2 showing age-specific mortality rates ( $q_x$ ) clearly illustrates the remarkable age-dependent mortality of all the populations. Mortality is very high for day 0 and again late in life for about the last ten days of the maximum life span. It must be remembered that these data are obtained from life tables derived from capture-recapture studies and that, therefore, all the insects have been caught and marked. As marking was only carried out when the insects were first captured and they were very young when marked, it may be argued that at least some of the high mortality recorded for day 0 may be attributed to the marking process. This may well be true, but it is unlikely that all or even most of the high infant mortality may be due to marking, as if this were so, it is difficult to see why all the populations should not show similar levels of mortality for day 0. Day 0 mortality for Pond 2 was 65.5 percent, whereas it was only 35.7 percent at Pond 3, with the Pond 1 population being intermediate at 50.5 percent.

When life tables are drawn up from the capture-recapture data relating to Ponds 1 and 3 in June, 1970, very similar results are obtained to those of 1965 and 1966 discussed above. The detailed life tables for the populations at Ponds 1 and 3 for June, 1970, are not presented here as a single month is not long enough to cover the maximum life span of *I. elegans*; nevertheless, day 0 mortality was again very high in both colonies. The population at Pond 1 in June, 1970, showed a 65.6 percent mortality between day 0 and 1, and at Pond 3 the first day loss was 46.7 percent. It seems likely that the apparently higher mortality rates for day 0-1 in June, 1970, were a reflection that the sampling period did not cover the maximum life span. These data for 1970 seem to support the view that the mortality rate (especially of young imagines) of the Pond 3 population is lower than the other colonies studied. PARR & PARR (1972) discuss the seasonal survival rates at these colonies and suggest that differential predation by birds (particularly of the teneral insects) can explain the observed specific survival rates at the three colonies.

## Life expectancy

Figure 3 of life expectancy further illustrates the considerable differences between the three populations. The life expectancy for all three colonies increased sharply from day 0 to day 1, but thereafter the pattern is different in each case. At Pond 2 from day 1 until day 28 the life expectancy fluctuates around 7.5 days before finally plunging towards zero for the last ten days. In contrast, the life expectancy at Pond 3 showed a consistent decline from day 3 to the end of the observed maximum life span of 39 days. For days 1-3 the life expectancy at Pond 3 was about 16.5 days, but by day 22 it had fallen to 8.6

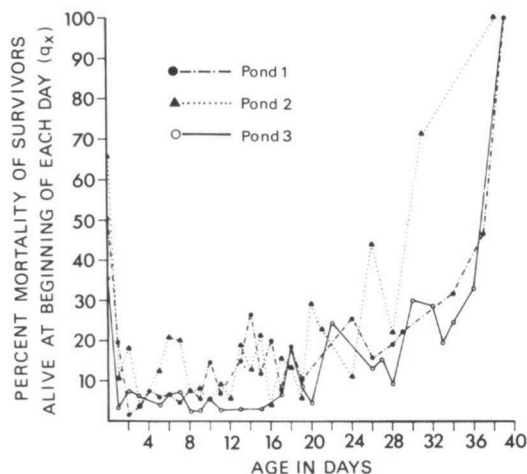


Fig. 2. The age-specific mortality rates for three populations of male *I. elegans*.

days. The life expectancy curve for the Pond 1 colony was intermediate in most respects between that for Pond 2 and Pond 3, although it was more irregular. The observations suggest that in habitats where bird predation is slight the life expectancy curve shows a consistent decline after the post-teneral period. However, when bird predation is heavy life expectancy may be nearly constant after the post-teneral period, until natural ageing begins to operate to reduce life expectancy. That is to say, the pattern of life expectancy for the Pond 3 colony represents a simpler case due to light predation, whereas at Pond 2 the life expectancy curve is complicated by the greater tendency for younger insects to be caught by birds.

### Maximum life spans

Although the recapture data do not allow the construction of reliable life tables for females, it is interesting that at Ponds 1 and 3 the maximum survival exceeded that for males. There is here some evidence that the biological life span of female *I. elegans* is greater than for males as two females which survived 45 and 42 days were both mature andromorphs when first captured. The addition of five days for teneral and *violacea* stages would give a maximum life span of 50 days and 47 days respectively for these females. However, the longest surviving males were under observation for 39 days and were green when first captured. The addition of a further 3 days to allow for teneral and early green stages would give a maximum survival of 42 days.

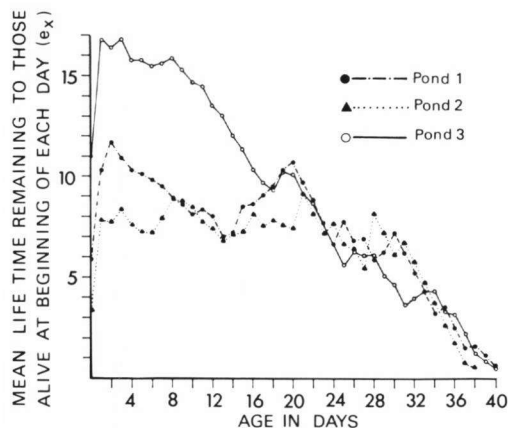


Fig. 3. The age-specific life expectancy for three populations of male *I. elegans*.

### LOCAL MOVEMENTS AND DISPERSAL

Relatively very little work has been reported on movement and dispersal in zygopteran dragonflies. The colonies in Dunham Park were studied in order to throw some light on the movement of individuals in the vicinity of the ponds. It is generally assumed in the literature (e.g. CORBET, 1962; MOORE, 1964; BICK & BICK, 1961) that teneral and immature imaginal dragonflies leave the neighbourhood of water until a maturation process of specific length has been completed. At the end of this time, which commonly ranges from two days in *Calopteryx splendens* (Harr.) (ZAHNER, 1960) to 30 days in *Lestes sponsa* (Hans.) (CORBET, 1956), the return to water is made. The recapture data for *I. elegans* at Dunham Park indicate consistently that many individuals show little or no tendency to move away from water during the sexual maturation process. In 1970 for example, out of 46 males which were marked when teneral and subsequently recaptured, 25 were recaptured at the waterside once or twice within four days of being marked. Other individuals do, apparently, appear to move away from the breeding site soon after emergence, only to reappear after several days or even weeks have elapsed. A large proportion are never seen again after the first occasion of capture and we must assume that some of these, at least, have moved permanently to other ponds; many others have undoubtedly died. *I. elegans* is, therefore, very variable in its flight activities when a young imago, and must be contrasted with other species of Zygoptera which demonstrate a 100 percent dispersal from water soon after emergence.

As far as can be determined from the present observations, *I. elegans* shows no territorial behaviour such as has been reported for *Calopteryx virgo* (L.)

(ZAHNER, 1960), *Calopteryx maculatum* (Beauv.) (JOHNSON, 1962) and *Hetaerina americana* (Fabr.) (BICK & SULZBACH, 1966). The two latter writers agree with earlier authors (KELLICOTT, 1895 and WILLIAMSON, 1923) that *H. americana* is an unusual dragonfly showing a high persistence at water. They further suggest that males of *H. americana* spend the night very near water. In these two latter respects *I. elegans* is closely allied to *H. americana*. As all individuals of *I. elegans* were marked uniquely and a record was kept of the sector in which they were marked and recaptured, it was possible to draw certain conclusions regarding the local movements and dispersal.

#### Local movements within the colony boundary

In order to obtain a detailed and fully comprehensive picture of the movements of individuals within the colony boundary it would be necessary to spend much time tracking individuals for days at a time. The other aspects of this study precluded such a possibility, but it is considered that some important conclusions may be reached using these results. Each insect which was recaptured at least once was classified according to its recapture history at the sectors of each pond (Fig. 4). The 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. These results were used to place individuals into one of four classes:

- (1) Those always caught in the same sector.
- (2) Those only moving to one adjacent sector.
- (3) Those only caught in two (but not adjacent) sectors.
- (4) Those caught in three or more sectors.

These observations were carried out in 1965 at Ponds 1 and 2 for the period May – September and in 1970 at Pond 1 for the month of June. The results are presented in Tables II and III. It must be emphasised that these results only provide a rough measure of mobility within the colonies, as many individuals only recorded from a single sector probably made some movements into other, possibly distant, sectors of the colony area. However, it seems clear from these results that most individuals do not show random movements within the colony area. If they did so, an insect would probably be more likely to be captured in a different sector than the one in which it was previously seen as they are potentially highly mobile, but this was not so. Most of those insects that were recaptured in a different sector from the one in which they were originally marked were taken in adjacent sectors. Furthermore, although many individual damselflies were captured three or more times, only 38 (from a grand total of exactly 1000) were recorded as visiting three different sectors, and none was observed to visit more than three sectors. A total of 600 individuals from the grand total of 1000 were always recaptured in the same sector in which they

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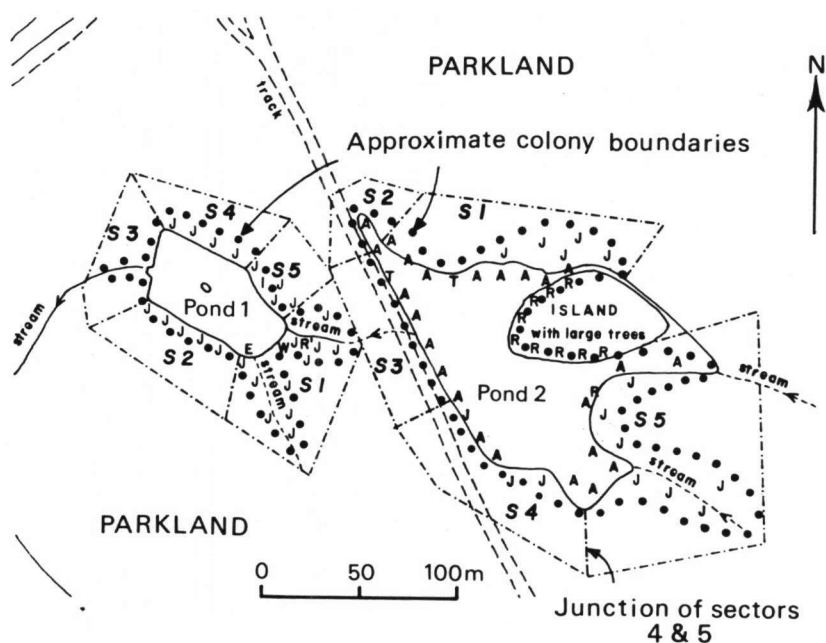


Fig. 4. Map of Ponds 1 and 2, Dunham Park, Cheshire, showing sampling sectors, approximate colony boundaries and the dominant waterside vegetation. (S1 = Sampling sector 1; S2 = Sampling sector 2, etc.; - J = *Juncus* spp.; A = *Acorus calamus*; - R = *Rhododendron ponticum*; I = *Iris pseudacorus*; - E = *Eleocharis palustris*; R' = *Nasturtium officinale*; - T = *Typha latifolia*; W = *Epilobium hirsutum*)

were first marked. In comparing the data from Ponds 1 and 2 it must be remembered that the sectors of Pond 1 were much smaller than the sectors at Pond 2 (Fig. 4) and it is, therefore, to be expected that more individuals would have changed sectors at Pond 1 than at Pond 2.

#### (1) Pond 1

Local movements within the colony boundary were studied in 1965 and 1970 and it may be seen from Tables I and III that the two years' results are, on the whole, very consistent. Both sexes show the same very uneven distribution, strongly preferring Sectors 1 and 2. However, Sector 4 was very much more frequented by both sexes in 1970 than in 1965, although it had not obviously

Table II

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 for a given pond, year and sex)

Sectors and combinations of sectors																	Totals
	1	2	3	4	5	1 2	1 3	1 4	1 5	2 3	2 4	2 5	3 4	3 5	4 5	1 2 3	
Pond, Year, Sex																	
1, 1965, ♂	30	39	0	2	5	36	0	4	9	1	3	19	0	0	2	0	163
1, 1970, ♂	59	41	0	22	3	66	1	11	9	4	13	5	2	2	11	1	261
1, 1965, ♀	7	26	0	0	1	13	0	0	1	0	3	1	0	0	2	0	56
1, 1970, ♀	14	17	2	19	3	13	1	3	3	1	4	2	1	0	1	0	88
2, 1965, ♂	80	0	42	50	37	1	20	6	10	1	0	0	4	6	32	0	294
2, 1965, ♀	31	0	18	39	13	1	10	0	4	1	0	0	5	1	15	0	138

Table III

Local movements within the colony boundaries: percentages caught in single sectors and combinations of sectors. (Data from Table II)

	Pond 1 (1965)		Pond 1 (1970)		Pond 2 (1965)	
	♂	♀	♂	♀	♂	♀
% always caught in same sector	46.6	60.7	47.9	62.5	71.1	73.2
% only moving to one adjacent sector	29.5	28.6	35.3	21.6	19.7	21.7
% caught in only two (but not adjacent sectors)	15.9	7.1	12.3	11.4	7.5	3.6
% caught in three sectors	8.0	3.6	4.5	4.5	1.7	1.5
	100.0	100.0	100.0	100.0	100.0	100.0
Sample sizes	163	56	261	88	294	138

changed in that time. Sector 3 was almost totally avoided in both years, probably because it was practically devoid of fringing vegetation except short grasses. There is some indication that females are apparently less mobile than males. If, as seems likely females of *I. elegans* resemble other Zygoptera in visiting water primarily to mate and oviposit, the regular appearance of the same individual in the same sector may indicate a geographical or topographical memory.

## (2) Pond 2

The distribution of individuals was less uneven than at Pond 1. Sector 2, being heavily shaded and with little open water, was almost completely avoided by both sexes, but the other sectors were well frequented. The high percentage of insects remaining in a single sector suggests that many individuals of *I. elegans* do not move much more than 100 metres from their emergence site. The results for Pond 2 show only a slight tendency for greater mobility of males than females.

### Dispersal-movement between ponds

The only attempts at quantitative assessment of dispersal of *I. elegans* which have been traced are those of MOORE (1954, 1964). The study of the *I. elegans* colony at Dale, Pembrokeshire (PARR, 1965) failed to reveal any evidence of dispersal from the four linked ponds although samples were obtained from other ponds in the area.

In July, 1968, a short mark-recapture experiment was carried out on an *I. elegans* colony at Gunkel Pond (Nat. grid ref. SM 818 047), Dale, Pembrokeshire. In the period 17-21 July, 184 (106 male; 78 female) individuals at Gunkel Pond were marked with cellulose paint. A green phase male marked on 17 July was recaptured in the blue-green phase at Watwick Pond, which is about 600 metres away from Gunkel by the shortest route. This was the only specimen of the Gunkel population which was recaptured away from the colony area, although four ponds within 1.8 km. of Gunkel were sampled in attempts to locate marked insects.

I am indebted to Mr T.M. Stokes (pers. comm.) for a record of a solitary andromorphic female of *I. elegans* (unmarked) on the tip of Dale Point, Pembrokeshire (Nat. grid ref. SM 825 052) on 24 July, 1968. A thorough search of the area suggested that the nearest possible breeding site for this individual would have been the pond at Gunkel mentioned above; this is about 1.2 km. distant by way of the coastline. It is significant that this specimen was sexually mature and that it was unaccompanied by other dragonflies. MOORE (1954) in his study of dispersal of the anisopteran dragonfly *Sympetrum striolatum* (Charp.) and *I. elegans* in the Scilly Isles states that the latter species appears to disperse much less far from its breeding areas than the former. The maximum distance he records *I. elegans* away from its nearest breeding site was about 360 metres for a single individual.

Table IV summarises the observed movements of *I. elegans* individuals between Ponds 1 and 2 at Dunham in 1965. Despite the closeness of the two colonies (about 35 metres at the nearest point; the open water of the two ponds was only 60 metres apart) very little movement between the colonies was detected. Only about 103 individuals (1.5 percent) out of a total season's combined

estimated population of 6746 were likely to have moved from one pond to the other. These results correlate well with the data obtained for the local movements of individuals at each pond, and suggest that many individuals move only very small distances throughout their imaginal lives. The small numbers recorded as moving from one pond to another precluded the use of the method of IWA0 (1963) for estimating total population exchange.

Table IV  
Movement between Ponds 1 and 2 at Dunham (1965)

<i>Movement from Pond 1 to Pond 2</i>		
	♂	♀
(a) Total individuals caught in season at Pond 1	359	187
(b) Total observed to change from Pond 1 to Pond 2	8	7
(c) Total season's estimated population at Pond 1	1018	1018
(d) Total estimated to move from Pond 1 to Pond 2 (bc/a)	22.7	38.1
<i>Movement from Pond 2 to Pond 1</i>		
	♂	♀
(a) Total individuals caught in season at Pond 2	877	601
(b) Total observed to change from Pond 2 to Pond 1	10*(9)	4
(c) Total season's estimated population at Pond 2	2270	2440
(d) Total estimated to move from Pond 2 to Pond 1 (bc/a)	25.9	16.2

\* Including one individual which returned to Pond 2. Total season's combined estimated population = 6746. Estimated total of individuals changing ponds = 102.9 (1.5%).

When the populations at Ponds 1 and 3 were studied in June, 1970, 793 males and 441 females were marked at Pond 1, and 326 males and 155 females were marked at Pond 3. Only a single individual (a blue-green male) out of the grand total of 1715 was detected changing ponds, although the ponds are but 270 metres apart. This individual was first captured at Pond 1 in Sector 2 on 10 June and was subsequently recaptured, still in the blue-green phase, at Pond 3 on 13 and 15 June.

Observations on the Dale peninsula, Pembrokeshire and at Dunham Park indicate that all age classes of both sexes may move away from one breeding site

to another, and, therefore, all age groups may be involved in the colonisation of new breeding areas as the species remains sexually active into old age. Most of the standing water on the Dale peninsula represents irrigation ponds constructed in recent years. The fact that these have been rapidly reached and colonised by *I. elegans* (ahead of other zygopteran species) shows the importance of the wandering activities of a small percentage of individuals.

With the foregoing results in mind it is possible to classify the common natural flight movements of *I. elegans* in the following manner:

(1) Short flights (few centimetres to several metres) at the water's edge or otherwise within the area occupied by the colony. These flights are particularly concerned with feeding, mating, oviposition and minor disturbances. (The only long flights at water were observed on releasing newly marked specimens: occasionally, if released carelessly the insect would fly out of sight and fairly high, sometimes over land, or sometimes over water. These flights were clearly unnatural in the sense that they probably never normally occur).

(2) Inconspicuous wandering (a haphazard type of movement characterised by short flights, often in various directions; MOORE, 1954) of both immature and mature individuals of both sexes. This type of movement is apparently only indulged in by a small percentage of individuals, but is, nevertheless, of great importance in allowing the formation of new colonies.

There seems to be no evidence to indicate a general movement away from water soon after emergence, nor is there evidence for any form of true, orientated migratory flights.

## GENERAL DISCUSSION

*Ischnura elegans* is in many respects a remarkable zygopteran. It is probably resident in all vice-counties on the mainland of the British Isles and is present on many British islands. It is widespread in Europe and Asia, and very closely related species occur over much of Africa. There is ample evidence that *I. elegans* is exceedingly adaptable, being able to exist in a wide range of habitats (LONGFIELD, in CORBET et al., 1960). Of great significance in relation to the success of *I. elegans* is that weather conditions are far less limiting than for other species of Odonata that commonly co-exist with it in Britain. A full range of activities may be observed in dull and cool weather, when, for example, *Coenagrion puella* and *Enallagma cyathigerum* will not fly. It shows an apparent cline in voltinism from the Scottish Islands to the Rhône delta in France (AGUESSE, 1961; CORBET et al., 1960; PARR, 1969, 1970).

In several other respects, *I. elegans* does not conform to what seem to be more general zygopteran characteristics. It is generally stated (e.g. CORBET et al., 1960) that the first part of adult life in dragonflies is spent away from water and that dispersal is the first action of the recently emerged imago. In fact, this

is probably true for most dragonflies, but many individuals, perhaps the majority, of *I. elegans* do not leave the waterside during their maturation period. *I. elegans* is capable of copulation after only 3-4 days of imaginal life, and it seems that, usually, males mature slightly faster than females (PARR & PALMER, 1971). *Pyrrhosoma nymphula* (Sulz.) was found to have a maturation period away from water of 9-15 days (CORBET, 1952) and *Lestes sponsa* spent from 16-30 days away from water (CORBET, 1956). However, *Calopteryx splendens* matures even more rapidly than *I. elegans*, as ZAHNER (1960) reported that the return to water occurred after only two days. The north American *Argia moesta* (Hagen) studied by BORROR (1934) spent between seven and 14 days away from water after emergence. There is clearly a very wide range of maturation times in the Zygoptera, as in species that hibernate as imagines (e.g. the European *Sympecma fusca* (Vander Lind.)) the reproductive period does not begin until the spring of the year following emergence (CORBET, 1962). Those individuals of *I. elegans* that were not recaptured at water on the days immediately following marking and first capture as teneral often reappeared several days to weeks later. In these cases it is difficult to be sure if they were overlooked when sampling or whether they were temporarily absent from the colony area. *I. elegans* contrasts with many other species of dragonflies, and Zygoptera in particular, in that the female is frequently seen at water. In fact, females may occur at water as frequently as males, but their lower and faster flight, and the cryptic colouration of about two thirds of the individuals may result in this sex being underrepresented in the samples. Also unlike the females of many other species, females of *I. elegans* are rarely molested by males. They are rarely seen to mate and are only occasionally sexually attacked; oviposition and feeding are usually undisturbed by males (PARR & PALMER, 1971). The copulation time of *I. elegans* appears to be the longest recorded for Odonata and frequently lasts longer than three hours and sometimes as long as five hours (KRIEGER & KRIEGER-LOIBL, 1958). The females of *I. elegans* always oviposit unattended by males and the *in tandem* position has not been observed in this species.

Thus, it appears that *Ischnura elegans* is very distinct behaviourally and ecologically from other coenagrionids which have been studied in detail. It would be interesting and informative to know in which ways other temperate and tropical species of *Ischnura* closely resemble *I. elegans* in their ecological and behavioural characteristics.

#### ACKNOWLEDGEMENTS

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