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SURVIVAL RATES, POPULATION DENSITY AND PREDATION IN THE DAMSELFLY, ISCHNURA ELEGANS (VANDER LINDEN) (ZYGOPTERA: COENAGRIONIDAE)

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Populations of *I. elegans* (Vander L.) were studied during 1965, 1966, and 1970 by means of the capture-recapture method at three ponds in Dunham Park, North Cheshire, England. The results seem to suggest that neighbouring imaginal populations between which there is little interchange may each have their own specific survival rates, which may be largely determined by the geographical features, vegetation and specific predators, and which are not directly related to the numbers of imagines present.

INTRODUCTION AND METHODS

During a comprehensive study of the population ecology of *Ischnura elegans* (Vander Linden) (Zygoptera: *Coenagrionidae*), interesting relationships were noted between survival rate, population density and predation of the imagines. The populations were studied by means of the capture-recapture method and the insects were marked with cellulose paint, using coded systems of spots on the wings to allow each marked specimen to be identified individually (PARR, GASKELL & GEORGE, 1968). This part of the work was carried out at three ponds in Dunham Park, north Cheshire, England, in the years 1965, 1966 and 1970. These habitats have been described by PARR & PALMER (1971). Ponds 1 and 2 were sampled at average intervals of 3.5 days in 1965. Pond 3 was sampled at average intervals of 2.6 days in 1966. The sampling in 1965 and 1966 extended throughout the flying seasons. In 1970 the populations at Ponds 1 and 3

were studied for the month of June only, and sampling was carried out at average intervals of 2.0 days and 2.1 days for each pond respectively. The mean sampling intensities (\bar{p}) (an estimate of the proportion of the total season's population captured) for both sexes were obtained by noting for each individual, the number of times it was caught (A) out of the number of times it was known to be available for capture (B) (excepting the first and last times of capture). Then \bar{p} was estimated from

$$\overline{p} = \Sigma A / \Sigma B$$

Table I Mean Sampling Intensities (p) of <i>Ischnura elegans</i>						
Year and Locality	Male	Female				
1965 Pond 1	p = 0.3468	0.2727				
1965 Pond 2	0.3115	0.2764				
1966 Pond 3	0.4243	0.2380				
1970 Pond 1	0.1740	0.1070				
1970 Pond 3	0.2881	0.1000				

The method of analysis used to estimate the mean season's survival rate for each colony was that of FISHER & FORD (1947). It has recently been shown (MANLY, 1970) that the Fisher and Ford method performs fairly satisfactorily in obtaining average survival values under the type of conditions of survivorship and sampling intensity occurring in this study. As survival is known to be age dependent in *I. elegans*, with tenerals having a much higher mortality rate than post-tenerals, the method of MANLY & PARR (1968) was used for estimation of population size. As the recapture rate and, therefore, sampling intensities for females were so low in 1970 (Table I) it was decided not to estimate other population parameters for the female populations. In order to obtain the highest possible sampling intensity in 1970, Ponds 1 and 3 were sampled by both authors simultaneously, whereas in previous years only one person worked in the field.

RESULTS

In 1965, when the populations at Ponds 1 and 2 were sampled it was found that the estimated population sizes were related to the linear dimensions of the ponds with which the colonies were associated. Also, survival rates and hence the mean lengths of life were inversely proportional to numbers in the colonies and sizes of the ponds (Table II). When the population of *I. elegans* was sampled at Pond 3 in 1966 it was found that the result was consistent with that of the 138

previous year in the sense that a very small pond supported a small population which had a high survival rate. This suggested that survival rate might in some way be associated with colony size and, therefore, further sampling was carried out in 1970.

The 1970 results are also summarised in Table II. It is noticeable that the

Year	Pond No. and Pond Size	Daily survival rate	Mean length of life in days	Max. ob- served surv. in days	Total est. popn. size	Largest single popn. estimate	Hirundines present (% of sampling occasions)
1965	1 55m x 24m	0.8958	9.1	39	1018.3	301.5	Frequent*
1965	2 165m x 114m	0.8724	7.3	38	2270.1	564.7	Frequent*
1966	3 45m x 21m	0.9234	12.4	39	218.4	105.0	Occasional*
1970	1 55m x 24m	0.8979	9.3	23+	1537.3	1328.0	66.7 (10/15)
1970	3 45m x 21m	0.9278	13.5	25+	601.6	561.0 [‡]	21.4 (3/14)

 Table II

 Population data for Ischnura elegans (males)

Actual numbers and dates of occurrence not recorded.

Maximum possible observed length of life was 30 days as observations were only carried out in June.

Almost certainly an over-estimate.

mean daily survival rates were extremely similar at Pond 1 for the years 1965 (0.8958) and 1970 (0.8979). Furthermore, the survival rates recorded for Pond 3 in 1966 (0.9234) and 1970 (0.9278) were also very similar. However, soon after sampling started in 1970 it became clear that the population densities were very much higher than they had been at Pond 1 in 1965 and at Pond 3 in 1966. This observation was supported by estimates of total population size for June 1970 and the estimated population sizes for the 1965 and 1966 seasons. The large population estimates obtained each sampling occasion for 1970 and the sampling intensity estimates are also strikingly different from those obtained for the same ponds in 1965 and 1966.

The maximum observed survival for individual insects was 39 days (Pond 1, 1965), 38 days (Pond 2, 1965) and 39 days (Pond 3, 1966). Thus, there is no evidence that the observed differences in mean survival rates are related to maximum longevity. The recorded maximum longevity at Ponds 1 and 3 in 1970 is respectively only 23 and 25 days, as observations were only carried out from 1 - 30 June.

DISCUSSION

Detailed meteorological data for nearby Manchester Airport indicated that the months of May – September 1965 were very similar to those of 1966, and that weather differences could not be used to explain the differences in survival rates noticed in those years. The weather in June 1970 was exceptionally warm, sunny and dry but these unusual conditions did not result in survival rates for the respective colonies being different from those of 1965 and 1966.

Other ecological factors apart from weather may be important in determining the survivorship and mean length of life in different colonies. Pond 3 is very sheltered in a deep hollow and is surrounded by mature oak trees (*Quercus robur*) and tall bracken ferns (*Pteridium aquilinum*), whereas Ponds 1 and 2 are exposed especially to the prevailing westerly winds. This factor may be important, as on several occasions teneral *I. elegans* were seen impaled on, or crushed by *Juncus* spikes at Ponds 1 and 2 during windy weather.

Predation may also seriously influence the survival of imagines. Spiders (*Tetragnatha* spp.), heteropterans (*Gerris* spp.), wasps (*Vespa* sp.) and birds have been observed as predators on both teneral and post-teneral Zygoptera at Dunham. The hirundines *Hirundo rustica*, *Riparia riparia* and *Delichon urbica*, and also the swift *Apus apus* are the most likely predators to have a marked differential effect on survival. They were seen to take Zygoptera high in the air (tenerals making their maiden flight) and low down near to the water's edge and over the open water. In this connexion it is interesting to note that tenerals, which are particularly liable to attacks from birds, showed much higher mortality rates than mature insects at Ponds 1 and 2, while at Pond 3 the difference was less apparent. The rarity of bird predation at Pond 3 (Table II) seems to have been due to the small size of the pond and the high banks and trees surrounding it, whereas at Ponds 1 and 2 the birds had a much larger area for free flight while feeding and drinking.

It is likely that populations of I. elegans at Ponds 1 and 3 in 1970 were at least five times as large as those at the same ponds in 1965 and 1966. More casual observations at Pond 2 in 1970 also indicated that the population of I. elegans was very greatly in excess of the 1965 number, and that, in all probability, a capture-recapture study would have been impracticable because of the large numbers. At present no explanation can be suggested to allow interpretation of these large population changes in relatively unchanged habitats. It is clear that populations of I. elegans may fluctuate to a considerable extent in numbers of imagines, even though there is no evidence that predation levels alter and it is known that imaginal survival rates are unchanged in what appears to be a stable environment. These results seem to suggest that neighbouring imaginal populations between which there is little interchange may each have their own specific survival rates which may be largely determined by the geographical features, vegetation and specific predators, and which are not directly related to the numbers of imagines present.

The large imaginal population increases at Pond 1 between 1965 and 1970, and at Pond 3 between 1966 and 1970 suggest a change in larval survival rates, but it has not been possible to relate this to any possible ecological factors such as nutrition, predation or weather. It is also possible that a specific factor operating sometime after 1966 resulted in ovipositing females being much more successful in depositing full egg batches.

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