

only three days have been far from convincing, because for most of this period the worms were in a dying condition, the prospect is now much more satisfactory, because worms are often more lively after they have been maintained *in vitro* for more than a week than they were on the first day after their removal from the liver. From a nutritional point of view the medium used is very imperfect; but its enrichment holds further promise of extending the period of survival *in vitro* of *Fasciola hepatica*, and providing a sound basis for physiological experiments.

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<sup>1</sup> Dawes, B., "The Trematoda" (Camb. Univ. Press, 1946).

<sup>2</sup> Stephenson, W., *Parasitology*, **38**, (3), 116 (1947).

<sup>3</sup> Gatenby, J. B., "Biological Laboratory Technique" (Churchill, 1937).

<sup>4</sup> Van Cleave, H. J., and Williams, C. O., *J. Parasit.*, **29** (1943).

<sup>5</sup> Stephenson, W., *Parasitology*, **38**, (3), 123 (1947).

### Seasonal Regulation in British Dragonflies

It has long been recognized that the reproductive stages of different species of dragonflies tend to be restricted in incidence, each being characteristic of a given season. During the period 1950-53, the life-histories of several British species were studied with the view of determining the principal ecological factors responsible for their seasonal regulation.

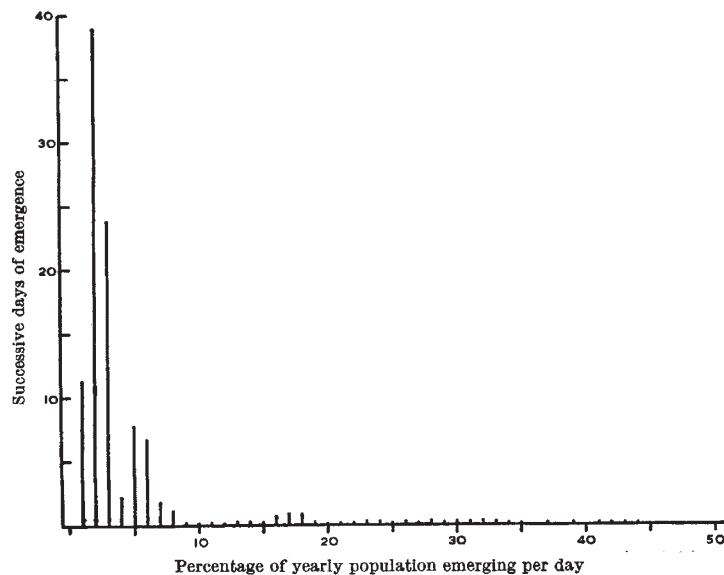


Fig. 1. Time-frequency distribution of adult emergences in a population of *Anax imperator* during 1953. Emergence began on May 25 and finished on July 7

In the Emperor dragonfly, *Anax imperator* Leach, it was found that, although larval populations showed a wide measure of temporal variation, yet emergence was restricted regularly to a period of about forty-five days each year, lying between mid-May and mid-July. The first fourteen days of adult life were spent away from water; after this, when sexually mature, adults returned to the aquatic habitat for reproduction. Oviposition extended from late June to early September. Adults did not survive the summer. The eggs hatched in about twenty-four days and

larvæ were half-grown (c. 24 mm., instar 11) by October, after which low temperature prevented further development. In the following April growth was resumed, and the final larval instar (c. 50 mm., instar 15) was entered in August, approximately one year after hatching of the eggs. A diapause occurred in the final instar, and morphogenesis was suspended until diapause development had been completed in the autumn. This did not take place until the temperature had fallen below the threshold permitting metamorphosis. In this way it was assured that final instar larvæ embarked upon metamorphosis simultaneously, as soon as conditions became favourable in the spring. Thus, the temporal variation accumulated during the long period of larval development was effectively erased in the final instar. Ecdysis, which directly succeeded metamorphosis, was closely synchronized, more than 90 per cent of the annual population of adults emerging within the first ten days of the emergence period (Fig. 1).

In this life-history the synchronization of emergence can be seen as a direct consequence of the diapause in the final larval instar. Recognition of this causal relationship means that species with a time-frequency pattern of emergence resembling that of *A. imperator* may be expected to feature diapause in the final instar and vice versa. This expectation has been confirmed in *Pyrrosoma nymphula* (Sülzer)<sup>1</sup>, the only other species of which the emergence curve is known throughout the flying season. Dragonflies typified by these two species have been termed 'spring' species, in contradistinction to 'summer' species in which a diapause, if present, is located elsewhere in the life-history. In summer species the final larval instar is usually entered in the year of emergence and, since growth is uninterrupted at this stage, larval variation finds expression in the emergence curve, which is temporally dispersed. Although not invariably the case, summer species usually emerge later in the year than spring species, since they have at least one extra instar to complete before commencing metamorphosis.

This ecological classification has been found to hold good throughout the British dragonflies, of which approximately half are spring and half are summer species. It corresponds with recognized taxonomic affinities at a generic level but shows departure when families are considered.

It is likely that the principles of this classification apply generally where there is a biological demand for rigorous seasonal regulation, and comparative treatment of other insect groups may throw an interesting light upon the colonization of temperate regions

and upon the evolution of different types of life-history.

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<sup>1</sup> Corbet, P. S., *J. Anim. Ecol.*, **21**, 206 (1952).