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THE PRESENT STATUS OF WORK ON THE ECOLOGY OF AQUATIC INSECTS AS SHOWN BY THE WORK ON THE ODONATA[1]

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For a measure of ecological work on aquatic insects in general we will use as a yardstick the present status of our knowledge of the Odonata or dragonflies. This group is more nearly ready for ecological study than are other orders of aquatic insects because it is small in number of species and these are conspicuous so that their description is farthest advanced; also we are personally familiar with the dragonflies and the literature in this field. The size of our problem is further reduced because the small amount of ecological study on Odonata has been limited almost entirely to areas in Europe and North America.

Before proceeding further we wish to point out that one other and more restricted group of aquatic insects has received more study than have the Odonata. This is the family Culicidae, the mosquitoes and their relatives, which as early as 1879 were shown by Sir Patrick Manson to be the carriers of filaria worms. With the discovery in 1898 by Sir Ronald Ross that mosquitoes carried malaria and the further discovery two years later that yellow fever was transmitted by mosquitoes, this group of insects has had more intensive study than has any other group of insects of equal number of species. Because of its direct bearing on human welfare the mosquitoes have had all the forces of medical entomology brought to bear on them. Students of aquatic insects in general would do well to study the methods of research developed by

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men in medical entomology. Several recent publications give methods of culture, of population study and of control. (Peterson, 1934, 1937, and Needham, 1937).

But to return to Odonata: About 3,000 species of dragonflies have been described for the world fauna which count ranks them as a small order of insects. That many beetles have been described in America north of Mexico. Dragonfly species are usually distinct enough from near relatives to be easily described. However, we find a few widely spread forms which can be broken up into subspecific groups. The taxonomic problem at this point becomes difficult as a careful study of subspecific forms has value in direct proportion to the amount of cytological study and of the field study of these forms. Unfortunately for the larger aquatic insects these cannot be crossed and bred in a bottle as can many small flies. Further, in the case of predator insects such as Odonata we lack the extra specific characters which Kinsey, working on Cynips, found in the species of host oak, type of gall and in characters of the alternate generation. Nevertheless, students are already recognizing, but so far not describing, physiological, geographic and hybrid forms of Odonata. We cite two or three such problems:

Didymops transversa (Say) is common on cold spring-fed hill streams about Ithaca, New York, but at Raleigh, North Carolina, this dragonfly thrives on warm muddy ponds. Neither E. B. Williamson nor I could find any morphological differences between specimens from these very diverse environments. Are we dealing here with physiological species? In the Zoological Museum at Ann Arbor is a series of Macromia from the White River, Arkansas. This series of several hundred specimens is a mixture of two described species and an almost equal number of intermediate forms. Are the intermediate specimens hybrids? On the Wabash River in Indiana, no intermediate forms occur; the same two species on the Wabash are always distinct. A careful study of some western dragonflies show a plains form, an intermountain form, a Sonoran form and a Pacific Coast form. This type of distribution is that usually labelled geographic. All of these taxonomic problems are now facing the museum men who in the past have been limited to the study of dead insects. What catalogue name the museum taxonomist will ultimately concede to the student of living insects for such types of living aggregations of interbreeding individuals has not as yet appeared. Kinsey has called them species. At this point we recommend the reader to Kinsey, "The Origin of Higher Categories in Cynips," 1936, and to Dobzhansky, "Genetics and the Origin of Species," 1937, and Anderson, "The Species Problem in Iris," 1936.

After naming his species the next great problem facing any field entomologist whether a student of land or of water insects is that of the population count. This is not a problem peculiar to aquatic entomology but is one of the more difficult problems facing all economic entomologists. The usual winged insect is an active animal which classes all moving objects larger than itself as possible enemies. Insects tend to avoid the census taker. The entomologist reporting an outbreak cannot assure his chief in Washington that he has not counted the same insect twice or even three times. Until entomologists can develop the technique of a fairly accurate census of insects in the field we will not be able to handle entomological problems statistically. Our mathematics of population will be too dependent on sampling which is something difficult to divorce from the desires of the sampler. Or just as bad, statistical studies may be based too much on laboratory populations. (See Snedecor, 1937.)

As Odonata are predators they occupy the peak of a food pyramid as defined by Elton (1927). Thus in general the individuals of any species in a limited area are not numerous as compared with the individuals of insect species on which they prey. In a small area dragonflies may appear numerous because the same conspicuous individuals fly constantly back and forth on the same beat. The only population study of value is that by Borror (1934) on *Argia moesta* Hagen, a common stream dragonfly of this region. In his study of Argia by a system of marks placed on their wings Borror was able to show the proportions of the two sexes, the sequence of color forms as individuals matured and to give a general idea of the total number in the area studied. C. B. Wilson (1920) attempted estimates on ponds at Fairport, Iowa, by counting the number of exuviae of nymphs at sampling stations.

The number of eggs laid by any species of dragonfly is unknown. Various estimates on partial data have been made. C. B. Wilson's studies on the Bureau of Fisheries' ponds at Fairport, Iowa (1920) are the best. This is data which will probably be difficult to obtain for the larger Anisoptera, but perhaps can be had with some accuracy for the Zygoptera which can be reared in large cages, if these are placed in the bright sunshine.

Females of such could be caged with males and the eggs deposited actually counted. This, then, could be checked against ovarian egg-counts of virgin females which might prove to be the only count needed. Until we get the basic data of sound population counts and of reproductive ability we will be unable to apply mathematical formulae accurately to ecological problems. On its face it appears to be difficult to count insects that fly as well as do Odonata, but Borror's studies of Argia and all field observations indicate that the majority of the aquatic Odonata (some tropical forms are not aquatic) live as adults in very limited areas. This is especially true where water is in small or discontinuous ponds.

In Odonata and in all aquatic insects one of the basic limiting factors in distribution is the selection of the place of oviposition by the female. The structure of the odonate nervous system and casual observation indicate that the dragonfly is probably eye-minded. On this assumption the place for the eggs is probably selected through the sense of sight. Many female dragonflies will attempt to lay eggs on a wet automobile top or in ponds and reservoirs of crude petroleum. Only a multiplicity of field observations on the habits of particular species will define egg-laying habits. The literature at present contains only casual observations which too often are on egg-laying sites that in some way are unusual. As compared with the much more exact knowledge of oviposition in the codling moth and other pest insects our knowledge of odonate habits is crude in the extreme. Such observations on the selection of habitat by the female which are vital to any study of ecological distribution have not as yet been put on even the simplest statistical basis.

After having been deposited, the eggs of many dragonflies are subject to parasitization by the minute wasps of the family Mymaridae which can fly to them if laid above the water, or can swim to them when deposited in the water. Casual observation indicates that these are especially parasitic on the eggs of dragonflies which inhabit the desert type of pond that contains water only during the spring and early summer. Life history problems of this type could be worked out on the numerous small ponds of our glaciated area.

We have little, if any, knowledge of whether small fish or other aquatic predators eat dragonfly eggs. Eggs of many species of Anisoptera are scattered in the water in June and July when the broods of small fry are just off the nest. Except for some insectivorous birds and a few predaceous insects, insect eggs in general are not often attacked by predators.

The ecological distribution of dragonflies depends first on the flying adult which selects the new territory for hunting and egg deposition. The flying adult is aerial and not aquatic. The finer distribution of the species within the general aquatic habitat may depend more specifically on the behavior of the larva which is truly aquatic. The newly hatched larva may burrow in the mud or the sand of the bottom, may burrow in loose trash on the bottom, may cling to vegetation, or cling to rocks at any one of several levels. In a few species (Archilestes) the larva may even swim rather freely as do the darters and fish that lack an air bladder. We have little data as to whether larval distribution is a response to degree of light, to touch, to temperature, to currents or to varying amounts of gases or other solutes. Probably it is not often a matter of food.

With the great amount of field work on Odonata we are just beginning to get fair data on the seasons of flight. Wesenberg-Lund, of Denmark (1913), gave us our first extensive diagrams of seasons of flight. His form of diagram has been adopted in this country by E. M. Walker, C. F. Byers, the present writer and others. There is considerable casual evidence that species of dragonflies, particularly the one-brooded spring and early summer forms, are ready for emergence but do not emerge until some certain water temperature is reached. Even such simple data have not been collected on the common species, though it could be had by the use of a pocket thermometer.

To do all the things suggested so far, the species of dragonfly must be positively identified, whether in the egg stage, in one of a dozen larval stages or in the adult stage. As already stated the taxonomy of the egg stage and of larval stages is hardly begun. We now know the grown larvae in approximately half of the species north of Mexico, but we have only fair descriptions of the early or first stages of less than 20 of the 365 species for this area. For several years the writer has been collecting from entomological literature the known complete life histories of insects, those which give the length of each of all the stages, and certain other data. Of American dragonflies we have only two or three such life histories. These species have been painstakingly reared by Professor P. P. Calvert and his student, Miss Lamb. (Calvert, 1929, 1934; Lamb, 1925.) Culture methods are summarized in the recent volume, "Culture Methods for Invertebrate Animals," edited by Professor Needham and sponsored by Section F. of the A. A. A. S. The usefulness of such work will depend on ample and exact illustrations of the various stages.

When we come to the food of dragonflies we have a few good papers based directly on stomach contents; one on Hawaiian species by Warren (1915) and the work of C. B. Wilson on dragonflies on the fish ponds at Fairport, Iowa, in 1920. Field observations have been brought together by Hobby (1933 and 1936).

In the matter of animals that eat Odonata we have a great many odds and ends of records in the literature on fish foods. The first important contributions in this field were made in Forbes' floating laboratory on the Illinois River in the early part of this century. The best bibliography of this literature is that by Gersbacher in the American journal, "Ecology" for July, 1937. Concerning animals which eat flying Odonata we have only the occasional published records of field observations. The present writer has just completed a manuscript which summarizes the data of the U. S. Biological Survey up to 1925 on dragonflies found in the stomachs of birds. Little of this material could be determined to species but it raises innumerable questions such as why certain species of birds take Odonata regularly while others closely related do not. It shows throughout the close relationship between the nature of the food, its abundance, and the size, structure and habits of the bird.

Concerning the actual ecological distribution of dragonflies we have many excellent lists of the dragonflies found in specific types of bogs, marshes, streams, ponds and the larger lakes. These are ecological data of a sort. Probably Professor E. M. Walker's papers on Canadian dragonflies deal more regularly with environmental conditions of the various species than do the writings of other American odonatists. I know of no paper which deals conclusively with the actual limiting factors of distribution as checked by experimental work of any extent.

No paper has appeared which deals with the ebb and flow of a dragonfly population over a period of years. In the

E. B. Williamson library on dragonflies, which is deposited in the Zoological Museum of the University of Michigan, are his detailed notes on the species of Odonata and their relative abundance each season over a period of more than twenty years as found flying on a button-bush woods-swamp (Vanemon Swamp) near Bluffton, Indiana. This is the best set of records we know of but they have never been organized or any part of them published. They show great fluctuations in relative abundance of species and apparently corroborate the writer's (Kennedy, 1922, p. 332) findings at Put-in Bay, Ohio, that gravid, fertilized females must fly long distances (one to five or more miles) and then must oviposit in any water available, where if unfavorable the species may exist one or more years then disappear.

This brief review of our knowledge of one of the most interesting groups of insects shows how little is really known concerning the lives of the less economic species. With the other aquatic insects in North America, the mayflies, caddisflies, stoneflies Hemiptera and Coleoptera less is known as in these groups even the taxonomy is in poor shape and little is known of geographic distribution.

The lack of knowledge of the distribution and habits of aquatic insects in North America can be laid partly to the fact that this area is so rich in undescribed species; the majority of men interested in insects have been tempted or even compelled to help describe new species. American insects are a biological gold mine. A graduate student at Ohio State University in two summers collected 2,000 species on the campus which is a flat city park. Many were new to science. This tremendous job of cataloguing has to go on before physiological and particularly before ecological work can be done with precision. Research on insects is no longer an amateur's job. Knowledge of insects has made amazing strides in two fields, that of medical entomology and that of agricultural entomology. In both fields large research funds have been available. Individual projects of study and control in the hundred thousand dollar level no longer cause comment and two projects, that of the European corn borer and that of the fruit fly in Florida have been operated in the ten million dollar level. In the United States and Canada are employed between 1,000 and 2,000 college trained men in research on insect pests. With the recent realization of the necessity of conservation in its various forms we can anticipate more funds for studies of aquatic biology. Social pressures will force more funds into these fields of research.

Some of the most advanced ecological research being done at present is that by economic entomologists on various of our farm pests. Out of these lines of research are beginning to emerge general biological principles which help in the control of pests and aid in the prediction of serious outbreaks.

As far as I know the majority of American Odonatists are mostly interested in problems of taxonomy and of geographic distribution. Probably in order to make specific advances in the knowledge of the physiology of aquatic insects we will have to turn to men trained in the techniques of economic entomology. Peterson's recent volumes reviewing insectory methods and apparatus (1934, 1937) show us the great variety of types of research now being carried on by economic entomologists. Such men trained in the study of habits and in the techniques of experimental zoology could show us how to handle the problems of the ecology of aquatic insects. Too much of the work to date on aquatic insects has been done on a few specimens of a species by one man on a single table in the corner of some poorly equipped laboratory. The economic entomologists, if given funds, could operate with the large scale techniques developed in recent years by state and federal entomological staffs.

We append to this review a bibliography of key books and articles especially those with methods and good bibliographies of use in this subject.

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