The Distribution and Relative Seasonal Abundance of the Indiana Species of Enallagma (Odonata: Agrionidae)

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Enallagma is a cosmopolitan genus of agrionid dragonflies in which about 96 nominal species or varieties have been proposed or placed by one or another author. Six of these, three of which are synonyms, belong to other clearly distinct genera and 26 others appear to be synonyms or names of races not deserving specific rank or separate consideration. Kennedy (1920) has further subdivided the genus, erecting six genera, but these are not generally recognized by other authorities, most of whom are inclined to consider the approximately 70 species as a single unified group.

The geographical ranges of the different species of Enallagma vary greatly in size—many species, some from regions where the fauna is rather well known, appeared to be quite limited in distribution, (one or a few adjacent states or similar areas in other parts of the world), others occur over wide areas—the major portion of a continent or more. One species, *cyathigerum* Charpentier, the type of the genus, is circumpolar in the northern hemisphere. It occurs in the British Isles, throughout the continent of Europe and across central Asia to China and as far south as Tibet and Kashmir but appears not to have been recorded from Japan. In America its range extends from Alaska to Newfoundland, southward to Indiana in the east and to Mexico in the west.

Although the genus is best represented in the Americas, especially in the Nearctic Region, about 24 species are known from the eastern hemisphere. Only one species occurs in Europe. About 16 species are known from Africa, most of them from South Africa or the Abyssinian region although species have been described from the Congo and the Cameroons, and one occurs in the Mediterranean coastal area. In addition to *cyathigerum*, seven other species are known from Asia and adjacent islands. These include two species from Japan, one from China, one from India based on a single female type specimen and of doubtful distinctness, one said to be "widely distributed through south Asia including Ceylon, India and Burma", another from India, Ceylon and Java and one from the Maldive Islands.

Three species occur in northern South America (Colombia and Venezuela) and two others have distributions extending into that continent—*civile* ranging from southern Canada to Colombia and *novaehispaniae* (sometimes considered a subspecies of *coecum*) from Mexico to Brazil. Two species (*eiseni* and *semicirculare*) are found in Mexico and two (*coecum* and *truncatum*) in the West Indies. *Doubledayi* occurs in the eastern United States and the West Indies, *cardenium* in Florida and the West Indies, and *praevarum* has a range extending from

Oklahoma and California into Mexico; all other (28) species of the genus are confined to areas in North America north of Mexico.

Of the 33 species occurring north of Mexico, five (*boreale, carunculatum, civile, cyathigerum* and *ebrium*), are transcontinental, three (*anna*—Ore. & Dak. to Ariz.; *clausum*—Br. Col. & Ont. to Nev. & Kans. and *praevarum*) are western, and the remaining 26 may be considered to be eastern although several of them extend westward to Kansas and Oklahoma. Thirteen species are limited to the Atlantic coastal regions, and another (*doubledayi*) appears to have been taken west of the Appalachian Mountains (Ohio) only once. All of the transcontinental and the eastern species except those confined to the coastal area and *doubledayi* have been taken in Indiana.

The season of flight (or period of adult life) of a species of Odonata is usually expressed by giving the earliest and latest dates. Wesenberg-Lund (1913) gave rather extensive diagrams of the seasons of flight for the Danish species and several American authors have used his form of diagram. Williamson (1917) summarized the seasons of flight of Indiana Odonata by thirds of months and his data for the Anisoptera were used by Kennedy (1928) in making a diagram of seasonal distribution.

There have been few population studies of the Odonata. Almost all references to the abundance of any species consist of such words as "rare", "common", "very abundant", "not rare", etc., and are purely subjective with the observer, although in most cases, they probably are accurate statements of the conditions. Wilson (1920) estimated the relative abundance of 15 different species around fish ponds by gathering and counting nymph skins at intervals of two weeks during the summer. Valle (1926) deplored the lack of any standard method of measuring or recording abundance of insects and proposed two standardized scales of seven degrees each, one a "local faunistic scale of frequency" and the other a "local faunistic scale of abundance." The first is based upon an area of observation ten kilometers square and varies from one occurrence in several years of observation (very rare, "*rarissime*") to general occurrence throughout the area every year (very common, "*frequentissime*"). The second is based on an area of 50-100 meters square and has a graded scale varying from one individual (very few, "*parcissime*") to more than 50 (very abundant, "*copiosissime*") in the area. This system seems not to have been used outside of Finland and certainly will need some modification for use in this country where collecting is less intensive and the average size of the usual unit of distribution in lists (the county) is much greater than ten kilometers square (about 38 square miles.) Borror (1934) marked individuals of *Argia moesta* in stations scattered along a river for about 700 yards and in an adjacent farm during two summers and made calculations of the population based upon "the relative number of marked individuals recaptured on successive days, with allowances made for shifts in population due to movements in and out of the area and to death and emergence."

Records of almost all Odonata collected or observed in Indiana since 1900 have been preserved in the note books of the late E. B. Williamson and of the author. These rather extensive records appear to be sufficient to provide some measure of the relative seasonal abundance of the different species in the state. The records for the species of Enallagma have been tabulated and the accompanying chart (Figure 1) shows the relative abundance of the different species throughout the season.

The records of captures (or observations) were tabulated by thirds of months and the time-frequency graph for each species was constructed by plotting the frequency for each third at the mid-point (5th, 15th and 25th of the month, respectively) of the third on the time axis.

The records are based upon collections made from 1900 to 1940, inclusive, except that *piscinarium* which is known from Indiana only from the male holotype collected in July, 1898, is included in the chart. However, there are no records of specimens of Enallagma taken in 1918 and 1923. The greatest number of species recorded for any one season is 13 and the average number recorded per year over the 41-year period is about 7⅓. No species is recorded for all of the 39 years for which species of the genus are listed; however, *antennatum* is recorded for 36 years, *exsulans* for 35 and both *civile* and *signatum* for 32. *Cyathigerum* has been found in only six years, *boreale* in eight, *divagans* in nine and both *aspersum* and *basidens* in 12. However, *basidens* was first found in the state in 1929 and has been collected every year since that time.

The number of collections rather than the number of specimens taken has been used in the tabulations because the numbers of specimens collected are not recorded in the notes for the years before 1908 as well as for the obvious reason that specimens are usually taken because of the rareness rather than the abundance of a species.

It is probable that the records tend to be weighted in favor of the rare species, both by selection of collecting places and by failure to collect specimens of the common species on many occasions when they were seen. These selective tendencies are overcome somewhat by other factors—the first by the collection of the more numerous species quite frequently during collecting trips not planned especially for Odonata and the second by the habit of both Mr. Williamson and the author of taking at least one specimen of every species found at each locality where collections were made.

Our species fall into three groups upon the basis of the season of flight—the spring forms (*boreale, cyathigerum,* and *divagans*) which are found on the wing from late May to early July, the early summer forms (*ebrium, hageni* and *traviatum*) which fly from May to the end of July, and the full season forms (the remainder of the species, except *piscinarium* for which there is insufficient information to indicate seasonal range) which are found as adults from May throughout the summer—to the end of August, into or through September, or even, in the case of *civile,* into October. There appear to be three peaks of abundance; the first which is the least distinct is in the middle of June,

the second which is very distinct and can be seen in almost all species occurs early in July, and the third which varies somewhat in the different species occurs late in August or early in September. Walker (1941) and other authors have noted "two periods of emergence" for certain species of Odonata.

The present abundance of *basidens* in Indiana relative to that of the other species is probably about three times that indicated in the

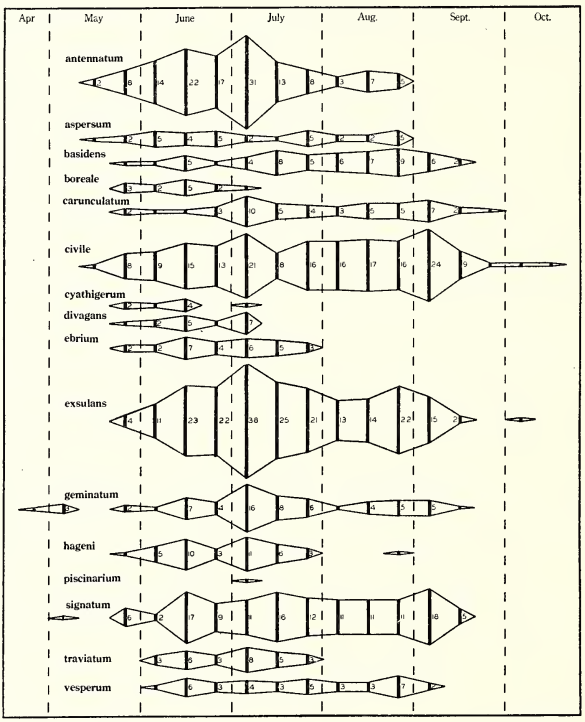

Fig. 1. The range of the flight season (or period of adult life) and the relative seasonal abundance of the species of Enallagma in Indiana. Collections made from 1900 to 1940 inclusive were tabulated by thirds of months and the graphs constructed from the resulting frequency distributions. Numbers near the bars in the graphs indicate the frequency of collection of each species in each third of a month; where no number is given the frequency is one.

chart. This species was first found in the state in 1929 but has been taken every year since that time and its frequency of occurrence and abundance as noted in the field appears to be almost, if not entirely, equal to that of *antennatum*, *civile* or *exsulans*.

Upon the basis of geographical distribution the Indiana species of Enallagma may be placed into three or four groups. *Boreale*, *cyathigerum* and *ebrium* are northern, transcontinental forms which reach or

approach their southern limits in Indiana. All of them are early season forms and comparatively rare in Indiana but are more abundant northward. *Antennatum, aspersum, exsulans* and *hageni* are northeastern species, occurring in the upper Mississippi valley and eastward; *aspersum* and *exsulans* are found from Ontario and New England to Oklahoma and South Carolina, *hageni* from Alberta and the Maritime Provinces to Kansas and South Carolina but *antennatum* appears to be confined to the area west of the Appalachian Mountains and there are few if any records from states south of the Ohio River although it probably occurs there as it has been taken in counties along the Ohio in Indiana. Five of the Indiana species (*divagans, geminatum, signatum, traviatum,* and *vesperum*) are found throughout the East—in general, from Wisconsin, Michigan or Ontario and New England or the Maritime Provinces on the north to Oklahoma and Florida on the south. *Carunculatum* is found across southern Canada from British Columbia to Ontario and southward to California, Oklahoma and New Jersey, *civile* from southern Canada throughout the United States, Mexico, the West Indies and Central America into Colombia. The type of *piscinarium* was collected in Wells County, Indiana, and specimens are also known from New Jersey and Pennsylvania; New York records for this species may be authentic although the specimens upon which they are based were lost, but records of *piscinarium* from Oklahoma, Illinois, and Michigan are almost certainly erroneous. When *basidens* was first taken in Indiana in 1929 it was known only from Kansas and Texas. It has since been found in Missouri, Ohio, North and South Carolina and New York. That this species has actually spread over the eastern United States during the past fifteen or twenty years appears certain. Many of the localities where it is now found in abundance had been visited by experienced collectors of Odonata for many years before it was discovered, and it seems unlikely that it would have been missed had it been present previously. It was first taken at Lake Garrett (formerly known as Franz Fish Pond) in Wells County in 1932 when it was comparatively common (44 specimens taken). This pond was a favorite collecting locality for the late E. B. Williamson who had visited it more or less regularly season after season for almost 35 years before 1932. The author found *basidens* in increasing numbers for three or four years after its discovery in 1929 at ponds in southern Indiana where he had collected for five years previously without finding it. The South Carolina record is from a locality beyond the Piedmont, at the very edge of the coastal plain and it would appear that the species has spread entirely to the Atlantic seaboard.

Although there is some correlation between the geographical distribution of a species and its seasonal distribution and abundance in Indiana, this relationship is by no means constant. Two of the "spring species" (*boreale* and *cyathigerum*) and one of the "early summer forms" (*ebrium*) are distinctly northern in distribution but the third "spring species" (*divagans*) and one of the "early summer" species (*traviatum*) have ranges which extend farther to the south than to the

north of the latitude of Indiana; *hageni*, an "early summer" species, but somewhat more abundant than the others, has a range more or less similar (although it extends farther to the northwest) to those of three "full-season" species. *Civile*, the species with the greatest north and south spread in its range has also the longest seasonal range.

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