9. THE LIFE CYCLE OF INSECTS; GENERAL DISCUSSION.

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In preparing for a general discussion of so large and complex a subject as that of this symposium, two choices were open to me. For one, I might have tried to summarize, generalize, and reduce to fundamental principles as well as I could on the spur of the moment the data and inferences presented by the specialists who have entertained and instructed us by their remarks on the life cycles of the various orders in which they have specialized. The alternative choice was a presentation and brief discussion of a limited number of topics, too general to come within the divisions of our subject treated by my predecessors on this program, and of kinds to which, in my judgment, we ordinarily give too little attention. Whether rightly or wrongly, I have made this second choice, with the idea especially of pointing out deficiencies in our knowledge by way of suggestion to the younger entomologists who are in the line of succession to the problems which we of the passing generation have solved imperfectly, mistakenly, or not at all.

One of the most fundamental features of the life history of insects, with its innumerable variations more or less adaptive in character, is the necessary inference that all these fixed differences are predetermined in the protoplasmic composition and structure of the fertilized egg, each succeeding step in any life history following upon the preceding one by a physical necessity; and the further fact that in each order of insects—each insect species, indeed—this minute, invisible, and possibly indeterminable structure of the protoplasmic egg must have been passed down by inheritance virtually unchanged from an extremely remote ancestry. On the other hand, all the variations and differentiations which have arisen to distinguish species from species, family from family, order from order, in respect to the general course and the minor details of their life histories, must have made their appearance as variations and differentiations in the egg protoplasm, which exhibits at once a constancy in some lines and an instability in others which, taken together, have made evolution possible. This *constancy* we see illustrated by the fact that the average course of the life cycle in any insect species is virtually uniform so long as the external conditions affecting it are uniform. The average lengths of the egg, larva, pupa, and imago stages of a holometabalous species are the same in any given locality, season after season, if the seasons average alike in temperature, humidity, etc.; but the *instability*, nevertheless, of this same protoplasm is shown by the fact that individual variations in the details of life history appear among insects of the same species and variety, hatched from eggs laid on the same day, and kept continuously under identical conditions. In Doctor Shelford's unpublished experiments, pupæ of the codling-moth, formed on the same day from the same lot of larvæ and kept side by side under the same conditions until the imagoes emerged, have had pupal periods of 9½ days, 10½ days, and 12½ days in one series, and in another series of 10½ days, 11 days, 11½ days, 12½ days, and 13½ days, and so on; and another colleague, Mr. P. A. Glenn, tells me of 24 codling-moth pupæ formed on the same day and treated precisely alike, of which one gave the imago in 8 days, six gave imagoes in 9 days, ten in 10 days, six in 11 days, and one in 12 days. Still more significant are some of his data concerning the incubation periods of the *eggs* of the codling-moth, these varying from 12 to 15 days for a lot of 46 eggs laid May 5, from 8 to 10 days for 162 eggs laid June 3, and from 8 to 11 days for 118 eggs laid June 5, all being kept under like conditions. He has had, indeed, occasional instances of single larvæ of the first spring generation surviving as pupæ until the following spring, representing thus a one-generation variety of the codling-moth, although their brothers and sisters took the usual course of two or three generations in the year.

These individual differences in the sensitiveness of the egg protoplasm to the stimuli of development furnish, *if they are heritable*, abundant materials for the action of natural selection in fitting a species more exactly to its environment in respect to its life history, just as other kinds of variation make possible an improvement of its structural adaptations; and a study of these variations in life history, of their continued heritability, and of their advantages and disadvantages to a species by way of its adaptation to the various environments in which it is found, is just as necessary to a knowledge of our subject as is the corresponding study of visible variations of structure to a knowledge of the phylogeny of the insect organism.

One of the environmental conditions to which an insect may adjust itself by reason of this flexibility of its life history is its relation to its food-plant and to its competitors for food. Remembering that the prosperity of a plant-feeding insect is dependent on the abundance and continued growth of its food-plant, and that this plant, for its own best prosperity, must produce for its insect guests timely supplies in quantities which can be spared without actual injury to the plant itself, we see a mutual advantage to insect and plant alike if the draft on the growing plant shall be distributed over as long an interval as possible, in order that the product of continuous growth may go as far as possible to supply the demand. Obviously, the demand of a thousand insects delivered in one day might effectually bankrupt a plant which could honor the draft without embarrassment if it were distributed over a fortnight or a month; and this advantage to the food-plant would react, of course, to the advantage of the feeding insect also. There is thus a standing reward offered to every insect dependent for food on a living and growing organism, for establishing and maintaining an individual variability in its sensitiveness to stimuli such as shall lengthen the period of its depredation.

Of course, individual differences in the rate and the period of development of the insects of the same generation, and even of the same parentage, are not all due to variations traceable to the egg, but many are consequences of different individual exposures to stimulating or retarding factors; as a consequence of them all, (some original and some incidental), the effect of an infestation is diluted and diminished by an extension of its period, to the common advantage of the infesting guest and the infested host.

Furthermore, it seems possible that this depredation period may be shifted as a whole, so as to come earlier or later in the season, if competition with another species of kindred habit may be thereby evaded. If two species infest a food-plant at the same period, their joint number must be so limited, as a general rule, that their attack will not destroy the food-producing plant; but if they can come to succeed each other so that each shall have the plant for a time to itself, both may maintain a higher rate of multiplication without permanent injury to their common host; and individual variations in the length of the stages of the life cycle already referred to make this easily possible. If there is any initial difference whatever between the competing species as to the period of their attack, natural selection may do the rest, and even if there is not, mutation of habit may have the same effect. I happened, many years ago, upon an apparent instance of this kind, when I was studying the life histories of the so-called root-worms of the strawberry—larvæ of three species of chrysomelid beetles which devour the roots of the plant. One of these larvæ, that of *Colaspis brunnea*, begins its work in southern Illinois in early spring and continues active through June; another (*Typophorus canellus aterrima*) begins in June and continues into August; and the third (*Graphops nebulosus*) begins in August and continues active through the fall, hibernating, in fact, in the larva stage.

It is a significant fact that another species (*Graphops pubescens*) closely allied to the last and with a like distribution, but living on another food-plant, refusing, indeed, the roots of the strawberry and feeding only on those of the wild evening primrose, has a very different life history from its near relative, wintering as an adult instead of a larva, as does the strawberry species. There is here a suggestion of a possible shifting of the life history of the strawberry *Graphops* in a way to adjust its demands for food to those of its competitors. Of course, this seeming adjustment may have been a coincidence merely, and I do not know of another instance of the kind; but, on the other hand, I do not know that such instances have been sought. Most of our best life history work has been done on insects infesting the crop plants, where the natural reactions of plant and insect are so generally disturbed or annulled by the overpowering agency of man that we must look for clear cases of interlocking life histories of competing insects among those dependent on uncultivated plants; and here but little has been done.

The foregoing case may at any rate serve to illustrate the fact that for a full understanding of the adaptations of insects to their environment by way of their life histories, we must not study merely the separate species in their natural habitats, but must make local ecological groups our units for investigation, and inquire into the system of competitions, and adjustments and avoidances of competition, exhibited in their relations to each other. We have much reason to expect, indeed, that an insect association of long standing in a geographical area, or in a set of situations of fairly uniform character, will have come to make many internal readjustments—adaptations of one species to another in habit and life history, of each species, perhaps, to several others, of different stages of the same species each to the other, such that the whole association may avail itself to the best advantage of the resources for existence and multiplication offered to it by any environment. The strains and pressures of competition will thus be in some measure relieved, and an internal equilibrium of the ecological group will be reached which will smooth and steady the system of interactions within the association, to the general advantage of all its members. It seems to me quite possible that a single species of wide range may have become a permanent member of unlike associations in different parts of its area of distribution; may have had to adjust itself, consequently, to different systems of interaction with its associates; may have acquired local peculiarities of life history not to be understood until these internal systems have been studied and made out.

The subject is, indeed, delightfully complex—a challenge to the curiosity and ingenuity of the accomplished naturalist equipped with apparatus for exact experiments with variations of temperature, moisture, light, rates of air movement and evaporation, such that he can produce any desired combination of these natural factors of the insect environment and determine their separate and conjoined effects on the life cycle of any species which he wishes to study in detail.

An equipment of this description is invaluable in testing the inferences of the field observer and in detecting reactions to features of the insect environment which are obscured or lost in the complex of the natural system out-of-doors. By such a means we are beginning to account for some, at least, of the almost explosive outbreaks of insect multiplication in certain species, which we find peculiarly sensitive to meteorological conditions by which others are little affected. Doctor Shelford tells me, for example, as a result of his studies now in progress on the chinch-bug, that these insects, whose numbers fluctuate enormously in successive years, are extremely dependent on relatively high temperatures; that with optimum humidity, multiplication is very slow and breeding experiments usually fail at a temperature of 70° F. (a much higher limit than that of any other insect studied), but that with high humidity and high but variable temperatures like those of a hot, moist day in summer, breeding experiments are highly successful, and the rate of multiplication is almost unbelievably rapid.

I am beginning to hope that, by vivarium work and companion studies in the field, we shall be able soon to standardize our life history data so that we can describe the life cycles of insects, not primarily in unreliable units of time, so variable as to be perplexing, but in ecological units of temperature, humidity and the like, invariable for a species whenever and wherever it may be found. An example of such a standardization is furnished by the product of recent work on the life cycle of the codling-moth done by Mr. Glenn at a well-equipped orchard station in southern Illinois, to the effect that in normal seasons, when the sum of all mean daily temperatures which fall between 50° and 85° F. reaches 550°, the eggs of the spring generation of the moths will begin to hatch, and when these totals reach 1550° those of the second generation will hatch, and when eleven hundred degrees is added to this sum, the third generation may begin to hatch; but that if this last total of 2650° is not reached before September 10, there will be no third generation at all in that year; and these statements may be expected to hold good every year without regard to the character of the season or to differences of elevation or latitude. Dr. Shelford is now working out in the vivarium a scheme of corrections to be applied to this forecast whenever the humidity factor is practically important.

Our present method of describing life histories in days or hours for each stage or phase is, indeed, thoroughly illogical, for mere lapse of time has, of course, no effect in itself; it is only the dynamic content or accompaniment of the time unit, especially in temperature and humidity, which really signifies. We must find our unvarying ecological constants and make up our life-history calendars of these and not of the uncertain units of time which we now use simply because they are the most easily obtainable.

Perhaps we shall never know just how and to what immediate profit the holometabola were differentiated, but that the differentiation was a fortunate one for the future of insect life in the world is shown by the present great predominance of holometabola over ametabola and hemimetabola, and by the obvious advantages which they have in the struggle for existence. By their premature hatching from the egg before the characters of the adult have been laid down in the embryo, their larvæ are much more capable of adaptive modification for their life as larvæ than are young Orthoptera or Hemiptera, already virtually adult at birth, except as to size, sexual organs, and organs of flight. Hence we see, in the vast majority of cases, the holometabolous larva taking its own course in its own interest, quite regardless of the coming necessities of the adult, with the result that larva and adult have widely different ecological relations, belonging, indeed, to different ecological associations, and do not compete with each other in any way. As the closest competitors of an ametabolous insect are the members of its own species, the division of any species into two non-competing groups diminishes by a certain considerable fraction the dangers of this interspecific competition. On the other hand, the fact that the holometabolous insect must alternate between two quite different environments, one for the larva and the other for the adult, makes its failure to find either one a fatal catastrophe, requires the coincidence of two favorable environments, instead of the occurrence of only one, for its survival; but this danger is largely overcome by the remarkable development of instinct which leads the female adult to deposit her eggs at a place and time as favorable as possible to the success of the larva; and in the social insects it is of course much more than compensated by the solicitous care which the young of all stages receive from the mature.

I think we may also count the holometabolous insect as relatively fortunate in respect to its exposure to predaceous enemies, parasites, and contagious diseases. A grasshopper is endangered during its entire life cycle by the same kinds of destructive agencies—the same species of predators (except as it outgrows some of them), the same kinds of insect and other animal parasites, and the same bacterial and other fungous diseases—but white-grubs and May-beetles differ one from the other almost completely in these respects. The attacks of parasites and contagious diseases commonly increase in intensity with the length of time during which their victims are exposed to them, so that they are much more destructive in the second half of the insect life cycle than in the first; but in a holometabolous insect with unlike larval and adult habits and habitats, this period is divided into two unlike periods of disease or infestation, and there is no second half to either of the two.

The multiplication of seasonal generations in some species is a consequence of a high degree of sensitiveness to temperature and other developmental stimuli; and this may enable a species to push its range into colder latitudes than would otherwise be possible, giving it at the same time a capacity for multiplication in the milder latitudes far in excess of that of its single-brooded competitors and enabling it to take prompt advantage of seasonal conditions temporarily favorable and to rally quickly from the effects of those temporarily injurious. I surmise that the many-brooded species have, as a rule, had an experience of frigid or semi-frigid life—that of a glacial period, for example—during which variations towards a quick physiological sensitiveness to heat stimuli have been selected for survival. Entomologists are but just beginning to determine accurately the so-called physiological zero or threshhold of development of the several insect species, and have accumulated as yet too little precise knowledge of the temperature at which development begins and of the effects of differences of humidity in shifting this zero up or down to enable us to base our surmises on experimental evidence. There is an almost limitless field for interesting investigation open to those who have command of a good experimental equipment, and the entomologist who first carries through a seasonal series of experiments on the army-worm with its three annual generations in comparison with one of the single-brooded noctuids, both kept together under identical conditions for a study of their differences of reaction to ecological factors, will get some new and important results.

As I piece together, after a fashion, these few scraps and fragments of observation, interpretation, and inference which I am offering here, it seems to me that the general pattern which they suggest is that of a wide-ranging, open-minded survey of insect life as it is actually lived by these complex and variable creatures, in constant interaction with the still more complex and similarly variable system of objects and energies which together constitute the insect's world—that we need to study that world from the insect standpoint as its center, to realize as clearly as we can, by insight and imagination, what it would be to a beetle or a butterfly, a caterpillar or a grub, if it were endowed with our capacities of observation, analysis and inference; how and to what ends and by what means it would act upon that world and how and by what means its world would react upon it in turn; and what has been the history of the system of actions and reactions through the agency of which it has become what it finds itself to be. Except as we can approximate this ideal—in so far, that is, as we adhere in our studies to the merely human point of view—our perspectives must be distorted and our emphases wrongly placed, to the confusion and disappointment of our efforts to solve the intricate problems of insect life.

THE EXTERNAL ANATOMY OF ANTHOMYIA RADICUM Linn.*

(Diptera, Anthomyidæ).

By Howard L. Seamans.

CONTENTS.

The North American Anthomyidæ, though belonging to one of the largest and most important of the families of the Diptera, are nevertheless in very unsatisfactory condition from the systematic standpoint. The permanent work that has been accomplished on these flies has been concerned largely with the economic relationships of individual species, and, in this country at least, very little thorough work along taxonomic or morphological lines has been done. It is apparent that there is a real opportunity for systematic work in this group, and, as a preliminary step in this direction, the writer undertook a morphological study of *Anthomyia radicum* Linnæus, one of our most common species in this family, and this paper gives the results of this study.

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*Contributed from the Entomological Laboratories of Montana State College.