OBSERVATIONS ON THE LIFE HISTORY AND HABITS OF HYDROMYZA CONFLUENS LOEW., (DIPTERA).*

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During the past three summers the writer carried on some biological investigations in the vicinity of Douglas Lake, Mich., in the extreme northern end of the southern peninsula of that state. The work was done in connection with the University of Michigan Biological Station, the facilities of which aided materially in securing the data which form the basis of this paper.

Hydromyza, one of the several small genera belonging to the *Cordyluridæ*, has only one species (*H. confluens* Loew) reported for North America. This species is northern in its distribution and seems to have been reported only from New Jersey (Johnson, '04, p. 162) and Michigan (Needham, '08, p. 270). Needham reported it from Walnut Lake, in southeastern Michigan, and predicted that it would probably be found common about *Nymphaea* beds in the United States. In looking over the literature relating to this insect the writer was surprised to discover how little has been written about it. Aside from a brief, two-page paper by Needham ('08, pp 270-271), nothing seems to have been written on the habits or life history of this very interesting insect. It occurred in sufficient numbers to make possible the accumulation of a number of interesting facts relating to this species. The data presented in Needham's brief paper were tested and found to agree with the observations of the writer in almost every respect. Data merely mentioned by Needham have been worked out in more detail and a number of new observations were made. Unfortunately the writer has been unable to observe the method of oviposition and the younger larval stages have not been studied.

THE LARVA.

Food Plant.—*Hydromyza confluens* was found in connection with the yellow waterlily, *Nymphaea americana*, (Provancher) Miller & Standley. This is the form which has until recently been included under the name *N. advena* or *N.*

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advena variegata, but Miller and Standley ('12, p. 78), have shown that the boreal species has several distinct characters which separate it from the true *advena*, and they have raised Provancher's name, *americana*, to indicate this northern species. *N. americana* occurs in some abundance in the protected bays, in the beach pools, in the mouths of some of the streams, and in sphagnum bogs of the Douglas Lake region and the insects under consideration were correspondingly abundant. Needham ('08, p 270), reported this insect in connection with *Nymphaea advena*, but judging from his description and figures it seems very probable that the species in Walnut Lake was *N. americana*, rather than the true *advena*.

A careful examination of all the aquatic plants occurring in the immediate vicinity of the *Nymphaea* beds was made with the view of determining whether or not other plants were used as food. In no case did the larva occur on plants other than *N. americana*. The white waterlilies (*Castalia odorata*) were entirely exempt in spite of the fact that white and yellow waterlilies mingled in the same beds. In every case the evidence pointed to the conclusion that this insect is restricted to *N. americana* in the region studied.

The Gall.—The immature stages of this insect were found in the long, constantly submerged petioles of the yellow water-lily. A large number of plants were examined and in no case did they occur on any part of the plant other than the petiole. Furthermore they were confined exclusively to certain petioles, namely, those of the floating leaves. Special effort was made to determine whether or not larvæ ever occurred on the peduncles or on the petioles of the submerged leaves. Both were found to be entirely free from infestation. Although the writer has no data on the method of oviposition, the reason for this distribution on the plant seems apparent. Needham ('08, p. 270) suggested that "Probably the attack of the gall maker begins when the first leaves reach the surface in late spring; then they have their first opportunity to reach the proper place of oviposition by crawling down the stalk." The writer regards this as the most feasible explanation since it will be shown later in this paper that it is possible for the adult insect to pass under water by crawling on a supporting surface and that it actually does so of its own volition. The short and wholly submerged leaves of *N. americana* do not at any time reach the surface and since this is true there would be no opportunity for the female to deposit the eggs, hence the constant freedom from infestation. Furthermore, in the region of Douglas Lake, the flowers do not reach the surface of the water until in late July and in August, a date which is much later than the time of oviposition, and as a consequence they are exempt from the attacks of the insect.

The gall first becomes perceptible on the petiole as a slight, ovoid enlargement and can be detected by pulling the petiole between the fingers. Each gall is produced by one larva only and in no case is more than one larva found in a single gall. It is very probable that in the early stages the presence of the larva is not perceptible since this enlargement really occurs at a time when the larva is well toward maturity. As the time of pupation approaches the gall begins to turn brown, ultimately assuming a deep brown color, thus making it easy to detect. The shape of the exterior of the mature gall varies somewhat, usually appearing as an ovoid swelling, although it should be noted here that many of the galls do not increase the diameter of the petiole. The galls also vary in size to some extent, the length of those containing pupæ ranging from 6 to 9 mm. They are always longer than broad, the long dimension being in the direction of the long axis of the petiole.

The number of galls per petiole varies rather widely. Sometimes only one gall occurs on a petiole, but usually the number is greater. In a large series of observations the maximum number on a single petiole was found to be 14 and many of the petioles contained as high as 13. In one of the series of counts in which 45 infested petioles were examined, 7 was found to be the average number of galls per petiole. No relation was found to exist between the length of the petiole and the number of galls. It might be assumed that the longer petioles contain the larger number of galls, but this was not always true. Numerous instances were observed in which a petiole, six feet in length contained only two or three galls, while a neighboring petiole, three feet in length, contained 10–12.

Galls occur irregularly along the petiole and may be situated near the bottom, even in those almost six feet long. They may be distributed along the entire length of the petiole and well separated from each other, or they may be distributed in such a way that some are widely separated and others so closely placed that two or three may appear to be continuous.

The interior of galls containing pupæ, or half to full-grown larvæ, can be easily examined by removing the infested petiole from the water and holding it between the eye and the light. The cavities are not at all uniform in shape. Each has a slightly elongated central chamber and one or more side channels which are usually just large enough to contain the larva. The total space in the gall of a full grown larva is commonly three or four times as large as the larva itself. The size of the cavity represents the bulk of the food which the larva has consumed during its growth and since there is no connection with the exterior all of the excrement is deposited within the gall. The consumed matter, as indicated by the amount of excrement, does not seem to decrease much in bulk so that near the time of pupation the greater part of the gall is filled with a brown excreta which almost surrounds the insect. This brown excrement has much to do with the brown exterior which characterises these excrescences and renders them conspicuous.

The full-grown Larva.—The morphological details of the full-grown larva will be included in a future paper which is in preparation. Needham's paper contains a very brief description of the larva and presents some of the more important anatomical details.

Variation in Maturity.—An examination of the galls on a given petiole often showed differences in the degree of maturity and when the larvæ on such a petiole were extracted and examined it was found that they too were not all exactly of the same degree of maturity. In some cases part of the number had pupated while others on the same petiole were still in the active larval stage. It thus appears that some of the larvæ lag behind the others in development and the question arises as to how this fact is to be interpreted. It is conceivable that this might result from the deposition of eggs at different times by different females, but the writer, after examining a large number of such cases, is skeptical of such a possible interpretation and believes that in the majority of cases at least, all of the galls of a given petiole are the result of eggs laid at one time since, (1) although some of the larvæ lagged behind others in development, the differences did not seem to be sufficiently marked to warrant the conclusion that the eggs were deposited at different times, and (2) in some cases those lagging behind occurred in the middle of the petiole, while those towards the upper and lower extremities of the petiole developed at the same time, a condition which would not be likely to happen in case the eggs were laid by different females. The above evidence is not entirely conclusive but it seems to support the more feasible explanation, namely, that the eggs on a petiole are all laid at one time, and that the variation in the degree of development is possibly due to internal or external factors, probably the former since the external conditions seem perfectly uniform for all those deposited on a given petiole.

Activity.—Like many other dipterous larvæ, this gall maker is very sluggish. Specimens, removed from galls, showed only slow, squirming movements which were very ineffective so far as locomotion was concerned. The activities of these larvæ could be observed to some extent by holding an infested petiole between the eye and the source of light. The feeding activities appeared to be very deliberate.

Effect on the food plant.—As mentioned above, the first evidence of infestation is the presence of a slight, ovoid swelling at various places along the petiole. Later these swellings begin to develop a brownish color, ultimately becoming a deep brown. About this time or a little later the entire petiole loses its green color, takes on a yellow appearance, and shortly afterwards the entire leaf begins to turn yellow, showing signs of deterioration. During the last week in July and the first week in August of 1913 one could readily pick out the infested lilies by the yellowish leaves. This work of the larvæ leads to the decay of both leaf and petiole. The nature of the injury is simple. The larvæ affect the plant in two different ways: (1) The larva, as it eats out the internal cavity of the gall, severs the vessels which connect the leaf with the rootstalk, this alone being sufficient cause for the decay of the leaves. It was found that the heavily infested petioles deteriorated no more rapidly than did the slightly infested ones and that one larva is just as efficient as several in causing the death of the leaf. (2) These galls produce weak spots in the petioles so that wave action breaks them at the points of infestation. Leaves with broken petioles were found floating about early in the season before the galls had begun to turn yellow, but the greatest havoc from this cause was produced during the first week of August of the past year when the larvæ were pupating. At this time in one of the badly infested lily beds approximately 40% of the leaves were broken off and were floating about in a semi-decayed condition.

The possibility of other insects playing a part in causing this deterioration of the petioles and the change in the color of the leaves was taken into account and, while other enemies were present, it was possible to observe many leaves and petioles which were infested only by the larva of *H. confluens* and which showed the same effects as those which happened to be affected by more than one enemy.

All of the lily beds in the immediate vicinity of Douglas Lake were examined and the degree of infestation observed. There was considerable variation in this respect since some were only slightly infested while in others the percentage of infestation was as high as 50 or 60. None were entirely exempt. It was found that the heaviest infestation occurred in a lily bed which was located at the end of a point which formed one side of a protected bay and was thus exposed to the wind and wave action to a greater extent than any of the other lily beds. In this particular case the infestation was almost twice as great in this exposed lily bed as in another in the protected bay only about one hundred feet away. The infestation in the lily beds in the beach pools and the sphagum bogs, which are protected from the action of the wind and waves, was very slight. The writer is not prepared at the present time to account for this distribution, but merely gives the facts for this particular region, realizing that the distribution just described may not agree with that of other regions.

It thus appears that the larva of *Hydromyza confluens* is a serious enemy to *Nymphaea americana* since every petiole which contains even one larva is doomed. Three summers of work on insects infesting waterlilies in the Douglas Lake region has convinced the writer that, although there is a rather large number of species which attack this plant, yet *Hydromyza confluens* has only one rival for first place as the greatest enemy namely, the larvæ of *Bellura melanopyga*, one of the *Noctuidæ*, which also plays havoc in the lily beds.

THE PUPA.

The detailed description of this stage is reserved for another paper which is in preparation.

Position.—The position of the pupa in the gall is variable, the only constant feature being the fact that its long axis always lies almost or quite parallel to the long axis of the petiole. However, the position of the head and the caudal end is not at all constant since in some cases the head is up (towards the surface) and in others it is down (towards the root-stalk). In galls which are well advanced in development and contain pupæ this point can easily be determined from the exterior without breaking into the gall by noting the position of the *window*, a feature to be described later. When the window occurs at the lower end of the gall it is positive proof that the head of the full-grown larva or the head of the pupa is down; if the window is at the upper part of the gall, the head of the larva or pupa is up. In a series of observations in which 242 pupæ were examined it was found that 130 occupied a position in which the head of each was up and 112 in which the head of each was down. Other statistics of the same kind showed a similar result, namely, that the majority of the pupæ lie in the galls with the head towards the surface of the water.

The Window.—The window mentioned in the preceding paragraph is a very interesting and unique provision for the emergence of the adult and, as stated by Needham, is constructed by the larva immediately before pupation. It is circular in outline and only large enough to allow the passage of the emerging adult. In constructing this window the full-grown larva works towards the exterior of the petiole until it reaches the epidermis. Here it removes all of the surrounding tissue (exclusive of the epidermis) from a circular area which is destined to be the window so that the latter is composed only of epidermis. A circular incision, which extends around approximately two thirds of the circumference, is made along the periphery of this area. The remaining one-third is left intact and thus a circular lid, attached at one side, is produced. The attached portion always has a definite relation to the position of the pupa, namely, it is constantly on the side of the circumference nearest the caudal end of the pupa. The larva evidently constructs this circular incision by rotating the head through about 240 degrees, cutting the epidermis with the mandibles as it goes. Needham ('08, p. 270) in discussing this matter makes the following statement: "Just before transformation to the pupal stage the larva eats a hole out to the epidermis and returns to the center of the cavity; this hole is a passage of exit for the adult, which then has only to break through the transparent epidermal window to gain its liberty." One would infer from this statement that the window is opened at the time of the emergence of the adult by the rupture of the epidermis, but this is not the case. Also no mention is made of the fact that the epidermis is cut in any way. The evidence is conclusive that the operation of opening the window is not a mere rupture of the epidermal tissue since: (1) Very careful examination shows that a circular incision is actually made and that the translucent window is merely pushed open at emergence, (2) it is an easy matter to open one of these windows on a gall from which the adult has not emerged by either carefully inserting the point of a needle between the edges of the incision, or by splitting the gall and applying very slight pressure against the inside of the window, which in either case opens as a hinged shutter with the attachment constant in position, and (3) an examination of a large number of petioles from which the adults had emerged showed that in every case the window opened as a hinged shutter, the attachment of which always had the above described, definite relation to the body of the gall and to the pupa. If the opening of the window was a matter of rupturing the epidermis there would be no possibility of this constancy in the form of the opened window. It should be mentioned in this connection that the incision is not an absolutely continuous one, since a few minute portions of the tissue are left uncut and serve to hold the window closed up to the time of emergence. It is therefore possible, under average conditions, to determine from the exterior whether or not the adult has emerged. If the window is not loose around the edges the insect is still within the gall, but if the window is loose and gapes slightly it is very strong evidence that the adult has emerged. An exception to this rule may occur in a petiole which has been subjected to side to side strains such, as are produced by wave action, and the window has thus been broken open.

According to the observations of the writer, pupation occurs shortly after the window is completed and the pupa lies with the cephalic end in close proximity to the window. In some cases the pupa lay so close to the window that the movements of the adult in escaping from the puparium would have been sufficient to open it.

One of the characteristics of *Nymphaea americana* is the shape of the petiole. It is conspicuously flattened so that approximately one-third of the circumference is quite flat while the remaining two-thirds are very convex. For convenience in discussion these surfaces will be designated as the plane surface and the convex surface. On the former there is a median, longitudinal ridge. Needham's paper indicates nothing as to constancy or variation in the position of the window with reference to the two above-mentioned surfaces although he figures a gall with the window on the convex surface. The position of this window is variable, sometimes occurring on the plane surface and sometimes on the convex, but not in equal numbers and the writer was lead to make some observations on this point. Of 226 galls examined at random the window in 137 occurred on the convex side and in the remaining 51 cases on the plane surface. Various other counts not recorded in the above numbers showed similar results. Available data does not seem to offer an explanation for the predominance of the windows on the convex surface.

THE ADULT.

Broods.—Although the writer has no positive evidence as to the number of broods per summer, there seems to be the possibility of at least two. A few adults were observed about the *Nymphaea* beds during the first part of July, at least three weeks before the larvæ in the petioles were grown. The maximum appearance of the adults in 1913 occurred between August 1st and 6th. During the period, July 10–25, adults were very rare and it may be that this represents the interval between two successive appearances of the adults. Very few of these insects remained in the pupal stage after August

6th. Adults were very abundant during August 1–6, and it was a common thing to find numbers of them copulating.

Local distribution.—In spite of the fact that these insects have well developed powers of flight they are not found at any great distance from the waterlilies. They occurred ordinarily on the leaves and flowers of these plants and when disturbed made only short flights, seldom taking to open water or to shore. Only in rare instances were flies found resting on plants other than *N. americana.* When undisturbed they assembled in the open flowers or ran restlessly about over the lily leaves, making short flights where leaves were not contiguous.

Relation to water.—These flies are related to the water in several interesting ways. Although the emergence of the adult has not been observed in the field it seems safe to assume that when the adult emerges from the pupal stage it must of necessity push the window open and pass up through the water to the surface, either by crawling up the petiole, or by independent passage through the water, presumably the former. It was found that the flies emerged and came to the surface when the infested petioles of *N. americana* were brought into the laboratory and completely submerged in water. In many cases individuals which develop near the base of the longer petioles must, in emerging, come up through about five feet of water before reaching the surface.

It seems almost certain that the female deposits the eggs by going into the water and crawling down the petiole to the place where the eggs are deposited. Careful watch was kept on adults for periods of an hour or more at a time and none were observed to go beneath the surface in open water. If perchance an individual did alight on the surface it immediately took to wing again. Adults which fell on the surface of the water did not sink, but appeared to be supported mainly by the surface film. The fact that they may and do voluntarily pass under water was demonstrated when the writer observed a few individuals walk over the edge of the lily leaf, go under water, and travel on the lower surface of the leaf for short distances. None were seen to go down the petiole.

Experiments in which adults were submerged showed that under such conditions the flies apparently have a specific gravity less than water, and consequently they rise to the surface if opportunity affords. They stay below only by clinging to some submerged object. While under water a goodly supply of air clings to them in the form of a dense, silvery coating. When allowed to come to the surface they immediately lose the silvery coating and are apparently as dry as if they had never been in contact with water. Experiments, in which adults were subjected to forced submergence for varying lengths of time, showed that they can remain under water for several minutes without apparent detriment to themselves, due without doubt to the generous coating of air which surrounds them. Submerged individuals usually appeared uneasy and made vigorous effort as if seeking release. The ease with which they apparently resist wetting and the quantity of air which they take below with them make possible the mode of emergence and oviposition suggested above.

Relation to the Yellow Waterlily.—The adults as well as the immature stages have a definite and interesting relation to the yellow waterlilies. This relation will be discussed under two heads, (1) food relation, and (2) possible agents in pollination. Although each of these relations will be treated independently, it will be understood that such separation is purely artificial and also that both are operative at the same time.

(*1*). *Food relation.*—The time of maximum abundance of the adults coincided closely with the opening of the majority of the flowers and it was very evident that the flies were deriving food products from them. Flies swarmed in the newly opened flowers in great numbers, congregating between the petals and the stamens to the extent that often the interior of the flower was black with them. In the case of flowers which had been open only a short time the anthers were crowded in a compact mass under the edge of the expanded stigma or were just beginning to spread out in a radial fashion, while the petals had spread out widely, thus forming a cup-shaped flower and producing a space between the petals and anthers into which the flies crowded. Flowers frequently contained as many as fifty adults. They regularly disposed themselves as described above with the heads in close proximity to the base of the anthers. It often required a distinct shake of the flower stalk to disturb them and this proved to be an easy way to collect adults since one of these flowers could be cautiously thrust into a bottle and the inmates dislodged. This habit resembles a similar one described by Fulton ('11, p. 300) for certain *Diptera*, the adults of which also congregate in the flowers of a yellow waterlily. Later when the anthers became spread out the flies found better concealment beneath them.

The conspicuous assembling of flies in the flowers is indicative of some rather strong attraction which the latter have for the former and it seems safe to assume that the flies profit therefrom. Nectar is said (Lovell, '02, p. 205) (Robertson, '89, p. 122) to be secreted on the outer faces of the petals in *Nymphaea advena* and it is also probably true of *Nymphaea americana*. Therefore it is possible that the visits of the flies are induced in part by the presence of nectar which forms a source of food supply. Flies were observed in the flowers from the time of opening to the time when the flowering parts began to disappear.

(*2*). *Possible agents in pollination.*—The information that insects are found in connection with yellow waterlilies is not new since species representing several orders have been reported as occurring on these plants by Robertson ('89, pp. 122-123), Lovell ('98, pp. 60-65), Bembower ('11, p. 379) and others. Furthermore Elliot ('96, pp. 117-118) and others claim that flower haunting *Diptera* are of considerable importance in the fertilization of many of the flowers which are visited. It is claimed that *N. advena* may be self- or cross-pollinated (Bembower, '11, p. 379) and this is probably true also of *N. americana*. There is good evidence in support of the view that the insect visitors of yellow waterlilies (*N. advena* and others) may transfer pollen from one flower to another, or from one part to another on the same flower. The writer had occasion to examine large numbers of the adults of *Hydromyza confluens* and it was discovered that many were carrying the pollen of *N. americana*. Swarms of adults taken from flowers in which they had congregated showed that the great majority, and often all, of the insects were dusted with pollen. Very frequently pollen occurred so thickly over the body that the insect was distinctly yellow in appearance. Adults collected August 5–22, showed that pollen was being carried during this entire period. While it was not demonstrated absolutely that these flies carry pollen from one plant to another, the circumstantial evidence seems to point definitely to these insects as being at least one of the factors in the cross-pollination (and possibly the self-pollination) of *N. americana* and may be summed up as follows: (1) The coincidence of the blooming period of *N. americana* with the maximum appearance of the adults of *Hydromyza confluens;* (2) The large numbers of flies limited in distribution to the immediate vicinity of the lily beds; (3) The assembling of the flies in large numbers within the flowers when the latter have opened sufficiently to admit them; (4) The heavy loads of pollen which are carried by many of the flies and the almost universal presence of varying quantities of pollen on all individuals; (5) The continuous blooming of *N. americana* throughout the greater part of August, so that at any given time there were flowers in all degrees of maturity, a fact which eliminates a difficulty due to the possibility that a given flower is proterogenous; and (6) The behavior of the adults in preferring to pass from place to place by crawling and by very short flights (usually the former when possible) rather than by extended flights, which means a maxium of contact of the insect with the various parts of the supporting plant.

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