MIGRATORY HABITS OF THE MAYFLY, *BLASTURUS CUPIDUS* SAY

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Blasturus cupidus Say is somewhat better known in its early stages than many other North American mayflies. The full-grown nymph was described by Berry in 1903, while the egg and other stages are figured by Morgan ('11, '13), who also gives information regarding the life history. More recently the species has been the subject of a paper by Traver ('25), who gives details concerning the habits, food, etc., of the nymph.

The present paper gives an account of certain nymphal migratory movements scarcely considered in the papers cited, but which appear to be important, locally at least, in the general ecology of the species. Most of the observations on which these notes are based, were made during 1927, 1928 and 1929 at various localities in the province of Manitoba.

TYPES OF WATERS AND MIGRATIONS

In the area indicated, there are comparatively few small permanent streams, most of the permanently available water supplies being in the form of rivers and lakes. In spring, however, large additional areas are covered with water formed by the melted snow, and some of these seasonal bodies of water drain into the aforementioned rivers and lakes by means of small temporary creeks and ditches. In autumn and winter, when the water supply is lowest, the nymphs of *Blasturus cupidus* are to be found along the margins of the Red River, Assiniboine River, Lake Winnipeg, and doubtless many other portions of the Hudson's Bay drainage system. In early spring, when these bodies of water are suddenly expanded, there is an annual migration of the nymphs into the newly flooded areas. Not only do they move to the new margins of the permanent bodies of water, but in many cases they push up temporary tributaries to a very considerable distance from their winter habitats. For example, on April 3, 1927, large numbers of nymphs were observed in a temporary creek which drains into the Red River about 5 miles south of Winnipeg (Fig. 1). These nymphs were all actively migrating upstream, and the foremost individuals had already reached a point more than half a mile from the river, although the creek could not have been in existence more than a few days. On April 1, 1928, large numbers of migrating nymphs were found at approximately the same place, and a few had travelled as much as 100 to 150 yards farther. By April 7, nymphs were plentiful up to this latter distance, at which point the stream took its origin in a marshy area. They were also present in numbers throughout the lower portion of the stream, and were found to be still entering it at its confluence with the river. In 1929 the half-mile mark had been passed on March 31, although the creek

FIG. 1. Mouth of temporary creek at time of migration. Red River (ice-covered) beyond.

was very small and was covered with new ice which was 2 inches thick in many places. On April 2, nymphs were traced in numbers to a point (3/4 mile from the river) where the creek drained from a maze of shallow channels and pools.

On May 7, 1929, another temporary body of running water in the form of a roadside ditch draining into the south side of the Assiniboine River about 7 miles west of the Winnipeg city limit was examined. Nymphs were found to a distance of a mile from the river. At this point the ditch connected with other channels and marshy areas (Fig. 2) in which many nymphs might pass unnoticed.

Actively migrating nymphs have also been observed at Ponemah, on the east shore of Lake Winnipeg, the medium again being a roadside ditch which in this case drains into the lake. The latter was entirely covered with thick ice at the time when the observation was made (April 14, 1929) except at the point where the ditch entered.

In each of the districts indicated it is evident that not all the nymphs succeed in entering creeks and ditches. Those which do not find their way into these temporary tributaries keep close to the water's edge and thus reach new habitats as the water rises in the spring. When the water retreats some of them are left in small isolated lagoons and pools.

It is sufficiently obvious from many such observations that this spring migration is of annual occurrence in this part of Canada and is of comparable importance, perhaps, in the life history of the species with the annual migrations of many species of fishes. The writer is not aware of any records of exactly comparable movements by any immature insects. Traver ('25, p. 215), it is true, writing of the present species, makes mention of a migration of some of the nymphs into shallow water just previous to transformation. This, however, has nothing to do with the larger movements described above, which take place from 5 to 10 weeks previous to transformation, at a time when many of the nymphs are only half grown. Moreover, they are not migrating into shallower water, most of them being already close to the water's edge, but are merely moving into new quarters.

FIG. 2. Temporary marshes—the farthest point reached by migrating nymphs.

DURATION AND SPEED OF THE MIGRATION

In the localities indicated, migration begins as soon as the melting or bodily removal of the ice permits. In the case of the first-mentioned creek, migration proceeds actively while thick winter ice still covers the river. The increased volume of the latter lifts up the ice, leaving open water along the bank, and thus establishing continuity with the creek. The latter reaches its maximum volume early in April and then declines, but as long as it retains connection with the river, nymphs continue to enter it and proceed actively upstream. The latest date on which this has been observed is April 23, giving a migration period of about 4 weeks in this particular creek. The creek then becomes cut off at its mouth from the river, and various other portions dry up at approximately the same time, so that all migration ceases and the nymphs are confined to little separate pools.

Some attempt was made to discover the rate at which the nymphs travel up the creek. When kept in still water in the laboratory, they commonly swim at a rate equal to 85 to 110 inches per minute, *i.e.*, 425 to 550 feet per hour. Of course this rate is not maintained over long distances. On the other hand, swimming nymphs can make headway against a current which is flowing more swiftly than the above mentioned rate. Swimming, however, though the most frequent, is not the only means of progression during the upstream migration. Where the current is uncomfortably rapid, the nymphs crawl along the sides or bottom, and when it becomes still faster they proceed to the extreme edge of the stream and partially or wholly quit it, crawling and wriggling forward along the wet border. In this way even diminutive waterfalls can be passed, if not too high. In this creek, however, the nymphs are able to swim most of the way, and the foremost individuals appear to reach the headwaters about 7 days after quitting the river, an average of nearly 600 feet per day.

Specimens captured soon after their entry into the creek, and confined in vessels of still water, frequently continue to swim actively around the edge of the vessel for a day or two after introduction. Apparently they are somewhat gregarious in habit, and all tend to swim in the same direction, resulting in a continuous procession, each individual stopping to rest at intervals but the general motion continuing. Later, the nymphs become more quiescent and rest on the bottom or on weeds, making occasional short irregular movements of a non-migratory nature. For several days afterwards, however, the introduction of a current, as for instance the stirring of the water in a circular vessel, stimulates them to swim against it for a time.

In the field, the nymphs cease their migratory movements when they become confined in small pools or even before this period (at the Assiniboine River locality) and are then much less conspicuous, lying amongst algae and other vegetation.

It may be noted that there is considerable variation in the size of the nymphs at the time when migration takes place. Measured individuals were found to range from 4.5 mm. to 8.5 mm. in length (excluding the setae). In general, the larger nymphs are the first to travel up the creeks.

Nature of the Migratory Impulse

One of the most striking features of the annual migration in the creeks is the persistence with which each nymph travels against the current. As a result of this propensity, the presence of eddies in the stream is a considerable hindrance to such nymphs as encounter them, for, instead of travelling straight through, they turn so as to face the current, and are thus brought in a downstream direction. The same reaction is noticeable in captive specimens. If the water in a circular vessel be stirred, the nymphs, as already indicated, swim against the current and reverse their direction immediately when the direction of the current is changed. Similarly, nymphs were induced to pass through several feet of glass and rubber tubing against a gentle flow of water, and were then brought back to the starting point by reversing the direction of the current.

Loeb ('18, Chap. XIV) appears to doubt the existence of rheotropism (rheotaxis), at any rate as a widespread form of response, and shows that in some animals the habit of orientating themselves with the head upstream is due not to the current but to a phototropic stimulus, the position being maintained with regard to visible objects on the bottom, banks, etc., of the stream. It is obvious, however, that these considerations do not apply to animals which are actively *moving* upstream. Furthermore the *Blasturus* nymphs react to current in the dark as well as in the light, as has been found by simple experiments in a dark room. In the field they frequently migrate under ice which must cut off most if not all of the light. It seems evident, therefore, that the upstream migration is not a response to anything seen. On the other hand, genuine rheotaxis also fails to explain certain features of the movement, as for instance the fact that the nymphs keep on "migrating" when confined in still water. Also, the advance of the nymphs into newly flooded areas must be made in the absence of any directing current.

It seems to the writer that the most important factor in controlling the direction when in running water is to be found in the distribution of the weight and shape of the body. Dead nymphs were taken and subjected to a current which was then allowed to slacken. The bodies always came to rest with the heads pointing upstream, no matter from what angle the current was directed on them in the first place.[1] The anterior end is comparatively heavy, smooth and rounded, while the lighter abdomen with its rows of flattened gills and hair-fringed caudal setae offers greater resistance to the water. The

[1] Similar orientation of dead nymphs can probably be obtained with most species of mayflies. The writer has obtained similar results with the nymphs of *Siphlonurus*, *Baetis*, *Callibaetis*, *Ameletus*, *Ephemerella* and *Heptageninae*. The tendency appears to be less marked in some burrowing forms such as *Ephemera* and *Hexagenia*. In many other nymphs, *e.g.*, damsel flies, there is little tendency to lie in any particular direction.

nymph sinks through the water head first, and, as the current strikes it, the tail tends to be pushed downstream, as a parachute is blown out to leeward of a falling man. As soon as the anterior end touches the bottom or any projecting object its progress is checked and the upstream orientation becomes complete. A swimming nymph would react similarly to a change in the current as soon as it relaxed its efforts for a moment. Not infrequently in still water a nymph will be seen to swim close to the surface and then, relaxing, sink without effort to the bottom. In so doing the head end always sinks to the bottom first, as in the dead nymphs. It seems, therefore, that the reaction to current may be largely a mechanical one. Close observation of living nymphs at times when the direction of current is changed seems to confirm this view. The nymphs do not appear to orient themselves by muscular effort, but to be swept by the current into a head-on position. In the absence of such interruptions they tend to travel straight ahead.

It seems probable, therefore, that the spring migration is not in any way a tactic response, but is the result of an internal instinct working in combination with the physical structure of the animal. It remains to consider briefly the conditions under which the instinct becomes apparent.

When living in large permanent bodies of water, *Blasturus cupidus* appears to be chiefly a shore line species, seldom occurring at any great depth. The writer has noticed this, not only in the localities previously mentioned, but also at Jasper in the Canadian Rockies. Living under such conditions the nymphs are undoubtedly forced to perform a certain amount of seasonal movement, particularly in a country such as Western Canada where marked changes in water level occur during the year. In autumn, as the water recedes, they are compelled to retreat, a movement which must be continued due to the formation in winter of solid ice to a depth of several feet. In spring, on the other hand, the living quarters of the nymphs may be covered by water, within a few days, to a depth of 10 feet, causing the nymphs to advance over the newly flooded shore. Such movements may or may not have provided an evolutionary basis for the stronger impulse which carries many nymphs for long distances up the temporary streams already described.

It is probable that the food supply is an important consideration in causing the nymphs to seek entirely different habitats in the spring. In their winter quarters the bottom consists principally of mud or stones, with very little vegetable growth. Examination of the alimentary tracts of nymphs from these waters shows that they feed mainly on diatoms,[2] with an occasional copepod. Mud was present in all the alimentary canals examined. The great variability in the size of the nymphs in early spring may reflect the uncertainty or relative unsuitability of the food supply. Associated with *Blasturus* are *Heptagenines* and stonefly nymphs. Among the latter, the most plentiful are forms belonging to the genus *Isoperla,* and the writer has frequently found

[2] The following forms were noted: *Navicula, Cymbella, Surirella, Synedra, Meridion.*

the remains of *Blasturus* nymphs in their stomach contents. Doubtless *Blasturus* is also preyed upon by other insects and by fishes.

At the time of entry into the creeks, the latter have an insectan fauna which is apparently limited to *Corixidae* and certain water beetles, these having flown thither. No larvae or nymphs are present. Although comparatively barren when first formed, these creeks usually develop a growth of filamentous algae, etc., on which the *Blasturus* nymphs browse. As soon as this food supply is available, the nymphs cease to migrate, even in cases where free passage up the stream is still possible. It may be noted that nymphs which have been kept in shallow vessels with an adequate food supply through the winter show no migratory tendencies in the spring or at any other time. As the streams dry up and the water becomes restricted to pools, a rich fauna develops, consisting of such forms as *Eubranchipus*, *Lepidurus*, Odonatan nymphs and the larvae of beetles, caddis flies, Diptera, etc., all of which have developed from eggs laid in the same locality, *Blasturus cupidus* being the only form which migrates into these waters in an immature condition.

In addition to the benefits of a plentiful food supply and relative freedom for a time from enemies, there is perhaps an additional advantage in escaping from the edges of the rivers and lakes at the earliest opportunity. A few days after a passage into the creeks becomes possible, the ice usually breaks up and the shores are in many places subjected to a scraping and pounding that must be very disconcerting to the fauna of these habitats.

On the other hand, there are certain obvious disadvantages attached to life in the creeks and ditches. Probably the greatest cause of mortality is the drying up of pools before the time of transformation. Many nymphs at both the Red River and Assiniboine River localities are trapped annually in this way—in fact in a dry season only a comparatively small number of the larger hollows remain habitable until the time of emergence, *i.e.*, from the latter part of May until the middle of June in this district. The photograph in figure 3, though taken in August, shows the condition of pools which have dried up before the adults have emerged.

Further, it seems obvious that those mayflies which emerge at a long distance from permanent water will have a correspondingly diminished chance of laying their eggs in a suitable place. Ovipositing by individuals which have emerged from temporary waters has not been observed, but it seems certain that some at any rate find their way back to the permanent rivers and lakes which are the only available habitats for the nymphs during the rest of the year. Otherwise the migration into tributary and outlying waters would be suicidal, and the species would depend for its existence on such individuals as fail to find a way out of the permanent bodies of water.

In conclusion, attention may be drawn to the great range of physical conditions to which the nymphs are subjected during a comparatively brief portion of their lives. The rapid change from a muddy river to the melted snow water of a newly formed creek, for instance, must be sufficiently great. Once in the creek, the nymphs pass through areas where the water runs over manure piles, etc., apparently without discomfort. Three weeks later they may be inhabiting stagnant pools. Many of the latter are very shallow and are subject to great extremes of temperature. Apparently the nymphs can also survive for a time with a very small amount of water, for a pool which ap-

FIG. 3. Dry bed of a *Blasturus* creek photographed in August. Assiniboine River in background.

peared to have dried up entirely was found to contain living nymphs a few days later, after replenishment by rain. The ability to withstand such a wide variety of external conditions probably enables *Blasturus cupidus* to make its annual migration with advantage. A greater susceptibility to one or more of these physical factors may explain the failure of all other nymphs and larvae to exploit the considerable feeding grounds which are annually available in the form of temporary waters.

SUMMARY

1. There is an annual migration of the nymphs of *Blasturus cupidus* Say, in the Winnipeg region, into temporary creeks and connecting waters in the

spring. Some of the migrants travel as much as a mile from their winter quarters.

2. The migration is due to an internal instinct, but in running water its direction seems to be controlled by the shape and weight of the body.

3. As a result of the migration, nymphs are brought into an environment in which the physical and chemical conditions and the animal and plant associations are very different from those in which they have previously lived.

4. The advantages of the migration include a plentiful food supply and relative freedom for a time from predaceous enemies. The disadvantages lie in the physical conditions of the new environment, such as the frequent drying up of habitats, and the distance which must be traversed by the adults before they reach suitable localities in which to lay their eggs.

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