THE DISTRIBUTION OF CERTAIN INSECTS OF REVERSED BEHAVIOR.*

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The recent researches of Loeb, Holmes and other students of animal behavior as well as the work of various entomologists on the reactions of insects to definite environmental factors, has given us a mechanistic interpretation of insect activities very different from the anthropomorphic interpretation of the earlier students. Shelford, Dean and others have related many insect adjustments in behavior with remarkable exactness to specific conditions of light, temperature, humidity, etc.

These reactions are frequently quite specific but many of them are the same for all the species of a genus. As, for instance, all species in a genus are nocturnal or all are aquatic. Such a generic tropism usually defines the generic habitat in a broad way. Within this general habitat the individual species will have individual habitats limited by other tropisms. Apparently the generic tropism that defines the generic habitat is seldom modified for any individual species enough that such a species may exist outside the generic habitat. But apparently a complete reversal of a generic tropism is more likely of occurrence than any lesser modification. When such occurs in a genus the individual species possessing this reversed generic tropism has entrance into an environment closed to all other members of its genus.

The writer has come across two species of insects, one a dragonfly, the other a mayfly, in which a reversal of one or more of the tropisms normal to the other species of the same genus has permitted the entrance of these reversed species into environments not open to the normal members of the genus. These finds have opened up so many interesting problems in behavior and distribution that they are well worth presenting in some detail.

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The first of these that was found is *Æshna nevadensis* Walker of the Sierra upland of central California.[1] This is a large, pond and shallow lake dragonfly that lives at elevations of 5,000 to 9,000 feet. It is known only from the southern Sierra Mountains. It has been recorded from Walker Lake, Mono Co., California, at 7,700 feet elevation, Hardin Lake, Tuolumne Co., at 7,775 feet elevation and from Elizabeth Lake, Yosemite National Park at the great altitude of 9,000 feet. The writer found it at its optimum development in shallow, weed-filled lakes on the divide between Lake Tahoe and the Rubicon River (Calif.) where at an elevation of 7,000 feet it dominated the subalpine dragonfly life. Here in an open, meadow-like mountain pass, fairly level for about two miles, lie four shallow lakes, two flowing into Lake Tahoe and the desert drainage, while the other two empty into the Rubicon River and the Pacific drainage. On both sides rise granite crags for a thousand feet above the lakes, their lower parts green with firs, while their gray upper slopes are blotched white with fields of snow. Three of the lakes are covered with yellow flowered pond lilies and are fringed with green sedges among clumps of silver gray willows. These shallow lakes are warm because of the black peat bottom and long hours of sunshine. They support great numbers of a few species of insects—such as are able to withstand the long winters and cold nights at this elevation, as this is a subalpine situation with nightly temperatures at or near freezing. Eight other species of dragonflies are common here. These are northern forms that occur in the mountains of Oregon at 3,000–4,000 feet elevation and in British Columbia at sea level.

The habitat of *nevadensis* appears to be entirely above that of all other species of North American Æshnas. It appears as strayed individuals at 4,500 feet but does not appear in numbers until an elevation of 6,000–7,000 feet is reached. From here up to 9,000 feet it appears at its optimum development. No other Æshnas have been found regularly at these higher altitudes. From about 4,500 feet down to sea level, however, Æshnas are a constant element of the North American Odonate fauna. Twenty or more lowland species have been described from north of Mexico while there are actually seven or eight species living

[1] Kennedy, *Proc. U. S. Nat. Mus.*, Vol. 52, pp. 483–635.

about the lower slopes of the Sierras. Thus *nevadensis* has a habitat entirely above or outside of that of the other North American members of the genus.

We do not know the behavior complex of *Æshna nevadensis* in enough detail to speculate on all the adjustments in reactions necessary to adapt this species of a lowland genus to a highland habitat. It shares with all other Æshninæ, and without any change, a positive reaction to shining water surfaces when the sexual instinct is not overbalanced by hunger. This is a reaction through the eye as *Anax*, a related genus, was found reacting just as positively to the glistening surfaces of the crude oil pools of the Bakersfield (Calif.) oil field where hundreds of *Anax junius* perished while mating and trying to oviposit in the crude oil. When hunger predominates over the sexual impulse the reactions change so that the Æshnas fly away from the water on hunting trips into the surrounding territory. They fly away from the water and roost on trees when the minimum flying temperature is reached, also at twilight on warm evenings when the minimum flying light is reached. The minimum flying light varies greatly with the different species as some will still fly when it is so dark to the human eye that the dragonfly can be seen only when it is outlined against the sky or some white surface.

As ponds for oviposition are the same on the Sierra upland as at sea level, we find the reactions of *nevadensis* while under the sexual impulse practically identical with the similar reactions of the lowland species. The adjustments to the upland come in the reactions of the insects when hunger and other impulses outweigh the sexual impulses, and have nothing to do with the coursing of the males and females over the surface of the water while mating and ovipositing.

Two of these adjustments to the conditions found in these high altitudes are quite obvious. First the hunting individuals react negatively to the warm stratum of air next the ground so that, except early in the morning when the ground stratum of air is still cool, they hunt high off of the ground flying from fifteen to one hundred and fifty feet in the air. It is a tree-top species. This positive reaction to cool air probably explains the attraction of *nevadensis* to this alpine habitat. All other species of Æshna, when hunting, react negatively to the cooler situations of the habitat, the warmer the place the better, until 100–105° is reached when some species begin to become inactive.

The second obvious adjustment necessary is in the time of emergence. All lowland species of Æshna, as far as known, emerge at night, those the writer has reared, *umbrosa* and *constricta*, emerging at or near midnight. This appears to be an adjustment of value in that the imagoes have hardened sufficiently by daylight for flight and so escape the blackbirds and other marsh fowl that enjoy soft freshly emerged insects. But at an elevation of 7,000–9,000 feet with snow fields spread about, the nightly temperatures are never far above freezing and frequently below, making night emergence precarious as the young dragonfly would be too chilled to crawl out of its nymphal skin. Here a second adjustment to this elevated habitat appears. The emerging nymph of *nevadensis* instead of being negatively geotropic in the dark is negatively geotropic in the light, so that the winged adult emerges in the broad daylight when the temperature is high enough to insure a successful withdrawal from the nymphal skin. The writer found numerous individuals emerging in the bright sunshine in the early afternoon hours.

Thus we see that *Æshna nevadensis* has left the general warm lowland environment of the genus and has entered an entirely different region through having two of the tropisms normal to Æshna reversed.

While in the mountains of eastern Tennessee last spring, the writer discovered a mayfly, *Ephemera guttulata* Pictet, which appears to occupy a habitat entirely different from that of any other species of Ephemera. It too appears to have certain of its reactions the reverse of those of the other species of this genus.

Ephemera guttulata is a most interesting mayfly in several ways. It is one of our large mayflies. Its wings are so heavily clouded that at a little distance they appear almost black, especially as contrasted against the abdomen, which is immaculate snow-white. This bizarre insect lives in the smaller of the perennial, spring-fed mountain torrents that flow down the higher of the Eastern Tennessee Mountains. On Chilhowee Mountain these streams pour down deep V-shaped ravines over beds of small stones and coarse grit, in a succession of miniature waterfalls, for they descend at a rate of several hundred feet to the mile. These mountains are covered with pines on their high, dry ridges but the deep ravines between these ribs of pine woods are filled with a dense growth of deciduous timber so that the torrents are heavily shaded by tall trees in their whole course.

The burrowing larva of *guttulata* lives in the meager areas of coarse sand and muck found in the little basins below the waterfalls. The subimago emerges during the day. Those the writer observed came out on dull cloudy days. These fly out of the shade over the stream, through the surrounding brush and up to the better lighted areas of the hill side where they rest in the full light. The dull gray subimago then sheds a thin skin and comes out a fully developed imago with its brilliant black and white colors and its sexual maturity. No observations were made as to whether this occurred on the day of emergence or the following day. Because of the few subimagoes seen it probably occurred the same day as the emergence. Unfortunately also, no mating dances were seen. These probably occurred among the tree tops, in the deep dusk, just before egg laying began.

When the evening twilight had deepened to the point where it became difficult to pick one's way along the streams, the females of *guttulata* would appear over the little pools hurrying back and forth about a foot above the surface of the water apparently laying eggs. Their conduct was more like that of female dragonflies than like the usual hurried visit of the mayfly female dropping all of her eggs in a single effort. No males were caught at these times over the streams.

It was in these flights in the dense twilight gloom of the bottoms of these mountain gorges that the probable value of the bizarre coloration came to mind. The enormous development of the eyes, the evidence of the rudimentary antennæ together with certain experimental work indicate that the major reactions of the mayflies are through the sense of sight. Except for the white abdomen, the mayflies, at the time of these twilight flights, were practically invisible to the observer. These white abdomens, as the *guttulata* females doged about in the gathering darkness, reminded one of the streaks of light of a flight of fireflies. Apparently then this white abdomen is useful to *guttulata* in the mating flights in the deep shade of the mountain gorges as its visibility is very obviously increased by this color pattern. A snuff-colored, lowland Ephemera would be practically invisible under the same conditions. It is interesting to note that of several species of mayflies flying on these streams at this time *guttulata* is the latest on the wing in the evening and flies after the others have ceased. Some of the smaller species fly a full hour earlier, so that, though, of dull colors they are quite visible.

We can check this series of reactions of *guttulata* by a comparison with the reactions of the other species of Ephemera, all of which inhabit either large open streams or lakes. Probably the reactions of *Ephemera simulans*, the common Lake Erie species, are best known. The nymph of this species burrows in the mud of the lake bottom, being obviously negatively phototropic. At the time of emergence it becomes positively phototropic and rises to the light of the sky. At Put-in-Bay this emergence takes place between eight and ten P.M. It sheds its skin as it rises through the ten to thirty feet of water so that on arrival at the surface it bursts out fully winged, when it becomes less positively phototropic and flies toward the dark land. It rests on the shore vegetation until the following evening when it sheds its final skin, becomes sexually mature and at twilight flutters up and down in the mating dance. At this stage it is evidently becoming positively phototropic again. In this twilight nuptial dance it leaves the dark foliage for the more open lighter spaces. The males grasp the females and release them after a contact of a few seconds. The female becomes at once completely, positively phototropic and flies out toward the light surface of the lake to deposit her eggs.

If we compare this series of reactions with those of *guttulata* of the shaded mountain streams, we find that two of the series of reactions of the latter are reversed. *Guttulata* is negatively phototropic as a nymph, is positive as it emerges, but *remains positively phototropic after emergence* as it flies from the heavily shaded creek to the lighter areas above the shade. Further, *after copulation it becomes negatively phototropic* and flies down to the densely shaded torrent to oviposit. Any of the open stream species of Ephemera would react themselves away from the shaded stream when they started to oviposit. So by these reversed reactions *guttulata* is able to occupy a habitat that the normal members of the genus *Ephemera* are not able to occupy, one that is ecologically outside of the general habitat of the genus.

Certain experimental studies in the behavior of mayfly nymphs point to possible explanations of some of this series of reactions. Wodsedalek[2] has demonstrated that the nymph of Heptagenia is negatively phototropic. Also that CO_2 in the water will make a nymph which has been negatively phototropic, reverse its reaction and become positively phototropic. It is then possible that the change in reaction at the time of emergence, when the nymph ceases to burrow and swims up to the light, is due to an accumulation of CO_2 in the nymph after its tracheal system has detached itself from the gills in the last nymphal ecdysis. The shedding of the skin actually starts by a general loosening of the chitin several hours before the final emergence occurs. During this time, if the gills are early detached, much CO_2 could accumulate in the tissues, enough eventually to reverse the phototropism and so cause the nymph to rise to the surface.

On emergence the nymph fills its tracheæ with air and simultaneously becomes negatively phototropic, so that it flies toward dark land. It appears to retain this reaction until the next evening at dusk or for about twenty hours when it mates and the female at once becomes positively phototropic and flies towards the light surface of the open lake. During the intense nuptial dance her tissues have been accumulating CO_2 and in some way the sexual orgasm overbalances the condition, giving the acid condition full sway.

The experiments of Allee and Stein[3] show that the reactions are not as simply explained as they have been sketched in the preceding paragraphs. The actual intensity of the light probably also figures in some of the reactions. Krecker's work[4] in the subimagoes of *Hexagenia*, a close relative, shows that these, in spite of flying to the dark land, are positive to certain bright

[2] Wodsedalek, "Phototactic Reactions and their Reversal in the Mayfly Nymphs of *Heptagenia interpunctata* (Say)," BIOL. BULL., Vol. 21, pp. 265–271, 1911.

[3] Allee and Stein, "Light Reactions and Metabolism in Mayfly Nymphs," *Jour. Exp. Zoöl.*, Vol. 26, pp. 423–458, 1918.

[4] Krecker, "Phenomena of Orientation Exhibited by Ephemeridæ," BIOL. BULL., Vol. 29, pp. 381–388, 1915.

lamps. Anyone who has seen the snow storms of mayflies that come to the street lamps of the lake ports realizes that the subimago can have a reverse tropism under such conditions.

We are beginning to recognize physiological species among insects—those based on habits and habitats. In parasitic insects particularly we recognize generic reactions to common hosts so that we unofficially recognize physiological genera. There is no reason why we should not, except the expediency of morphological characters. Viewed in this light *Æshna nevadensis* and *Ephemera guttulata* are physiologically outside of their respective genera.

When the writer first thought through the habits and distribution of the North American species of the genus *Æshna*, his conclusion was that the positive thermotropism of the lowland species was perhaps different in degree and distinct for each species, thus explaining the restriction of each species to its specific thermal belt. Thus it appeared, at first, that this difference in positive thermotropism accounted for the fact that some Æshnas lived in hot Arizona, others in the cooler northern states, while still others are restricted to the northern parts of Canada and Alaska. However on investigating further this does not appear to be true.

The restriction of each species to its specific thermal belt is probably not due to a limitation of the positive thermotropism of the adult to the narrow limits of the particular thermal belt inhabited by that species. This is quite contrary to Merriam's theory of distribution by thermal zones.[5]

This distribution of the various species in different thermal zones however is a very striking thing and some of the thermal conditions are easily sketched. Except for *mutata*, *californica* and *multicolor*, which are early spring species, the majority of the species of Æshna are on the wing in August, so the writer has worked out the flying temperatures for August at four points, Yuma, Arizona, St. Louis, Missouri, St. Paul, Minnesota, and Sitka, Alaska. Each of these is representative of the flying conditions for a restricted group of Æshnas. The Yuma temperatures apply to *jalapensis*, *multicolor* and *arida*. The St. Louis

[5] Merriam, "Life and Crop Zones of the United States," Bull. U. S. Biol. Survey, No. 10, pp. 1–79, 1898.

temperatures apply to *constricta*, which is the only species broadly distributed across the central states, while the St. Paul temperatures apply to a series of several species such as *interna*, *canadensis*, *umbrosa*, etc. Under the Sitka temperatures we find *sitkensis*, *subarctica* and *septentrionalis*. Such species as *palmata* and *constricta* are found in two or three of these zones.

To define the flying temperatures the mean maximum and mean minimum day temperatures for August have been taken from the Weather Bureau Report for the above stations.[6] Ten degrees was then added to the mean maximum day temperature to give the approximate maximum sun temperature, which is the temperature to which the local dragonflies react positively, while the mean minimum day temperature remained unchanged, as it is a shade temperature to which the local dragonflies react negatively. Thus these temperatures show roughly the range of day temperatures which the species of *Æshna* meet during their flight season in each of the general zones represented by the temperature records. These records for August are as follows:

	Mean Maximum in the Sun.	Mean Minimum in the Shade.
Yuma, Arizona	114°	77°
St. Louis, Missouri	96°	69°
St. Paul, Minnesota	90°	60°
Sitka, Alaska	72°	45°

From the above it is obvious that the temperatures during flight do differ greatly for the various species of *Æshna*. However our observations indicate that all lowland Æshnas are always positive to heat so that the higher the temperature, the greater the activity of the insect. Hine's observations[7] on Kadiak Island were that *palmata* was most active on the warmest days. Walker's observations[8] on the Canadian species are that increased temperatures always increased the speed of Æshnas but his observations do not include temperatures above 90°. Somewhere above 90° there may be a limit for this increase of

[6] "Climatology of the United States," Bull. 2, 1906. Temperatures for Yuma, St. Louis and St. Paul. *Monthly Weather Review*, Dec., 1898, p. 549. Temperature for Sitka.

[7] In conversation with the writer.

[8] Walker, p. 33. "The North American Dragonflies of the Genus *Æshna*," Univ. of Toronto, Biol. Studies, Biol. Series, No. 11, 1912.

speed as the temperature rises, which limit may be actually reached by some of the southern species on very warm days. The writer [9] has made one interesting observation in this regard. *California* and *multicolor* on very hot days when the temperature is from 100° to 105° take frequent rests, by hanging up in the shade every few minutes. This was noted in the Yakima desert at Sunnyside, Washington. Apparently, for these at least, somewhere in the higher nineties a temperature is reached above which increase is depressing and no longer stimulating. However we can safely say that for all lowland species of *Æshna* an increase of temperature up to 95° increases activity so that all are equally positively thermotropic.

The thermal distribution of the four groups of species outlined above must then be conditioned through some indirect check on the life history. Some temperature condition of the water for the nymph or the developing egg may be the limiting factor rather than the flying temperature for the imago. Undoubtedly individuals of each species continually fly beyond the limits of the optimum habitat but the offspring of such do not survive or we would have a spreading species. This constant pressure of the species of dragonflies into surrounding but unsuitable habitats was worked out by the writer [10] on Put-in-Bay Odonata in 1922. Until we know the life histories of the various species in minute detail we will not be able to define all of these limiting factors except as we stumble onto them accidentally.

A further conclusion appears indicated from this study. As all Æshnas, except *nevadensis*, have one type of reaction to temperature in the imago, and all the Ephemeras, except *guttulata*, have one type of reaction to light and the reactions of these two odd species are just the reverse of the other species in their respective genera, we may conclude that a given type of insect nervous system can be completely reversed from its usual reaction more easily than it can be modified in a lesser degree. This would appear logical from the theoretical grounds of the mechanics of the nervous system. Because of its minute size, the insect nervous system is characterized by the relatively

[9] Walker, see ref. 8, p. 33.

[10] Kennedy, "The Ecological Relationships of the Dragonflies of the Bass Islands of Lake Erie," *Ecology*, Vol. III., pp. 325–336, 1922.

small number of units (either cells or combinations of cells) that comprise it. Such simple nervous systems obviously cannot produce the extended series of finely graduated reactions that are possible to a more complicated type of system. On the other hand the mechanism is already present for the reversal of any particular reaction. So a complete reversal of a generic reaction which puts the species entirely outside of the normal generic habitat, is more likely than the slight modification necessary to put it into a near but only slightly different habitat in which it would be held by only a slight gradation of the general reaction.

At first thought, if it is easier to have a reversed reaction in the insect nervous system than to have a graduated reaction, one might think that the genus would fly apart as to any unity of environment, so that each species would have a habitat strikingly different from that of each other species, that there would be no such thing as a generic habitat. Observation shows that this is not so. Species are superimposed and habitats overlap in a most confusing manner and in any large genus there is usually an easily recognized generic type of habitat. So far not enough experimental work on behavior has been carried out to determine if the species of any one genus of insects are distributed by graduated reactions to one type of stimulus. However an analysis of some of the factors of the problem appear to indicate that such a distribution, for instance as the species of *Æshna*, show in a series of temperature gradations, may not be due to a slight difference in reaction to a specific stimulus, but may be merely an apparent series each species of which is held in its particular zone by some different positive or negative reaction to any one of a variety of stimuli.

An insect with incomplete metamorphosis passes through two stages, nymph and adult, in each of which it may pass through several physiological stages of development. The nymph has at least two, its feeding stage and its quiescent preëmergence stage. The imago has at least five stages, the teneral, the sexually mature stage, which can be divided into periods of hunger, periods of sexual lust, periods of egg-laying, and finally the stage of senility. The last need not be considered in a problem of species distribution as it is beyond and outside the genetic cycle. In each of these stages several stimuli control the individual, the reaction to anyone of which may be the factor that limits the species to its particular environment. If we consider only ten of the more easily recognized tropisms then in the six physiological stages enumerated above we have one hundred and twenty positive and negative possibilities for a reaction to an individual stimulus that might limit the species to a specific habitat. The problem is really much more complicated than this as many more reactions enter and all are more or less conditioned by morphological factors. So there is no difficulty at all in accounting for a great variety of factors, any one of which may limit the species to a rather narrow habitat.

In building the conception in the student's mind of the group of habitats occupied by all the species of a genus the mind automatically picks the most obvious habitat characteristic that is common to all the habitats under consideration. If this habitat characteristic, such as flying temperature for *Æshnas*, varies from habitat to habitat the mind automatically considers each species delicately adjusted to the exact degree of this variation in its specific habitat. This may not be true at all. And the factor which limits each species may not be the obvious one but some inconspicuous factor and it may be in each species in the genus a factor from a different category. It may be a temperature factor in one, a moisture factor in another, a chemical factor in a third species, etc. Thus graduated generic factors may largely be a compound figment of the mind of the observer.