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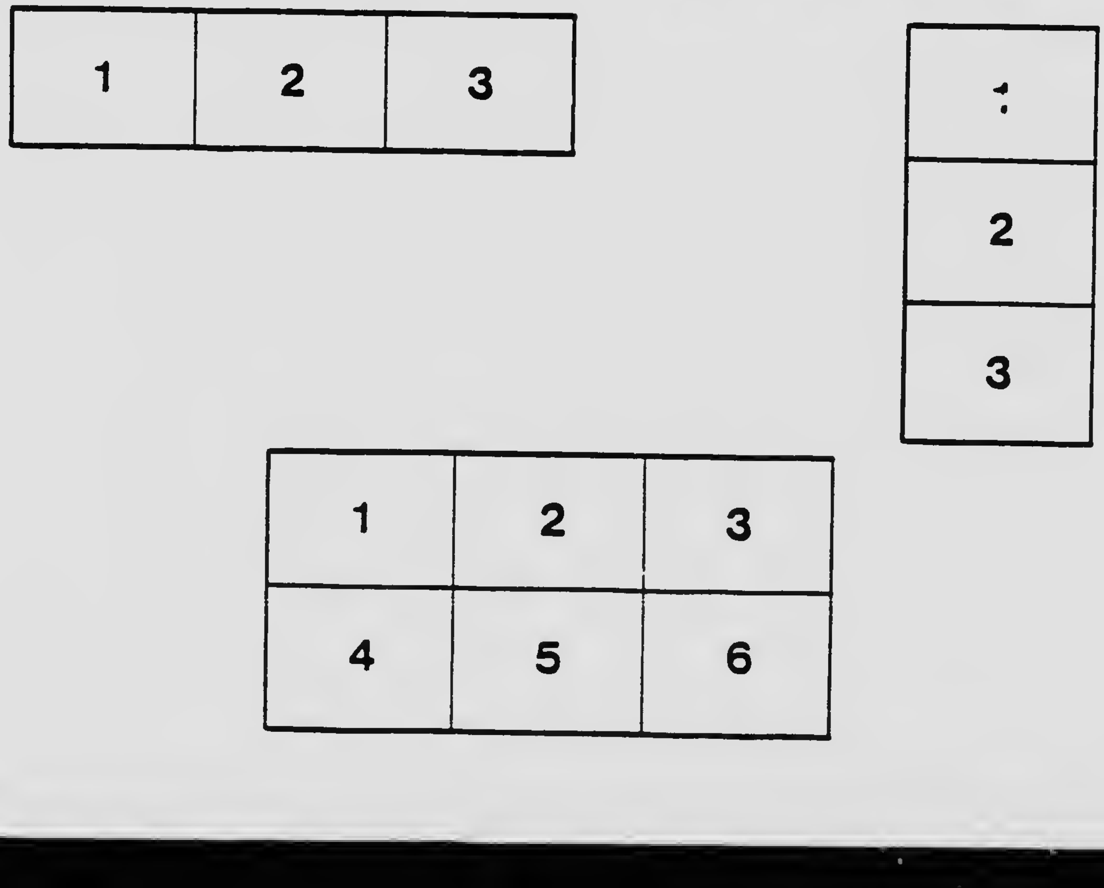
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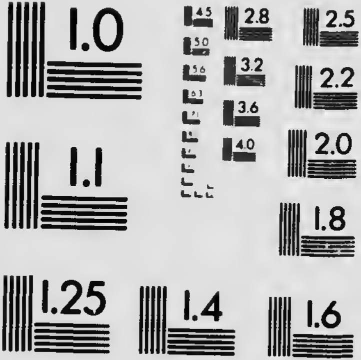

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INSECT BEHAVIOUR AS A FACTOR IN APPLIED ENTOMOLOGY

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INSECT BEHAVIOUR AS A FACTOR IN APPLIED ENTOMOLOGY

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In determining the choice of a subject for my address I have been guided by a feeling that, owing to the extraordinary progress that has been made in the knowledge and methods of applied entomology during recent years, the time at my disposal could not be occupied to better advantage than by an examination of what I believe to be fundamental to an adequate appreciation of the problems with which we have to deal and their successful solution.

We have accumulated an enormous mass of facts relating to insect life in all its manifold relations to the welfare of man, and many of these facts have furnished us with the means of determining methods of preventing or controlling the noxious effects of insect activity. But it would appear to me that we have reached a stage where our accumulated knowledge is rather like a city that has developed along the paths marked out by ancient trails and where a need has arisen for the earnest consideration of a town-planning system. Our further progress must be based upon principles that modern experience has indicated as being fundamental to a rightly conceived and an orderly development of future investigation.

Insect behaviour constitutes the basis of applied entomology and, while that fact may now be more generally realized, I feel that if the point of view such a conception implies were constantly borne in mind we should be able to approach the solution of our problems in a manner that would lead to even greater success than has already crowned our efforts.

Action is the result of the manner in which man experiences. So, also, the reaction of an insect to its environment finds expression in the behaviour of the insect. Behaviour, as Jennings has stated, "is merely a collective name for the most obvious and most easily studied of the processes of the organism, and it is clear that these processes are closely connected with, and are indeed outgrowths from, the more recondite internal processes." Stated briefly in another way, behaviour consists in the adaptation of the insect to its environment. Anything injurious to the insect causes changes in its behaviour and conversely anything advantageous to it produces a change in the behaviour. Of the factors which regulate behaviour in insects, as in other organisms, internal conditions and processes are effective no less than external, and both may be, and generally are, the product of environment. Further, to be effective the external stimulus of the environment, whether it be physical or biological, must produce a change in the physiological state of the organism.

The activities of injurious insects which furnish the problems of applied entomology are more pronounced in countries where, for various reasons, the stability of the physical and biological environment is changed. This affords the reply to a question often asked, namely, why entomologists are faced with more problems in newer countries, such as our own, than in older countries? One of the chief causes affecting the stability of the environment and consequently the activities of the insects in such countries as the United States and Canada is the extension and development of agriculture and of agricultural areas. In countries of an older civilization the environmental conditions, particularly the agricultural conditions, are fairly stable by reason of the long period of their gradual development. In such countries we find a conservative type of husbandry with which careful rotations of crops and a fairly intensive system of cultivation are associated. In the newer countries, not only has widespread development within comparatively brief periods of time been responsible for extensive changes in environmental conditions, but such development, particularly in agriculture, has necessitated, among other things, the importation of large quantities of the natural products, including vegetation, from older countries with the inevitable introduction of the insects affecting those products, thereby not only modifying the environmental conditions for the native insects in the new country, but also introducing into a new environment insects from another country and from a native environment more conducive to stability in behaviour Thus the conditions are altered for both the insects native to the new country and the insects fortuitously introduced.

Formerly, the investigations of the entomologists did not extend very far beyond a study of the life-histories of insects, and control measures were largely based on such knowledge supplemented by a limited study of the insects' habits; the idea being, as we were told, "to find the weak spot in the insect's life-history." The limitations of such methods of solving entomological problems were demonstrated by an inability either to account for the outbreaks of certain insects or to discover effective means of control. Not until the behaviour of insects, that is, their reactions to their environment, to each other and to the different biological constituents of that environment, was studied with true appreciation was it possible to make satisfactory progress in the control of certain serious pests. The corn root-aphis (*Aphis maidi-radicis*) furnishes a good example of this fact. It was not until Forbes and his assistants worked out the relation of this insect to the ant *Lasius niger americanus*, on which it depends for its well-being, that any success in controlling this serious corn pest could be attained; and such control measures as the breaking up of the ant colonies in the spring and the destruction of weeds on which the ants plant their wingless aphid captives before the growth of the corn, are based solely on a knowledge of behaviour.

The reaction of an organism to environmental influences is known as a tropic reaction or a *tropism*. The external stimulus may induce a physiological state that exhibits response in movement, or the physiological condition of the organism may be changed in a more fundamental manner with the result that not only is the organism itself affected permanently, but the progeny experience the effects of the stimulus and react by a change in behaviour or even in structure. For the sake of convenience we may term such tropic reactions as *individual* and *racial*, respectively.

It will not be possible in the time at my disposal to deal with more than the main types of tropic reactions to physical factors and a treatment of these must of necessity be brief in character. Let us, therefore, consider the chief tropisms: Chemotropism, thermotropism, hydrotropism, phototropism, and anemotropism. If time permitted, a consideration of that extensive realm of insect behaviour included within the category of instinctive behaviour would be desirable, but we must content ourselves with the knowledge that this type of behaviour is the result of reflex responses to the various types of tropisms.

Chemotropism is the reaction to stimuli of a chemical nature perceived through the olfactory sense. Inasmuch as odour is undoubtedly the most important factor in the environment of insects the significance of this tropism is evident. The chief objects of animal or plant life, are feeding and reproduction, and in the search for food or for the sexes, or in oviposition, chemotropism plays a predominant part. The sexual chemotropism of insects, particularly among the Lepidoptera, has long been a familiar phenomenon to entomologists. But it is in their response to chemical stimuli as affecting the search for food and oviposition that we find a tropic reaction that has untold possibilities in its practical application.

The vital functions of search for food and oviposition are closely associated. The female insect deposits its eggs on substances best suited for the nourishment of the larvæ. The females of *Pieris rapæ* and *P. brassicæ* select the leaves of cruciferous plants, attracted thereto by the mustard oils, a group of glucosides present in these plants, as shown by the experiments of Verschaffelt. The same investigator showed that the larvæ of the sawfly *Priophorus padi* (L.) Thomas, which feeds on the foliage of certain rosaceous plants, are probably attracted by a glucoside, amygdaline. The chemotropic reactions on the part of carrion beetles, and to excrement on the part of coprophagus Coleoptera and Diptera, are well known. Howlett induced *Sarcophaga* to oviposit in a bottle containing scatol, a decomposition product of albuminous substances; and he stimulated the oviposition response in *Stomoxys calcitrans* by means of valerianic acid. Richardson's recent work on the oviposition response of the house-fly, in which flies were induced to oviposit in response, apparently, to an attraction of ammonia in conjunction with butyric and valerianic acids, opens up suggestive lines of investigation. Barrows finds that the positive reaction of *Drosophila* to fermenting fruit is due in a large measure to amyl, especially ethyl alcohol, acetic and lactic acid and acetic ether.

While the aforementioned cases, which might be multiplied, illustrate the chemotropic responses of insects in so far as they affect the oviposition response, that is, the search for food as affecting the future larvæ on the part of the ovipositing female, there is the large class of chemotropic reactions which affect only the adult without reference to the progeny. An illustration of this class is afforded by the investigations of Howlett on the fruit-flies of the genus *Dacus* in which the males are attracted by the eugonol oils, iso- and methyl-eugonol, which are constituents of oil of citronella.

The control of outbreaks of the larvæ of Arctiid moths in India by the capture of the adult moths in bait traps of the Andres-Maire pattern is an example of the manner in which practical advantage may be taken on a large scale of a chemotropic response.

The negative chemotropic reaction of insects is illustrated in the practical use of repellent odors. *Musca domestica* is repelled by certain coal-tar products such as phenol; the protection of cattle from biting flies and of man from mosquitoes is secured by the use of repellent mixtures.

Turning now to a problem of great biological interest and practical importance, namely, the different behaviour of the same species of insect to different plants, we find that what would appear to be fundamentally a chemotropic reaction is sometimes responsible for the creation of a biologically different race of the same species. In his investigations on blueberry insects in Maine, Wood has found a form of *Rhagoletis pomonella* infesting blueberries (*Vaccinium*) and huckleberries (*Gaylusaccia baccata*) that is below normal size, and this form appears to be long-established as efforts to get the apple-bred race to oviposit on blueberry and *vice versa*, failed. The physiological influence of the host plant upon the insect feeding upon it and the creation of biologically different races which may differ sufficiently to be separated as species by the tendency of members of a single polyphagous species of insect to become adapted to a particular food plant is strongly suggested by Cameron's study of the leaf-miner *Pegomyia hyoscyami* Panz. which feeds on belladonna (*Atropa belladonna*). Within this category we should also include, I believe, the case of the Arizona wild cotton weevil (*Anthonomus grandis thurberiæ* Pierce). The production of morphological changes by a change in food plants has been observed in like manner in the case of Aphides. These chemotropic responses, for that is essentially their nature, have as important a relation to the work of the taxonomist as to that of the applied entomologist.

A subject which promises results of great practical value is the study of the resistance of plants to insect attack with a view to the production of insect-resisting varieties in crops subject to injury. Comparatively little attention has been paid to this further example of chemotropic reaction, but the development of strains or varieties completely or even partially resistant to the attacks of particular insects attacking them, would place a valuable preventive measure in our hands. This is a field for joint investigation by the entomologist and the plant-breeder.

The realization that in the ultimate control of the gipsy moth in North America, the silvicultural aspect of the problem must receive serious consideration is an indication of the importance of chemotropism in the control of this pest. The elimination of favored food plants and the substitution of unfavored species such as pine are measures largely based on the principle of food attraction, that is, of chemotropism, and should be so regarded.

Enticing and suggestive as the subject of chemotropism has been shown to be, we must pass on to the next tropic reaction, namely, thermotropism. In temperature we encounter an environmental influence which is as far-reaching as it is universal in its relation to insect behaviour, and while it is inseparably associated with other factors, especially that of moisture which we shall consider later, it is in itself sufficiently potent to determine the range of insect activity in both time and space. The relation of temperature to the distribution of insects is too well known to require demonstration by examples. Merriam's laws of temperature control, namely: (1) that "animals and plants are restricted in northward distribution by the total quantity of heat during the season of growth and reproduction," and (2) that "animals and plants are restricted in southward distribution by the mean temperature of a brief period during the hottest part of the year," in general, hold true in regard to insect distribution. The importance of determining the optimum temperatures for the reproduction and development of different insects has been realized by a number of investigators, although their conclusions have sometimes been defective through neglect to take into consideration the coöperative effect of other environmental factors such as humidity. The influence of temperature on development is illustrated very strikingly in the Aphides. For example, Ewing has recently found that a constant temperature of 90° F. is sufficient to prevent completely the development of *Aphis avenæ* and that the optimum temperature for the production of wingless agamic forms of this species is about 65° F., these forms only being produced at a mean average daily temperature of about 65° F.

Practical use is now made of our knowledge of the temperature relations of insects in the employment of high temperatures as a means of insect control, and "superheating" offers great possibilities.

An interesting case of the use of temperature as a means of control is afforded by the employment of the method of close-packing of horse-manure for the purpose of preventing the breeding of *Musca domestica.* About ten years ago I found that a temperature of about 105° F. was fatal to the larvæ of *M. domestica* and in an account given before this Association in 1913 of further studies of the effects of the temperature of the manure pile on the larvæ I showed that the larval habitat in the well packed pile was peripheral, and that excessive internal heat became practically a larvicide. Recently, Copeman has shown that practical use can be made of this principle and that close-packing of the manure is all that is necessary to prevent the breeding of flies. In a recent letter to me Copeman states that this method of control is being taken up by the military authorities on an extensive scale both in England and abroad.

Just as high temperatures are effective in insect control so also low temperatures have a like value, as is now well known. And the utilization of low temperatures in applied entomology offers a fruitful field for further investigation. Further, in northern countries exact knowledge concerning the relation of low winter temperatures, associated as a rule with degrees of humidity, to the distribution of insects is highly desirable.

The activities of all insects are so closely related to temperature that no study of their behaviour can be made without full consideration of its effects.

Closely linked with thermotropic reactions are the effects of hydrotropism, and particularly humidity. This is especially the case in the effects of climate on insect distribution and migration. The theory advanced by Ellsworth Huntingdon in his "Civilization and Climate," that as climates change nations either change with them or migrate when the change is unfavorable to more suitable climatic environment, is equally applicable to insect life. We must ever take into account the effect of the climatic stimulus on insect behaviour.

In a recent suggestive paper Pierce has called attention to the fact that "a careful study of the records of any species, charting for the time required for each activity and the temperature and then similarly for the humidity, will disclose temperature and humidity points of maximum efficiency. With the boll weevil these points lie approximately near 83 degrees F. and 65 per cent of relative humidity." This author has also pointed out the practical applications of a knowledge of the relation of climatic conditions to the control not only of the cotton boll weevil, but also to such pests as the cattle tick and the fall army-worm. Other cases are numerous.

We have always to bear in mind that a tropism may include reactions to a stimulus existing in very diverse forms. This fact is well demonstrated in the case of hydrotropism. The negative hydrotropism of the salt-marsh mosquitoes of New Jersey and San Francisco is a reaction to water *en masse*, as is the positive hydrotropism of aquatic Coleoptera and Hemiptera. On the other hand, the reaction of insects to humidity is a hydrotropism that may be brought about by diffused moisture in the air. Similarly, moisture in the soil affects the behaviour of insects considerably, as Wheeler has shown in the case of many species of ants, and as Parker has demonstrated in his study of the sugar-beet root-louse (*Pemphigus betæ* Doane) in which it was found that soil moisture is a very important factor in controlling the rate of increase in colonies of this insect. The attraction of the so-called "watershoots" of trees such as apple for aphides should be regarded as being in effect a hydrotropism.

The importance of moisture as a factor in insect behaviour is strikingly illustrated in the case of some of our most important grain insects. Forbes has discussed the effect of drought and rainfall upon the abundance and suppression of the chinch bug in Illinois. In Canada we find that the prevalence of the western wheat-stem sawfly is governed by humidity. A lack of precipitation causes a dearth of flowering stems among the grasses in which this insect normally breeds, resulting in a decrease, the abundance of the insect depending primarily upon the prevalence of suitable grass stems. Similarly, a lack of moisture is an important natural check on the Hessian Fly, a dry season being generally recognized as prejudicial to the fly. In Manitoba, Criddle finds that the partial second brood is frequently destroyed completely by the premature ripening of the grain due to the hot weather conditions in late July. Further instances might be given of the effect of moisture on other classes of insects but sufficient has been said to indicate the diversity of the hydrotropic type of behaviour.

Reaction to light plays a prominent part in insect behaviour and numerous are the examples that might be given, were it necessary, of phototropism in insects. But while entomologists are familiar with the manner in which adult insects such as Lepidoptera are attracted to light and with the negative phototropism of many larval forms, and of adult insects such as *Anopheles*, we are still far from anything approaching a working knowledge of this reaction. Such knowledge will undoubtedly place a valuable weapon in the hand of the applied entomologist. In some cases we are able already to take advantage of this type of behaviour. Swaine finds that the destruction of piled logs by the wood-boring larvæ of the sun-loving *Monohammus* can be prevented by forming a dense shade over the logs by means of brush. In his study of the army cutworm (*Euxoa auxiliaris*) in Alberta, Strickland found that the larvæ are negatively phototropic and hide beneath the soil till about four or five o'clock in the afternoon when they come to the surface and feed. With the weaker light they become positively phototropic and a general migration in a westerly direction takes place. When food is scarce hunger may overcome their aversion to sunshine with the result that the larvæ come above ground, but they still display a modified negative phototropism and migrate in a northwesterly direction. These facts are of practical value in controlling outbreaks of this insect.

The two previous tropisms, operating together, constitute perhaps the most widely operative of all environmental stimuli as affecting insect life. The daily activities of insects, their movements on the soil, on vegetation or in the air, are largely governed by them. And in referring to the dual influence of these stimuli it may be remarked that the various types of stimuli are very frequently coöperative. Years ago, when collecting Diptera by sweeping, Wheeler was impressed with the fact that there must be a regular diurnal up and down migration of insects in the low vegetation, comparable to the phenomenon exhibited by the pelagic fauna in the sea. The insects descend to the ground at night and with the return of light and heat rise until they reach the upper surface of the plants. There is little doubt that this diurnal migration is of economic importance and demands further careful study. Its dependence on the coöperative effect of several stimuli such as light, heat, and probably air currents, indicates the necessity, which should always be borne in mind in studying insect behaviour, of a careful analysis of tropic reactions.

The relation of the dispersion of insects to air currents is an aspect of insect behaviour that has had wide recognition since, and perhaps before, the locusts descended on the land of Pharaoh. Anemotropism is well exhibited in the case of the Rocky Mountain locust which moves with the wind and when the air current is feeble is headed away from the source. The brown-tail moth owes its distribution in New England and eastern Canada largely to wind-spread and the investigations of Collins and his associates have shown that the general spread of the gipsy moth in New England is most probably due to the fact that the first-stage larvæ are carried in a north and northeasterly direction by the warm prevailing winds rather than to dispersal by artificial means, as formerly believed. The practical value of knowledge of this type of behaviour is shown by the experiments of Le Prince and Zetek on the flight of Anopheles with the use of Quinby intercepting planes in Panama. Le Prince has suggested that where antimalarial work is to be undertaken in badly infested regions observations on the flight direction will indicate which of several possible production areas is the source of the particular species of mosquito it is desirable to eradicate.

If time permitted it would be profitable to discuss other types of tropisms and to show how this line of study throws light on the complicated instinctive behaviour of insects, particularly those exhibited by the social Hymenoptera. The latter, however, is a subject in itself and has received the attention of more competent hands than mine; the studies of Wheeler in particular have thrown much light on this fascinating problem. As Wheeler has stated: "We know that the insect responds not only to external stimuli but also to certain unknown stimuli originating within the cells of the alimentary tract, reproductive organs, etc., and that the responses to these stimuli are often remarkably complex, as *e.g.*, in the elaborate feeding and nesting instincts of ants, bees and wasps. Nor does the complication of the problem end here. It is greatly increased by two further considerations, first, by our complete ignorance of the protoplasmic changes, chemical and physical, which precede or accompany these tropisms or the response to stimuli in general; and second, by the difficulty of explaining why all these responses are so marvelously adaptive. I venture to assert, nevertheless, that it is better to face these difficulties, insuperable as they appear, than to continue investigation in that spirit of anthropomorphism, which has been such a fruitful source of misinterpretation in the comparative study of habits and instincts."

Reference has already been made to the control of the corn root aphis (*Aphis maidi-radicis*) which is based on a knowledge of the instinctive behaviour of the ant *Lasius niger americanus*. The most notable example in applied entomology of the practical value of a knowledge of instinctive behaviour is seen in beekeeping. A knowledge of the behaviour of the bees enables us to mould their instincts along those lines most desirable from the point of view of our convenience and pecuniary profit.

Incomplete as this account is of the manner in which insects react to the various constituent factors of their environment, I trust that in the time at my disposal I have indicated the fundamental character of insect behavior in relation to the solution of the problems that confront us. We have reached a stage in the progress of our work that demands on the part of every investigator and entomological practitioner, whether he be working at problems as wide apart as taxonomy or quarantine administration, as thorough a knowledge as possible of the manifold nature of insect behaviour, that is, of the relations and reactions of insects to the physical and biological factors in their varied environments; for it is through such knowledge that applied entomologists will find solutions to some of the greatest problems that now occupy our attention and are certain to confront us in the future. Great as the contribution of entomological science to the advancement of civilization has been in the past, it is slight compared with promise of future achievement.

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