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FOOD, DRINK AND EVOLUTION[1]

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THE three primary animal instincts, to secure sustenance, to gain protection and to enjoy the opportunity of reproducing their kind, are related either individually or collectively to every biological problem, however narrow its scope. Although the impress of each of these necessities is to be found in the behavior and structure of every species, it is by no means evident to the same extent, nor alike at all periods of ontogeny. Reproduction is confined to a limited part of the life span even in the most primitive types of animals, and the period of reproductive activity is still more obviously restricted in the insects, where it becomes an attribute of only the final, unchanging imaginal stage. This stage must thus suddenly disclose all the adaptations of the sexually mature animal.

Protection from destructive agencies is on the other hand a constant necessity, common to all periods of the life span. It is, however, in part passive, as it may depend to a great extent upon bodily characteristics, not necessarily associated with specialized behavior.

The instinct to secure food is equally a constant necessity during post-embryonic growth, for only by its gratification can growth and development take place. Even more than reproductive activity the taking of food by animals is rhythmic, cyclical or interrupted by periods of varying length. Furthermore, food requirements in insects are proportionally much greater during the preparatory stages, when large reserves of fat are produced and stored within the body. Feeding is thus by no means a uniform or continuous process, but its association with the several stages is far more extended than is reproduction. Also, it is a purely active, never a passive, process, and in consequence we find that it has modified struc-

[1] Annual public address of the Entomological Society of America at its meeting in Richmond, Va., December 29, 1938.

ture and behavior even more profoundly than have the needs for protection.

The relations of insects to their food supply are very diverse and complex and taken together are unparalleled in any other group of living organisms. We have as yet made slow progress in unraveling the details and have been tempted to make many assumptions and generalizations which it must be admitted rest upon a rather flimsy basis. For this reason I feel that it behooves us as entomologists to take brief stock of our present knowledge concerning the food and feeding habits of insects as they appear to have influenced the course of insect evolution.

With reference to their choice of foods we may roughly group the insects into two categories, one of which includes herbivorous species, feeding directly on plants, and the other represented by those that are carnivorous, preying on other living animals or consuming those dead from other causes. The number of species in each group is approximately equal, but it is a striking fact that the great majority of the carnivorous forms depend upon other insects on which they are either predatory or parasitic. In this respect the insects are almost human, for the most important predatory and parasitic enemies of civilized man are other groups of men. Some of them accept and thrive upon the foliage and other tissues of numerous, often unrelated plants without evincing a pronounced preference for any particular kind. The number of such polyphagous species is large, but not so great as we once thought. Even some of our common grasshoppers restrict their feeding to one or at most to a very few species of plants. They may, however, under stress of hunger partake of many plants they would otherwise avoid, while other Orthoptera and even lepidopterous caterpillars may occasionally become cannibals. Such transgressions again are "almost human" and recall the behavior of mobs. They are of definite biological significance, for they show conclusively that the normally restricted diet of these insects is not a physiological necessity, since the unaccustomed substances cause neither digestive disturbances nor other metabolic derangement sufficient to interfere with normal growth and development.

Viewed in the light of our own appetites such a restricted dietary is utterly incomprehensible. We, as entomologists, are so accustomed to this peculiarity among many insect pests that we take it for granted and have shown little inclination to inquire into its evolutionary history.

Carnivorous insects exhibit many of the fundamental characteristics of their vegetarian relatives with reference to food, despite their more spectacular behavior. They are almost equally fastidious in confining themselves to diets as circumscribed as those affected by vegetarian species. Thus, certain ground beetles of several related genera restrict their food to snails. Lady-beetles consume great numbers of aphids and scale insects either generally or with great specificity. The solitary wasps store their nests with spiders and insects of all kinds, but we find, generally, that each species limits its provisioning to members of a single family or still more closely restricts its choice, sometimes, to a single species of prey. Such behavior is again difficult to reconcile with our own human appetites.

Parasitic insects present undoubtedly the most striking series of highly specialized food habits to be found in the whole animal kingdom, and their behavior is modified for several reasons. The vast majority, known as entomophagous or insect-eating, parasites, present a picture that is fundamentally different from the more conventional types of parasitism among other organisms. They are members of the holometabolous orders of insects in which it is almost invariably only the preparatory stages that dispense with a free-living existence. One result of this dual mode of life is the acquisition of totally different food-habits by the larval and imaginal stages of the insects concerned. This is paralleled, but to a far lesser degree, by the nectar-loving butterfly that suddenly discards the carrots or cabbage that nurtured it as a caterpillar. Such vagaries should not surprise us, as they are quite in keeping with our own personal habits when we feed our offspring on milk and spinach and deny them the liqueurs and lobster that we smugly reserve for the age of discretion. Nevertheless, this proved to be an innovation for insects as it initiated the development of the many remarkable modifications which now follow independent lines of evolution in the larval and imaginal stages. This condition reaches its highest development among parasitic insects. The free-living imagines are morphologically of quite ordinary structure, but the female is endowed with very highly adaptive and complex instincts associated with host-selection and oviposition. The larvae on the other hand commonly show unusual physiological, morphological and behavioristic peculiarities that enable them to develop successfully within the eggs or bodies of the many diverse insects on which they are parasitic. Individual species are narrowly restricted in the selection of host insects, even more regularly so than the free-living vegetarian and predatory types.

We have already mentioned the fact that one of the most extraordinary features of this horde of entomophagous parasites is their selection almost exclusively of other insects as hosts and that the same is true of predatory insects. For this reason the insects are a much more self-contained series of organisms than any other group of animals. That is to say, the balance of nature which determines the fluctuations of organic populations is among the insects dependent to a large extent upon the abundance and activities of other insects.

It is perfectly obvious from the foregoing very inadequate summary that food and food-selection play a very important part in the present economy of the insects as a whole. Thus we may readily surmise *a priori* that their evolution and diversification through the ages have been determined in great measure by the changes and specializations that have established the complex picture just presented.

We may now inquire to what extent the evolution of insects has been directed or modified by the persistence of stabilized food habits and by the acquisition of new methods of securing sustenance in a living world that has itself undergone vast changes.

Since vegetarian insects are at the present time the mainstay of the entire series it is natural to suppose that this type was the first to appear on the earth, but this appears dubious when we examine it critically. The present vegetarian insects depend mainly on the seed plants, and these were not in existence till long after insects had become highly differentiated. Moreover, specialized predators, like the dragon-flies and mantids, are included among the early arrivals, quite contemporaneous with the precursors of vegetarian types.

The obvious conclusion to be drawn from these facts is that the several types of food habits have persisted without change for very long geological periods. This may be most naturally attributed to physiological or anatomical necessity. That is to say, to assume that animal foods are the only ones suitable for the proper nutrition, growth and reproduction of carnivorous insects and that plant foods are similarly required by vegetarian insects. Two plausible reasons for such an assumption readily come to mind. The restriction may be functional or physiological, depending upon the ability of the animals to utilize the materials which they eat. Or it may, on the other hand, depend upon the morphology of the mouthparts and digestive system or upon structures accessory to the feeding process such as prehensile legs or unusually delicate sense organs. Such mechanistic explanations do not suffice, so as a third alternative we may blame it on the pure cussedness of the "critters" and call it blind instinct. We shall have to leave this question in abeyance till we have considered some other aspects of the problem.

It is quite axiomatic that there is usually a high correlation between form and function in animals, meaning form in a wide sense. An extension of this idea to behavior, habits or bionomics as an integral part of "function" is justified, partly because of the necessarily loose way that these terms must be applied to the activities of animals. Also, it is impossible to find any discontinuity as we pass gradually from a purely physico-chemical type of functional activity to the complex train of events involved in the search, capture, mastication, digestion and final utilization of food by a predatory insect. Such associations are the essence of the division of labor between the parts of the animal body, and they lose their true significance once we attempt to deal with them as independent or even separable units. Nevertheless, we shall proceed to do this very thing, as there seems to be no other approach. We perceive everywhere niceties of structure that are obviously suited to the food-habits of their possessors. The asymmetrical grinding mandibles of a grasshopper are better fitted for chewing foliage than for tearing flesh, although they may draw blood from our finger if it is offered to them. The composite sucking jaws of an ant-lion suit their purpose admirably, but they would make little headway if their owner elected to eat a tasty bit of spinach. The scissor-like mandibles of the worker amazon ant are fine for a formicine pogrom, but render the ants useless in their own nursery as they can not even pick up their babies without danger of inflicting mortal injury.

Without prolonging this familiar inventory, we will agree that such profound modifications are important factors in limiting the choice of food.

Nevertheless, if we should continue to enumerate further such similar structural adaptations of mouthparts we would reach the point where the correlation was far less patent. Then we could not honestly say that a transition, for example, from predatism to vegetarianism would entail any mechanical difficulties.

Indeed, some of the most interesting and instructive evidence bearing on the evolution of food habits is furnished by the sporadic appearance of aberrant diets in insects belonging to groups that are otherwise homogeneous in this respect. The acquisition of carnivorous habits by butterflies or moths and the occurrence of a few vegetarian members among the enormous series of parasitic chalcid flies are examples of this phenomenon.

Clear-cut examples are to be found which show that there have occurred occasionally shifts in food habits whereby changes comparable to structural mutations have resulted in the appearance of vegetarian habits in a purely carnivorous group or *vice versa*. Likewise between the four types, phytophagy, predatism, parasitism and saprophagy, similar shifts may be noted. One of these relates to the very obnoxious Mexican bean beetle.

It is well known that the lady-birds or coccinellid beetles form an almost uniformly predatory group. They spend their entire developmental and adult life gobbling up helpless aphids or scale insects and hence represent the acme of virtue to the economic entomologist. To him the bean beetle is *persona non grata* for the subfamily Epilachninae into which she was born gave up the murderous habits of their ancestors and became gentle vegetarians many millions of years before it became a fad in America to visit Battle Creek for this purpose.

Together with a number of similarly degraded relatives the bean beetle forms the cosmopolitan genus Epilachna, so named because it has a fuzzy back in the place of the hairy chest that adorns the real meat-eating he-beetles. For this reason the term lady-bird is particularly appropriate. A few distant cousins forming two other genera are equally disreputable vegetarians with specific food plants. A second species, *Epilachna borealis,* is common in eastern North America, feeding on the foliage of our native wild cucumber and also mutilating cultivated squash and pumpkin vines. We have thus in our region two species, each with sharply restricted food plants. In Europe two species feed on cucurbits, usually on native palearctic species, and one of these may on occasion attack potato foliage when its preferred food plants are absent, but no European species are known to feed on legumes. Further eastward, from India to Japan, Malaya and Australia a common oriental species is often a pest of potatoes and may be frequently found feeding on other solanums and related genera, while a Japanese species feeds on both Cucurbitaceae and Solanaceae. In South America two species eat cucurbits, but none are known to eat solanums. Finally in Africa no less than five species attack cotton, a malvaceous plant that is never known to harbor the beetles on other continents except in one or two isolated cases that have been reported.

From this complicated situation we may draw several inferences. The integration of food plants and Epilachnas throughout their entire range demonstrates quite conclusively a genetic relationship in their diets traceable to a common origin of their vegetarian habits. Since that time, which was probably at least well back in the Tertiary, the genus has attained its present cosmopolitan distribution, has undergone differentiation into numerous species and split off two minor vegetarian genera. On the basis of related food-plants in adjacent areas we might even trace its migrations in space and time just as paleontologists have done for certain mammals on the basis of their fossil remains. From the foregoing it is evident that phytophagy appeared full-blown, like a structural mutation, and that the insects became addicted to particular plants which they were loath to leave even during the long period required for speciation to the present level. Other coccinellids are known to feed occasionally on foliage, pollen or fungi although retaining their primary predatory habits. The fixation of such an aberration would produce the kind of sudden change that we have just described.

Changes from parasitic to vegetarian habits are well illustrated by a number of chalcid flies of the order Hymenoptera. The members of this enormous group of minute insects are entirely parasitic, except for scattered genera or species that have turned to plants for food. In such cases this involves changed instincts in the adult wasps and an utterly strange environment for the larva, which becomes an internal feeder within the seeds or other plant tissues, sometimes with the production of galls or malformations in the host plant. Contrary to the condition in the lady-beetles, the food of the adult chalcid-fly undergoes no change. Phytophagous habits have appeared in at least six of the fifteen families that compose this group, and they are so scattered that no one can question their independent origin. A quite recent inception is indicated in some cases where the vegetarian forms are not even generically distinct from the parasitic ones.

Here again we encounter fundamental changes in larval food and imaginal instinct, but no correlated structural modifications. As a matter of fact the changes are occasionally not so great as they appear at first sight when we come to examine them closely. For example, in the Eurytomidae, the primitive members of the family are parasites of gall-making insects, so that the mother wasp must lay her eggs within the galls in order to reach the host larva that is enclosed therein. Some of the derived forms, like the abundant and destructive species of Harmolita, still lay their eggs within the tissues of grains and other grasses, but the larva is a vegetable feeder and, what is most remarkable, its larva also produces gall-like swellings of the grass-culms within which it feeds. It is thus in the same sort of immediate environment as its parasitic forbears, but is eating the plant directly.

We have mentioned the great age of the derived vegetarian habits of the bean-beetle and we could readily present evidence to show the antiquity of other similar shifts from one method of feeding to another that have taken place.

We have already referred to the development of quite independent lines of evolution in the larvae of insects without correlated modifications in the reproductive stage. This condition is involved to some extent in shifts from one type of food habits to another, but we have seen that these do not necessarily involve a high correlation between form and function, but that rather the reverse is true.

However, slow-moving, non-aggressive larvae tend to be vegetarian and the opposite holds for predatory forms. Glaring exceptions come to mind, such as the highly degenerate apodous, blind and almost jawless larvae of syrphid Diptera and certain predatory gall-midges that suck the juices of aphids for a living.

If we turn from these poor moronic maggots to the trim aphis-lion, enjoying the same diet, we are confronted with the very quintessence of adaptation: good vision, strong active legs, jaws of marvelously complicated and appropriate form and all in all a creature that looks and acts the part. "Ain't Nature wonderful" when we contemplate the inscrutable tenacity of purpose that enables all these creatures to keep "off relief" and successfully cope with their environment?

This leads us to another phase of the food problem among insects that has had a profound influence on the evolution of many vegetarian groups, especially among the social insects. I now refer to those that have established symbiotic relations with, and cultivated certain fungi and micro-organisms of several types. In this way they have been able to exploit their environment by fostering the growth of plants for food just as civilized man has done through the development of a farmer class. But we must not apply this comparison too closely, for the similarity is quite superficial. They have not bartered away their own products, wishing to acquire others in their place, but have lived the self-contained life that is characteristically theirs as insects. Consequently, they have been able to maintain themselves in a biocoenosis that excludes many undesirable meddlers and parasites.

The mycetophagous food-habits of the ambrosia beetles and the fungus-growing ants and termites are familiar to all of us. Their origin is obscure, but we may be reasonably certain that they arose through chance associations with fungi growing in the wood or other vegetable material where the ancestors of these insects fed. During the course of time, at least some of the fungi have undergone marked evolutionary changes which set them off from their non-symbiotic relatives. At the same time various structures have been developed by the insects like the bristly heads of the ambrosia beetles and instincts like the leaf-cutter ant-queen, who takes a neat little packet of the fungus spawn along when she goes in search of a new home. The precious treasure is stuck in her cheek like a quid of tobacco to be later erupted as the nucleus for the garden that is destined to nourish her future household. Here we see that in spite of the fundamental changes in food habits only slight structural or instinctive modifications are required to render the new system at once self-perpetuating.

Concerning the symbiotic relations of termites to the fauna of highly specialized flagellate Protozoa that inhabit the alimentary tract of these insects we have quite a complete picture. The ability of these symbionts to digest cellulose renders them at once absolutely necessary in the economy of the wood-consuming termites, by a direct trophic relationship. This is perpetuated by the unhygienic habit prevalent among socially minded insects of transferring food from one to another just as the communal lolly-pop insures the propagation of mumps and measles. The great age of this association is shown by the large number of termite protozoans and their differentiation into many taxonomic groups.

Concerning the intracellular symbionts that occur in many insects, we have as yet insufficient knowledge to do much more than speculate about their probable origin and present importance to the insects that harbor them.

From their irregular distribution among insects and the occasional occurrence of more than one species of symbiont in a single insect we are safe in assuming that symbionticism is of multiple origin. That they have played a part in guiding the evolution of food-habits in insects seems quite certain.

Another interesting corollary which greatly strengthens the conclusions we have reached concerning the great age of the numerous sorts of food habits may be derived from an entirely independent source. Over the course of many years I have devoted some time to purely taxonomic studies of certain Tertiary insects, especially those in Baltic amber of Oligocene age. Gradually the impression has developed that the insect fauna at that remote period, at least so far as certain groups are concerned, was not only as extensive and varied as the living one, but that many of the complex associations like myrmecophily and parasitism existed in the form that we encounter them to-day.

What in brief are the general conclusions that may be drawn from the material I have endeavored to parcel out in more or less independent categories? Has the evolution of insects been influenced and guided to an exceptional extent by their highly specialized food-habits? If so, can we point out any obvious reasons why they should differ from any other group of animals in this respect?

Many lines of structural evolution (if you will pardon the term) owe their origin and direction to the several types of food-habits. You may say this is putting the cart before the horse, but I think not, for it is the persistence of instinctive feeding habits over long periods that has provided a long, straight course for natural selection to act in the good old-fashioned way. Lest you throw me out as a nineteenth century biologist I hasten to repeat an earlier statement, that at least many of the shifts in food habits so conspicuous among insects have arisen as mutations in instinct that appear *de novo* and unexpectedly in perfectly serene ecological associations.

This is, I believe, the crux of the matter in that instinctive behavior, particularly with reference to food, is in insects of such paramount importance that its influence has transcended the cruder characteristics on which we can put our fingers and resolve into smaller particles under the microscope.