INTERRELATIONS OF INSECT-EATING INSECTS

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Scope of Entomophagy. Sweetman has found published records showing that 224 insect families, distributed among 15 of the 25 insect orders, contain species already known to live more or less by eating relatives of their own class. I estimate that about 100,000 of the million species of insects catalogued to date possess structural or physiological adaptations fitting them to make such use of their kin. These adaptive modifications for entomophagy find full opportunity for expression in the amazing variety of form and mode of life exhibited by the prolific and ubiquitous insects in their several metamorphic stages. Grubs in soil are hunted by fossorial predatory and parasitic wasps; caterpillars excavating herbaceous and woody plants are reached by the boring ovipositors and supersenses of ichneumonids; eggs, whether laid on exposed surfaces or in prepared crevices, are penetrated by the piercing mechanism of numerous microscopic serphids and chalcids, some of which even use wings as oars to swim in water where the host eggs occur; the malodorous nymphs and adults of bugs afford no defense against the ovipositors or larvipositors of tachinid flies, and neither the jumping nymphs of grasshoppers or the flying, hard-shelled adult of beetles are immune from parasitization by sarcophagid and other dipterous parasites. This small series of instances serves to show that insects, regardless of developmental stage, place of residence, mode of defense and manner of locomotion, are sought out and devoured, either at once or by small degrees over a period of time, by some entomophagous hexapod possessed of equally effective means for overcoming the defensive positions or structures of some relative. However, it would be worth while, if space permitted, to consider whether the predatory and parasitic ten per cent are actually equipped with the variety of senses and structures necessary to reach and employ as sources of nutriment all the bionomic types occurring among the non-entomophagous nine-tenths of the insect class.

Predatism and Parasitism. The relations entomophagous insects sustain to their non-entomophagous kin naturally form two classes, predatism and parasitism. Both these expressions of entomophagy are richly exemplified, and excepting some annoying borderline cases, are readily distinguished by the features presented in the following characterizations.

Predatism appears in both the major insect subclasses, Heterometabola and Holometabola. In the former, both the nymphal and adult stages are predatory, if either is so, and in the latter either the larval or adult stages, or, in some groups, both, practice predatism. The predator is mostly larger than the prey it devours or sucks out, but those equipped with grasping and inactivating devices of unusual efficiency commonly overcome insects of more bulk than themselves. In either case, the prey is killed quite promptly after seizure, and more or less consumed during the time that follows immediately. Inactivation is achieved by stinging, injection of a deadly digestive secretion through the mouth parts, or by simple mechanical biting with chewing jaws. While not a few are fitted fo watchful and patient waiting until prey comes into reach of legs or mouth parts the majority use legs and/or wings t hunt aggressively. This locomobility brings the predator over a wide terrain and hence in contact with a numerically high average diversity of prey forms and helps to account for its utilization of a different captive at each meal. Wher the adult, as well as the young, is preda cious, its faculties for locomotion resul also in the wide distribution of the eg progeny,— as a consequence the preda tory nymph and larva may hatch more o less remote from the essential prey food This imposes on them the obligation t hunt for the living insect to be victimize and ingested.

Parasitism, on the other hand, expresses itself only in the Holometabola, and with few questionable exceptions, the feeding-growing larvae alone are parasitic entomophags. Many adult female ichneumonid, chalcidoid, sphecoid and vespoid Hymenoptera, and a few true flies feed on the individuals of the species used as a host by the larva, or even on one not so used, but since these do not confine themselves to any one individual and live there only irregularly, this relation is more akin to predatism than to parasitism. The parasitic larva, particularly early in its development, is smaller than the stage of the insect it employs as a host. And because it generally avoids feeding on the vital viscera but utilizes at first only such reserve materials as nutriment in the blood or fat body, the parasite usually permits the host to live as long as, or even somewhat longer than itself, thereby assuring itself with a food supply adequate to complete its parasitic life. In a few known cases the host dies early, hence the parasite becomes obliged to feed in its later phase in a scavengerous capacity. Many adult parasitic Hymenoptera, exclusive of the true wasps, paralyze the host by stinging. Here the size differential between parasitic and host stages is such that the latter provides the food bulk needed by the former despite cessation of its growth due to inactivation. Adult parents of the parasitic larvae resemble the parental predators in their locomobility, but are generally selective, not promiscuous in their choice of hosts for reception of the egg or larva. This comparative selectivity seems to be determined on the one hand by such inherited specialized mechanisms as sensory organs and ovipositors, and on the other by the structural, physiological and bionomic limiting factors of the hosts or their habitats. This is equivalent to stating that the larva has little to do with host selection, hence, in the case of polyphagous species, the parasite seems to be adjustable to diverse hosts. Because the parasitic larva is mostly legless from hatching to maturity, its placement on the hosts by the parent is obviously essential to survival. But this principle does not apply to the considerable number of species whose first larval instars are active planidia or triungulins. However, also, these undergo a degenerative metamorphosis that leaves them increasingly sessile and helpless after the first molt.

Forms of Parasitism. Parasitism seems to assume a greater variety of forms than predatism, hence also a greater diversity of relations to their food species. The principal relations or forms have been fairly well defined to date, but numerous further variations of these are readily found among the species whose bionomics have been investigated. The chief relations are distinguished on the basis of the position the parasite assumes with reference to the host, the number of parasitic individuals or species attacking a host, and the relation of the several parasites to each other.

First, classified as to position, the larvae are ectoparasitic or endoparasitic. Although the large majority attack the host exclusively either from without or from within, a few species initiate the attack externally and terminate their development as endoparasites, and a few cases of the reverse relation have been recorded.

Second, entomophagous parasitism is solitary when but one individual attacks one host, but gregarious or supernumerary when two or more parasitic larvae attack one host simultaneously and sustain like, i.e., parallel relations to it. Gregariousness may involve a number of larvae of a single species,—a relation termed superparasitism, or the number may represent two, and possibly more, species,—a condition described as multiparasitism.

Third, where several parasitic species are associated with one host, but sustain a successive instead of a simultaneous relation to it, each successively attacking its immediate predecessor, a relation known as hyperparasitism exists. Here the primary or non-parasitic host (e.g. a leaf-eating caterpillar) is first attacked by the primary parasite (e.g. an ichneumonid); the latter, in turn is utilized as a source of food by a secondary parasite (e.g. a chalcid), thus becoming the secondary host. Hyperparasitism of the secondary degree is richly exemplified among the ichneumonid and chalcid Hymenoptera, but well demonstrated instances of tertiary parasitism seem to be infrequent. In a few cases (e.g. the chalcid *Dibrachys cavus*), the species work at one time as a primary and at another as a secondary parasite.

Fourth, since only the larvae and not the adults of Holometabola are entomophagous parasites, the parasitism described here is exclusively transitory in character; no absolute parasitism, in which all the life stages live entomophagously on or in the host, occurs. The nearest approach to the permanent relation appears in certain Scelionidae whose adults ride the adult host, thereby facilitating oviposition in the host egg. But these phoric adult forms are not known to derive their food from the parent host, hence do not constitute entomophagous parasites.

Fifth, entomophagous parasitic insects vary greatly from facultative to obligatory from the standpoint of their dependence on the host. A few seem to be limited to one stage of one species, others to a few of close taxomic relationship or of similar modes of life or habitats, whereas a large number exhibit a wider adaptability and utilize hosts of more varied taxonomy and bionomics. These several degrees of dependence may be expressed as monophagous, oligophagous and polyphagous. Predators are largely polyphagous, but some forms that stand close to the borderline between predatism and parasitism are restricted to few prey species (e.g. blister beetles predatory exclusively in the egg masses of locusts).

Phoresy. This relation, in which one species utilizes another as a carrier but not as a direct source of food, serves merely to facilitate parasitism and does not in itself constitute entomophagy. Two varieties of phoresy occur among entomophagous insects. In one, exemplified by the scelionid, *Rielia manticida* Kieff., the adult female rides largely the female, more infrequently the male, of certain mantids. When the mantid deposits her egg mass, covering it with a frothy matrix as she proceeds, the *Rielia* females descend to the host eggs and insert their own into them. It appears to be essential for success that parasitization be accomplished while the host matrix is yet soft and the host embryo exists in an early phase of development.

In the other variety of phoresy, the active first instar larva of several parasitic groups ride the adults of their hosts, which are ants, bees and wasps. These larvae hunt or wait for the Hymenoptera on the nest site or in flowers in order to ascend upon them and to be carried to the host nests. The larvae of some blister beetles are carried by bees and wasps,—largely solitary, and eat the egg and the store of pollen-nectar mixture. Several rhipiphorid beetles gain entrance thus into the nests of wasps and bees, but parasitize the larvae. Four families of Strepsiptera possibly are carried by adult bees and wasps, and also utilize the carrier or other adults of the species as hosts. And the eucharid Hymenoptera affix themselves to worker ants whose advanced larvae and pupae they subsequently parasitize.

BIONOMIC TYPES OF ENTOMOPHAGY

The following classification of predator-prey relations is based on the kind of metamorphosis, the structural or foreign preying devices and the degree of predatism exhibited by entomophagous predators. On the other hand, the parasite-host relations are divided according to the stage or succession of stages the parasite employs as host.

PREDATOR—PREY RELATIONS

I. Hyphenic Relations. There exists a considerable number of entomophags which live as predators for only a part of the entomophagous stage, or which may exhibit predatism only occasionally, and meet the rest of their food requirements as phytophags, scavengers or even as temporary parasites. These combination food practices are here designated hyphenic relations. A few examples will make the meaning clear.

The maggots of the anthomyid fly, *Hylemya cilicrura* Rond, sometimes feed upon planted seed corn and again prey gregariously on the egg masses of grasshoppers. This case illustrates phyto-predatism. A variety of this occurs in the gland-bearing caterpillar of *Lycaena* which eats foliage in its first instars and devours the subterranean brood of ants in the last phase of its development. This abrupt change in diet is compelled by the ants that feed on the glandular secretion of the caterpillar. Predato-parasitism is exhibited by the sarcophagid fly *Wohlfartia euvittata.* Its larvae are capable of opportunistic interchange between predatism on the subterranean egg masses of locusts and parasitism in the nymphs and adults of the same locust species.

II. Absolute Predatism. This category embraces the large majority of predatory entomophagous insects, and is characterized by the fact that the food taken by one or both feeding stages consists exclusively of insect prey.

A. *Hetermetabolous Predators.* It may be taken for granted that both nymph and adult are predators if either proves to be so, and that both possess some similar adaptations for pursuit, seizure, retention and ingestion of the prey. Several noteworthy but not fundamental differences in fitness for predation occur here.

The numerically dominant type displays front legs fitted with enlarged or spiniferous femora and tibiae, and, in the mantids, with greatly elongated coxae. Beside the Mantidae, many families of Hemiptera are thus equipped—including the well known giant water bugs, backswimmers, assassin bugs and ambush bugs. Yet the mechanical features of the front legs vary greatly in their efficiency. For example, the damselbugs use small non-resistant prey forms, whereas the ambush bugs capture insects having up to several times their own bulk. The latter make use of most flower-visiting insects ranging in size from gnats to bumblebees. In three years of collecting near Urbana, I have found *Phymata* feeding on representatives of 7 orders, 54 families, 131 genera and 195 species of insects. Its efficiency is due also to the deadly substance it injects into its victims, killing them in a few minutes and liquefying the body contents as it feeds.

Another method of attack is employed by the asopine Pentatomidae. Thrusting the forward-extended proboscis against the caterpillar, beetle larva or other prey, the stylets are simultaneously jabbed into the body. The needle-like mandibles then recurve laterally, holding the captive until inactivated, presumably by a lethal injection, whereupon the contents are drained out.

In the Odonata the metamorphosis is hemimetabolous, hence, the dragon and damselflies secure their prey on wing, while the aquatic naiads employ their extensible mask-like lower lip and its pair of apical hooks for securing prey and bringing it to the jaws.

B. *Holometabolous Predators.* Several variations of predatism are represented among insects characterized by a complete metamorphosis. In the carabid and coccinellid beetles and in the chrysopid, hemerobiid and sympherobiid Neuroptera both larva and adult have thysanuriform bodies, hunt aggressively in like habits, and seize their similar prey with their jaws. True these neuropterous larvae possess grasping-sucking jaws, whereas the adults have the simple chewing kind. But the adults and larvae of many other Holometabola live and feed in dissimilar ways. Striking cases are the Mantispidae which are presumably predacious as adults but whose larvae prey on small spiders in the egg sac, and the tiger beetles, which as adults employ their efficient running legs and sickle-shaped jaws to hunt aggressively, whereas the S-shaped body, hook-bearing dorsal abdominal bump and powerful jaws of the larvae form a remarkable machine for elevating soil, clambering up and down a vertical shaft in the ground and lying at the burrow mouth in wait for prey running across. Many solitary wasps not only paralyze prey by stinging before storing it in a nest for the future legless larva, but themselves malaxate the prey to obtain the body fluids as food. Such treatment may be accorded to prey to be stored subsequently or to a victim that serves solely to satisfy the adult wasp.

In another form of relation, only the adult uses prey as food. The calliphorid genus *Bengalia* feeds on winged termites or robs ants carrying their brood; several genera of sawflies prey on the larvae and pupae of beetles, and other insects; mecopterous hanging flies suspend themselves by the front legs to capture Diptera with the dangling hind legs, and numerous ichneumonoids, parasitic as larvae, jab their ovipositors into host insects and imbibe fluids thus liberated, not a few constructing feeding tubes to facilitate the process where the host lives under cover. The larvae in these instances are largely or wholly non-predatory.

Again many species prey only as larvae. I do not include the solitary wasps here; presumably the adults, like the larvae, will be found to feed largely if not entirely on insects or other small arthropods. Among the ichneumonoids and chalcidoids, which are predominantly parasitic, occur a few species predatory as larvae. A *Habrocryptus* consumes successively the eggs and larvae from several adjacent cells of an andrenid bee; certain *Spilocryptus* destroy the numerous larvae of *Pteromalus* parasitic in the chrysalis of the cabbage butterfly, etc. Also nonhymenopterous instances are known. The larvae of some mosquitoes eat aquatic insect larvae; the remarkable worm lion, *Vermilio vermilio* L., a rhagionid fly, imitates the pit-making ant lions in its mode of preying; most syrphid larvae feed on aphids, whereas the adults utilize plant fluids, honeydew and the like, and not a few minute caterpillars regularly prey on various Coccidae as contrasted with the nectar-siphoning practice of the adult moths. And while many blister beetles are hyphenic in that the larvae first prey on the egg or larva, then on the stored pollen-nectar mixture of bees, the larvae of *Epicauta* and some species of *Mylabris* and other genera, destroy masses of grasshopper eggs, as do also the maggots of several bee flies.

III. *Opportunistic Feeders.* Studies of stomach contents indicate that caddis worms, an entirely aquatic order, use almost any manageable organic matter either in a state of life or decay. This seems to be true of both those fashioning portable cases and the trapnet builders, although the more primitive families of the latter group display a feeble preference for prey. In any case, however, prey forms only a variable part of the total diet.

TYPES OF PARASITE—HOST RELATIONS

The larvae of Holometabola constitute all the true parasitic entomophagous insects. The adults that practice phoresy seem not to feed on the parent host which they ride, and the behavior of the flies and Hymenoptera that feed on fluids released by thrusts of the ovipositor comes closer to predatism than parasitism.

Parasitic entomophags form a sizeable minority of the order Diptera, at least half of the order Hymenoptera and all the small tiny order Strepsiptera. Also a few beetles and Lepidoptera are entomophagous parasites. Most of the Diptera seem not to possess a piercing ovipositor, hence place their eggs or young larvae directly upon the host or at the entrance to the shaft or burrow occupied by the prospective victim. However, the female hymenopterous parasite is invariably equipped with a boring ovipositor which is employed to penetrate either the body wall of free-living hosts, or the protecting cover and, in some cases, the host as well, that lives in some sort of shelter such as a cocoon or plant cavity. Accordingly, the legless majority of the larvae find themselves on or in the host when they begin their active life. However, both the Diptera and Hymenoptera include a considerable number that are of unusual interest for their practice of depositing numerous eggs remote from the host. Parasitization then depends on (1) ingestion of the egg by the caterpillar host as it eats foliage or (2) the locomotor or waiting activity of the young larvae, that attach to and bore into the host when it is reached. The primary larvae of the Strepsiptera seem to rely on their fleet-footedness or a carrier to bring them to the new hosts. In the former instance, the hosts are saltatorial Homoptera, in the latter aculeate Hymenoptera.

The classification of parasite-host relations presented below is based on the host stage or succession of such stages the parasitic larva requires for its development. Usually also the egg, and in many cases the pupa, are found on or in the host, whereas the adult lives free.

I. Parasites of Hetermetabolous Nymphs and Adults. Many Hymenoptera and Diptera and some Strepsiptera use this subclass of insects as hosts. Ichneumons and chalcids commonly parasitize the nymphs and adults of both Hemiptera and Homoptera, and the dryinid wasps mostly initiate their attack within jumping Homoptera and complete it externally in a sac formed of the larval exuviae. Some sphecoid wasps, typified by the cicada killer, *Sphecius speciosus* store but one paralyzed insect, hence fall within the realm of parasitism, whereas most species store two or more prey insects hence must be rated as predators.

The chironomid fly, *Trissocladius equitans* Claas. is ectoparasitic on a may fly nymph, an aquatic host; the planidia larvae of cyrtid flies stand up by aid of a caudal disc in order to attach to spiders; certain sarcophagid flies larviposit on grasshopper nymphs or even the flying adult, and the tachinid *Trichopod* and others inject eggs or larvae int various terrestrial bugs.

Members of several strepsipterous fam lies endoparasitize jumping Homopter: The active primary larva issues from puparium-like case occupied by the grul like female on the old host and moun new nymphs of the host species, borin into it at the intersegmental membranes and absorbing nutriment from its blood. In the final or seventh instar, the larva pushes the cephalothorax out between the abdominal segments of nymph or adult. The apodous female undergoes no recognizable pupal stage, whereas the male does so and bears legs and a pair of functional wings.

The minute caterpillars of several moths parasitize various coccid Homoptera internally. The Epipyropidae, however, should probably be regarded as scavengers, not as entomophags, because their food, in observed cases, consists of wax or excretions derived from their homopterous hosts.

II. Parasites of Insect Eggs. Most of the numerous Mrymaridae and Scelionidae, and some other miscroscopic Hymenoptera, pass their entire egg, larval and pupal stages exclusively as solitary endoparasites of the eggs of other insects. However, a few species of this order that attack eggs laid in masses, e.g. Mantidae, do so externally. Again, *Trichogramma* species are gregarious, the number of individuals developing in one egg being correlated with the size of the host. More than 150 host species of six orders are known to be used by *T. evanescens* Westw.

III. Parasites of Insect Larvae. Insect larvae doubtlessly are utilized to a much larger extent as hosts than any other metamorphic insect stage. Numerous examples are known to occur among the Hymenoptera and Diptera and a few in the order Coleoptera, and their larval hosts belong principally to the Lepidoptera, while the beetles, flies and Hymenoptera also appear on the list. Altogether they represent almost every kind of relation to the host, living outside or inside singly or in numbers, and as primary or secondary parasites. In addition, the female ichneumonoids, chalcidoids, parasitic vespoids and others may puncture or malaxate the host and feed on it previous to oviposition, or, in some cases feed without subsequently placing an egg. The above wasps and some ichneumonoids paralyze the host, either in part and temporarily, or wholly and permanently, before depositing the egg.

A parasitizing process of unusual interest appears in the primitive Trigonalidae. The numerous microscopic eggs are placed in foliage remote from the hosts, and the larvae have been reported as secondary parasites of ichneumons in caterpillars or sawfly larvae, and as primaries in the larvae of *Vespa*. According to observations, the trigonalid eggs are ingested by the caterpillar or sawfly as they eat foliage, whereupon the small parasitic larva attacks the primary ichneumonid parasite already present in the primary host.

However, the *Vespa* grub does not eat foliage and contains no ichneumonid primaries. How, then, does the trigonalid gain entrance into the wasp host? Clausen theorizes plausibly that the parent wasp fed parts of trigonalid-parasitized caterpillars or sawfly larvae to her grubs, a mode of feeding practiced generally by social vespoids. Thus, he believes, the parasitic larva was ingested along with the prey larvae provided by the parent,—a simple mechanical, incidental transfer of the trigonalid from its original host to a second.

The Eucharidae, Perilampidae, a number of tachinid flies, and others likewise place numerous microtype eggs on leaves, buds or in soil irrespective of the host's location. The parasitic, active first instar, primitive-type larva then gains entrance in one of several ways: ingestion by the host of the egg along with its plant food (some Tachinidae); the locomotor activity of the larva itself (Perilampidae and some Tachinidae); exploratory movements of the larva while supporting itself caudally on the chorion of its egg during the wait for the caterpillar host (some Tachinidae), or by riding a worker ant whose intranidal larvae or pupae it uses as hosts (Eucharidae). The known Perilampidae are secondary parasites on ichneumons or tachinids in caterpillars. In all these cases, as also in the Trigonalidae, the larvae assume progressively reduced forms during their ontogeny, thus displaying various degrees of hypermetamorphosis.

IV. Parasites of Prepupae or Pupae. While the lines between parasitism of larvae and of pupae are naturally not sharply drawn, some Hymenoptera and a few Coleoptera develop at the expense of only the pupal stage of their hosts. For example, the chrysalids of Lepidoptera, the pupae of ladybeetles, lacewings and caddis flies, and the puparia of Diptera form the hosts of many ichneumonoids and chalcidoids, and the active running primary larvae of aleocharine Staphylinidae complete their parasitic life within the puparia of cyclorrhaphous flies.

V. Parasites of Adult Holometabola. A few examples are cited to elucidate this relation. First, *Elasmosoma* inserts her eggs into the abdomen of *Formica fusca* within the nest, *Syrrhizus* parasitizes *Diabrotica* beetles, and *Perilitus coccinellae* Schr. uses lady beetles exclusively. These are braconid Hymenoptera. In the order Diptera, we find certain ceratopogonid flies suck blood from the wings, or other body parts, of caterpillars, dragonflies, etc., while a conopid makes the ovipositional attack on wasps and bees in air, and the tachinid, *Chaetophleps setosa* Coq. likewise seems to attack *Diabrotica* when these are on wing exposing the vulnerable dorsum of the abdomen. The Strepsiptera concerned here are endoparasitic in wasps and bees. The procedure in parasitization and development is similar to that of those which utilize homopterous hosts, with the possible exception that the primary larvae may practice phoresy which facilitates finding new hosts, particularly such as are social.

VI. Parasites in Consecutive Host Stages. This category embraces not a few ichneumonoid, chalcidoid and even serphoid Hymenoptera which utilize either two or three successive stages of holometabolous hosts to accomplish their life cycles. Three such combinations have been shown to be employed to date, namely egg-larva, larva-pupa and egg-larva-pupa. The hosts include Lepidoptera, Diptera and Coleoptera. For example, the chalcidoid, *Tetrastichus asparagi* Cwf. inserts an egg into that laid by the common asparagus beetle on its food plant. The parasite does not interfere with the embryonic development of the host, but makes its development at the expense of the beetle larva. The latter is permitted to complete its growth and to proceed normally to the soil and form the usual pupal cell. But its life is terminated before pupation by the final feeding activity of the endoparasitic *Tetrastichus* larva.

Representatives of the chalcidoid genera *Ageniaspis*, *Encyrtus*, *Copidosoma*, *Berecyntus* and *Litomastix* similarly utilize the egg-larval stages of Lepidoptera, whereas the serphoid genus *Platygaster* may employ the egg-larval host sequence of tiny nematocerous Diptera; these genera are, in addition characterized by polyembryony that works itself out in the larval host.

Several examples are known also in the Braconidae and Ichneumonidae. Where the host relation involves the larva-pupa succession, the parasitic larva hatches in the larval host but, in some cases, larval feeding and development is delayed until the host attains the pupal period. In such instances it is believed the histolytic changes accompanying pupation constitute the stimulus necessary to initiate parasitic activity. It may therefore be surmised that this fact, plus the unfavorable size differential between parasite and host, explain at least in part the need for a succession of host stages required in the above instances for the success of the parasite.

CONCLUSION

An extensive panorama of entomophagous food relations has passed in quick review. Only a small fraction of the known cases exemplifying the several relations described are cited above. Moreover, a considerable number of confusing exceptions have been omitted in the interest of simplicity. Readers interested beyond this brief attempt to portray the diversity and fascination inherent in the bionomic relations of entomophags and their prey and hosts are invited to consult the several more comprehensive treatises cited below.

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