

Parasitism in Insects

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INTRODUCTION

MOST animals have their natural enemies which are usually grouped into two classes: predators and parasites. The former only attack for food and after feeding for a short while on their victims, which are usually killed in the process, give them up. The latter may attack for egg-laying as well as for food and their association with their victims is of a more permanent nature and generally lasts till the parasite reaches the adult stage. The distinction between predators and parasites is sometimes arbitrary and many workers often regard them as merely two extreme examples of a type of life in which one insect lives at the expense of another.

Parasitism is more common among insects than perhaps in any other group of the animal kingdom with the exception of the helminth worms. In its simplest form one insect parasitises another which is not a parasite (primary parasitism). When the attacked insect is itself already a parasite the phenomenon is known as hyper- or secondary parasitism. Sometimes two or more species of insects attack the same host simultaneously leading to multiple parasitism or, according to some authors, super-parasitism, though the latter term is better restricted to cases where the attacking insects belong to the same species. Most dipterous and hymenopterous parasites often eventually destroy their hosts and, on this account, are termed by some authors as 'parasitoids' to distinguish them from other parasites whose presence to their hosts usually does not prove fatal.

ORIGIN OF PARASITISM

It is generally believed that insect parasites originally evolved from free living and phytophagous forms which took the first step towards a parasitic existence by living in harmless association with other animals. Later, physical proximity, habits of cannibalism, which gradually widened to include other species, a kind of rough similarity between certain plant and animal foods, such as lichens, coccids, etc., induced one insect

to feed on the other. The predatory habit thus acquired was maintained so long as the predator did not find enough nourishment on one host and had to attack several of them but if the host was large enough to supply the full requirements of its enemy the necessity for changing the host vanished and a more lasting association leading to a parasitic mode of life came into existence. A border-line case is that of two micro-moths, *Zenodochium coccivorella* Ch., and *Euclemensia bassettella* Cl. which parasitise coccid hosts (*Kermes* sp.). The caterpillars of these moths each live on a single *Kermes* individual though the latter's substance is hardly adequate to sustain the parasite till it is full grown. It is conceivable that the caterpillar would have had to attack more than one host if the substance afforded by a single host was much under requirement. In other words, parasitism here is only just in advance of predatism (Balduf, 1938).

Parasitic life among Epipyropidæ, a group of small moths, seems to have evolved in an analogous manner. It is now certain that the ancestors of these moths were phytophagous and fed on plant juices as do their homopterous hosts of to-day. The epipyropid caterpillars found equally palatable food in the anal and other excretions of the homopterous insects living alongside with them, from which it was a short step to living on the bodies of the latter and not only obtain their excretions very much near at hand but also get the benefit of shelter and transport. Parasitism in Epipyropidæ, therefore, is considered to be of a very simple order, not advanced yet to the higher specialisations of efficient parasites (Balduf, *op. cit.*).

Change in feeding habit led to change in body structure. In the attacking insect certain morphological characters became unnecessary and in turn certain others were developed to suit its new requirements. The bed bug and the flea, for instance, seem to have lost their wings as a result of parasitic existence. Among bird lice the eyes are greatly reduced or even absent.

obviously because, living as they do on the cuticle and feathers of birds, they hardly need them. In many first instar hymenopterous larvæ there is complete absence or at least feeble development of the spiracles and the tracheal system and respiration is cutaneous, the blood of the host providing the necessary oxygen. An anal vesicle or caudal appendage is present in the early instar larvæ of *Exochilum*, *Limnerium*, *Dinocampus*, *Meteorus*, etc., which is undoubtedly respiratory in function though it later gets absorbed in the body as the larvæ develop and begin respiring by means of spiracles.

Another view regards parasites not so much the creatures of necessity as the natural result of an intelligence in insects, with predatory instincts, following up an advantage. According to this view parasitism is an achievement in which the mode of living illustrates specialisation rather than degeneration. Obviously the greater the specialisation for extracting nourishment from the host for the longest period of time the more successful is the parasite. Indeed the perfect parasite will not kill its host as by doing so it will only starve itself, and the one that would kill its host will not be so well evolved as the other that would not. Hermes (1926) cited a number of cases to show that many parasites which habitually live and breed on their hosts are not so troublesome to the latter as those that attack only occasionally. The mosquito, *Anopheles maculipennis*, which is a vector of the causative organism of malaria, is 'benign' in its bite but *Aedes dorsalis*, a wild salt marsh species, is viciously irritating, though harmless.

SOME TYPES OF PARASITISM

From the standpoint of their feeding habits, parasites are divided into two categories: endoparasites, which feed inside the body of their hosts, e.g., many dipterous and hymenopterous parasites, and ectoparasites which feed on but live outside the body of the host, e.g., the ticks and lice of various birds and mammals and many braconid parasites of insects. Among insects Diptera and Hymenoptera provide the commonest examples of parasitism. Three families of beetles and two of moths also contain parasitic species while stylops or Strepsiptera are exclusively parasitic. Most ectoparasi-

tic insects are drawn from the order Anoplura. In the groups just enumerated several families, e.g., Cecidomyidæ, Anthomyidæ, Evanidæ, Cynipidæ, Staphylinidæ, etc., contain both predatory and parasitic species.

Parasites depend for their existence on their hosts and have, therefore, adapted themselves, in many cases very finely, to the habits and characters of the latter. Perhaps the most varied examples of adaptation are met with in the tachinid flies which include oviparous as well as larviparous species. In America the females of *Sturmia scutellata*, a parasite of the gypsy moth, lay their tiny black eggs on the foliage which are swallowed by the caterpillars and the hatching of the parasitic egg actually takes place inside the alimentary canal of the host. The females of another tachinid, *Prosenia siberita* Fabr., a species widely distributed in Europe and Asia and introduced in America to control the Japanese beetle, deposit their larvæ on the soil which wander about till they find host larvæ into whose bodies they penetrate and develop. In such cases the parasitic larvæ have to be active migratory forms well adapted to seeking their hosts (Sweetman, 1936).

The majority of hymenopterous parasites, however, lay their eggs in or on the eggs, larvæ, pupæ and even adults of their hosts. Many species of Mymaridæ, Trichogrammidæ and Seclionidæ parasitise the eggs of various bugs, moths, butterflies, beetles, flies, grasshoppers, mantids, etc. One of the most important of the egg parasites, is the famous *Trichogramma minutum* (Riley), a cosmopolitan species parasitising an unusually large variety of hosts in the egg stage and employed extensively to control codling moth, moth borers of sugarcane and several other pests in various countries. Many braconids and ichneumonids parasitise the larvæ and pupæ of their hosts. *Melchior nursei* Cam., a well-known parasite of the spotted bollworms of cotton in various parts of India, lays its eggs on the body of the host pupa by puncturing its cocoon. Parasitisation of the adult is rather less common than those of the immature stages but the braconid genera, *Perilitus* and *Dinocampus* are known to parasitise some adult beetles. An interesting case is that of a cecidomyid (*Endopsylla* sp.) in Scotland, which lays its eggs on the wings of *Psyllia mali* race

peregrina. The larvæ that hatch feed for sometime ectoparasitically on the body of the host and then bore into the abdomen near its base and develop endoparasitically till full grown when they come out of the body and pupate in the soil (Lal, 1934).

HOST SELECTION

The number of hosts which a parasite will attack is often limited and is at times confined to only one species which means that it exercises some discrimination when out for oviposition. Parasites must select their hosts and before they can select they must find them. It seems now generally agreed that the first concern of a parasite is not so much to seek a host as the particular type of environment in which it is likely to be present and then only to look for it. In doing this the parasite restricts the field of its search and increases the chances of its coming into contact with a suitable host.

The factors that guide parasites in host finding and host selection have been subjects of great controversy and some experimentation. It was believed by Thompson and Parker (1927) that the laws underlying the problems of host relations could not be scientifically ascertained and expressed in scientific terms, a view which was refuted by Salt (1935) as a result of his work on *Trichogramma evenescens*. Salt showed that the chief criterion which guided an ovipositing female of this species in selecting its host was that of size since out of several objects selected and attacked by the parasite many were unsuitable and from which no progeny could develop. More recently Laing (1937) has analysed the factors for host selection and concluded that not only *Trichogramma* but many other parasites, e.g., *Alysia manducator*, are first attracted by the qualities of an environment irrespective of the fact whether their host happens to be present in it or not, but within the environment itself sense of sight is their chief guiding factor. To the extent that sight helps the parasites to distinguish size Laing's conclusions may be said to agree with those of Salt.

Ulyett (1936) on the other hand, working with the chalcid, *Microplectron fuscipennis* Zett., and its tenthredinid host, *Diprion* sp., showed that this parasite could exercise a high degree of discrimination between

healthy hosts and those already containing well-grown parasitic larvæ, although a parasitised host merely harbouring an egg of the parasite was distinguished. This discrimination was ascribed to the presence or absence of movements of the host larva and it was also inferred that a definite proportion of every host population was not subject to random oviposition. Ulyett, therefore, concluded that "a wholly mechanistic view of host selection is untenable and that the underlying basis of behaviour is of a psychological nature".

EFFECTS OF PARASITISM ON HOSTS AND PARASITES

The presence of a parasite is undoubtedly inimical to its host but the extent of this injury varies widely, from simple annoyance to death. Most of the biting lice live upon their bird hosts for a long time merely causing deep irritation to their skin by the scratching action of the claws of their feet. Some parasites, although they themselves do not prove fatal to their hosts directly, may cause the latter's death by transmitting various disease germs. The louse, *Pediculus humanus* L., is known to transmit typhus and relapsing fevers and some other human diseases through punctures of the skin made with its mouth parts or by its infected excreta coming in contact with an abrasion on the skin. Many Ichneumonidæ, Bethyliidæ, Scollidæ, Tiphidæ, etc., habitually sting and paralyse their hosts before ovipositing in them and in the process even kill them. *Tiphia popilliavora* Roh., a parasite of the grub of the Japanese beetle, stings its victim so many times before egg-laying that the latter dies through mere mechanical injury.

Usually some distortion or change of colouration of the host occurs sooner or later after parasitisation. Psyllid nymphs, as a rule, when parasitised by encyrtids turn brown and become bloated. Many aphids, e.g., *Aphis rumicis*, when parasitised by species of *Pachyneuron* and other chalcids, turn black. The effects of parasitisation of several hymenopterous and homopterous genera by stylops are now well known and in many cases are so characteristic as to be known by the special name of 'stylopisation'. In the bee genus *Andrena* some curious results follow parasitisation by the female stylops. The 'stylopised' bee has a more globular abdomen and a shorter

head: in addition certain secondary sexual characters are also affected. The parasitised female bees have the pollen collecting apparatus so reduced that their hind legs resemble those of the males, the sting is shortened in size and often the yellow colouration of the male is acquired. In the male the copulatory apparatus suffers atrophy. Indeed in *Andrena* the changes due to 'stylopisation' have been regarded not merely degenerative but as inversions of development in which the female acquires certain characters of the male and *vice versa*.

Several cases are on record in which the rate of development of a host insect is accelerated by the presence of a parasite 'Stylopised' insects of several species of *Andrena* (*A. crawfordi*, Pierce, 1909; *A. wilkella*, Perkins, 1918) were shown to emerge earlier than the healthy bees. According to Alston (1920) the larvæ of the blow-fly, *Calliphora erythrocephala*, were stimulated to immediate pupation if attacked by the braconid, *Alysia manducator*. The larvæ of a chloropid fly, *Lipara lucens* Meigen, which are full grown in autumn, normally hibernate in winter and pupate in the following May but pupation may ensue in autumn if the larvæ are parasitised by the braconid, *Polemon liparæ* Giraud (Varley and Butler, 1933). In a general discussion of this phenomenon the authors conclude that the effect of parasitisation in such cases is to provide a shock which can be and has been simulated mechanically and in nature with very much the same results.

The above instances have dealt with the effect of parasites on their hosts. Recently Salt (1937) has recorded the case of a host affecting its parasite. The eggs of *Sialis lutaria* (Neuroptera) are parasitised by *Trichogramma semblidis*, the males of which occur in two forms, both of which are equally large but differ in important characters and are not connected by intermediates. Rearing experiments with four different hosts, including the original one, showed that males bred from the original host were of apterous form while those reared from the other three (all moths) were of winged form. According to the author the dimorphism has a nutritional basis but it is not the amount but the kind of food that produces the difference. Here, therefore, it

is the host that determines the character of the emerging parasite.

HYPERPARASITISM

Primary parasites are about as liable to parasitisation by their insect enemies as the hosts they themselves attack but while secondary parasitism is quite common parasitism of a higher order, tertiary, quaternary, etc., is progressively rare. It seems that sometimes insects come to attack primary parasites but alight upon a secondary parasite and find themselves actually in the role of a tertiary parasite. It is also doubtful if some cases of tertiary parasitism are not merely cases of multiple parasitism in which several parasites try to live in the same host. In this struggle some of the parasites are naturally killed and the survivors, though they themselves are not directly responsible for the deaths, get the appearance of secondary parasites. The prevalence of this competitive parasitism creates considerable confusion in the determination of the exact status of a parasite, a matter of great significance in the biological control of insect pests.

The extent of hyperparasitism, a term which may include all grades of parasitism higher than primary, though some authors restrict it only to secondary parasitism, in nature depends largely upon the degree and the period of exposure or concealment chiefly of the primary parasites, specially in the cocoon stage. In general hyperparasites are not as discriminating in the selection of their hosts as primary parasites and this fact accounts for the great abundance of hyperparasitism in the field. Thus even one species, *Perilampus hyalinus*, may parasitise hosts belonging to groups Tachinidæ, Braconidæ, Ichneumonidæ, and Chalcidoidea.

CONCLUSION

The problems of parasitism in insects are important in relation to several branches of natural history and in applied entomology. Their study sometimes leads to interesting conclusions about the phylogeny of host insects. Similar parasites, at present, attacking very divergent groups of insects are taken, along with other evidence, to denote a common ancestry for the latter. Questions of multiple and hyperparasitism furnish interesting material for the study of insect

populations while the interrelationships between hosts and parasites provide valuable aid in the understanding of insect behaviour. In protecting crops and domestic animals from their pests, both insect and weed, the method of controlling the latter by means of their natural enemies is coming to the fore every day but the very complex problems involved make it essential to study and thoroughly understand the parasite in relation to its hosts and environments. Few groups of insects seem destined to be more important than those collectively grouped as parasites.

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Nicotine and Citric Acid Content in the Progeny of the Allopolyploid Hybrid *Nicotiana rustica* L. × *N. glauca* Grah.

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ALLOPOLYPLOID di-*rustica*—di-*glauca* originated by chromosome duplication in the first generation of the hybrid *Nicotiana rustica* ($n = 24$) × *N. glauca* ($n = 12$).¹ It had 72 somatic chromosomes and was partially fertile and dwarf in size, while the F_1 -hybrid developed normally and was self-sterile.¹ In studying the procedure of the meiotic processes in the allopolyploid di-*rustica*—di-*glauca* hybrid, I found quite often the appearance of multivalent chromosomes (quadrivalents and trivalents with univalents) during the first meiosis due to auto- and allosyndesis. I shall mention here that allosyndesis between *glauca* and *rustica* chromosomes was also observed in the F_1 -hybrids which formed a variable number of bivalents (sometimes until 12), some of them being heteromorphic. The appearance of univalents and rarely one bivalent in *N. rustica* ($n = 24$) haploid² indicates that bivalents in F_1 -*rustica* × *glauca* result from allosyndetic pairing, i.e., from chiasma formation between *N. rustica* (r) and *N. glauca* (g) chromosomes.

Allo- and autosyndetic chiasmata (r-r-g-g) of the multivalents formed among *N. glauca* and *N. rustica* chromosomes in the allopolyploid di-*rustica*—di-*glauca* are

responsible for the formation of unequal gametes. The inconsistency, i.e., the segregations in the subsequent generations of this allopolyploid is consequently due to the exchange of parts between *N. rustica* and *N. glauca* chromosomes in the multivalent groups as it was clearly shown for the allopolyploid *N. glauca*—*Langsdorffii*.³

The progeny of the dwarf allopolyploid *N. rustica*—*glauca* differed enormously in respect to their morphological, physiological and biochemical characters. In the second, third and fourth allopolyploid generation (A_2 , A_3 , A_4) there were dwarfs (about 40 cm.), giants (about 250 cm.), and all transitional degrees between these two extremes. Similar amplitudes of variations were observed in the leaf sizes and shapes, the flower sizes and shapes and the vegetation periods, the latter and the length of the petioles showing even a transgressive segregation in respect to those of the parental forms. There were segregates that developed very rapidly and formed a larger amount of green mass (leaves and stems), than the parental species *N. glauca* and *N. rustica*. A more detailed description of their morphology and cytogenetic behaviour will be given elsewhere. I shall call attention here to the alkaloid and citric acid