The Amateur Entomologists' Society

Rearing Parasitic Hymenoptera

by

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General Editor MIKE BONSALL

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INTRODUCTION

IF, LIKE J.B.S. HALDANE, you thought God had an inordinate fondness for beetles (of which there are just under 4000 British species) pause a moment to reflect that there are more than 5500 species of parasitic Hymenoptera in Britain, which is about a quarter of all British insects. They are all very specialised insects, and they do some almost unbelievable things. For example, some lay eggs that swell to 1000 times their volume before hatching; others produce whole broods, which in extreme cases may number thousands, from just a single egg laid; some inject venoms that, after a delay, make their hosts change their development; others insert virus-like particles, which they produce in their reproductive tracts, along with their eggs, to interfere with the host and help their larvae develop; and almost all can choose and control the sex of their offspring. Yet parasitic Hymenoptera remain the least known, least studied, and least understood part of the British insect fauna - we do not have a really good knowledge of what species occur here and, for the very large majority, literally nothing is known of their precise host associations.

This booklet aims to provide enough background information on the general biology of parasitic Hymenoptera to enable relatively inexperienced entomologists to understand what is likely to be going on when they rear them accidentally, and especially to give practical advice on how to rear and study parasitic Hymenoptera for those who wish to do so deliberately. Perhaps most importantly of all, I will try to stress how to ensure that the best scientific advance can be made from the results in either case. I also hope that it will encourage a general interest in parasitic Hymenoptera, in particular so that these extremely specialised and vulnerable insects are given the much greater conservation attention that they need and deserve, as our fauna is undoubtedly diminishing much faster than we can appreciate at present.

Parasitic Hymenoptera belong to the life-style group (guild) properly called parasitoids. Put at its simplest, insect parasitoids obligatorily feed as larvae on the single body of another animal (nearly always an immature insect) which is killed by the association and which provides all the food necessary for the full development of the parasitoid. In the vast majority of cases the adults are free-living and search for the hosts on or in which to lay their eggs. The word "parasitoid" has now become generally used to describe this life-style, in distinction from "parasite"

which is usually reserved for an organism that is not inevitably lethal to its host. Nevertheless, "parasitic wasp" and "parasitic Hymenoptera" are terms still often used and widely understood. They are also acceptable because they are merely descriptive, like "aquatic insect", without any classification connotation. In contrast "Hymenoptera Parasitica" (or just "Parasitica") is a term that has largely fallen from use as it incorrectly implies that there is a classification system that includes "Parasitica" as a natural (monophyletic) group. The evolutionary history (phylogeny) of the Hymenoptera is far from clear, but most systematists now recognise that dividing the order into suborders is difficult because some of the major groups that used to be regarded as suborders arose from within others, rather than as a clean split at the origin of each. Thus the old suborder "Symphyta" (= sawflies) is almost certainly not really a whole unit, but rather a grouping that includes somewhere within it the (extinct) ancestor of the suborder Apocrita. In contrast Apocrita is, in fact, regarded as a whole unit (monophyletic group) that not only had a single ancestral origin but also includes all of the descendants of that ancestor. The Apocrita consists of all the Hymenoptera that are not "Symphyta", and they used to be split up into "Parasitica" and Aculeata. But we now believe that only Aculeata is a whole unit (monophyletic group) because it arose from somewhere within the diverse old-style "Parasitica", which is thus not a natural group including all its descendants (i.e. it is paraphyletic). So of these four names ("Symphyta", Apocrita, "Parasitica" and Aculeata) only Apocrita and Aculeata are natural groups and the other two terms, though in some contexts still very useful, are best used with inverted commas. Even then, Apocrita and Aculeata are not of equal rank, because the former includes the latter.

There are lots of groups of insects that are parasitoids outside the Hymenoptera, particularly in the Diptera in which the large and important family Tachinidae is one of the main groups of parasitoids encountered by entomologists in general. To some extent the principles outlined in this booklet will apply to all parasitoids, but mainly it is directed towards parasitic wasps. Some of the Aculeata are in fact parasitoids, or have life-styles that are very similar, but the general thrust is directed towards the other Apocrita. The few phytophagous groups of Apocrita such as most gall wasps (Cynipidae) will not be covered by this treatment of "parasitic Hymenoptera".

Almost all groups of terrestrial insects in Britain are subject to parasitism from parasitic Hymenoptera at some stage in their lives, but

the groups most heavily attacked are insect eggs (fairly generally, provided they are durable and can be reliably found), the larval and pupal stages of the terrestrial endopterygote orders (that is, the groups that have distinct larval and pupal stages, like Lepidoptera, Coleoptera, Diptera, Neuroptera and indeed Hymenoptera), and also the relatively sedentary plant-feeding exopterygote order Homoptera. In general, parasitic Hymenoptera do not attack adult endopterygote insects, but there are just a few that do - especially one group of Braconidae (the subfamily Euphorinae) that is mostly associated with restricted groups of Coleoptera, Hymenoptera and also Hemiptera and Psocoptera (at least in Britain: a few other orders are attacked elsewhere in the world).

There is a fairly clear primary adaptation to endopterygote insects underlying most of the main radiations of parasitic Hymenoptera, and exopterygote insects have only attracted much parasitism when their life-style is particularly easily exploited. On top of this bias towards endopterygotes, however, what influences whether or not the early stages of an insect will be parasitised by Hymenoptera seems to be very much to do with how reliably it can be found. In general, if an immature terrestrial insect is easy for humans to find by searching, then parasitoids will have easily latched onto it. In addition, however, parasitic wasps have well developed chemical senses. Thus, potential host species that live on or inside plant tissue and leave a clear physical or chemical indication of their presence are easy for adult parasitoids to detect, and in consequence they have, over evolutionary time, attracted their attentions and provoked their specialisations. Some parasitoids can also sense the presence of the slow moving wood-boring hosts they attack (possibly "hearing" their chewing), enabling them to exploit that niche even more effectively. On the other hand, many highly mobile larvae that live in chemically concealing substrates, like water, wet mud or the soil, largely or entirely escape. However, some aquatic insects are exploited by parasitic wasps; often in the egg stage (e.g. the larger aquatic beetles and Odonata by tiny Chalcidoidea that are reputed to "swim" underwater) or sometimes in the prepupal or pupal stage (e.g. some Trichoptera by an ichneumonid, *Agriotypus armatus* (Curtis), that lays its egg in the hosts' cases fixed to submerged rocks for pupation, and can develop inside them by using a special gas-exchange breathing device called a plastron). If aquatic insects leave the water to pupate in a conspicuous way - as do, for example, whirlygig beetles (*Gyrinus* species) - then parasitoids will respond to them just like anything else that is, for a sufficient time, quite easily discovered.

Rearing parasitic wasps as a deliberate activity is extremely rewarding - if it is done carefully, with the results being observed and recorded accurately. Undoubtedly the easiest way to become interested in rearing and studying parasitoids is from a good knowledge of a major host-group, so that the ability to find, identify, and rear the immature hosts is already in place. That is obviously helpful from a practical point of view, but it also highlights an extremely important consideration that everyone rearing parasitoids ought to keep strongly in mind. Simply, it is this: the host associations of parasitoids are so poorly understood that, like it or not, when you rear and preserve parasitoids you are at the frontiers of knowledge and potentially contributing scientific data that you should presume will be trusted and *used* at some stage, by someone or other. This brings with it a scientific responsibility: the greatest care needs to be taken to avoid providing mis-information by mistake, which will confuse the true picture we are striving to see. If the adult parasitoid is preserved it is there to be seen and re-identified as often as necessary, but the identity of the *host* is a one-off event not so easily verified, and I shall return again and again to the need for care over this. For now I would like to emphasise it in its most positive form: if you do it well and strive for accuracy, the scientific contribution you can make by rearing parasitoids is considerable.

Most of the rest of this booklet will provide advice about how to achieve good results in the actual rearing you do, how to avoid mistakes, and how to preserve and study the parasitoids you rear, including what to record on the data labels and how to express various levels of certainty about the host. The bare essentials of what will be covered are worth listing here in the introduction as a guide and summary.

General principles:
- apply all the control you possibly can (p. 17)
- express doubt fully - make no assumptions (p. 20)
- know something about the host group (p. 21)
- understand the limitations of what you are doing (p. 21)

Efficient practices:
- work in "biological time" (p. 25)
- standardise your rearing equipment (p. 26)
- ensure great cleanliness (p. 27)
- prevent putrefaction and moulds (p. 28)
- keep imaginative - be experimental (p. 30)

Dealing with the adults reared:
- best ways of killing them (p. 31)
- mounting and preserving them efficiently (p. 33)
- optimising data labels (p. 36)
- how to start studying them (p. 37)
- sending them by post safely (p. 38)
- breeding them in culture (p. 39)

First of all, however, an outline of the general biology of parasitic wasps will be helpful. Without this understanding there will be more likelihood of jumping to the wrong conclusions when parasitic wasps are reared, instead of correctly interpreting and recording the real events.

GENERAL BIOLOGY OF PARASITIC WASPS

IN ALMOST ALL parasitic wasps the adult females are highly mobile (even if, as is the case for a few, they may lack functional wings) and adept at searching for and detecting exposed hosts or those that are hidden in a relatively static way. Typically they have a well-developed ovipositor - in many species projecting conspicuously beyond the apex of the abdomen, but in others largely concealed - and it is through this needle-like tubular apparatus that eggs are injected into, or placed on or near to, the host. In the case of concealed hosts the ovipositor may be the only part of the female parasitoid to actually contact the host, as it is first used to probe or drill through the concealing substrate, and in general the ovipositor tip also has a sensory role. Another important function of the ovipositor is to inject various secretions, from a wide range of internal glands that the female has, either just before or at the same time as the egg is laid. Sometimes these venoms (in the widest sense) cause temporary or permanent paralysis, but they may also have much more subtle effects that help to control the host's physiology for the benefit of the parasitoid and/or prevent the host from mounting an effective physiological defence against it.

The trophic relationship that a reared parasitoid has to its apparent host is not always as simple as it seems. **Primary parasitoids** attack and eventually kill the host itself, but surprisingly often the parasitoids you rear will be **secondary parasitoids**, also known as hyperparasitoids, that are in fact parasitoids of the primary parasitoid. There are two main categories of hyperparasitoids. First, there are **true hyperparasitoids**, which attack the primary parasitoid while it is still growing inside (or occasionally on the outside of) the host, which is usually still alive at this time. Almost all true hyperparasitoids are fully specialised to that way of life and cannot behave as primary parasitoids. Usually they do not kill the primary parasitoid until after it has killed the host and made its own apparently normal preparations for pupation, such as a cocoon - but within that structure the primary parasitoid is eventually killed by the true hyperparasitoid, and it is the adult of the latter that eventually hatches. Adults of the most frequently found true hyperparasitoids (e.g. the ichneumonid subfamily Mesochorinae) look for hosts such as caterpillars in much the same way as adults of primary parasitoids, and they are often able to oviposit into and develop in most or all of the kinds of primary parasitoid larvae they find inside them. But a few

groups of very much rarer true hyperparasitoids have remarkable - almost unbelievable - life histories, involving laying a great many tiny eggs (often several thousand) on vegetation. In some (the ichneumonid subfamily Eucerotinae) the eggs are laid on stalks and the tiny heavily sclerotised larvae that hatch wait for days or weeks on their pedestal to be brushed against by a caterpillar or sawfly larva, to which they rapidly attach themselves; in others (some members of the chalcidoid family Perilampidae) the larvae, which are similarly armoured against desiccation, wander around in search of a host; and in others again (the family Trigonalyidae, with just one very rare representative in Britain) the eggs are laid on the edges of leaves and have to be ingested by a caterpillar or sawfly larva as it eats. In all of these cases, the parasitoid can only develop further if the host to which it gains access is either already parasitised or subsequently becomes so (or, in special cases, is carried off by wasps to be fed to their grubs), and it is on the body of the primary parasitoid that it eventually feeds. One might say small wonder that these various parasitic wasps whose females do not make direct contact with their host are all rather rare - but they are widespread in the world and may possibly be the remnants of a once much more successful life-style, so it is perhaps interesting to reflect on the kind of ecological circumstances that may in the past have promoted what now seems such an unusually hopeless individual existence. Similar behaviours also occur in a few parasitic wasps that are primary parasitoids, and, among non-hymenopterous parasitoids that lack the sophisticated ovipositor that is so characteristic of Hymenoptera, these remote oviposition strategies are quite common.

Pseudohyperparasitoids are the other main category of secondary parasitoids. They attack the primary parasitoid only after it has completed its feeding, by which time the host will usually be dead and finished with. The primary parasitoid will typically be attacked in its cocooned or pupal stage. Although having less to do with the original host than true hyperparasitoids, pseudohyperparasitoids are also secondary parasitoids in the sense of the host's population dynamics because, like true hyperparasitoids, they reduce the effective population of the primary parasitoid rather than that of the host. For this reason it is sometimes helpful to account for them in the parasitoid complex of the host (in which context they are often collected), although really they are usually simply opportunistic parasitoids of a range of hosts in small cocoons etc., some of which just happen to be those of primary

parasitoids. Some, however, are obligatory pseudohyperparasitoids in the sense that they only ever attack ichneumonid or braconid cocoons (which are all parasitoids).

It is quite common for some kinds of parasitoids (almost always idiobionts - see below) to be capable of being either a primary parasitoid or a pseudohyperparasitoid of a given host, in which case they are said to be **facultative hyperparasitoids**. Tertiary or even higher levels of parasitism sometimes occur, but they are almost always merely facultative - and the longer the chain the smaller the effective food resource, so a practical limit is fairly quickly reached.

In a few situations another interaction known as **cleptoparasitism** can occur, whereby a parasitoid preferentially develops on or in a host which has already been attacked by another species (the same term is used for aculeate Hymenoptera that usurp another species' food store). One of the best known obligatory cleptoparasitoids is the ichneumonid *Pseudorhyssa alpestris* (Holmgren), which has a long but frail ovipositor that it uses to thread down the bore hole made by similar looking but better equipped ichneumonids that drill through wood to reach deeply concealed hosts: the *Pseudorhyssa* lays its larger egg on the already parasitised host and the resulting larva is armed with huge mandibles with which to kill the young larva of the original parasitoid, so that it alone has possession of the host's body.

Perhaps the weirdest habit of all is the **autoparasitism** practiced by a few Aphelinidae (chalcidoid parasitoids of Homoptera), in which the females are ordinary primary parasitoids and the males obligatory secondary parasitoids, developing on immature females of their own species.

Whether primary or secondary, parasitoids whose larvae feed on the host from an external position are called **external parasitoids** or **ectoparasitoids**, while those which feed from within the host's body are called **internal parasitoids** or **endoparasitoids**. Sometimes they are termed **ectophagous** and **endophagous** respectively. The larvae of parasitic wasps are mostly relatively immobile whitish maggot-like creatures with very thin skins, and ectoparasitism is largely restricted to hosts which live in concealment, e.g. in stems, wood, leaf mines, galls, cocoons etc., where the vulnerable and fragile parasitoid larva can safely develop. Typically in these cases the host will be killed or permanently paralysed by a venom injected by the female parasitoid just before she lays her egg on or near to it. There are, however, a few ectoparasitoids

whose eggs are attached to exposed mobile hosts, but these usually either develop extremely rapidly (e.g. the ichneumonid subfamily Adelognathinae, on sawfly larvae) or else delay their growth until the host has constructed a retreat as though for pupation, in which concealed site the parasitoid develops instead (e.g. the ichneumonid subfamily Tryphoninae, on sawfly and moth larvae). Ectoparasitism appears to be the ancestral condition, and endoparasitism has probably arisen basically as an adaptation to exposed hosts, and also to take advantage of the great protection afforded by the hard and streamlined ("obtect") structures that are the pupal stages of many endopterygote insects (e.g. cyclorrhaphous Diptera and most Lepidoptera).

There is another way to categorise parasitoids by their developmental characteristics that can be useful because it correlates better with certain parameters, such as the potential for a wide host range, than ectoparasitism or endoparasitism. In this case the emphasis is on the immediate effect on the host's development. If it is permanently arrested, or even killed, at the time of parasitisation (or so soon afterwards that the immature parasitoid still effectively experiences no challenge and so has no need to be adapted to a living host) then the parasitoid is said to be an **idiobiont**. If, on the other hand, the host is permitted to continue to develop, or move around and look after itself, for at least a time following parasitisation (so that the immature parasitoid has to be adapted to withstand the challenges that may be mounted by a living host), then the parasitoid is said to be a **koinobiont**. One reason that these distinctions are made is that koinobionts generally have to have relatively narrow host ranges, while idiobionts - at least potentially - can adapt to what they find within their searching niche (although some idiobionts have such successful and narrowly specialised host searching behaviours that they, too, can have very narrow host ranges). For example, the true hyperparasitoids mentioned above are all koinobionts, while the pseudohyperparasitoids (many of which behave as facultative hyperparasitoids and have host ranges that thereby often span at least two insect orders) are idiobionts. There is quite a high degree of correlation between ectoparasitism and idiobiosis, and between endoparasitism and koinobiosis - but it is an important fact that when idiobionts are endoparasitoids, as a few are, they tend to have broad host ranges; and when koinobionts are ectoparasitoids, as occurs in quite a number of groups, host ranges are usually extremely narrow. Thus it is idiobiosis and koinobiosis, rather than ectoparasitism and endoparasitism, that gives us the best simple prediction of a parasitoid's role and ecological performance.

Parasitoids may be **solitary**, when a single individual develops in or on each host, or **gregarious** when a brood of two or more develops from one host. Usually a given species of parasitoid is consistent in being either solitary or gregarious, but there are some species that invariably have small brood sizes that may typically range from one to about three or four, a very few others that have strictly single sex broods and are gregarious in one sex (usually the female) but not the other, and others again which differ according to the host, or its size or stage, that is attacked. While both strictly solitary and gregarious species can occur in the same genus in several groups of parasitoids, there are many sizeable groups at family or subfamily level in which all species are believed to be strictly solitary. The first instar larvae of strictly solitary parasitoids usually have efficient fighting adaptations or some other means to ensure the elimination of competitors, so that only one survives even if by accident more than one egg has been laid (which in such cases would usually happen as a result of several independent discoveries of the host). But this is just one of a range of possible outcomes of situations in which separate oviposition events lead to extra parasitism of an already parasitised host, which are referred to as **superparasitism** if the parasitoids are of the same species, or **multiparasitism** if different. Sometimes, though rarely, even multiparasitism can be successful in the sense that both parasitoids survive, especially if it involves an ectoparasitoid and an endoparasitoid, or two species that are each tolerant and capable of gregarious development.

As might be expected, most gregarious parasitoids lay several eggs in or on the host, each of which gives rise to one of the brood. But in a few disparate groups of koinobiont endoparasitoids **polyembryony** occurs, whereby a single egg laid in the host grows by absorbing nutrients and divides repeatedly as it develops, resulting in a brood that (depending on the parasitoid species, and also the size of its host) may range from less than ten right up to a couple of thousand. The parasitoids that do this include some Encyrtidae (Chalcidoidea) and Braconidae (in the genus *Macrocentrus*) that are regularly reared from the larvae of certain Lepidoptera, and some Platygastridae that commonly attack gall midges (Diptera: Cecidomyiidae). The broods, coming from single eggs, are all of one sex: if mixed sex broods are found it will indicate that more than one egg was laid.

Most primary parasitoids attack their hosts at a fairly precise life-history stage, and they can be categorised to reflect this. Thus all **egg**

parasitoids oviposit into and kill insect eggs (and in due course all known egg parasitoids, in this strict sense of the term, emerge as adults from them). **Larval parasitoids** attack and also kill the host in its larval stage (if it is an endoparasitoid the parasitoid larva may leave the host to pupate elsewhere; or in some groups it pupates inside the dead host's larval skin, from which the adult emerges in due course). **Pupal parasitoids** oviposit in or on the host pupa (and if they are endoparasitoids they almost invariably later emerge as adults from it) - the term **puparial parasitoid** is sometimes used for the apparently endoparasitoid species that oviposit into the puparia of cyclorrhaphous Diptera in recognition that the puparium (made of the last larval instar's skin) is not the same as a pupa, and within the puparium such parasitoids often in fact develop externally on the true pupa. By definition, for idiobionts the stage attacked is also the stage killed, but many groups of koinobionts attack one stage but delay their development until killing the host at a later stage, and they are then known as **egg-larval parasitoids** or **larva-pupal parasitoids**. The terms **nymphal parasitoid** or **nymph-adult parasitoid** would be appropriate for relevant species attacking exopterygote groups, but the term "adult parasitoid" would obviously be confusing if applied to the species that attack adult insects, so it is best avoided in that context. Finally it has to be conceded that there are a few parasitic wasps that - using strict definitions - are not really parasitoids at all. Some of the most easily reared are those whose larvae develop inside spiders' egg sacs, in which they consume a succession of eggs rather than just the "single" individual allowed by the term parasitoid. But it seems pedantic to push this difference, especially when the species concerned are demonstrably closely related to absolutely conventional parasitoids and, in fact, in some cases can consume either a gravid female spider (= parasitoid) or the eggs she lays (= predator), whichever happens to be found in the egg-nests sought.

However they develop, the larvae of parasitic wasps are rarely very mobile and they generally pass through up to a maximum of five instars, the first and last often being of rather different form from the middle ones. This is presumably to do with the specialised roles these instars have - the first for hatching from the egg, establishing itself in the host, and often also for fighting competitors, and the final one for preparing a pupation site, either inside a cleaned-out host skin, or as an externally spun cocoon or naked pupa that in some cases may be positioned some

distance away from the host remains. The final instar larva may also need to burst through the host's skin and even, notably in several subfamilies of Braconidae but also in some other groups, make a transition from endoparasitism to ectoparasitism for its final feeding period.

Koinobiont parasitoids often produce more or less subtle alterations in the behaviour of their hosts which, among other things, may mean that it is hard to be sure that parasitised and unparasitised hosts are equally easy to collect by any particular method so that accurate "sampling" for parasitism levels may be a real problem. Often the changes produced in the host's behaviour are most manifest just before the parasitoid larva is ready to kill or leave it, and hosts such as caterpillars may then be induced to climb high up vegetation, or perhaps move down to soil level or below, in a way or to a degree that is abnormal for the species, or they may construct tougher than normal pupation retreats, or seek a twig of a particular size to rest on, before being killed by the parasitoid. Although there has been some argument as to whether these changes are beneficial to the parasitoid in the sense of improving its chance of survival, in the properly investigated cases it seems clear that they are, and the popular notion that the host is attempting suicide by exposing itself and its parasitoid to increased danger now appears entirely fanciful. The larvae of some kinds of Braconidae feed mostly on their host's blood and fat, rather than its muscles, and these species may leave the host and spin a cocoon externally without killing the host outright, though the host generally does not resume feeding and slowly wastes away to die later. Sometimes the cocoon remains attached to the host and is carried around by it for a time, but in some other cases after the cocoon (or cocoons, for some are gregarious) are spun the host very reliably moves away for at least a short distance to die and perhaps putrefy where it will not effect the cocoons. Some warningly-coloured hosts, in contrast, are induced to remain with and conceal or protect the cocoons of their parasitoids - a familiar example is the brownish spindle-shaped cocoon of the braconid *Dinocampus* (= *Perilitus sensu lato*, in part) *coccinellae* (Schrank) upon which its adult ladybird host (usually *Coccinella 7-punctata* (Linnaeus) (Coccinellidae)) sits immobile (though still capable of walking if picked off) for a time and eventually dies.

Ichneumonoidea (= Ichneumonidae + Braconidae) have soft easily damaged pupae that are thin-skinned and untanned, with the appendages loose ("exarate"), and almost all ichneumonoids make

protective silken cocoons of some sort in which to pupate. Even those that pupate *in situ* deep in plant tissue or inside tough host cuticular structures (pupae, puparia etc.) usually at least line the pupation site with a smattering of silk, and some go so far as to form a strong discrete cocoon. Cocoon formation is also a feature of some (but not all) of the Aculeata that have parasitoid-like life-styles and rather similar pupae. In contrast, the so-called "microhymenoptera", that includes Chalcidoidea, Proctotrupoidea, Scelionoidea, Ceraphronoidea and Cynipoidea, pupate without the benefit of silken cocoons as such, though they often make some sort of protective modification of the sites in which they pupate. In many cases microhymenoptera develop inside protective structures such as cocoons, puparia, eggs, galls and other woody plant tissue, and in any case these groups tend to have tougher more obtect pupae with better tanned cuticles - as is especially evident in some groups that pupate in relatively exposed situations.

Despite the protective value against invasive microorganisms, mechanical damage, desiccation and generalised predation, one big disadvantage of cocoons is that silk is rather easily detected and so cocoons are themselves attractive to parasitoids. Indeed pseudohyperparasitism rates are often heavy in ichneumonid and braconid cocoons spun exposed on plant vegetation, even when the cocoons are protected, for example by being suspended from threads or double wrapped. This may be one reason why so many koinobiont ichneumonoids using exposed hosts delay the destruction of their host until it has left its relatively dangerous feeding site to construct for itself a safer pupation retreat, but for some parasitoids such as those attacking aphids and other Homoptera, galls, some sorts of leaf mines, etc. there is no opportunity to do this and the parasitoid complexes of these hosts typically involve a rich (and in some cases very specialised) hyperparasitoid element.

In Hymenoptera generally there is an unusual form of sex-determination known as **haplodiploidy**. In this, unfertilised (haploid) eggs develop and become males (which is also known as **arrhenotokous parthenogenesis**), while fertilised (diploid) eggs become females. It seems to be usual for the females of haplo-diploid Hymenoptera, once they have mated, to be able to control the sex of each egg laid by regulating access of the stored sperm to it as it passes down the oviduct. Both the overall sex-ratio and, for gregarious species, the sexual composition of broods thus reflect reproductive strategies that have

presumably been optimised by natural selection. Also, in the case of solitary idiobionts in particular, female progeny are often invested in the larger-sized hosts attacked while males tend to result from the smaller hosts. However, in a good many Hymenoptera species males are practically unknown and females develop from unfertilised eggs by a process known as **thelytokous parthenogenesis**, or **thelytoky**.

Many parasitic wasps in Britain are univoltine and attack univoltine hosts, with complete synchronization of life cycles. Others may be plurivoltine and attack plurivoltine hosts, again with synchrony. In both these cases there is a potential for parasitoids to be absolutely host specific, i.e. entirely dependent on a single species of host, and indeed many parasitoids do - at least locally - seem to be in this position. However, for a fairly large number of plurivoltine parasitoids it is clear that different sets of univoltine hosts are being used at different times of year, potentially leading to highly complex population dynamics, of course, but also resulting in ecological requirements and reflecting evolutionary origins that may be quite difficult to discover and understand. Even for parasitoids in complete synchrony with their hosts, it is often clear that it is not in fact only a single species of host that is being used but rather a (usually fairly small) number of species, perhaps as much just physically and ecologically similar (within an overall taxonomic grouping) as bearing really close evolutionary relationships to one another, as a core **host range** for the parasitoid.

The idea that each parasitoid species has a more or less definite host range is important, although in practice such host ranges are not always easy to express in exact terms. A useful conceptual definition of the host range of a particular parasitoid species is that it includes only the species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behaviour enabling it to encounter them regularly. This immediately suggests that host ranges will need to be assessed through quantitative data, and also that there may be some *de facto* variation in host usage by different populations of a parasitoid species, over both space and time. One of the best features of the approach demanded by such a definition is that it marginalises not only freak events but also mis-identifications when host ranges are being assessed. To understand the host associations of particular parasitoid species, through building up extensive collections of preserved reared specimens that will generate the essentially quantitative data needed to reveal actual, realised, host ranges, is why it is so well worth rearing

parasitoids - and in particular parasitic wasps - with great care as a sustained activity over a broad front. It is quite a challenge, but a good conceptual start has been made, and it is the only way to gain a clearer understanding of parasitic Hymenoptera in terms of both community ecology and also their underlying evolutionary biology.

In addition to those rather lofty aims, rearing parasitic wasps is by far the most interesting and rewarding way just to study our huge fauna of these Hymenoptera - there are lots of species that have only ever come to notice in Britain by being reared, and without a doubt hundreds (at least) are still waiting to be found here. And that is on top of thousands of species that we know are here, but for which we have no idea what they are doing.

REARING - GENERAL PRINCIPLES

MY OWN BACKGROUND is as a lepidopterist, and it was principally through rearing caterpillars that I got interested in parasitic wasps. As this host group is by far the most straightforward to collect and keep as immatures, much of the following narrative will be written as though Lepidoptera are the hosts from which parasitic wasps are being reared - but the general guidance applies whatever the host group, needing only a little imagination from the reader. In fact, although the early stages of Lepidoptera are among the most heavily parasitised of insects and a great deal remains to be discovered, their parasitoids are relatively well known in comparison to those of several other orders, and a determined effort to study parasitism of, say, larval sawflies or particular groups of Diptera or Coleoptera may well bring even greater rewards.

Apply all the control you possibly can

This is necessary in order to ensure that the parasitoids you rear really do come from the host you think they do. A surprisingly high proportion of the mistakes in the literature giving host-parasitoid records have been made because the host was misidentified or, even more to the point, the real host was totally overlooked. For example, a parasitoid cocoon from something else might already be present on leaves being fed to caterpillars and, if the cocoon is seen only later, it would be easy to make the mistake of presuming it came from one of the captive caterpillars. Or a different species of insect may be concealed and overlooked deep within the plant being introduced as food, and may produce its own parasitoid subsequently without the presence of the real host species ever becoming evident. Often mistakes of this sort come to light most clearly when the parasitoid that hatches is of completely the wrong group to have attacked the supposed host. For example, parasitoids of aphids are all too easily reared from leaf mines of certain Lepidoptera because parasitised aphids often enter slightly torn mines and die within: as there is no overlap whatsoever between parasitoids that attack aphids and those that attack Lepidoptera the problem is easily detected and understood. But it may be harder to know that a similar event has happened when, for example, a leaf mining nepticulid moth larva has entered a torn leaf mine of, say, a gracillariid moth in which to spin its cocoon, as the parasitoid that later hatches may not so obviously be "wrong".

There are some very simple rules to follow that will reduce this category of error enormously, especially in relation to hosts that can be isolated and counted. Taking exposed hosts such as leaf-feeding caterpillars first:

(1) Search the foodplant to be fed to the hosts very carefully, removing any bits that might conceal other insects, and look out for parasitoid cocoons, mummified aphids, scale insects, hoverfly puparia etc. - all of which may produce parasitoids that could otherwise confuse you. Many careful insect rearers would do this anyway, if only to remove leaves fouled by bird droppings etc. in an effort to control disease - it is just a matter of extending the search a bit.

(2) Only ever rear one species of host per container. Even if you can very easily tell apart two kinds of caterpillars (for example) that might conveniently be fed on the same foodplant in the same container, if one of each produces a (different) parasitoid cocoon it will often be impossible to be sure which came from which. The same applies to containers used later on for pupae - even if it is the host and not the parasitoid that is the main objective, it is very easy to keep pupae in clear plastic or glass topped pill-boxes, only one species (and locality) per box, and the resulting moths (or whatever) will expand their wings perfectly satisfactorily given just enough clearance. A lot of larva-pupal parasitoids of Lepidoptera have unclear host ranges because too many of the reared specimens have arisen from large "emergence cages" in which lots of different hosts were kept together - an unnecessary practice even for lepidopterists, and one that greatly limits the usefulness of the parasitoids reared.

(3) Count and record the individuals present in the container and, *every time* the container is turned out, account for each one. In this way any parasitoid cocoons (etc.) found can be related clearly to a definite host mortality, and any apparently missing host will provoke a sufficiently close inspection of the debris to reveal, for example, the cryptic mode or site of its parasitoid-induced death. Be aware, too, that some parasitoids do not kill the host outright when they leave it to spin their cocoons - there may be moribund but active hosts (often with clear exit wounds near posterior spiracles) still pottering around, equatable with parasitoid cocoons found elsewhere in the container.

(4) Each parasitoid cocoon (or brood of cocoons in the case of gregarious parasitoids), along with the remains of the host concerned,

should be removed when detected and kept in isolation from others in a separate container to await the emergence of the adult parasitoid, with its pertinent data. Do not keep more than one cocoon (or one brood, if gregarious) in a container or else it may not be possible to relate adults to the cocoons from which they hatched. Apart from anything else, there may be several primary parasitoid species (even if the cocoons all look similar) or a mixture of primary and secondary parasitoids emerging overall. And always keep the full details of the host, its origins and dates of all pertinent events (e.g. date parasitoid cocoon made; date parasitoid adult emerged) written on bits of paper inside each container at all times: these are the details that, eventually, will be permanently recorded as the data label for the adult specimen. Never trust your memory - write everything down straight away! (It is sometimes worth storing host remains separately until parasitoid cocoons have hatched, especially if the latter will overwinter, as the host remains may deteriorate badly under the somewhat damp conditions needed by unemerged parasitoid cocoons. If this is done it is, of course, vital to devise an efficient system for reassociating them accurately later on.)

(5) Preserve everything that relates to the adult parasitoid reared. The cocoon (etc.) may reveal the intermediate host of a hyperparasitoid, and in any case its appearance and mode of construction, the way the adult parasitoid has emerged from it, and the skin of the final instar larva that it will contain, are all valuable for systematic studies. Parasitoids preserved with the remains of the actual host individual from which they were reared have the added value that the identity of the host can be checked and verified in the future if needs arise. For this reason it is important that the host remains preserved are of the actual host individual (not just an example of its species), or else that the labelling makes it clear that the remains are mixed up.

The procedure outlined above is all very simple for countable hosts that can be picked out and transferred to substrates previously checked to be clear of other hosts, and to some extent hosts that develop wholly inside structures like galls or leaf mines can be treated under similar levels of control by the simple expedient of isolating each one (for example in a corked glass tube) so that if a parasitoid emerges the correct individual structure can be opened to verify the exact host. Much more difficult to deal with are substrates that contain an unknown number of host individuals, and often an unpredictable range of species.

principle this is fairly easy to address: ideally hosts need collecting at as many life history stages, and from as many different situations and areas, as possible and then, given effective techniques, it will become clear what parasitoid species are attacking them. There will, of course, be practical problems - for example for many kinds of host the pupal stage will be far more difficult to find than the larval stage, and so pupal parasitoids will be less readily investigated. The same may be true of egg parasitoids. But even without these problems it is often not easy to get much further than establishing the simple host/parasitoid relationships, for the following reasons.

Firstly, it is usually very difficult to get an accurate idea of the percentage parasitism suffered by a host, for three main reasons: (1) unparasitised hosts and those parasitised by koinobionts do not always behave in exactly the same way, and thus they may not be equally amenable to sampling; (2) parasitism can be a continuous but uneven and transient process, so that at a particular sampling date part of the host population may have already been killed by parasitoids (and so be absent, undetected) and some of the parasitoids that will later on attack the host's generation may not have yet done so; and (3) koinobiont endoparasitoids rather often somewhat retard the development of their hosts (less often they can accelerate it) so that, most noticeably at the end of the normal time of year for a host such as a caterpillar to be feeding, many more of the unparasitised ones will have left the population to pupate, leaving parasitism over-represented in those still available for collection. This can, of course, provide the alert rearer of parasitoids with a kind of efficiency bonanza, but nevertheless it adds to the problem of assessing the percentage parasitism in the host population overall. Furthermore, as not all of the parasitoids of a given host will be causing equivalent effects, you can not even really be sure that the parasitoid you rear most of is actually the one causing the most mortality. It is important to realise that even in principle being able to evaluate quantitatively the generational mortality due to parasitism arises only as a special case. In essence it is only for hosts that complete their entire pre-imaginal development in a single site such as a gall or a leaf mine, and that can therefore be sampled comprehensively at or after the end-point of their generation, that (at least in principle) it is possible - and even that rests on there having been no differential removal from the sampling arena by predators etc.

Secondly, even if we can get a good idea of the parasitoids of a given species of host, the question that is in almost every respect much more

Fig. 1.
A rearing shed with lift-out framed chicken wire door.

Fig. 2.
Painting the roof white can help reduce thermal gain in a partially shaded shed. As well as the door, the window is left permanently open and the space covered with chicken wire.

Fig. 3.
Standardisation provides for efficiency and convenience. Corked tubes in a carrying box, especially useful in the field.
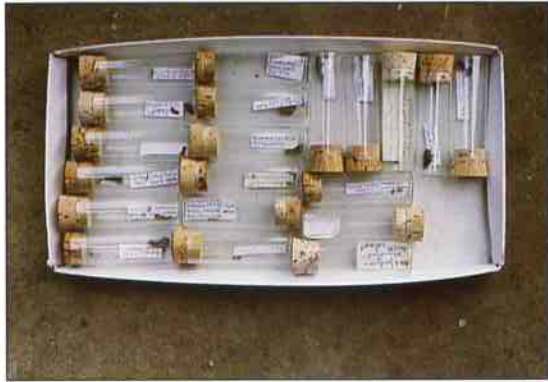
Fig. 4.

Emergence of adults is easily detected if corked tubes containing parasitoid cocoons are laid out flat. Shoe-box lids make convenient trays.
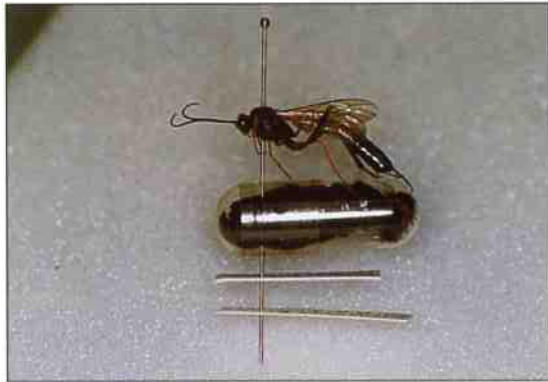
Fig. 5.

A direct pinned mount. The insect's relatively high position up the pin leaves plenty of room below for associated items in a clear gelatine capsule as well as the data label and a determination label.
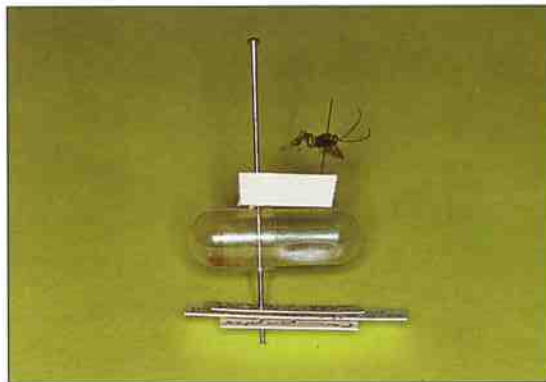

Fig. 6.

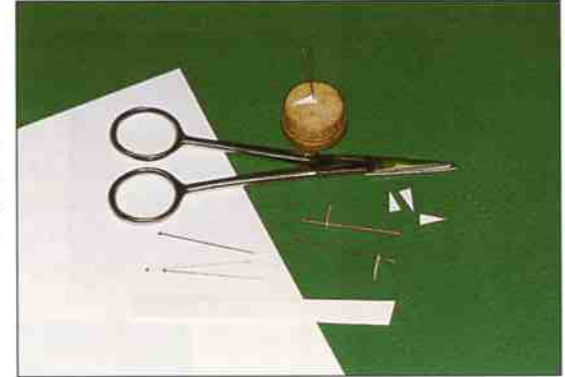A specimen micropinned to a stage.

Fig. 7.
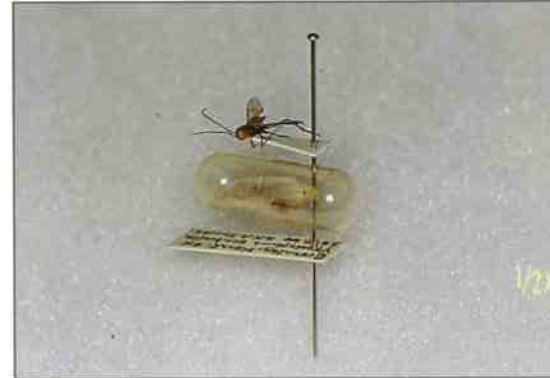Preparing card points is straightforward but needs practice.

Fig. 8.

A pointed specimen (with the wings closed above the thorax).

Fig. 9.

A pointed specimen (with the wings in the open position).

Bee... ...umbria.
Nematus leucotrochus
on Ribes uva-crispum
with 2 ectos 25·5·1991
em 22·4·1992 M.R.Shaw
W:24 NMSZ 1993.143

Fig. 10.
A carded specimen.
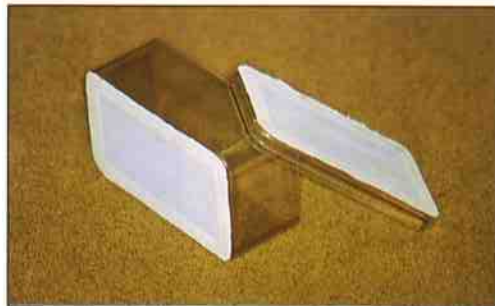

Fig. 11.
A specimen glued to the pin.

Fig. 12.

A badly mounted specimen.
Although it looks neat and tidy and
used to be popular, this method
makes it hard to examine any of the
venter, much of the face, and the
side of the thorax.

Fig. 13.
A mating chamber providing for a
through draught.

interesting is "what else do they attack?" or, to put it in more general terms, "what are the hosts of a particular species of parasitoid?", and that is very much harder to evaluate in a simple direct way. It is far easier to look at parasitism of, say, a moth like the poplar hawk, *Lathoe populi* (Linnaeus), than to discover the host range of any of its parasitoids, and yet - even in relation to parasitism of *L. populi* - the latter is rather an important consideration. In extension from this you should realise that trying to make a thoroughly comprehensive collection of any given group of parasitoids purely by rearing them will usually prove to be practically impossible.

REARING - EFFICIENT PRACTICES

TRYING TO REAR parasitoids is taking things one trophic level further than usual, and the labour cost per specimen therefore tends to become worse. A lepidopterist may want a few specimens of the oak eggar moth, *Lasiocampa quercus* (Linnaeus) (Lasiocampidae), and feel fairly sure that collecting half a dozen caterpillars will usually provide for that without difficulty. If I want a few living specimens of one of its specific but rather rare parasitoids, ichneumonid *Metopius dentatus* (Fabricius), how many caterpillars must I collect and rear? I'm not sure, but I have gone far beyond a couple of hundred and I have still not reared that parasitoid.

This means that efficiency is very important - optimising rearing conditions not only to reduce mortality but also to save time and trouble becomes essential. As high numbers of hosts may have to be reared, there are scale-up problems in animal husbandry that need consideration - in particular, the risk of disease.

Work in "biological time"

There are two main reasons for working in "biological time" - i.e. under conditions that are as near natural as possible. The first is simply that survival rates are higher. One of the two most important causes of failure in rearing parasitoids is desiccation of the cocoon or pupal stage (the other is using small and completely airtight containers such as plastic stoppered tubes, to which I shall return). By far the best way to redress desiccation is to conduct all rearings - and certainly to store parasitoid cocoons etc. overwinter - in an unheated outbuilding, preferably a detached shed (Plate A, Figs 1, 2) that is: (1) efficiently shaded from the sun at all times of year; (2) well ventilated (e.g. replace a window and remake the door with chicken wire); and (3) reserved entirely for rearing insects.

A rearing shed needs electric light, but a water supply is probably not worth the burst pipes as you should not heat it in winter. If you can't run to a well-shaded rearing shed, at the very least make sure that *from the time they appear* parasitoid cocoons or pupae are kept under approximately natural cool (shaded) conditions, and that they are overwintered in relatively cold and damp but airy surroundings. Be aware that sheds, outbuildings or other devices that are in sunny situations will usually be prone to disastrously high internal temperatures, in which case they will not be much help. Painting partially shaded sheds white can improve their performance.

Working in "biological time" refers also to the benefit of knowing that the things that happen with the parasitoids (and indeed the hosts) you rear are what is also happening at the same time in the wild. This will be the case if you use an efficient rearing shed for all livestock at all stages of the rearing process - parasitoid cocoons that ought to overwinter will do so, and those that hatch the same year will be the ones that should hatch the same year. This will allow you to evaluate the parasitoid's voltinism and also its synchrony with the host species you reared it from. In turn this indicates whether or not it could be host specific, or whether it clearly needs alternative hosts. It is a category of natural history information that is entirely lost under more artificial rearing conditions, whether they be controlled constant temperature and light/dark environments in the laboratory, or the chaotic regimes of fluctuating heating and lighting we employ for our own domestic comfort. And you should appreciate that whether or not insects will enter diapause is often determined by the environmental conditions experienced well before the time that it actually does or doesn't happen, so providing natural conditions of daylength and temperature for potentially parasitised hosts during the whole rearing process is important - even a few days under artificial conditions can interfere.

Standardise your rearing equipment

This is another very obvious suggestion, but it is easy to undervalue the huge efficiency savings involved. For example, glass tubes all the same size (Plate A, Fig. 3; Plate B, Fig. 4) are easier to: (1) wash up; (2) find the cork for; (3) store when not in use; (4) lay out on their sides in (e.g.) shoe box lids for easy daily inspection to see if adult parasitoids have emerged; (5) transport and use in the field in an effective purpose-made box; (6) learn to judge and use efficiently for tricky rearings. And so on. The same will apply to plastic boxes, plastic-topped cardboard pill boxes, and anything else people may like to use.

What you find best will depend on what you are trying to rear, and also, no doubt, on what you are able to lay your hands on or are willing to spend. For what it is worth, dealing especially with parasitoids of leaf-eating Lepidoptera and sawflies and also spiders, I regularly use just two sizes of corked glass tubes (7.5 x 2.5cm and 5 x 1cm), two sizes of clear airtight plastic boxes (about 18 x 12 x 6cm and 14 x 8 x 6cm), and plastic-topped card pill boxes (supplied as nests of three, often needing repair but worth it) for all the controlled rearing I do. In the main, the

large sized tubes are used for small things that don't need feeding, including the parasitoid cocoons removed from rearing boxes, and the smaller sized tubes are used only for very minute items that would otherwise be liable to unwanted desiccation or loss; the plastic boxes are used to rear caterpillars, especially relatively large ones or cohorts (but small singletons, and also parasitised spiders, are usually best reared in the large sized tubes), and also for some substrate rearings; and the pill boxes are used for particularly large parasitoid cocoons and all but the smallest of host pupae awaiting emergence. For substrate rearings I occasionally also use plastic sweet jars, cotton pillow-cases (excellent for dead wood and other material that is not entirely dry), plastic buckets with fine netting over them (old nylon tights are ideal), and well made shoe box bottoms with glass sheets on top. This basic set of equipment would do very well for rearing parasitoids from almost any insect group.

Ensure great cleanliness

To avoid too long a discussion of the merits of washing-up I will just say that, short of time though I am, I find it very definitely worth adopting the following procedure: (1) Containers in which nothing has died of a disease (or inexplicably) or in which no mould or putrefaction has occurred are wiped physically clean, if necessary with damp tissue, and used again; (2) Washable containers in which there has been disease, unexplained death, putrefaction or mould of any kind are washed-up before re-use.

In order to control disease and anaerobic fermentations completely it seems essential to employ disinfectants in the wash-up. You may wish to experiment, but I offer my domestically simple process for what it is worth:

Fill sink with warm water (not hot, as that makes some plastics go opaque); add enough Dettol to make it stay just cloudy; totally submerge glass and plastic items (in fact it is more efficient to do plastic boxes and glass tubes separately - the process can be done much hotter for glass alone) but not corks; leave water to go cold (causes Dettol to precipitate onto all surfaces) and let stand a few hours; drain thoroughly; refill sink with warm water; add a very generous dose of full strength washing-up liquid; leave everything submerged for a few hours; mechanically clean/wipe very thoroughly (test-tube brush for glass tubes, sponge for boxes); rinse well and dry (glass tubes in very hot water, then stand to drain - for plastic boxes it is worth drying-up with a tea-towel after a

merely warm rinse). Corks should not be subjected to Dettol or washing-up liquid as they will retain enough of either to kill insects or cause other problems. Instead they are easily sterilised in a sweet jar with cold water and Miltons crystals or fluid (as used for baby feeding apparatus) followed by a long rinse - do not boil as many corks are glued and will fall apart, and also boiling would strip out some of the included tannins (beneficial in having a slight fungicidal/bactericidal effect). After the wash-up process, all containers are stored open for at least a week (to lose the persistent perfumes found in washing-up liquids - though I have no evidence that they are harmful).

Although it may seem rather a palaver, this wash-up procedure ensures that diseases are not transferred, and it also prevents potentially lethal anaerobic conditions and food-spoiling moulds developing from pre-existing infection in closed containers which, at the very least, would cost the rearer time unnecessarily. If you are rearing large amounts of material it really does repay the time invested, and if you are rearing only small amounts then it won't take much time anyway. On the whole I find it easier to follow the above procedure than to boil or autoclave glassware, but that is of course an alternative way to sterilise it. Microwaving is also effective and will not damage most kinds of plastic containers, provided they are dry.

Physical cleanliness has to be stressed for re-used containers between wash-ups. In particular, it is important for lepidopterists to ensure that parasitoid cocoons (or adults) are not put into containers contaminated with moth scales, as these will collect onto the parasitoid's body and result in a dirty specimen that is difficult to examine. As a general rule, containers that have had powders or chemicals in them (even medicines, or liquids like alcohol that may appear to have fully evaporated) are not suitable for livestock until washed-up.

Prevent putrefaction and moulds

Many parasitoids are highly vulnerable during the few hours between leaving the host and completing their cocoon, so a general aim should be to disturb the contents of rearing containers as little as possible. This means that processes causing deterioration within the container have to be slowed down.

Good washing-up, and the resulting sterile containers, provides only part of the answer to controlling putrefaction and moulds, as it only addresses cross-infection. A general problem remains when insects are

reared in closed containers, especially using natural pabula like plant tissues that are subject to decay - and it is particularly dangerous for parasitoids because they are often already living in a way that makes getting enough oxygen a problem, and they do seem to be on the whole very much less tolerant of anaerobic fermentations than their hosts. Moisture control is a very important first start. If plant tissue that is not required as food is being coincidentally tubed along with an insect (e.g. with a cocoon, as a fully-developed leaf mine, etc.) then it should be allowed at least to wilt beforehand. While it is not normally advisable to use tissue paper in containers in which adult parasitoids may soon emerge (as they are likely to burrow into it and die in a crumpled state), any closed container used for feeding hosts should have sufficient absorbent tissue (plain white lavatory roll is unbeatable) well fitted over its entire base to absorb moisture, so that condensation of droplets is completely avoided (a single ply from a single sheet is enough to crumple down very firmly into the bottom of a 7.5 x 2.5cm tube; for my large sized plastic boxes I normally use a total of 14 double ply sheets placed flat and for small ones seven). This provides a good buffer also ensuring a fairly high relative humidity, so it will prevent introduced foodplant (if present in sufficient quantity for the space) from drying out at the same time. It is important that closed rearing containers are not subjected to unduly wide fluctuations of temperature (for example, leaving them overnight on the floor, or on a good conductor of heat, may lead to surprisingly high condensation, especially following a period in a heated room) or, of course, struck directly by sunshine, and they should be inspected regularly enough to ensure that they are changed out before stressful conditions arise. Many parasitoids kill their hosts as prepupae, and often hosts such as caterpillars will descend into the wad of damp tissues to prepare pupation sites. Such sites should not be unduly disturbed until the host has either pupated successfully or produced a parasitoid larva that has had an opportunity to complete its cocoon - sometimes it is best to leave the tissues for a period and simply transfer the active hosts that remain to a new box, as parasitoid larvae are extremely vulnerable to disturbance, often being unable to make a cocoon except in a tightly confined space, and they will nearly always die if interrupted during this crucial process. Once cocoons do appear, however, whether among the tissues or on the leaves etc., they should be carefully cut round and removed, with the host remains, to clean dry airy containers (such as a cardboard pill box) and allowed to dry out completely before being confined again in closed containers (such as

corked tubes) to await emergence of the adult parasitoids. Failure to allow all bits of associated plant or host remains to dry completely at this stage will severely threaten the parasitoid, as mouldering or putrefaction within the container almost always has lethal results. Note that *corked* tubes have been stressed throughout. The cork allows the contents to lose or gain a little moisture, and also the exchange of a little air, and both help enormously to control moulds. The use of tight plastic stoppered tubes is almost invariably lethal to the pupal (or earlier) stage of parasitoids, and virtually guaranteed to render any adult that does happen to emerge uselessly mouldy as soon as it dies. Use of a rearing shed was said earlier to be one of the two best ways for the average entomologist to reduce mortality and spoilage of parasitoids. Replacing plastic stoppered tubes by corked ones is the other.

Keep imaginative - be experimental

This is really the best advice of all. During rearing, if something you try doesn't work well, question why not, and try a different way next time. Was it too dry, too wet, too hot? Did that kind of host need soil, sand, sphagnum in which to pupate? Is this soil or potting compost suitable, full of fungal spores, treated with pesticides? Was the container less than ideal, too overcrowded, left too long? During fieldwork, try to work out how to give yourself the best chance. If a particular species of host - say a caterpillar - is abundant, collect all sizes in case only the small (or large) ones harbour a particular parasitoid. And collect plenty - especially if you will be able to release the unparasitised surplus at the same locality later on. Always be on the look out for opportunities to collect good samples of potential hosts that are rarely collected at that stage - for example, if the caterpillar is abnormally abundant it may be abnormally possible to find the pupal stage a bit later on, too. Many plurivoltine hosts become progressively more heavily parasitised as the season progresses, so late generations may yield better than early ones; but sometimes (though not commonly) a particular parasitoid will be wholly absent from some generations of a plurivoltine host that it attacks heavily at other times of year. Recognise also that it is the quality of the habitat, not the rareness of the host, that is most likely to determine whether or not you get unusual parasitoids. Although rare hosts sometimes do, they most often don't have rare parasitoids. Very good quality sites usually do have rare parasitoids, but often they will be associated with quite mundane hosts.

DEALING WITH THE ADULTS REARED

HAVING GONE to all the trouble (or had the luck) of actually rearing an adult parasitoid, it would be a real shame to fail at the stage of ensuring that it had some worth. The first point to address is whether or not you want to keep it for your own collection and research or whether you will pass it on to a specialist. If the latter, the best advice is to make contact with the person to whom you will pass it on as soon as possible (preferably beforehand!) as some specialists will certainly want it preserved in a particular way, and in particular may not want it mounted by someone who is not experienced. Also, they can provide advice and perhaps more practical help over safe transit. If you can, use the phone (or at least give your phone number in any letter) - by the time a letter in reply gets to you some of the advice will probably be too late. In view of the potential scientific value of reared parasitoids, most people who rear fairly small numbers as a by-product of other activity are happy to pass them on to specialists, content in the knowledge that they are accumulating in appropriate collections where the best use of them can - over time - be made. However, this booklet is also aimed at those who want to rear parasitoids more intensively for their own research so this section mostly addresses that presumption.

Best ways of killing them

The first thing is to ensure that they are still alive when you first notice them. Ideally, you will have a well-organised rearing shed and make the time to inspect everything twice a day - this gives several chances of seeing adults alive with even cursory glances over (for example) arrays of clean corked glass tubes laid out flat in shoe box lids in which parasitoid cocoons or other structures have been placed to await adult emergence, before they die and become much less noticeable in a few days. Similarly with your other containers - organisation and standardisation is the key to efficiency. Any container with only one item in it should already have all the relevant data in it as well, and provided it is physically clean and also roomy all that is needed is to add the emergence date and wait for the parasitoid to die of starvation (in some cases, especially parasitoids of wood borers, you will need to ensure that the adult will not chew through the cork and escape - if it looks likely to do this put the whole thing into a plastic box). If adult parasitoids appear in, say, pill boxes in which there are several host pupae, each host remains should be

removed and kept with its adult parasitoid (and also with transcribed data) immediately, in case some of the other pupae are about to produce another kind of parasitoid which might lead to confusion in the correct association of host remains.

Death by starvation is a semi-natural process for parasitoids, arguably a less stressful end than poisoning, and it ensures a number of things: (1) the cuticle, and especially the wing membranes, will be fully matured; (2) the stored fats in the body will be consumed rather than tending to leak out over the insect's exterior after death, which can distort colours and make sculpture and setosity very difficult to appreciate; (3) the insect will die in a state relaxed enough to be easily mounted over the following day or so; (4) very often the insect will die in a much more suitable configuration for mounting than if it is killed by chemicals, which often induce violent contortions; (5) usually the insect will groom itself until shortly before death - if it is a bit dusty it will still be relaxed enough to be brushed clean with a small paint brush before being mounted (in which case this is well worth the trouble). If for any reason you will not be able to deal with the parasitoid quickly once it has died, put it in the fridge while it is still alive to postpone that necessity - this can hold things over a summer holiday, for example, and insects that die in the fridge (or freezer) stay relaxed for longer and do not moulder quickly.

If the adults will not be mounted fresh, then extra care is needed to ensure that they are not damaged after they dry out, or moulder if this process is inhibited. On the whole parasitoids are best kept dry if possible - if not mounted very soon after death they must be allowed to dry out completely in sufficient space, and then stored in such a way that they cannot be broken. Further advice is given in the section on sending parasitoids by post. Although parasitoids from spirit do not make such good specimens as those that have been kept dry, for large specimens short term storage in 70-80% Industrial Methylated Spirit (IMS) (do not add glycerine as it is hard to wash it off completely) may be a sensible option because at least then the legs and antennae will not become dry and liable to breakage. It is preferable for the adult to have had at least a day to harden off fully, but then if necessary it can be killed by putting it straight into 70-80% IMS. But do not put host remains and cocoons into fluid: they are always best kept dry (unless destined for wet storage permanently) as they are troublesome to restore. Microhymenoptera (mostly having short legs and antennae, in particular) are less liable to damage and can usually be kept dry but unmounted reasonably safely provided nothing can rattle around with them.

Mounting and preserving them efficiently

Most parasitoids are hard to identify, and will require much manipulation under a microscope. Not only must an efficient mount provide for good direct views of all parts of the insect's external anatomy, but also it must be extremely easy to handle without damage or else the specimen simply will not survive. There are several methods of mounting that can be used to provide for ease of view and safe handling. For large specimens, direct pinning is by far the best (Plate B, Fig. 5). The pin should be long (preferably "continental" length, 38mm, though of course this sets limitations on the storage boxes and drawers that can be used) and have a good head (for handling) and sharp point (to minimise damage to the insect). It should not be too stout as it must be capable of passing through the dorsum of the mesothorax and out ventrally well behind the fore coxae on a line that keeps it entirely to the right of centre - i.e. so that any features of the central line of the thorax, either dorsally or ventrally, are not spoilt (to the right, as opposed to the left, is just a convention - but so universal that it is worth following). On the other hand the pin cannot be too fine either, or it will bend in use and put the insect at risk: there is therefore a downwards limit on the size of insect that can satisfactorily be direct-pinned that is quite quickly reached. The ideal for direct pinning is the continental length, thickness size 1, nylon headed, stainless steel "anticorro" pin produced in Austria by Emil Arlt and costing (in 1995) around 4p each when bought economically in huge bulk! But much cheaper alternatives exist. In direct pinning, the aim will be to get the insect about two-thirds of the way up the (38mm) shaft towards the pinhead, but ensuring that the pinhead is clear for easy handling (the antennae, especially, should not be left near enough to be put at risk), also leaving the legs well clear of the shaft and not extending too far downwards so that there is plenty of room underneath for the data label and determination labels etc. Obviously, pinning deeply into something like Plastazote and using pins to position antennae and legs may be helpful while the insect is drying, but there is no real advantage in "setting" the insect like a lepidopteran: indeed, sometimes features of the side of the thorax are much easier to see if the wings are positioned more upwards and the legs a bit more downwards. Direct pinning should always be done in preference to indirect mounting (staging, pointing etc.) when possible, as indirect mounts are always less efficient and more accident-prone, at least for large specimens. Never use headless pins when direct pinning - finger and thumb will always be the safest and most desirable means of manipulation.

There are two main methods of indirect mounting. In the first (Plate B, Fig. 6), a short headless thin stainless-steel micropin ("minuten") is used to pin the insect onto a stage of some sort (usually a strip of polyporous, or of Plastazote or some other high density and elastic foam; but never use polystyrene as this holds pins very poorly) that, at its other end, is pinned through by a handling pin (= carrying pin) that should be relatively robust (e.g. continental size 3) and have a good head. The stage should be as short as is practicable because long stages increase the risk of damage through swinging around on the carrying pin, as well as unnecessarily consuming storage space. As well as carrying the stage about two-thirds up its shaft this handling pin also takes the data and determination labels, so it needs to be long. Although the point of this pin will not pass through the insect, it still needs to be sharp to avoid its punching too loose a hole through the stage, which might cause it to swing (especially if it was occasionally accidentally rotated a little during use) and put the specimen, and also surrounding specimens, at risk. You have guessed it: the best carrying pins again cost 4p each at 1995 prices. The minuten can either pass through the dorsum of the mesothorax downwards and out of the venter in the same way as a direct pin, and then be pinned into the stage (with a good gap left between the insect and the stage, so the insect should be pinned quite high on its minuten), or else it can be passed upwards through the stage and have the insect pinned onto its tip, through the venter but not quite breaking out of the dorsum (this last method is only really suitable for insects mounted fresh, as it depends on the presence of internal fluids to stick the adult to the pin. With relaxed specimens, or those dried from alcohol, there is a risk that the insect will fall off - especially if stored upside down or sent through the post). Some people like to micropin specimens on a lateral, or a more diagonal, line in an effort to leave important features intact.

The second main method of indirect mounting involves glue. The carrying pin needs to have exactly the same properties as before, but this time it passes through a small piece of card two-thirds of the way up its shaft (thick card is best, as it grips the pin well and is less prone to swinging), onto which the adult parasitoid is glued. There are two main ways of doing this: either the card is a somewhat narrow isosceles triangle (pinned just in from, and half way along, the short side) and the insect is glued, usually on its side by a mesopleuron and the extreme base of the adjacent set of twigs, to the narrow tip in such a way that much of it projects beyond the area of the card allowing good views (this

method is called "pointing": Plate C, Figs 7, 8, 9), or else the card is usually a rectangle, pinned at one short end, onto the middle of which is glued the insect, preferably on its side so that fairly good all round views can be had even though the specimen is nowhere projecting (this method is called "carding": Plate D, Fig. 10). Pointing and carding each have advantages for different kinds of parasitoids - most microhymenopterists prefer carding, which affords greater protection to small insects and is also easier, while pointing can produce excellent mounts of small to medium sized ichneumonoids with a bit of practice. As with other indirect mounts, the overall size of the card needs to be kept down so as to reduce the distance from its centre of gravity to the carrying pin. Whether pointed or carded, it may one day be necessary to remove the insect in order to see some obscured part, so it is important that a soluble glue is used. Seccotine is an ideal glue as it is water soluble, and it is easily thinned to an appropriate consistency for any size of insect. Resist the temptation to reduce the labour of writing data labels by stacking several carded or pointed insects on the same carrying pin. Not only will the insects be difficult to examine without damage, but also they may belong to different species (i.e. needing different taxonomic arrangement). This is especially likely to be the case if they were solitary parasitoids, but it can also arise if a gregarious brood had been partly hyperparasitised.

A further method of mounting, developed especially for speed when dealing with large catches (e.g. from Malaise traps), is to glue the specimen directly to the shaft of a continental length pin (again about two-thirds of the way up) with a more permanent glue such as a gel of white shellac (which is shellac with the wax still in) in alcohol (Plate D, Fig. 11). Though quick, it is a somewhat less neat method and offers no real advantage over direct pinning or careful indirect mounting; and for reared specimens a little extra time to produce a better mount is more than justified.

However reared parasitoids are mounted, the host remains and the cocoons or pupal cases etc. from which the adults emerged also need preserving with them. It is best to keep these as part of the same mount as the adult if possible, most conveniently in a transparent gelatine capsule pinned through the handling pin immediately below the adult or stage. It is preferable not to glue these various bits to card etc., as they may easily fall off - and become lost or muddled or perhaps cause damage to adjacent specimens. Even if they don't, the parasitoid's larval exuvium (which may be of importance) is liable to fall from the

emergence hole of ichneumonoid cocoons when inverted. Gelatine capsules are also useful for keeping unmounted adults if only part of a gregarious brood is needed mounted, and again the capsule can best be included as part of a mount. If the cocoons (or host remains etc.) of solitary parasitoids are not exactly individually matched to particular adults it should be indicated in the labelling that cocoons (etc.) are mixed up - e.g. "1 of 4 cocoons mixed up".

The final advice on mounting is to take some of what you have done to a specialist and ask him or her to be critically helpful. Most will be glad to show you how you could improve, and it may help you to avoid developing inappropriate mounting techniques (Plate D, Fig. 12). For some groups (notably Chalcidoidea and some other microhymenoptera) quite different new techniques have been developed that are not needed for other groups (see "further reading").

Optimising data labels

The most important thing to appreciate is that you are not writing the label just for yourself, but rather you are providing a scientific document for posterity: it has to be legible and meaningful to others, probably even to foreigners, who may have absolutely no idea where or what you tended to collect or perhaps even in which country or century you lived. The data needed to write the label should have been accumulating on bits of paper kept with the insect as events unfolded. If possible this all needs putting on a single label: even if that makes the label a bit larger than usual the temptation to put it onto two smaller ones should be resisted as it is important that the full data can always be read without having to handle the mount unnecessarily. Two labels also have a tendency to end up pressed together: prizing them apart to read their data will then loosen their pin holes and cause the labels to swing around. A largish label has its good points as it helps to protect the specimen - not only in the collection, but also if the mount is accidentally dropped - and the high value of reared specimens is worth the bit of extra space. While labels should of course still be as small as possible in the interests of saving storage space (which is expensive), it is foolish to try to write smaller than is legible. Modern word-processing and printing facilities can be a big help with this.

The need to recognise and express uncertainty as clearly as possible, particularly in the host's identity, has already been discussed. If the host determination was provided by someone other than the collector whose name is given on the data label, then that fact should be so indicated.

There is also a need not to raise unnecessary uncertainty: for example ensure that locality names are not ambiguous, and do not use single dates without indicating "coll." or "em." to show what they mean. If possible provide both dates (even if only to the month or even year), and when applicable a middle date giving essentially the host's death (with a suitable indicator applying to the parasitoid such as "coc[oon]" or "mum[my]") is also helpful; especially if the collection and emergence dates occur in different years, for example, when it will indicate how the parasitoid passed the winter (in temperate areas). If the host is a plant feeder the plant from which it was collected should also be recorded - not least because sometimes phytophagous insect taxa become split partly on a foodplant basis and an undetectably erroneous host determination may otherwise be left over, but also because some parasitoids may not attack their hosts equally evenly over all the host's foodplants. If the plant is not known, or if some other substrate is involved, then give the best indication you can (e.g. "low plants", "fallen twigs", "leaf litter", "dry sheep dung" etc.). If the parasitoid is gregarious with respect to the host then this also should be indicated - if possible with the size and sexual composition of the brood. And finally data labels should be written in permanent ink on fairly thick *card* (of good quality - preferably acid-free and capable of lasting indefinitely): paper curls, and even card that is too thin is less well gripped by the pin leaving a label prone to twiddling. Of course, if you are passing unmounted parasitoids on to a specialist, it may be the specialist who writes the actual label - but ensure that he or she has the data on which to base it absolutely clear.

How to start studying them

Whether you want to find out more about their biology and host associations or learn how to identify the parasitoids you rear, the best advice is to seek direct contact with a specialist. If you wanted to start investigating the parasitoids of a host group such as, say, Neuroptera, a person knowing something about the general biology of parasitoids could quite easily point you to at least some of the relevant older literature, and more modern leads should come to light through computerized bibliographic searching of current and recent literature that you could do for yourself. This would establish what is known in a fairly straightforward way, though it may involve your reading quite a lot of papers. If on the other hand you had a growing interest in a

particular group of parasitoids such as, say, Ceraphronoidea, and wanted to know what was known of their biology and host associations, then the detailed and exact literature would still be best got from a specialist. If you have a *serious* interest don't hesitate to ask them: that is at least partly what they are for, especially if employed by the taxpayer.

It is not practicable to give an exhaustive list of relevant literature here, but fortunately a book on Hymenoptera (with particular reference to the British fauna) has fairly recently been published (Gauld & Bolton, 1988: reprinted and revised 1996) and this contains a large bibliography on their biology and also gives a good guide to the most usable identification literature up to that time. The suggested "further reading" given at the end of this booklet therefore concentrates on material additional to that found in Gauld & Bolton (*loc. cit.*).

Sending them by post safely

This section will apply particularly to people willing to pass reared parasitoids on to specialists, though of course it is to be hoped that anyone having their own collection of reared parasitoids will ensure that material can be borrowed from it. In either case, the postal system is often the only practical means of transfer. Unfortunately, however, some of the world's greatest entomological disappointments have happened in the post. If you have regularly received insects by post you will know that packaging has to be good enough to withstand: (1) being stamped on, (2) being thrown at a wall, and (3) being shaken vigorously for several minutes. Armed with that knowledge, and a little imagination, you will be reasonably placed to devise good packaging protocols that do more or less guarantee safe transit. The essential features are crush-proofing, shock absorbance, and eliminating rattle. For the first two, it is necessary to double pack, as follows: (1) the outer container must be strong and crush proof - e.g. a cardboard box (jiffy-bags are only good if the inner container is very strong, such as a small tin, or small and well wrapped further), (2) the packaging between outer and inner containers must be highly shock absorbent - e.g. bubble-wrap, expanded polystyrene "frass" - and thick enough *all around* the inner container to do its job. Finally, if the inner container is something like a corked glass tube containing an unemerged cocoon or an unmounted adult parasitoid, its contents must not be permitted to rattle, either loose in the container or with other bits and pieces (emerged cocoons, host remains, even data labels) in the container that are not adequately

separated and wedged from the adult parasitoid or other vulnerable item (e.g. unemerged cocoon). Wadges of cotton wool, firm but not too tight, are sometimes excellent - but there is a danger that small dry insects will get irreversibly tangled in the strands, and then be damaged as they are removed. Such small insects do well in small gelatine capsules which are themselves wedged against rattling. If the inner container is a box into which mounted specimens are pinned it should have a pinning base that holds pins very well (e.g. Plastazote - certainly not any low density foam or any kind of expanded polystyrene). It should also be strong but light (low momentum), and have a little fluffed cotton wool securely pinned into each corner to help trap anything that breaks loose in transit, and the mounts pinned into it should be firmly cross-pinned if there is any risk of their swinging (or of the pin not being held by the base - if the box lid is only a very little clear of the pin heads that in itself will prevent them from coming free). Finally, if livestock is being sent it will be prone to disastrous anaerobic fermentations in small airtight containers, especially if associated bits are not dry (or packed separately), so be mindful of that risk. First class post is well worth it. It also helps one to plan so as to ensure that extra time at weekends is not spent in the post unnecessarily. It is harrowing indeed to receive through the post a living host with a visibly dead parasitoid (such as a spider with a koinobiont ectoparasitoid larva on board), but this is a regular result of airtight containers and slow delivery. The pupal stages, too, of most parasitoids are very much more sensitive than most of their host groups, both to physical shock and to disease etc. - perhaps because their pupal cuticle is so thin.

Breeding them in culture

So long as their proper hosts can be provided in the right stage and condition, it is sometimes surprisingly easy to get parasitoids to oviposit on or into them in captivity. This enables one to observe their behaviour, to follow their developmental biology, to rear extra specimens (in thelytokous species females will result as the progeny of unmated females, but for all other Hymenoptera it is possible to rear a generation of males from an unmated female) and to investigate the success and willingness with which they may attack a range of different potential host species. Once parasitoids are in culture it is also possible to investigate various aspects of their developmental physiology, effect on the host's development, sex allocation strategies, and many other things.

Much of this is beyond the scope of this booklet, but for small-scale rearings under captive conditions (i.e. with the oviposition event taking place in captivity) a few tips and suggestions can be made briefly. The requirements are for good performance in all of the following: (1) mating, (2) longevity, (3) oviposition. This is, however, an area where experimentation really comes into its own: species of parasitic wasps will be rather idiosyncratic, and what has worked for one may not do so for another.

Mating can be a problem. Usually it works best if the female is introduced to the male (the other way round carries the risk that the female will be sitting in such a high concentration of her sex pheromone that the male can't respond to it in a directional way - but try both if necessary). They may require a roomy container, and it may need to have a through draught - plastic boxes with two sides cut out and replaced with gauze can provide for this (Plate D, Fig. 13). Often females are receptive only for a short time after emergence, but males may be reluctant to mate until they have fed: this is, however, very variable. Often an excess of males seems to be necessary to stimulate a female, even though she will usually mate with only one of them. Finally sunlight, shade, and the time of day can all be crucial.

Longevity is achieved particularly by *continuously* providing suitable food, and ensuring that the temperature and humidity do not exceed the parasitoid's tolerance limits (in general lowish temperature and highish humidity are best). Honey is a food-processing invention of Hymenoptera, and it proves to be as excellent for parasitic wasps as it is for bees. It contains proteins and vitamins as well as sugars, and (no doubt along with fat reserves) it seems to be adequate for egg maturation for most, possibly all, of the species that nourish and mature their eggs successively through their adult life (= synovigenic species) as well as being fully sustaining for the energy requirements of these and also the rather less demanding pro-ovigenic species that have a full complement of virtually fully developed eggs when they emerge as adults. It should be diluted about one part honey to three of water, and most parasitic wasps cope well with small droplets touched onto the insides of corked glass tubes, so that the droplets stand proud and do not "wet" and run down the glass. The food should be replenished daily as water evaporates, for it soon becomes too viscous. Any stock of 1:3 dilution should be discarded before moulds or alcoholic fermentations arise (sometimes within a day). Adults being kept alive and fed seem to do best if they are allowed to experience small rises and falls in

temperature/humidity and also natural daylight and darkness transitions. I keep them in my rearing shed, or somewhere a bit cooler in warm weather, and use 7.5 x 2.5cm corked glass tubes, stood upright, for all but the very largest species. In the case of synovigenic ichneumonids and braconids, even very small ones, the females of many species (that do not overwinter as adults) seem to live for about six to eight weeks, but most can be slowed down very satisfactorily in a fridge and can be kept alive for even longer. Some pro-ovigenic species, however, do not live more than two to four weeks even with a lot of care.

Oviposition is, of course, the crucial requirement. It is important to appreciate that some species (especially those that attack fully concealed hosts) will not parasitise naked hosts, only those offered *in situ* and - sometimes - even then only if there is frass or silk or some other necessary cue to turn them on. For these, the hosts must be set up and allowed to establish in their appropriate substrate well beforehand. If observation of the oviposition process is not a requirement, sleeving parasitoids with herbivorous hosts is often successful - and sometimes (e.g. for koinobiont parasitoids of leaf miners) almost the only practicable approach. Parasitoids (especially koinobionts) are often very particular about the stage and size of the host - and quite often subactive hosts will be ignored (so, for example, larval hosts in mid-instar may be more attractive than those approaching ecdysis - though there are also some parasitoids that will only accept hosts in the latter condition, usually so as to be on hand to parasitise the host as it moults). Many parasitoids whose hosts live fully exposed will parasitise them very smoothly if they are presented naked in glass tubes, and they are therefore easy to observe and subject to experimentation. Sometimes, however, when they are aged or have been deprived of hosts for long periods, they may exhibit abnormal behaviour, and in general it must always be borne in mind that there are liable to be limits to the inferences that can legitimately be drawn from behavioural observations on constrained parasitoids.

FURTHER READING

This list concentrates on material subsequent to, and therefore not listed by, Gauld & Bolton (1988) but also reiterates a few of the classic general texts (Clausen, 1940; Askew, 1971) and some papers particularly relevant to rearing and host associations from the perspective of host group. A few of the most recent overviews on evolutionary ecology etc. are included too (Waage & Greathead, 1986; Godfray, 1994; Hawkins, 1994; Hawkins & Sheehan, 1994).

Achterberg, C. van, 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandelingen (Leiden)* **283**. 189pp. [Deals with the world fauna. Well-illustrated keys, covering all situations.]

Askew, R.R., 1971. *Parasitic insects*. xvii + 316pp. Heinemann, London. [An admirable synthesis, giving biological overviews of not only parasitoids but also fleas, lice, blood-sucking flies etc. Well illustrated and very readable.]

Askew, R.R. & Shaw, M.R., 1986. Parasitoid communities: their size, structure and development. *In* Waage, J. [K.] & Greathead, D. [J.] (eds) *Insect parasitoids*: 225-264. Academic Press, London. [Explains the terms idiobiont and koinobiont, and develops host range concepts from them.]

Clausen, C.P., 1940. *Entomophagous insects*. x + 688pp. McGraw-Hill, New York. (Reprinted 1972. Hafner, New York). [Quite detailed accounts of the biology of parasitoids and predators on a group-by-group basis. Drawn mainly from the economic entomology literature, this excellent work still provides a reliable and well-illustrated wealth of information at species level despite its age. The classification followed is, however, very out of date.]

Fitton, M.G., Shaw, M.R & Austin, A.D., 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* **90**: 65-93. [Key to genera of the parasitoids involved (aculeates dealt with only very briefly), with summaries of knowledge at the time on their biology and host associations. Substantially more is now known.]

Gauld, I.D., 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society* **35**: 351-377. [An evolutionary rationale for the overall host associations and radiations seen.]

Gauld, I.[D.] & Bolton, B. (eds), 1988. *The Hymenoptera*. British Museum (Natural History), London & Oxford University Press. xi + 332pp. [Account of the biology and systematics of Hymenoptera, with special reference to the British fauna. General information on evolutionary biology etc.; keys to family level; biological information at subfamily level; guide to species-level identification literature for the British fauna. Extensive bibliography. [Minor corrections are made in the 1996 reprint edition.]

Godfray, H.C.J., 1994. *Parasitoids: behavioural and evolutionary ecology*. 473pp. Princeton University Press, New Jersey. [Comprehensive synthesis and rigorous analysis of hypotheses.]

Goulet, H. & Huber, J.T. (eds), 1993. *Hymenoptera of the world: an identification guide to families*. vii + 668pp. Agriculture Canada, Ottawa. [Essentially an identification guide, with simple and well-illustrated keys down to family or (usually) subfamily level. For each group a brief diagnosis and biological sketch is given, together with references to the most important regional species-level identi-fication keys and other literature, though this is rather patchily done.]

Hawkins, B.A., 1994. *Pattern and process in host-parasitoid interactions*. x + 190pp. Cambridge University Press. [Broad patterns and analysis gleaned from the global literature.]

Hawkins, B.A. & Sheehan, W. (eds), 1994. *Parasitoid community ecology*. x + 516. Oxford University Press. [Chapters were mostly given as papers at a symposium; a mixture of case studies and conceptual overviews.]

Noyes, J.S., 1990. Chalcid parasitoids. 2.7.2.5 in Rosen, D. (ed.) *The armoured scale insects: their biology, natural enemies and control* **B**: 247-262. Elsevier, Amsterdam. [Advice on killing, storing and mounting reared chalcidoids, also applicable to various other "microhymenoptera". Includes notes on critical-point drying not found in his more general 1982 paper: Collecting and preserving chalcid wasps (Hymenoptera: Chalcidoidea). *Journal of Natural History* **16**: 315-334.]

Shaw, M.R., 1990a. Parasitoids of European butterflies and their study. In Kudrna, O. (ed.) *Butterflies of Europe* **2**: 447-479. Aula Verlag, Wiesbaden. [Introductory guide to the study of parasitoids, focused on those attacking European butterflies.]

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Shaw, M.R. & Askew, R.R., 1976. Parasites. *In* Heath, J. (ed.) *The moths and butterflies of Great Britain and Ireland* **1**: 24-56. Blackwell, Oxford. [General biological overview. Nomenclature and parts of the classification now substantially out of date.]

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Shaw, M.R. & Huddleston, T., 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). *Handbooks for the Identification of British Insects* **7(11)**. 126pp. [Key to subfamilies occurring in Britain and review of the overall host associations and biology of each in some detail. Literature for species-level identification is also listed. Extensive bibliography.]

Waage, J.[K.] & Greathead, D.[J.] (eds), 1986. *Insect parasitoids*. xvii + 389pp. Academic Press, London. [Papers from a symposium; several aspects of parasitoid biology are covered.]

ACKNOWLEDGEMENTS

NOTES

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THE AMATEUR ENTOMOLOGISTS' SOCIETY

THE SOCIETY was founded in 1935 to promote the study of entomology, particularly among amateurs and the younger generation.

THE BI-MONTHLY BULLETIN, issued free to members, contains articles on all insect orders in a style suitable for the amateur, as well as observations by members. The Society relies upon its members to contribute articles as much as possible. A WANTS & EXCHANGE LIST, issued with the *Bulletin*, enables members to buy, sell or exchange entomological material, etc.

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