Mining bee *Anthophora plumipes* female　　　　Robin Williams, Wedmore

An Introduction to

Bees in Britain

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-from original work by members of the Bees, Wasps & Ants Recording Society

Technical editor, Mike Edwards

Bees in Britain

Foreword (by Robin Williams)

This project started back in 1997 at the AGM of the Bees, Wasps & Ants Recording Society (BWARS), when I raised the possibility of producing a well-illustrated book which would introduce people to the fascinating world of bees. The last British work which really went into the subject in detail, was Saunders (1896). So clearly there is a gap. Other groups of British insects have been raised to public awareness in recent years by modern introductions; one well-known example being that of Hoverflies, Stubbs & Falk (1983), resulting in many people taking up a special interest, often with great enthusiasm and benefits to our overall knowledge.

George Else, a prominent member of BWARS, is busy writing a comprehensive, scientific work on British bees, due to be published by the Ray Society in due course, but that is to be aimed at the professional or serious amateur, already steeped in the terms in use, techniques required and knowing a reasonable amount about the subject. We felt there was a need for a true introductory volume, bringing those who wish to know about bees sufficient information to enthuse them into seeking yet more, and to go out into the countryside with a blueprint for finding and enjoying these insects.

This volume has been designed to meet this need. A large introductory section answers many of the questions with which a newcomer to the subject is faced, starting with 'What is a bee?' It goes on with headings such as 'nesting', 'life cycles' and 'foraging'; all of which are basic to understanding about bees. 'Finding out more about bees' takes the reader further into detail, together with 'where to look', 'gardening', 'recording' and 'photography in the wild', as well as other techniques. A third chapter on conservation spells out why we should be concerned about changes in habitat and what we can do about it, as well as other important questions.

We spent a considerable while deciding how detailed the chapter on identification would be and settled eventually for printing two separate keys to genera. Why two? Most experienced entomologists will tell you that they are rarely satisfied with a single key. They always have the nagging feeling that they may be wrong and need confirmation. The other reason is that keys to bee genera have always been known to be difficult and we felt that two different approaches would be most acceptable. These keys have been tested by various groups of people and work well, but the final proof lies in how the new user finds them; it would be helpful if any comments could be fed back into our website .

The final chapter comprehensively covers descriptions of all the genera together with selected species from within each, plus excellent photographs to give a taste of the beautiful and varied insects found in our country. These descriptions have been laid out to a set pattern to make comparisons easier, giving sizes, physical characteristics, nesting behaviour, general abundance, when they are to be found and where, as well as availability of keys or other information.

Finally a number of appendices on specific subjects are included, with a large table covering all bee species, showing a brief description, flight times, sizes and other useful bits of information. This provides a unique guide to confirm other methods of identification, as well as where and when the bees are likely to be found.

I must thank the various authors of the sections and chapters for their hard work, tolerance and continuing good humour, in spite of various changes and editorial decisions which affected them. In particular, I must comment on a few individuals; Geoff Allen and Graham Collins for the intensive work on the keys, Geoff Allen again for the many beautiful drawings used to illustrate so many chapters, Andrew Philpott for selecting and editing the photographs, to all the photographers who have contributed their images and Mike Edwards & Geoff Allen for editing the final draft for technical accuracy. Finally, special thanks to my wife Romey for copy-editing the much-fragmented manuscript, after my own efforts in the same direction. It has been a long and hard slog, but we feel it has been worth all the effort put into it and hope that it will attract others to the fascinating world of bees to be found on their doorsteps.

REFERENCES

Edward Saunders, **Hymenoptera Aculeata of the British Isles**, L. Reeve & Co, **1896.**
Alan E. Stubbs & Steven J. Falk, **British Hoverflies,** BENHS, **1983.**

What is BWARS? (by Mike Edwards)

The Bees, Wasps and Ants Recording Society (BWARS) is a group set up for enthusiasts for aculeates (bees and their cousins), with nearly 500 members in 2010. The society developed from a project to map the distribution of British Bumble bees, inaugurated in 1970 as part of the European Conservation Year. This project collected records, historic and contemporary, for a period of 5 years. These were all mapped onto master sheets by David Alford and eventually produced as the Atlas of the Bumble bees of the British Isles (1980).

For several years after this date no mapping distributions of any bee or wasp species were collected. Although BWARS, as a recording scheme, had been created with the support of the Biological Records Centre (BRC) at Monks Wood in 1978, and participated in a memorable field meeting in Devon in the May of that year, together with the newly created Dipterists' Scheme, it lacked sufficient organising members to make much headway. It was left, by default, to George Else at the Natural History Museum.

In early 1986 a meeting was held in London at the Natural History Museum. All the major contributors to BWARS, plus some of the original Bumble bee Scheme, were invited and about twenty people had a very interesting afternoon reminiscing and planning. The outcome was the re-launch of BWARS as an active recording scheme, with a steering group, newsletter and regular meetings.

The first steering group meeting was held at Monks Wood over a weekend in June, 1986, and the first newsletter, a two-page roneo-ed affair, produced in the Autumn. There was no formal membership, individual applications to be included on the circulation list being sent to BRC.

An early decision was made to make recording the distribution of all the Aculeate Hymenoptera (ants, bees and wasps) the focus of the scheme, but this was clearly too big a task to be done at one go. Consequently it was decided to map sets of about sixty species, over a two-year period, with a Provisional Atlas for this set of species being produced at the end of the period. It was estimated that it would take something like twenty years to complete the set for all British aculeates. This approach was similar to that in which the original Bumble Bee Atlas was produced.

The scheme grew steadily in contributors and by 1995 it was decided to create a formal Society, with subscription and constitution. Membership is predominately drawn from Great Britain and Ireland, but there is a network of contacts, known as Corresponding Members, from many European countries, as well as several individual members. The Society also elected to become an affiliate of the long-established British Entomology and Natural History Society.

This connection has proved to be invaluable, most notably in providing a suitable location for annual workshops at its base at Dinton Pastures. The Society now holds several workshops a year, one in association with its AGM and others at regional centres, such as the National Museum of Wales at Cardiff.

The Newsletter has grown from the original two-pages of A4 paper to a very respectable, bound A5 journal with its own ISBN number. The spring 2006 edition had 56 pages, with colour plates on the covers. It still carries draft maps and species accounts of the current set of species for mapping, but also contains a good variety of articles about the aculeates of the UK. It is produced in the spring and autumn of each year.

The Provisional Atlas series has proved a very sturdy individual, with data for Atlas 7 being collected at the time of writing, for publication sometime in 2008. The number of people contributing data to these Atlases has grown enormously. This is both in response to the support which Society members have been able to give to new members and, very significantly, to the growth of home computing.

The first Bumble bee maps were laboriously hand-coloured on pre-printed maps, several times, with the associated transcription errors. The BWARS initial maps followed a similar process, but it was soon apparent that the way forward lay with using computing power, which allows the collation of lots of records from different sources as well as the ready production of maps. The implications of the development of the mapping scheme are dealt with further in a later chapter.

With all these successes, why then this book? The latest treatment of all the Aculeates of Great Britain and Ireland was published in 1896 (Edward Saunders, Hymenoptera Aculeata). It is an unfortunate quirk of history that, whilst the wasp and ant groups (just over half the approximately 600 aculeate species in the region), can be broken quite easily into smaller units which have attracted a number of authors to provide more modern treatments, the bees have not fared very well, despite their general attraction and 'better press' than wasps. This book aims to give the fascinated, or potentially fascinated, observer an introduction to the major groups of bees found in the region, their biology and behaviour. Once exposed, it is hoped that readers will become hooked and join the ranks of BWARS.

For further information see our website: www.bwars.com

Chapter 1- Introduction

What is a bee? (by Geoff Allen)

To the casual observer this may seem clear. The large, round, furry insects visiting the fruit tree blossom in the garden in spring are known to be bumble bees. The more observant will see that there are also smaller, more elongate, brownish insects, which look slightly different, flying with them, and these may possibly be honey bees.

However, should this observer look at the flowering mint in the herb garden in summer, it may be seen that, amongst the bumble bees, there are many small insects resembling flying ants actively visiting the flowers. However, winged ants do not toil in this way. The insects appear every day when the sun shines – flying ants do not do this either. Some will be metallic green or brassy in colour. Examining a flowering shrub may add to the interest. Amongst the same metallic insects may be found small, winged, black specimens with yellow spots on the face and thorax, equally intent on taking nectar. These are all bees. With the bees there may be equally small, black wasps, sometimes with silver "moustaches" and yellow spots, usually sunning on, or scent marking, leaves. If bees can be so varied, and some wasps so similar to them (even when under the microscope), how does the novice tell them apart? There are even harmless flies which appear very similar to bees and wasps, and so gain protection from vertebrate predators.

The bees are a closely related group of aculeates (stinging insects) placed in a series of taxonomic families, in the vast insect order Hymenoptera. Female bees provision their larvae in the nest with pollen (protein), sometimes moistened with nectar (carbohydrate), and are hence classified as phytophagous (feeding on plants). This contrasts with the wasps, most of which use insect prey. The adult female bee depends on pollen as a protein source to develop her as yet unlade eggs.

It is not surprising that structural modifications have developed in the bees corresponding to the above diet. All bees have sparse to dense, **plumose** (branched to feathery**) hair** somewhere on the body, for gathering pollen and carrying it, providing a key character for the separation of bees from wasps. Wasps all have **unbranched** hairs. Some bee species lay their eggs exclusively in the nests of other bees – so-called cuckoo bees. Such bees may have lost most of their plumose hairs in their evolution, as they no longer need to provision their own nests. They may look very like wasps, some even having bold red or yellow markings to deter vertebrate predators. In most such bees, however, at least a few plumose hairs still exist, particularly near the wing bases.

A structural modification of the hind metatarsus occurs in bees. This segment, the first of the five tarsal joints of the hind leg, (see **Glossary** at end) is expanded more widely than the remaining tarsal joints, compared with that of the related wasp families and is flattened from side to side. There may be a brush of stiff, bristly hairs on the inner face of this segment. This character state is associated with the habit of manipulating the collected pollen.

Bees have modifications to the mouthparts, which are adapted for gathering nectar from flowers, and this enables them to be split into two main groups. These are the "short-tongued bees", including four British families (Colletidae, Andrenidae, Halictidae and Melittidae) and the long-tongued bees (Megachilidae and Apidae).

In some of the most primitive bees e.g. *Hylaeus* and *Colletes*, the tongue is short, blunt and bilobed, resembling that of many wasps; this group is sometimes known as the 'wasp-tongued' bees. It is thought that this shape of tongue is an adaptation to the habit of lining the walls of their breeding cells with a glandular secretion, which hardens to a fine film. It has been suggested that this tongue shape is a reversal in evolution.

In the remaining short-tongued bees, the species nest in the ground and the tongue is short and pointed. Many female short-tongued bees have an additional feature, which can be a useful identification character: the fifth upper plate of the gaster (near the tip or apex) has a tuft of hairs called the preapical tuft. This is very apparent in a bee such as the common *Andrena haemorrhoa*. As the female sits sunning on a stone, the gaster can be seen to be shining black, apart from the apex, which has a bright, foxy red, preapical tuft, matching the thorax in colour. In the Halictidae, there are three British genera. In two of these, *Halictus* and *Lasioglossum*, there is a median, longitudinal parting of the preapical tuft, giving rise to a specialized hair structure known as the "rima". This is characteristic of most Halictinae, though in the cuckoo *Sphecodes* the preapical tuft is considerably reduced. In many short-tongued bees, the collected pollen is carried on pollen brushes not just on the tibia but much of the legs. In most Halictinae, there are additional scopal hair fringes on the underside of the gaster. Some *Andrena* have pollen carrying "baskets", on the sides of the propodeum.

The last main group is that of the 'long-tongued' bees (Megachilidae and Apidae), which has the tongue pointed, sometimes with a tiny spoon shaped development at the apex, and is long to extremely long. The flower bees, *Anthophora*, and some of our bumble bees, particularly *Bombus hortorum*, have very long tongues. These bees tend to specialize in collecting nectar from flowers with long corollas. In Britain, Megachilidae are recognised by the pollen brushes being found only on the underside of the gaster of the female. There are no pollen brushes on the hind legs. In Apidae the pollen carrying apparatus is usually on the hind tibia of the females. In the worker Honey bee and female *Bombus*, the hind tibia and metatarsus are expanded and flattened, and the scopa (pollen brush) is replaced by a pollen basket or corbicula. The outer surface of the hind tibia is smooth, shining and flattened. The pollen is held in place in a dampened mass by the stiff, curved, corbicular hairs surrounding this flattened area.

Foraging for Nectar & Pollen (by Mike Edwards)

Together with the majority of the aculeate Hymenoptera, bees are unusual among insects in that they concentrate the food for their larva in one place and then lay an egg on this concentrated store, rather than just laying their eggs wherever the larval food supplies happen to be. In this respect they behave more like birds than insects. In fact they are said to have nests, just like birds, and some species have developed into cuckoos, laying their eggs in other bees' nests.

This nesting behaviour allows female bees to place their eggs where the larvae will have the best chance of eating all the provisions provided by the female, but it also increases the essential requirements she has to meet if her reproduction is to be successful.

Partial habitats

Bees are said to occupy a number of partial habitats, each of which provides one essential component for the completion of the life-cycle. Most of these partial habitats are associated with nest-building and provisioning and it is these which are considered here. Cuckoo species short-circuit the process by searching out completed cells of their host species and laying their eggs there. However, ultimately these species rely on the presence of all the partial habitats as well, as they cannot exist in the absence of their hosts and their requirements.

No single dominant requirement

Although all the partial habitat components may sometimes be found in close proximity and may equate to a botanically-defined habitat, they may also be, and often are, separated by quite large distances, over several kilometres in the most extreme instances. The female bee needs to actively search (forage in a wide sense) for all these components and all partial habitats need to be present, or the life-cycle is broken; there is no one dominant requirement. Bees are strong flyers and the distances they can regularly cover in relation to their size gives the landscape a very different scale to the one inhabited by many other insects.

Partial habitat 1: the nest site

The nest site needs to be warm, as this reduces the time which the larvae take to complete development. Female bees can often be seen searching for areas of warm bare soil, if ground-nesting, or old beetle burrows and other holes in dead wood, in sunny places, if cavity-nesting. Sometimes male bees will use actual or potential nest sites as mate-searching areas. For instance, males of the snail-shell nesting *Osmia bicolor,* perch on an empty shell and try to entice the female to consider it as a nest site. His reward for finding the site is to mate with the female. The nest site forms one partial habitat.

Partial habitat 2: a source of nest-building material

Having found a suitable nest site this often requires modification to hold the eventual supply of larval food. Most ground-nesting species just use the excavated earth, but the situation for many cavity-nesting species is very different. Awkward and too large spaces can be built into something more suitable by the careful working of building materials, usually soft mud or plant material. Some species even utilise more than one material for different purposes and require specialist sources for their provision, such as mud or leaves. This makes another partial habitat.

Partial habitat 3: suitable flowering plants

Once the completed brood chamber, or cell, has been created within the nest site, it must be filled with larval food. Although popular mythology connects bees with gathering nectar, this is not the major larval food; even for the Honey bee, which certainly does collect large quantities - but not for larval food. If you want to build new bodies (larvae and maturing, newly-emerged adult bees) you need protein above all else. Nectar is basically sugar; for protein, the bee collects pollen, and the collection of this material drives much of the flower-visiting behaviour of bees.

A small quantity of nectar is often added to the pollen in the larval cells and the bees themselves certainly need to consume plenty of this energy-giving substance in order to do their flying, but the *gathering* of nectar for larval food is not the prime reason for flower-visiting. Failure to appreciate this fact, coupled with an incomplete understanding of the specialised nature of honey bee colony dynamics, is one of the commonest ecological misunderstandings about bees.

Pollen has several features which make bees what they are. It is a very concentrated source of protein, is locally abundant, and is readily collected and packaged according to the carrying ability of the bee. The secretion of concentrated sugar solution (nectar) by the flower, in more-or-less the same place as the pollen, is an added bonus. These concentrated resources allow bees to cover large distances and yet still obtain an adequate reward for their effort. Suitable flowering plants from which the bees may gather pollen and obtain nectar form a third partial habitat.

Generalist or oligolectic?

Some species collect pollen from just one flower species or, more often, family (specialists or oligolectic). Others visit a wide range of flower species and families (generalists or polylectic). There is a human tendency to value specialisation over generalisation, but this judgement has no ecological value, they are just different ways of getting a living and their relative value depends upon the resources available in the landscape. Nectar collection tends to be much less specific than pollen collection.

It is thought that oligolecty is maintained by the new female bees looking for pollen with the same scent as that which they fed on themselves. This connection to particular pollens may be very strong. On the other hand, some bees, notably those of the currently evolving *Colletes succinctus* group, seem to be able to switch pollen sources fairly readily. Hence you have three very closely related bees foraging for pollen associated with three different flowers. *C. succinctus* at the flowers of heathers, *C. halophilus* at Sea Aster and *C. hederae* at Ivy flowers.

How this may have happened is suggested by the fact that in some places where heathers have disappeared recently *C. succinctus* is still present, but now gets its pollen from Ragwort. It is thought that *C. halophilus* owes its origin as a species to extensive flooding by the sea of the Rhine Delta in the Netherlands. This flooding rapidly killed the heathers on the coastal dune systems, and Sea Aster, a close relative of Ragwort, replaced the heather as a major pollen source in the landscape.

Selection pressure on the optimal emergence time of *C. halophilus* (Sea Aster flowers several weeks later than heathers) has adjusted the flight period and this species now flies in late August and September, rather than *C. succinctus* in late July and August. Something rather similar may well have happened to drive the emergence of *C. hederae* as a distinct species, although the details of how this may have happened are not currently clear.

Where a specific flower type is dominant in a landscape, such as legumes in temperate grasslands, it will suit specialists as long as conditions do not change. Temperate grasslands are home to many species closely associated with legumes, such as some bumble bees. There will always be other plant types which do not dominate their landscape and this component may be more suited to visits by the generalist species. Generalists tend to win when conditions change dramatically. The balance between opportunities to develop specialism and to remain generalists is constantly changing and closely related bee species may exhibit one or the other behaviour.

Specialist equipment

It may be in the plant's interest to tie its pollinating insects to itself, for instance the highly complex flowers of the legumes require special techniques on the part of the visiting insect to get to the pollen. Sometimes this has required the bee to develop special organs or behaviours, but all female bees (apart from cuckoos) need to be able to carry their booty back to the nest. This requirement has given rise to the defining taxonomic feature of bees as compared with wasps, the presence of branched hairs on the body, 'all the better to get the pollen stuck to'.

These branched hairs may be concentrated in special areas known as scopa, usually, but not exclusively, on the hind legs or under the abdomen. The scopa often form distinctly coloured patches of hair, which differ between closely related bees and which can be very useful to humans when trying to name the bees.

Some bees have got rid of most of their specialised pollen-gathering hairs and adopted other ways of getting their larval food. Clearly cuckoo species do not gather their own pollen and it can be quite hard to find the diagnostic hairs - between the legs is a good place to look for these. The small, almost hairless bees of the genus *Hylaeus* have taken to carrying their pollen inside their crop, along with nectar, and these bees fill their specially water-proofed cells with a very runny mixture of pollen and nectar. Honey bees and bumble bees have altered their leg hair brushes so that they form a rim around a concave, shiny area of the hind leg, known as the pollen-basket. The front and mid legs are then used to comb pollen from hairs elsewhere on the bee into these baskets.

The tongue, which is the second specialised major adaptation for foraging at flowers, is the same for all aculeates. Several joints of the mouthparts have become specially shaped to form a long tube which can be folded up, out of the way under the head, when not needed. This tube can be inserted in the specialised nectar-producing glands of flowers, or nectaries, and the nectar drawn up into the mouth through the tube. The nectar forms the fuel the bee needs to search out all the other parts of its life-history requirements. When the bee has taken on a load of fuel it stores it in its crop, also known as its honey-stomach.

Tongue shapes

It is often convenient to divide all the bees into two large groups, the 'long-tongues' and the 'short-tongues'. In its basic taxonomic form this distinction relates to the actual pieces of the mouth-parts which are modified to form the tubular 'tongue'. In practice, the *actual* length of the tongue relates to the size of the individual. For instance, even among 'long-tongued bees', a large queen *Bombus terrestris* (a shorter-tongued bumble bee species) has a physically longer tongue than a small worker of the longer-tongued *B. pascuorum*.

This physical difference in length, rather than the relative lengths of tongues to body, can affect the sort of flower which bees visit for nectar. *B. terrestris* queens will readily visit flowers of Red Clover, a flower with a very long corolla tube, inserting their tongues to reach the nectaries from the front of the flower. However, the much smaller workers cannot reach the nectaries by this, the 'legitimate', route and resort to 'robbing' the flower by biting through the corolla at the base and inserting their tongues in a much shorter route to the nectaries. Although Honey Bees, which also have relatively short tongues, do not usually make the first bite into the corolla, they are very quick to follow the bumble bees' lead once the hole has been made.

Long-term storage

Going to more extreme lengths to get nectar is not just a feature of 'lazy' species. Honey Bees, and to much lesser extent bumble bees, have good reasons for needing to collect more nectar than they need for their immediate requirements. These bees live in colonies, with a number of workers, a non-foraging queen, who does (almost!) all the egg-laying and, of course, the males who do nothing but eat (drones).

The need to maintain the temperature and activity of the colony, often over a much longer period than the life-time of an individual worker, means that it is necessary to store adult fuel against lean times - the nest has its own honey-stomach - and keeping this filled up becomes important. It is this extra-insect store, which we raid to provide us with the tasty honey and in doing so stress the colony, which we then try our best to relieve by putting back a fairly tasteless concentrated sugar solution.

Life Cycles (by Geoff Allen)

Bees have a complete metamorphosis, or four-stage life cycle, i.e. egg, larva, pupa and adult. The adults are the only stage usually seen, as the young forms are reared hidden in cells constructed by the females in their nests. The egg is small, pearly white and sausage shaped, and hatches into the larva after a few days. This larval stage is white and maggot-like, lacking legs, wings and eyes, and is the only phase in the life of the bee in which it grows. The larva consumes the food provided by the adult female and moults its skin several times as it grows from egg-sized to having a body mass a little larger than the adult. It then metamorphoses into a pupa, usually first spinning a cocoon. In the pupal stage the whole tissue structure is reorganised, from maggot-like to the fully coloured, winged adult. Whilst in this stage, the young bee takes no sustenance and so gradually loses some body mass until the completion of the life cycle, when the fully formed, winged adult emerges. The adult bees do not grow.

Bees, along with most other Hymenoptera, have an unusual method of sex determination. Males come from unfertilised eggs and so have only a single set of chromosomes, whilst fertilised eggs produce females, having the normal paired sets. The female bee is instinctively able to decide the sex of her eggs and so lays male-determined eggs in smaller cells than those for females, (except for the limited number of species where the male is larger than its female). The female achieves this when laying by releasing sperm, stored in her spermatheca, if the egg is to be female. This has great significance in the social forms; all worker bees are female and so the queen needs to lay female-determined eggs until it is a suitable time for males to be reared. Males appear only at a specific time in the annual life cycle and serve but one purpose - to mate with eligible females. It is frequently the case that the males, having carried out this function, vanish quickly and are not found again until the next generation in the life cycle appears. In solitary species the females usually work on for several weeks after the males are gone, having greater longevity.

Most bees are solitary animals, each female constructing her nest, and provisioning it independently. Only a comparatively small percentage of species live in complex societies. A look is taken here at some of the transitional stages to sociality.

The female *Andrena fulva* is a solitary mining bee appearing in the spring a few days after the males. Females mate with a male after a minimum of courtship. Mating takes place only this once in her life and she stores the sperm, which is viable for several weeks, in the spermatheca. (In the queen honey bee the sperm remains viable for her lifetime, up to five years). Now fertilised, the female *A. fulva* starts to build her nest. This begins with a vertical burrow dug into the soil, often in short turf; lawns are favoured nesting sites. The spoil from the burrow is heaped around the entrance where it forms a small, crater-shaped mound. When the initial burrow reaches the required depth, depending on soil conditions, a cell is constructed. This cell is an oval shaped widening of the burrow, which gently curves at the cell; the long axis of this cell is almost horizontal.

The Dufour's gland, an internal organ near the apex of the bee's gaster, produces a secretion which is painted onto the wall of the cell. The secretion rapidly dries, forming a waterproof lining to the cell, which is then provisioned with pollen moistened with nectar. A favourite forage plant is dandelion and the bee makes eight to ten trips for the required pollen, which is packed into a ball. An egg is then laid on this dampened mass and the cell sealed with earth and tamped into place. Another cell, a little further towards the entrance, is then constructed from a side burrow and the cycle repeated. The *Andrena* female may produce about 4 or 5 cells and then construct another nest. All told, she may dig and provision two to three nests before she dies from her labours. However, the care taken in protecting and providing food for the young means that a very high proportion will survive to adulthood. But the female *A. fulva* never witnesses this, as the new generation of bees does not emerge until the following year. These new bees have metamorphosed to adults by late summer but remain in their cells within maternal nest until the following spring.

A slight variation of this life cycle is found in some *Andrena,* which produce two generations each year. In such species, there is a spring brood which provisions nests giving rise to a second, summer emergence. The latter brood females construct nests to produce bees which do not appear until the following spring. There is not usually much overlap in the flight periods of the first and second generations though sometimes a first brood female lives long enough to be still flying when the second brood males appear. The two broods of a species may slightly differ in appearance and in a few cases have erroneously been described as separate species.

Andrena flavipes is a double-brooded bee, which has another interesting form of behaviour. The females nest in aggregations, which can sometimes be vast, with thousands of bees burrowing separately but in close proximity. Besides the clear advantage given by the favourable nesting conditions in the aggregation, the incoming and outgoing of the foraging female bees probably acts as a distraction for would be parasites and predators. Nevertheless they are all solitary bees, merely sharing the same earth-bank.

A further step is communal behaviour. The females of at least three British *Andrena* species share a common nest entrance tunnel. Each individual female is believed to build her own burrow off this and provisions it independently. In the abundant *A. carantonica (= scotica)* the number of females sharing one entrance burrow may be a dozen, or sometimes more. In the related but rarer *A. bucephala* and *A. ferox* this number can rise to several hundreds.

Some mining bees in *Halictus* and *Lasioglossum*, both genera in the family Halictidae, have taken the first steps to sociality. The females mate in the autumn when the males are present, and frequently over-winter in the maternal nest. In the spring, the females dig burrows, usually solitarily. In *Lasioglossum fratellum* this sex has a long life-span, up to a year. A female founds a nest solitarily and the first generation reared is largely female. A daughter will often remain with the foundress in the maternal nest; the latter has more developed ovaries and usually guards the nest burrow entrance, whilst the daughter carries out most of the foraging. The nest comprises an earth cell cluster held within a chamber by pillars. In a nest with only one female, there are up to nine cells, whilst a nest with more than one may have 17. To provision one cell a female may make 10-13 foraging trips, the final few being for nectar only. Provisioning a cell may take two days.

In *L. malachurum* the colonies formed in each nest are more complex. The nest is again initiated by a solitary foundress in the spring, sometimes in close proximity to others. She rears a small brood, of perhaps a half dozen small females. The new brood are all workers and have no chance to mate, there being no males present at this time of year. In this species, the workers are differentiated enough from the queens to have been described, in error, as a separate species. These workers enlarge the nest and forage to produce a second brood of about twenty slightly larger workers, from eggs laid only by the foundress. The sexual forms are produced as a third brood, from up to 70 or so cells, in the late summer. These mate and the females hibernate. This is a truly "eusocial" species. A number of other halictid species are known to be fully social; in some groups they are a significant percentage of the total species. The autumn mating strategy may be a prerequisite for sociality to evolve, as it occurs in all temperate social bees and wasps, apart from the highly evolved honey bee.

In the social halictines, as with the solitary species, each brood cell is provisioned, an egg laid and then the cell sealed. It has been speculated that this may be a limiting factor in the evolution of halictine societies. In all other social Hymenoptera, there is some contact between larva and adult.

In a few halictid species, more than one female may co-operatively found an initial nest. The females may all be sisters. Here it is usual for one of the females to become the dominant alpha individual and hence the egg layer, whilst the others mainly forage, even though they are fertilised. At this stage in the life cycle, the species is subsocial but workers may be reared in many cases, when the colonies become fully eusocial.

The three conditions for eusociality, as set out by EO Wilson, are:

1. Members of the same generation use the same composite nest and co-operate in brood care.
2. There is reproductive division of labour.
3. There must be overlap of generations, so that offspring assist parents.

These conditions are met in several British halictid species. However, some species, such as *Lasioglossum calceatum*, are eusocial in the south of their range but in more northern parts may be solitary. Also, it is believed that some formerly primitively social halictines may have reverted to being solitary across their range.

The societies of bumble bees, genus *Bombus*, start in a similar, solitary manner but grow to include many more workers, up to about 450 in *B. terrestris*. Each queen starts nest foundation in the spring, often selecting an old rodent nest as a basis. She secretes wax to construct an egg cell and honey pot. The brood are fed on pollen collected by the queen and hatch into worker bees, very like their queen but much smaller. The brood nest grows at a controlled rate, the queen forming egg cells on top of the larger pupal cells in a manner such that there will be enough workers hatching out to care for the larvae resulting from the eggs. The gradually increasing proportion of workers over larvae result in each brood of workers being better fed, and hence larger than the last, until males and then the large queens are produced. In the majority of cases, the queens then mate and hibernate but some species occasionally have a second nesting cycle before the autumn sets in. With the warming climate this is becoming more frequent.

Why have complex bee societies evolved? The unusual sex determination in aculeates, where males have only a single set of chromosomes while females have paired sets, means that a daughter female has more genes in common with her sisters than she would her own daughters. Helping rear sisters does more to propagate her own genes than nesting independently, particularly if some of these sisters become future queens. Where the queen mates with a number of males, through the need to produce large numbers of workers in complex societies, this close relationship between sisters becomes diluted. A consideration here must be that more bees make for better defence of the young and the queen, particularly in light of the ability to sting.

Colony structure in eusocial bees and caste control by queen pheromones

In the most primitive of bee societies, such as those found in some Halictidae, there are only a few workers in a colony. The presence of workers is diagnostic of eusociality. The foundress female (queen or gyne) is dominant and to some extent directs work in the nest. For example, she may lead a succession of pollen laden workers to a freshly dug cell to deposit their loads before she lays her egg. In some species, workers may only be distinguished from egg-laying foundresses by less developed ovaries, being similar in morphology and approximately the same size. The differences, particularly at a subsocial phase where it exists, may even be statistical – some females in a colony mainly lay eggs and do little foraging while the converse is true of others; further individuals may lay some eggs and carry out some foraging. Experiments have shown that even at this primitive level there may be a common odour to the colony-members which distinguish them from intruders.

Bumble bees have achieved a higher level of eusociality. The queen is larger but otherwise very similar in structure to the workers. She is certainly dominant and this is not determined solely by her size. It has been shown that the queen produces a chemical signal to indicate her rightful position in the colony. This chemical is an example of an external hormone or “pheromone”. It not only informs the workers that she is alive and well, but also inhibits development of their ovaries, thus preventing them from laying eggs in her presence. As the season progresses and the colony gets larger, the queen substance has to be shared among ever greater numbers of workers and being finite in quantity, some of the workers become incompletely inhibited. These undergo some ovarian development and manage to lay unfertilised, hence male-determined, eggs. The queen, still behaviourally dominant, eats most of these. Approaching the end of the colony cycle there is a point where, to enable the colony to rear new queens, the foundress queen ceases to produce the queen substance. The result is a gradual breakdown in social order and the larger workers, more dominant than the smaller ones, can become aggressive towards the queen and in some instances will even sting her to death. At this stage, there are usually young queens who will mate and carry on the species into the next colony cycle, but not in the original nest.

The honey bee has the largest eusocial colonies of bees in Britain. Each hive has one queen and tens of thousands of workers; the maximum number is probably 75,000 to 80,000. There are distinct differences between the queen and her workers. (For example, the queen does not have the corbicula present on the hind tibia of the workers, used for carrying pollen). The males, known as “drones”, are usually present only during the swarming period, May to July. The queen is dominant in as much that she is fed by the workers and never feeds workers in return, but this is entirely due to pheromone control. Variations in composition of the queen pheromone compounds inform the workers not only of her presence but also whether she is unmated or in laying condition. Reproduction is at the colony level, by swarming, sometimes known as "colony fission". The old queen slows down production of her queen pheromones because she has not been fed so well for a week or two. Her body mass reduces, enabling her to fly from the hive with a proportion of the workers. A new colony is set up by this swarm. In the original colony a new queen is reared from developing queen brood, enabled by the low levels of queen substances, and after her mating flight, starts to lay the first of her eggs.

Nesting habits (by David Baldock)

Bees, wasps and ants are the only insects in Britain that build nests and provision these for their young. All other orders of insects lay eggs without any form of nest construction, except for some of the dung and burying beetles, which construct very simple chambers in the soil. Grasshoppers and crickets deposit eggs into the ground or into plant stems; dragonflies lay eggs on plants or scatter them in water; butterflies and moths deposit eggs on plants or scatter them randomly; flies and beetles lay eggs on the ground or on other animals.

All species of bees, except the cuckoo or parasitic bees, construct some form of nest for their offspring, this being one of the reasons that they are armed with such strong mandibles for burrowing into the earth or cutting stems and leaves. The type of nest varies enormously from one species to another. The majority of bees dig underground nests, some in level ground and others in banks, but some use existing cavities above ground, in old beetle holes and natural holes in wood or walls etc. The young in their cells are thus kept safely away from predators until they emerge as adults, although many insects, including other bees, have found ways of attacking them. But because they live the whole of their pre-adult life in a cell underground or in a hole, the mother has to ensure that their offspring have enough food in their cell for them to grow from an egg to maturity.

Most species of bees are solitary but some are social in varying degrees. Solitary bees make a burrow, or use a cavity, in which they construct a series of cells; they provision each cell with pollen and nectar on which they lay an egg before closing the cell. When all the cells are provisioned the burrow is sealed and the female then starts constructing another, and she continues to do this until she dies after a few days or weeks. She will never see her offspring, which emerge from the cell in the following spring, or later that year if the species is double-brooded. A few solitary species may share a nest entrance with other females but they are not social.

A few of the mainly solitary, halictine bees, the small *Lasioglossum* and *Halictus* species, are primitively social (or more correctly eusocial). The queen rears a small brood of worker females, which guard the nest and help the queen to rear a larger second brood of queens and males. Bumble bees have reached a more advanced state of sociality, having a life cycle similar to the social wasps. The mated queen hibernates underground or in a hole, and in the spring makes a nest in an underground hole or in leaf litter, in which she constructs a honey pot from wax in her body. She fills this with nectar and then lays some eggs on a mass of pollen, which she then incubates. The emerging adults are all female workers who build more cells and forage for pollen and nectar. After more broods of workers have emerged, and the nest has grown to its maximum size, males and queens emerge. The new queens mate and hibernate, but the males and the old queen and workers die off. The honey bee, *Apis mellifera*, is the most advanced social bee. Unlike bumble bees, the nest is perennial, and the old queen leaves the nest with a swarm of workers to form a new colony. Honey bee nests are occasionally found in the wild, usually in a hollow tree or hanging from a tree branch, and such nests can contain as many as 50,000 workers at the height of the season.

All the solitary mining bees, Halictidae, Melittidae and all species in the genera *Andrena*, *Colletes* and *Panurgus*, are subterranean nesters. The female digs a burrow in the soil, using her mandibles for digging and her legs for pushing the soil out of the burrow, sometimes forming conspicuous mounds of earth at the nest entrance. The cells are lined with a wax-like substance, or in the case of the *Colletes* waterproofed with a cellophane-like material. The cells of *Macropis europaea*, the nests of which are often constructed in damp ground, are lined and water-proofed with a unique yellow material, made from the oils of Yellow Loosestrife. Some species, e.g. *Panurgus banksianus* and the spectacular *Dasypoda hirtipes*, nest in bare, level, hard-packed soil, such as paths, while others, such as *Andrena argentata*, only nest in very soft, level sand. Some, e.g. most *Colletes*, only nest in vertical banks while others, *Andrena bimaculata* for example, prefer sloping banks. The beautiful spring tawny mining bee *Andrena fulva* usually nests in flat grass-covered ground, such as lawns, throwing up characteristic spoil heaps. Although most species prefer nesting in well-drained soil, such as sand or chalk, there are some that are normally found nesting in clay, e.g. *Lasioglossum malachurum* and *Andrena labialis*. Some species nest close together in aggregations which are relatively easy to find, but many others nest solitarily in herbage and these nests are almost impossible to find; while nests of certain species are still unknown.

All the species of Megachilidae, or leaf-cutter bees, are solitary bees but they differ from the mining bees in collecting pollen on brushes of hair beneath their abdomens, rather than on their hind legs. These leaf-cutter bees are mostly aerial nesters, using a great variety of holes and crevices. The large and robust *Anthidium manicatum* nests in dead wood, hollow stems and mortar crevices and lines its cells with silk hairs shaved from plants. Most species of *Osmia* use crevices, making cell walls and partitions from chewed leaf pulp. The mason bee *Osmia bicornis* often nests in the crumbling mortar found in old walls. *Osmia bicolor* and *O. aurulenta*, as well as their close relative *O. spinulosa*, specialise in using old snail shells. After the snail shell has been filled with cells and sealed with leaf mastic, the female covers it with grass stems and other debris, presumably to hide the nest from predators. *Heriades truncorum* and both species of *Chelostoma* use old beetle burrows in dead trees or posts. All the species of the genus *Megachile* cut pieces of leaves and petals with their mandibles to use in making their cells; they can sometimes be seen flying to these carrying the leaves rolled up beneath them. Each hole is lined with many rolled-up pieces of leaves and the ends of the cells are made from smaller circular pieces. Most species are crevice nesters, but some make holes in the ground.

Solitary bees in the genus *Anthophora* carry pollen on their hind legs; some are aerial nesters in crevices in walls or in dead wood while others are subterranean, burrowing into the ground. They often nest in aggregations. The beautiful small blue *Ceratina cyanea* is the only British representative of the 'carpenter bees', so called because the female excavates its nest burrow in dead pithy stems, usually of bramble; the cell partitions are made from wood dust. This bee is unique amongst British bees because in late summer the adults of both sexes enter the old nest stem and hibernate there till the spring, sometimes as many as ten in a stem.

About one third of solitary bees parasitise other solitary bees; though they are not strictly parasites, as they do not consume their hosts, but are cuckoos, stealing the nests of other bees. In varying ways, depending on the species, they crawl into a nest burrow when the host is away and enter a fully provisioned cell; they lay an egg on the pollen ball, and then crawl out again. The cuckoo bee larvae, on emerging, destroy the host's egg or larva and then proceed to eat the pollen and nectar provision, eventually emerging as adults in the spring. Cuckoo bees can often be seen hanging around the nest sites of their hosts, especially of those nesting in large aggregations. Six species of bumble bee are social parasites of other bumble bees; the queen enters the colony of its host, kills the queen, and the host workers rear the new cuckoo females and males.

Parasites and parasitism (by Geoff Allen)

It has long been known that to thrive, species produce more offspring than can possibly breed themselves and that only the fittest of these survive to do so, in competition mainly with others of their own species. A female solitary bee, through nest building and provisioning pollen for the young, ensures that a high proportion of her offspring survive to adulthood. Solitary bees thrive with this strategy and the mining bees visiting fruit tree blossom in the spring, for example, can often outnumber the foraging honey bee workers. It is not surprising to learn that some solitary bees have evolved to parasitise others and live off this bounty. These bees are cuckoos, or “cleptoparasites”. Their way of life is to lay eggs in the nests of their host bee species, and they are dependent on the latter to ensure the successful rearing of their brood. The host and parasite are thus reared in similarly sized host cells, which are provisioned with the same amount of food, so there is a good correlation in size between the two species. The flight periods of the two will also be timed to coincide closely.

The origins of cleptoparasitism can be inferred by observing a nesting aggregation of mining bees. The pressure on an individual female to compete for a suitable nest site in the “village”, as these aggregations are sometimes called, is intense. If she succeeds in digging in a suitable spot, she must defend her nest and forage to provision each cell, competing mainly with bees of her own species. A female bee which successfully manages to sneak her egg into the cell of another female of her own species and have the work done for her, has taken the first step on the road to parasitism. This could be a good survival strategy. The next step is to facultatively parasitise a closely related species, only nesting herself if conditions are favourable. But the adaptations needed to be a successful facultative cleptoparasite must accelerate the species into full parasitism, as few actual facultative parasites are known. The non-British *Halictus scabiosae* has been reported as occasionally taking over the nests of other halictids, most frequently *Lasioglossum nigripes*, and this has been interpreted as a possible precursor to obligatory cleptoparasitism.

A number of modifications may be observed in cuckoo bees. The pollen gathering and carrying hairs have become reduced; the integument, or outer surface, is thicker and harder, and the segments fit more closely, to combat the stings of the host; the compound eyes and antennae may also be larger than in related independent species, indicating the increased sensory abilities needed to locate the host and its nests. As these bees spend much time lurking around the nests sites of the hosts, they often have bright warning colouration to inform vertebrate predators of their stings or nasty taste and hence may look like wasps.

As might be deduced from the above, most cuckoo bees are closely related to their hosts. This is Emery’s Rule. Thus, *Sphecodes* is placed in the same tribe (Halictini) as the usual hosts *Halictus* and *Lasioglossum*. *Stelis* specialises in the related *Anthidium, Osmia* and *Heriades*, while *Coelioxys* usually parasitises *Megachile*, a genus to which it is certainly close. However, *Epeolus* and *Nomada* are parasites (both in the long-tongued Nomadinae), which do not appear to be close to their hosts – the former is found on the short-tongued *Colletes* and the latter on several genera, usually *Andrena*, but also other bees. One is led to assume that *Nomada* has been a parasite for so long that it has had time to radiate to other, unrelated hosts.

It is known that some *Sphecodes* females “conquer” the nest of the host, driving away or sometimes killing her, and laying an egg in the cell after destroying that of the host. This is a more primitive behaviour. In contrast *Nomada* sneaks into the required nest while the owner is foraging and hides her egg by laying it in a depression in the cell wall, before it is fully provisioned. The *Nomada* egg is microsculptured to resemble the surface of the wall and the *Andrena* does not recognise its presence. In this more advanced case, the young parasitic larva has powerful modified mandibles for destroying the host egg or young larva, and loses these when moulting to the next instar. It would appear that this parasitic way of life is not always successful, as many cleptoparasite genera are scarce. Only *Sphecodes* and *Nomada* possess common species among the British examples. Some of these can be frequent, however, particularly where the host is abundant.

The number of species utilised by one parasitic species can vary enormously, even within a single parasite genus. The genus *Sphecodes* may be considered first, where the main hosts are other halictids. *S.*

geoffrellus is a small, common bee which selects several similarly sized species of *Lasioglossum* to rear her offspring. The main host in southern Britain is *L. parvulum,* an equally common bee. Sometimes *L. nitidiusculum* is selected but this latter is less frequent. There are a few localities where neither of these *Lasioglossum* species are to be found but the *Sphecodes* is present. Here the host remains unknown. Occasionally, very small examples of *S. geoffrellus* are found and a smaller host may be suspected. It is therefore considered that this cleptoparasite will exploit a variety of *Lasioglossum* (and possibly *Halictus*) species and this may be true of the majority of *Sphecodes*. However, it is known that some are very specific in their needs, i.e. only one or two host species are known. *Sphecodes niger* is a rare insect in Britain but the believed host is the abundant *Lasioglossum morio*. A few *Sphecodes* have radiated to parasitise other genera, particularly *Andrena*. *S. pellucidus* is found solely on *A. barbilabris* and the two are to be found together in sandy habitats in the south of England.

Nomada cleptoparasitises *Andrena* species in the main and one parasitic species often selects a small range of related hosts, sometimes in a single species group. The common *N. flava* is found with several species in the *A. trimmerana* group, usually the abundant *A. carantonica*. However, this bee has more than one *Nomada* parasite, an additional one being *N. marshamella*. This latter parasite has a small emergence in the late summer, coinciding with the second, summer brood of *A. trimmerana,* which may provide an additional host. Very similar to *N. flava,* is the less common *N. panzeri*. The taxonomist struggles to separate the males of these two species but the host species groups are different. The latter is found on *Andrena helvola* group bees. A few *Nomada* are found on other genera; the small *N. sheppardana* on *Lasioglossum parvulum* and *L. nitiduisculum,* whilst *N. flavopicta* parasitizes two or three *Melitta* species. Finally, the very rare *N. sexfasciata* is found on the scarce, long-tongued bee *Eucera longicornis*.

A survival strategy of a parasitic nature is found in some social bees. Readily observed in Britain are the cuckoo bumble bees, now placed with their hosts in *Bombus*. The female of this kind of bumble emerges from hibernation a little later in the spring than her independent relatives and searches out a small nest of her host. Her choice is quite critical. There must be enough host workers to rear her own brood but not so many as to jeopardise her attempt to take over. Once in the host nest, the female cuckoo tends to spend time in the material near the bottom until she has acquired the nest odour. After this, she is free to move around without constraint. She does not always kill the host queen but may simply depose her as the alpha individual, by domination. This takes the form of mauling and bullying, and sometimes extends to the host workers. In some cases the host queen may still able to lay in the presence of the parasite but the latter consumes the resultant eggs. This behaviour is not well known for all species and there may be considerable variation in detail. The grip of the parasite on the host nest is not always secure. She needs to produce a pheromone simulating that of the host queen to inhibit the aggressive behaviour of the workers. Having succeeded in becoming the dominant female, the parasite lays her eggs in the manner of the rightful queen in her own nest and the host workers rear them to adults. However, the parasite has no worker caste to forage, and only males and females are produced. These leave the nest, mate, and the females then hibernate to complete the life cycle. The usurping females are often killed by the host-workers at the end of the season, in a similar manner to the normal execution of a rightful queen in a nest.

The adaptations needed for this type of life cycle, called social parasitism, are similar to those of the cleptoparasites. The cuticle has become more armoured and the abdominal segments fit closely. The pollen gathering and carrying hairs have become reduced, so a parasitic *Bombus* has a thinner coat, through which the cuticle reflects light. The pollen carrying hairs are reduced and the stiff corbicular hairs lost. Also, the ‘tail’ of the female tends to curl under the fore part of the gaster, so that the sting is more easily deployed against the defending host queen and workers.

The hosts of the British social parasites in *Bombus* are quite well known. *B. vestalis* is found on *B. terrestris* and occasionally *B. lucorum. B. bohemicus* parasitises *B. lucorum,* and *B. hortorum* is parasitised by *B. barbutellus. B. sylvestris* has several hosts: *B. pratorum, B. jonellus* and *B. monticola*. *B. campestris* is found on *B. pascuorum* and occasionally on *B. humilis, B. muscorum, B. ruderarius* and *B. sylvarum* and finally, *B. rupestris* is hosted by *B. lapidarius*.

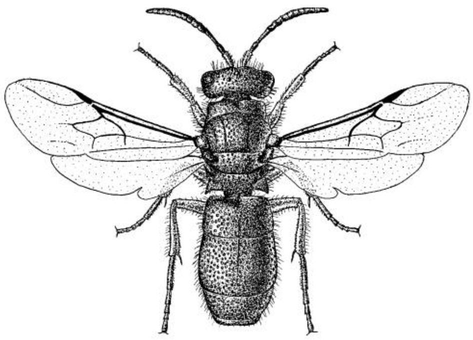
It is usual that the social parasite closely resembles her host. This is particularly true for *B. rupestris* and *B. vestalis.* The resemblance is not so clear in *B. campestris*, where the female is black with a yellow collar and frequently has a yellow tail whilst the usual hosts are reddish brown. The resemblance between host and social parasite can be quite striking but it is believed that this is not an adaptation to dupe the hosts when the parasite attempts to invade a nest. The host bees recognise nest mates solely by the possession of the nest odour which is common to all of the rightful inhabitants. It must therefore be a form of mimicry to deter vertebrate predators, which consequently have to learn one less warning livery.

Parasites from other orders

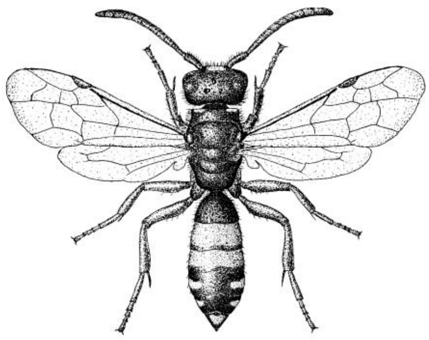
One cannot leave parasitism in bees without mentioning the many kinds of non-bee parasites found both on the bees themselves and in their nests.

Nematode worms have long been known as internal parasites of a variety of insects and *Sphaerularia bombi* is to be found in *Bombus* queens. A female nematode enters a queen's body as she hibernates and then develops. When this queen emerges in the spring she feeds and the nematodes, situated in her gaster, lay eggs. As the season progresses, the eggs hatch and the juvenile nematodes develop. The parasitised queen is unable to found a nest; instead she digs a hole in the soil at a hibernation site for queen bumbles, where the nematodes leave her body, moulting twice and mating. The fertilised female nematodes then wait for new queens to come to hibernate in the autumn, whilst the old queen dies.

Parasitellus species (Acarina: Parasitellidae) are common mites found on queen bumble bees in the spring, when they feed on pollen picked up by the coat of the bee as she feeds. When the queen begins nest foundation the mites crawl off her body and into the new nest, where they act as scavengers. Several generations of mites are produced over the period of nesting. When the autumn arrives mites climb onto the newly reared queens to over-winter, completing the life cycle.



♂ *Chrysura radians*



♀ *Sapyga quinquepunctata*

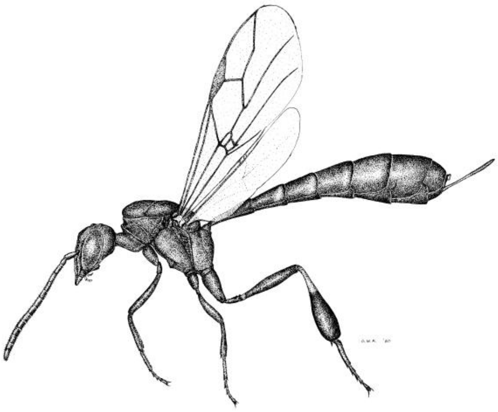
Other mite species are found in solitary bee nests, but in general their life cycles are not well known. However, *Chaetodactylus osmiae* is found on *Osmia bicornis* and its life cycle has been well studied by opening up trap nests. *O. bicornis* is also host to a fly, *Cacoxenus indagator* (Drosophilidae), which acts as a kind of cleptoparasite. A beetle, *Ptinus sexpunctatus*, behaves in a similar fashion in the nests of *O. bicornis*. An aculeate wasp called *Sapyga quinquepunctata* is a nest parasite of various *Osmia* bees. This species provides a rare example of the larva of a wasp feeding on pollen rather than insect food but, of course, the wasp does not provision it herself. Various ruby-tailed wasps (Chrysididae), including *Chrysura radians*, attack *Osmia* species but here the wasp larva feeds on that of the bee, killing it. *Chrysura* is therefore a parasitoid.

Bombyliid flies are nest parasites of *Andrena* and some other mining bees. The flies tend to look rather like mining bees but have a long, straight tongue protruding forwards from the head, sometimes forked at the tip. *Bombylius major* is a common example. The female lays her eggs at the nest entrance of the mining bee and the rapidly hatching larvae make their way into the nest, where they consume the food supplied for the host larva and sometimes the larva itself.

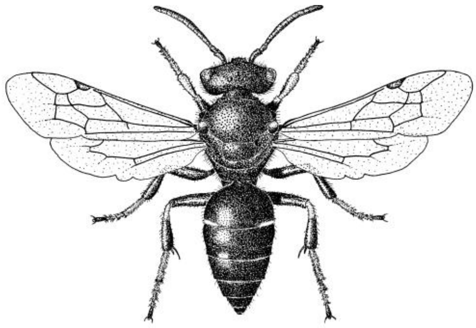
Volucella bombylans is a hoverfly which resembles bumble bees and the larvae of this fly are scavengers in the nests of various bumbles. There are several colour forms of the fly, each of which mimics a different species of *Bombus*. Conehead flies (Conopidae) are extraordinary endoparasites. The female fly shadows and pounces on a bee or wasp, depending on her species, and lays an egg through an intersegmental membrane of the aculeate into the gaster. The conopid larva slowly consumes the fluids and then the organs in the gaster of its host, which continues to work until shortly before its death, although it is made sterile by the parasite. The fly pupates inside the bee gaster and the aculeate dies not long before the adult fly hatches out.

It is not unusual to find *Andrena* mining bees in the field bearing female *Stylops* protruding between the gastral tergites. These parasites develop internally but the males fly after the bee has hatched out, leaving a gaping hole between the segments where they emerge. *Stylops* are highly modified insects and their true affinities are not clear. They may be related either to beetles or Hymenoptera. An individual *Andrena* may carry more than one *Stylops*, which reduce its fertility and may cause it to exhibit characters of the opposite sex. A stylopised male *Andrena fulva* has more luxuriant development of the gastral hair, like the female, whilst a similarly parasitised male *A. chrysosceles* sometimes lacks the yellow-marked clypeus of its sex, instead having black integument.

There are a number of small hymenopterous species which are parasites in bee nests. Some are chalcids and many are not host-specific, although sometimes specific to a nesting microhabitat, e.g. wooden posts, twigs and trap nests. *Gasteruption* (Evanioidea; Gasteruptiidae), is a parasitoid of *Hylaeus* and other bee genera. The female seeks out host nests and pierces the cell-seal with her ovipositor, laying an egg which hatches a few days later. The hatchling larva feeds on at least one bee larva, possibly more, during its growth. The scarce *G. minutum* is believed to be a parasite of *H. hyalinatus* and possibly other species.



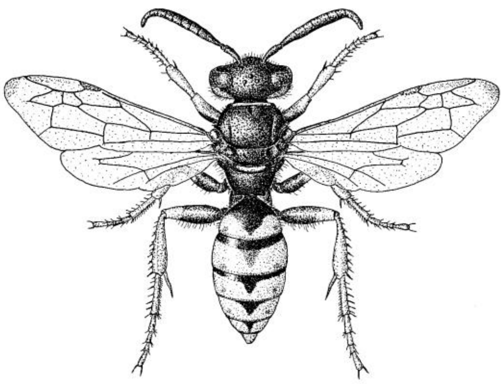
♀ *Gasteruption minutum* from the side



♂ *Hylaeus hyalinatus*

Predators of bees

The uninitiated might think that bees, with their potent stings, would be immune to the attacks of predators. Whilst there are comparatively few predators of bees, some do have considerable effect on bee numbers. Social wasps are generalist predators and have been recorded as taking bees, but the main victim is probably the honey bee. At the end of the summer, when wasps are most common, honey bee colonies are often in a fully alert state, with many guard workers near the hive entrance. Most attacks are repulsed and only weak colonies succumb. Some other generalist insect predators probably capture bees, particularly robber flies (Diptera: Asilidae) and dragonflies (Odonata: Anisoptera).



♀ *Philanthus triangulum*

There are solitary wasps which are specialist predators of bees. Two British species are in the crabronid subfamily Philanthinae. One, the common *Cerceris rybyensis*, largely preys on small halictid bees but will sometimes take bees of other families, most notably *Hylaeus* and the smaller *Andrena*. The bee wolf, *Philanthus triangulum*, preys almost exclusively on worker honey bees; it was a rare insect until the early 1990s, when it started expanding in abundance and range. It has now spread over much of southern Britain and, in the sandy localities where it occurs, can affect the honey crop.

Vertebrate predators generally leave bees alone but badgers and foxes dig up bumble bee colonies as readily as they do social wasp nests. Rodents will occasionally eat small bumble bee nests but avian predators may be significant in taking adult bees. Many a queen honey bee on her wedding flight has finished up as a meal for the humble house-sparrow.

Chapter 2 – Finding out more about bees

Where to look for bees (by Geoff Allen)

It soon becomes apparent to the field biologist that most bee species strongly prefer open habitats and that dense woodland is definitely not the place to look for such insects, which thrive in a higher temperature. It is thought that many aculeate species may have increased enormously in range and population size as a result of prehistoric and historic human activity; i.e. the cutting down of oak and beech woodlands in southern Britain. Before this woodland clearance, aculeates may have been rare opportunists, nesting at gaps created in the canopy of dense woodland where old trees had fallen. It is interesting that some modern bee records, of species such as *Lasioglossum parvulum* and *Andrena trimmerana*, are from nests in the earth root plates of fallen trees. It is known that some bee species are widespread, whilst others have very restricted distributions and some are common within their small range. It is clear that there are important factors which influence where a species can thrive and where it cannot, and that these factors can be different even for similar species. In this section, a look is taken at some of the habitats where bees may be found.

Sandy soil types

Lowland heath. This is one of the most prolific habitats for finding aculeates, including many bee species. It is thought that important factors for this are the high insolation (warming through sunlight) found on open heaths, and the soil texture, in which it is easy to dig burrows. The female of one bee, *Colletes succinctus,* is to be found in numbers in August foraging on heather species, upon which it is dependent. Other bees of common and heath include: *Andrena argentata, A. barbilabris, A. bimaculata, A. fuscipes, A. ovatula, Nomada baccata* and *Bombus jonellus. Andrena argentata* and *N. baccata,* its cleptoparasite, are good indicators of dry, sandy heathland.

Coastal sand. Some bees are found almost exclusively in coastal areas, which also offer good insolation. *Megachile dorsalis* and *M. maritima* dig nests in the sand of coastal dunes, whilst other species of this habitat type such as *Osmia aurulenta*, adopt specialist nesting strategies.

Sandpits. Some of the bees listed in the above two categories will also frequent sandpits, which can prove fruitful sites for recording.

Calcareous soil types

Chalk grassland, including downland. A small guild of species specializes in this habitat and they are infrequently found elsewhere. These include: *Andrena bucephala* and its cleptoparasite *Nomada hirtipes, A. hattorfiana, A. marginata, Lasioglossum fulvicorne, L. xanthopus* and *Osmia bicolor*. Other, more ubiquitous, species are also found here, such as *Lasioglossum morio* and *L. calceatum*.

Upland limestone areas. Bees particularly renowned for this habitat type are the rare *Osmia inermis* and *O. parietina*. Both of these bees rely largely, if not entirely, on Birdsfoot trefoil for pollen, as do several other species of *Osmia*.

Acidic areas other than heath

Moorland, with its boggy areas, is the upland equivalent to heath, and heather grows in many such sites. Bees specially associated with bilberry on moorland are *Bombus monticola* and *Andrena lapponica*, although the latter is also found on some lowland commons.

Woodland

Very few species of aculeates are found regularly in woodland, as there is usually not enough sunlight to warm up these heat-loving insects. Hence those bees found in this habitat type tend to select the more open parts, particularly on the edges of paths and rides.

Lowland coppiced woods. A few species are found here, including *Andrena clarkella, A. coitana, A. denticulata* and *Osmia pilicornis*. *A. coitana* sometimes forages on wood spurge in 1-2 year old re-growth in coppiced chestnut woods.

Upland ancient (Caledonian) pineforest. The very rare *Osmia uncinata* is found in this habitat, probably largely foraging on Birdsfoot trefoil.

Rapidly changing habitats

A few bee species nest in habitats which may change considerably over a relatively short time span. The most obvious type is cliff habitat, particularly soft cliffs such as are found in Dorset in the 'Jurassic Coast'. These coastal cliffs regularly change, due to erosion by the sea, which undermines the structure, and by water-logging from rain, both of which can cause landslips. Some bees are specialists in this habitat, such as the rare *Lasioglossum laticeps.* Sometimes a land slip can entirely wipe out a local population. Other ephemeral habitats harbour opportunist species which are widespread and common elsewhere.

Garden habitats

Many bee species are to be found in suburban gardens. Some bees are found mainly where people reside, and clearly find human gardening activities much to their advantage. It has been suggested that one limiting factor for the size of bee populations is the availability of nesting sites; in gardens there is a large variety of such sites, e.g. a diversity of flower beds, lawns, wooden posts, canes, pots, etc., supporting a wide range of aculeates. Many bee species, including the six common bumble bees, forage on various garden flowers and their larvae are able to utilize the variety of pollen. All bees need flower rich areas for foraging, and those which have long flight periods will require a succession of suitable flowers throughout their flying season. These particularly include the bumble bees but also many halictid bees, both solitary and eusocial. Gardens frequently provide such an ideal floral succession.

Brown field sites

Post-industrial sites are now important habitats for some scarce bees, which have benefited from stable management regimes, sometimes over many decades of industrial use. Since the recessions of the late 1980s, many engineering and other works have disappeared, leaving their often-extensive grounds as temporary refuges for nature. These brown field sites may support a variety of shrubs and wild flowers, and have the bare ground so important for mining bees; some bees have all but vanished from other habitats and brown field sites are important refuges. The possibility of new development, usually housing, on these sites is often a threat to endangered invertebrates in general, as well as the bees.

Boundary sites

Finally, species with complex biotic requirements may be found at the boundaries between habitat types, e.g. nesting requirements may be met in one habitat, whilst forage plants are found in another. This occurs frequently and it is evident that the best sites for recording are those with a complex mosaic of habitats in a small area. Thus, heathland which has occasional but regular, controlled fires, will have patches of heather and grass at various stages of regeneration resulting from different burns. This will be a much healthier habitat than vast areas of aging, monospecific heather growth, which supports only a small fraction of the potential flora and fauna, and at times can resemble an ecological desert.

Some nesting microhabitats

A few bees will build their nests in almost any suitable cavity that is large enough to contain the brood cells they construct, provided it is not so large as to expose the cells. Others species are more selective in this respect. Many mining bees require bare or sparsely vegetated ground; bare paths often provide exactly the right mix of hot and easily-excavated soil. Aerial nesters will require shrubs, brambles or dead wood in which to nest. It is likely that nests in walls are an adaptation from cliff face nesting and that humankind has enabled these species to proliferate. Examples of burrowing wall nesters are *Colletes daviesanus*, *Anthophora plumipes* and two *Lasioglossum* species, *L. smeathmanellum* and *L. cupromicans*. *Osmia bicornis* can adapt to this habitat but prefers to nest in preformed cavities. Broken twigs with the pith excavated out provide good sites for bees such as *Ceratina cyanea* and *Hylaeus* species. Aerial nesting species of *Osmia*, *Chelostoma*, *Heriades* and some smaller *Megachile* frequently can be found in vacated beetle borings in posts. One of the most interesting nesting habits is the construction of brood cells in empty snail shells by *Osmia aurulenta*, *O. bicolor* and *O. spinulosa*.

Trap-nesting (by Robin Williams)

A number of species of bees nest in hollow stems, holes in logs and other openings, or are involved in preying on those that do. This provides marvellous opportunities for home-entertainment in the garden, by channelling their nesting behaviour towards a distinct and definite area where you can watch them.

Trap-nesting is the art of persuading wild insects to nest where they may be easily observed and studied, and has come to mean the provision of artificial sites in a garden. It has been in use for many years and has both practical and enjoyment factors in its favour. In recent years, trap-nests have been used to improve the pollination of various crops throughout the world but, just as important for many people, is the sheer fun of watching wild insects going about their daily business, attracted to a convenient area near the house.

There are many types of trap-nest, a term which has come to mean the artificial provision of suitable nesting sites at a location selected by the provider. This can take many forms; bundles of hollow stems such as Hogweed; bamboos tied together or inside a plastic drainpipe; artificial purpose-built cardboard tubes; large-diameter drinking straws; glass tubes wrapped in paper to darken them; air-bricks; or holes drilled in logs. All have a common purpose, to persuade bees to enter and lay their eggs in a number of cells, which they construct from natural materials such as mud, pieces of leaf or chewed up vegetable matter. It all sounds very simple but it is actually a complex matter, which has echoes in choosing the sex of the eventual adult, providing food for the larvae and determining how each adult emerges in the correct order when they are ready.

Solitary bees and wasps

The Honey bee is a social insect, as is the black and yellow Common wasp which buzzes round jam pots in the autumn. ‘Social’ means that the queen lays her eggs to produce a brood of workers which then help her rear and feed the rest of her off-spring, whether workers, males or new queens. The majority of solitary bees and wasps have a quite different existence, with none of the adult flying insects surviving over the winter and without any social existence – though there are species that provide a halfway house to a fully eusocial existence.

Ignoring these variations, solitary bees emerge in the spring or summer; with either one or two broods each year, depending on species. The females are fertilised by waiting males and prepare their nests, after which each finds a hole, cleans it up, lines and caps it at the end, then brings in food for her future larva. The egg is laid on top of this and she seals the cell, then producing another. She works until she has prepared a number of cells, eventually dying from her labours. The eggs hatch and the larvae emerge, eat the food store, pupate and stay dormant until emergence. This occurs either in the spring or in the case of the second of two broods, later that summer. The obvious difference between solitary bee and solitary wasp nests is that the first is provisioned with pollen and nectar, while the second is stocked with living but paralysed prey, often caterpillars.

Species using the nests

A most remarkable book was written by an American professor, Dr Karl V. Krombein, which was the result of many years’ study, and sums up the scientific findings from over 3000 nests. Although it refers to American species, the results are very similar to what may be expected here

Of all the species that are likely to use trap-nests, *Osmia bicornis* is the most obvious. They are brightly-coloured mid-sized bees, often present in large numbers, notable for the females having golden pollen brushes in the form of hairs beneath the gaster. They seem equally happy to come to bamboos, tubes or drilled logs. In my garden I have both bamboos and logs. The bamboos are bought in a local garden centre and then cut so as to contain one node; one cut is close to the natural partition and the next just before the next node, giving a hollow length of around 25cms and total length of 28cm. The diameter of the hole should be between 6 and 10mm, though this is not too crucial – if one bee won’t use it, another species will. These bamboos are tied together in bundles and suspended horizontally on a hot southern-facing wall, ideally with the ends facing south, though against the wall is nearly as popular. And that is it! There is nothing else to do; nature takes care of the rest. All you have to do is to watch what is going on.

Logs are more difficult to discuss with precision; the state of the log, whether rotten, fresh, or of which species, all appear to have relevance. I favour a variety of different types of log, from upright boughs, to those with holes drilled in the face. If bees do not go for them, then various species of solitary wasp will almost certainly do so, which all adds to the excitement of watching the colonies develop. Logs are selected which are thick enough, so that the drill does not penetrate right through – a closed hole seems much more attractive than one showing light at the far end. Within reason, the longer, the better. I drill holes quite close to each other but in varying diameters, from 3mm up to 8mm, using the longest drills available. Seasons vary a great deal; in a good year, every hole in log or bamboo is in use, perhaps 200 or more; in 2002, with its very wet spring, only a small proportion was taken up, while the number of species was considerably less than in a busy year. The number and variety of insects may be affected in two ways; first by the weather, which may reduce numbers considerably, and second, by parasites. Many insects are parasitised by parasitic wasps and bees, by flies and by other orders. A good year for the primary insects may be followed by a few years where populations of parasites build up and primary numbers fall. When few of the originals emerge, the parasites die out for lack of food; so populations of bees, such as *Osmia bicornis*, will rise and fall over a period of several years, which is a perfectly natural event.

Nest construction

Whether log or bamboo, the process is the same for nesting species. Males usually appear a week or two before the females and hang around the holes, buzzing other males and gradually losing their clean, beautifully coloured fur to become worn and tatty. Some males, especially the specialised leaf-cutter bees, sit inside the holes for days on end, hoping a female will arrive. Eventually she does and the males descend to mate, often right by the hole in which she will later nest. She spends a great deal of time searching holes with her antennae, sometimes going in and emerging again, distinctly ruffled, after finding another inhabitant in possession. After mating and taking possession of a hole, the serious business starts and the female flies in with her raw material slung underneath, or in her jaws, ready to start cell construction. She enters head-first to start with, and walks into the darkness of the end of the hole to seal it off and make it habitable. In spite of apparently only just fitting the hole, she still manages to turn round inside and often emerges head first.

Each species has its own distinct method of construction, which may be studied by splitting the tube open. A bee makes a long cell, lays an egg on a pile of nectar-moistened pollen, which provides all the food the larva will need before emerging as an adult. The end of that cell is sealed before starting the next one. The outside, final cell, is closed off with a different structure, sometimes using a different mix of materials which may be of a different colour to the remainder. Once a solitary bee has finished its nesting activities, it dies, leaving the next generation to rear itself. There may be 8 or even more cells in a cane and the obvious query is how the insects emerge, since the first-laid egg is in the innermost cell?

There are several answers to this question, each contributing part of the story. First the female lays female eggs in the inner cells and males in the outer, a process she can control; second, she varies the food supply in each; as a result, males tend to complete the process to emergence in some days less than females. The insects then emerge from the outside/in, initiated by the outer bee starting to gnaw through the cap. Professor Krombein found that the vibrations of chewing started the following bee on the same action. In this way the bees emerge in the right order, the males well before the females.

Cuckoos and parasites

Not all bees seen going into the nests are the original inhabitants, or even nest-makers; a number are cuckoos in the nests. Among these are *Coelioxys* and *Stelis.* These insects do not collect their own food supply for their larvae, nor do they make nests. Instead they rely on their host bees to undertake these tasks – then take over from them, exactly like the avian Cuckoo does with a Meadow pipit. However, there is one major difference, inherent in the life of a solitary bee; these cuckoos do not actually receive food directly from the host for, by the time the larva is feeding, both mother and cuckoo are dead. The cuckoo bee lays her egg in the cell after the pollen and nectar food store has been placed in the cell and the host egg has been laid, but before the cell has been closed – a tricky matter of timing. The cuckoo egg hatches before the host egg and the resultant larva immediately sucks fluid from the other egg to destroy it, before feeding in a normal way on the pollen store.

Various wasps also act as cuckoos on the bees, including the dazzlingly beautiful chrysidid or 'Jewel' wasps, which are metallic green, blue or red in colour. They hover round the holes, chemically 'smelling' the state of hole and nest by constantly moving antennae before darting inside to lay their eggs on the food store. Some species of cuckoo wasp larvae hatch ahead of the host and then eat the egg before surviving on the original food store, while other species feed directly on the living host larva.

A variety of species may be found using trap nests; my own have held over sixty hymenopterous species to date, including 3 mason bee species, 4 leafcutter bees (*Megachile*), 2 cuckoo bees, 4 chrysidid wasps, 22 crabronid wasps and numbers of chalcids, ichneumons, and other parasitic wasps. Other observers have identified more than this in their trap nests.

How to set up trap-nests
The most important factor for achieving success is to site the trap-nests in a really hot spot that gets the maximum sun during the day; ideally a south facing wall which has an open aspect, with little or no shade. It is easy to see how this affects the bees if you sit and watch the site on a day where the sun comes and goes. Within moments of the heat hitting the nests, bees will appear and go to work; the moment the sun goes in, the bees vanish.

If you want to see what is going on, or to photograph events, then set the nests at eye-level when sitting on a comfortable chair. The easiest way to do this is to cut up bamboos and bundle them up together, or hang them in small bunches below each other, on the hottest part of the wall. I am fortunate to have a south-facing wall and have set them facing forward on one of the corners, with the open holes outwards; this lot is always used first. They may also be hung flat against the wall, tied in thick bunches of 16-20 bamboos in the sun or, alternatively, with the bamboos inside a 6.5cm plastic drainpipe cut to the same length. Try them all and see which suits the local bee population best. It is worth experimenting with different nests. Some people use hogweed stems tied together as with the bamboos. If it is planned to dissect the nests during the winter, these are easy to split and cost nothing. The old, wide, artists' plastic straws have been used with success but they are not easy to obtain now. It is sensible to hang all these so that the outer end slopes down, minimising rain damage, although it does not stop Blue tits and other birds looking for a meal.

Log trap nests, with plenty of different-sized holes, may be set up vertically against the wall or, as some people recommend, hung horizontally. Bees seem just as interested in these as the bamboos but may end going to the latter – the holes are much longer at over 20cms and suit the multi-celled nests they favour. Small wasps seem drawn to logs rather than tubes of any sort.

Oxford University helped set up the Oxford Bee Company to promote the use of solitary bees as pollinators for orchards, allotments, horticultural crops and in gardens. The connection with the University ensures on-going research, while a main objective is the spreading of interest and knowledge of solitary bees in Britain. To this end they sell bundles of special cardboard tubes inside an outer cover, which can be hung directly in the site without further preparation, and should help popularise the study of these fascinating insects and their parasites.

The company recommends that nest tubes are brought into an unheated shed for the winter, and then set out again in March. My bamboo and log nests are left out the whole year, simulating wild conditions. More bees may be lost to birds or weather but the system seems to work, because the materials are little affected by rain or frost, and the whole process seems well suited to building a hardy population.

Examining the nest contents
An important role for trap-nests is to find out more about the biology of the inhabitants. Single generation bees, such as *Osmia* and *Megachile*, over-winter as adults, which stay within the nest cocoons before eating their way out in the spring. Many wasps pass the winter as resting, fully fed larvae; then form pupae just before emerging as adults. It is possible to disturb them at this stage without affecting their survival and examine what is taking place. Tubes of various sorts lend themselves to opening without damaging the contents; bamboos may be split – with great care – while hogweed is easy to break into, without damaging the contents. An even better solution is to split the canes and reseal them before putting them in position, though this does involve a great deal of work if there is a large number. In this way it is possible to look at cell-construction, determine feeding methods or find out what has been parasitised. If the pupae are kept in a dark container, inside gelatine capsules, at outside temperatures, accurate records of emergence dates, contents of cells, parasitism and measurements of the adults can all contribute to our knowledge. If complete knowledge of emergence dates and parasitism is required, it is necessary to bag

the end of each tube with very fine Terylene netting at the end of winter. This must be examined daily for an accurate record. It may be surprising to find out the ratio of bees to parasites.

Further reading

Brian L. Griffen, **The Orchard Mason Bee**, Knox Cellars Publishing Co. **1999**.
Karl V. Krombein, **Trap-nesting Wasps & Bees**, Smithsonian Press. **1967**.
Christopher O'Toole, **The Red Mason Bee**, Osmia Publications. **2000**.

Recording (by Mike Edwards & Stuart Roberts)

Most of this book is concerned with what the British bees look like and what do they do. This section looks at how you can contribute to the increasing knowledge about British bees once you can identify individual species. This includes finding additional facts about what species do, where they are and why their distributions change.

The main process through which this information is gathered is the programme of Provisional Atlases. BWARS Provisional Atlases are issued on a two-yearly basis. In each one we target some sixty aculeates (ants, bees and wasps) and between twenty and thirty will be bees. For each designated target species we ask members to send in any records they may have, and then collate these, producing a distribution map from the results. We have decided to keep the same date-classes (pre 1900; Pre 1970 and post 1970) for all the maps in one Atlas series, thus keeping the maps consistent. As data becomes available via the National Biodiversity Network on the Web, it will be possible to view maps in different date-classes as required.

Each target species is the subject of a synopsis of what is known about it; very like the species accounts elsewhere in this book. This synopsis is written by a Target Species coordinator, and the membership is asked to contribute additional information when the draft account is published in the Society's newsletter. This section may contain indications whether the species is changing in frequency and/or range and possible reasons for this.

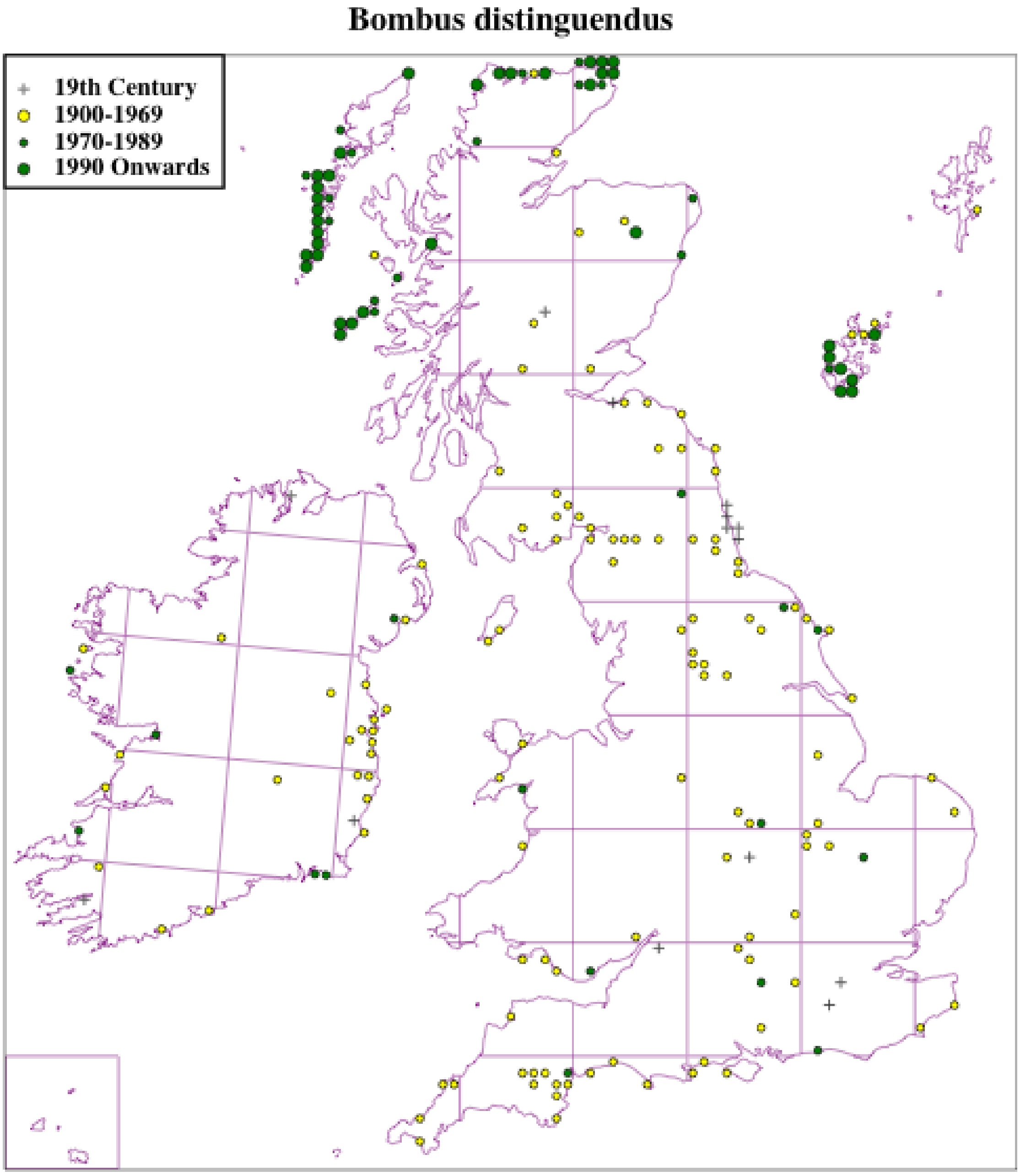
In order to do this we need to know more than just where a species was seen and a record, as submitted to the Society, should have a standard set of information. This is:

- The species name - Genus and species.
- The species number. (Provided by BWARS and included in the call for records.)
- The National Grid reference for where it was found. (Preferably to four or six figures.)
- A Locality name.
- The date of the record in 'dd/mm/yyyy' form.
- Collector of the record.
- Who named the species - determiner. (Often the same person as the collector, but some difficult species may need a second opinion,)
- Location of the specimen, source of published information or whether it is a field record only.
- Watsonian Vice-County name
- Watsonian Vice-County number (These have been marked on a standardised map available from the Biological Records Centre, and can help check for errors in grid references - we all make them!)
- Any additional information, such as what flower the insect was visiting.

This is explained further in Section 5 of the BWARS Member's Handbook. This publication also explains how any information you send in may be used.

Clearly with a lot of information it is necessary to get the data onto a computer so that it can be quizzed readily and we prefer to receive information in a computerised format, but this is not essential. The really exciting part comes once we have a large data-set. At the time of writing, this stands at over **300,000** records, spanning a time scale from the mid 1800s to the time of writing, and is growing daily. With all these records we can start to look at changes over time in the distribution of species and relate these changes to other changes in the environment, such as the loss of clover flowers in the countryside (decline in many bumble bee species), warmer summers and autumns and colonisation from the near continent (spread of several mining bees). This is illustrated here by distribution maps for three bumble bees; *Bombus distinguendus*, *B. sylvarum* and *B. ruderarius*, and the mining bee *Colletes hederae.*

When looking at the maps it is very important to be clear what the different symbols mean. The key at the left-hand top of each map gives the required definitions.



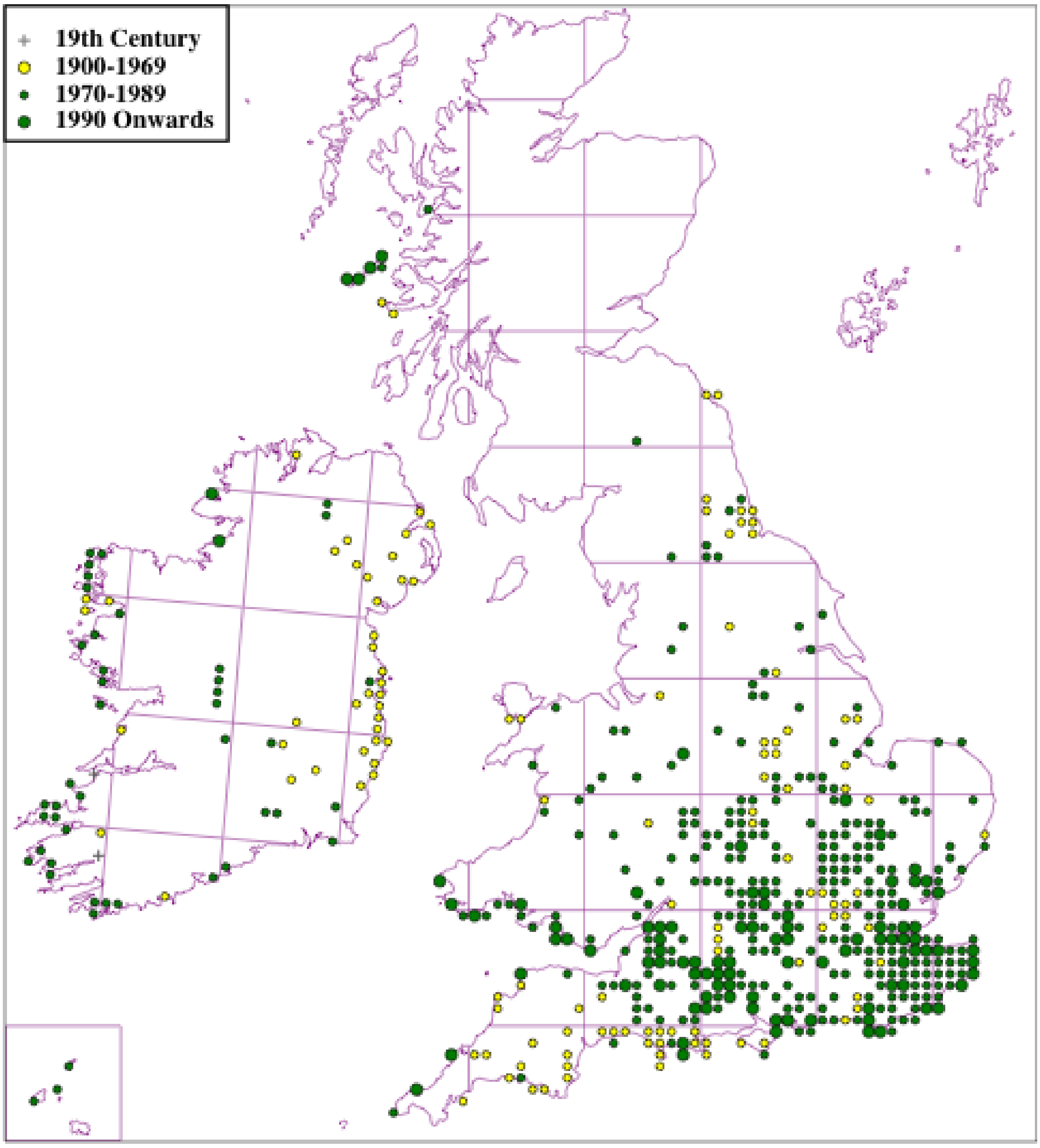
This first map is for *Bombus distinguendus* and shows data for four date classes. The post 1990 date class has been shown to be very important when looking at changes in distributions among bumble bees as most change has happened since the mid 1960s and is related to changes in farming, particularly the decline in clover-rich grasslands as part of the farming system.

This bumble bee was always living towards the southern edge of its climatic range in the UK and, as it became harder for it to find the resources that it needed to complete its life-cycle successfully, it has generally retreated to the north. Note, however, that the post 1990 distribution also highlights the regions where the most extensive areas of resource-rich grasslands remain, especially the machair of the Western Isles.

The second shows the map for *Bombus sylvarum*. This is a bumble bee on the northern edge of its climatic range and the change in distribution here is towards the south. Note, however, that the presence of extensive flower-rich grasslands in is also very important in defining the actual areas which remain occupied within this general southward shift in distribution.

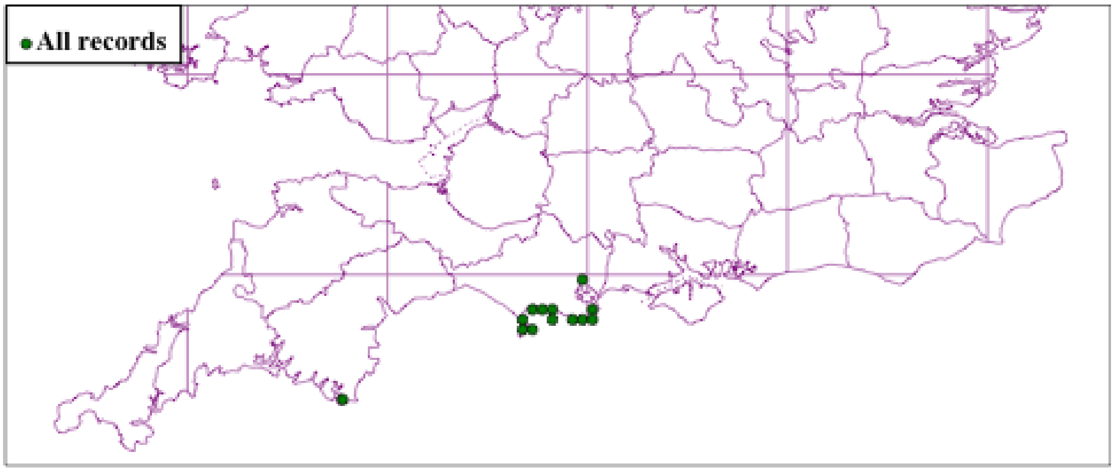
The next map shows the situation for *Bombus ruderarius.* It is less obvious what is happening here. It is clearly a species with a more southerly distribution than *B. distinguendus,* but the retreat to the south is not as clear as in *B. sylvarum*, and there are still good populations on some of the western Scottish islands. The general trend to an over-all decline in the number of occupied locations (actually 10km squares) since 1970 is very clear, although the trend, compared with before 1970, is much less dramatic than that shown for *B. sylvarum.* We are less clear about which factors, beside the restrictions of overall climatic range, are causing the changes.

Bombus ruderarius

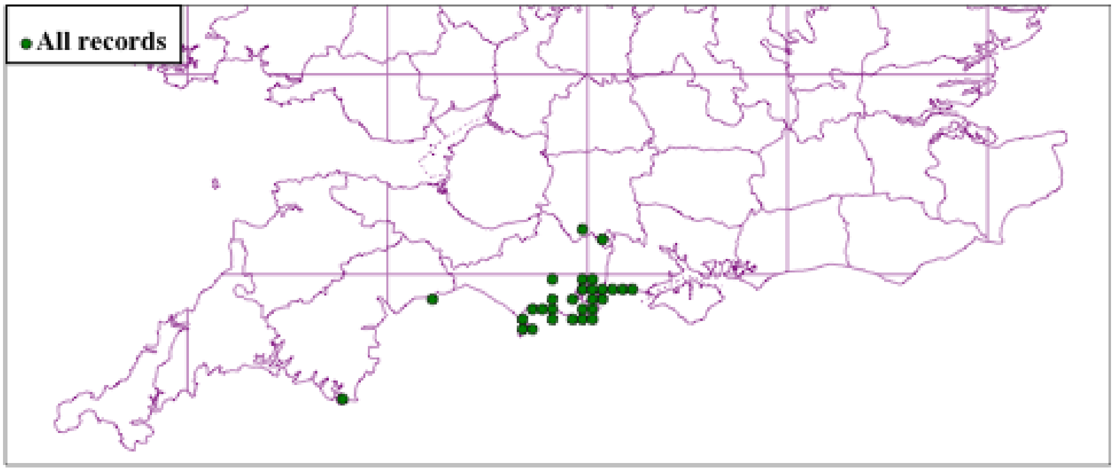


The next set of maps show the opposite to what has happened to many of the bumble bees. In 1970 the mining bee *Colletes hederae* was not known from anywhere covered by our mapping scheme, other than the Channel Islands. It was first found in 2001, in a well-visited locality on the Dorset coast. Many bees were found and the species clearly had been present before then, but it was felt unlikely to have been located there for more than 10 years at the most. Searches of other areas on the south coast that year produced the first distribution map shown here.

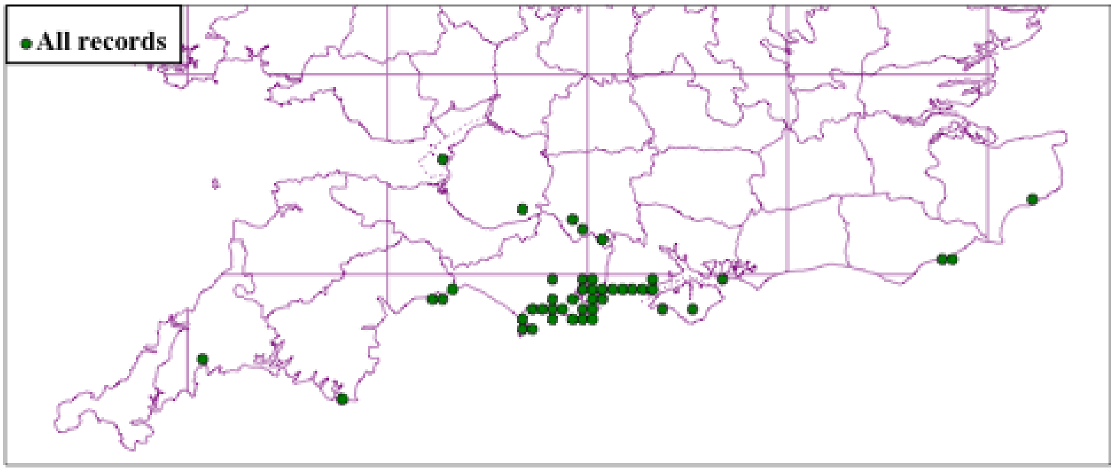
Colletes hederae (2001)



Colletes hederae (2003)



Colletes hederae (2006)



It now seems that this is a species which can build up very large populations very quickly and the real period it was present in the UK before being first recorded may well be more likely to be within five years. Its spread in the southern part of the UK since 2001 has been dramatic, as seen from the maps.

The bee collects its pollen at the flowers of Ivy *Hedera helix*. This is a widespread plant throughout Europe, yet the bee has always been much more restricted in its distribution. Over the last ten years it has been noticed spreading through Europe and the colonisation of the UK is part of this spread. These maps well illustrate the value of recording and give a flavour of the excitement involved in spotting such trends. This is at the heart of the activities of the Society.

BWARS atlases (by Robin Edwards)

The distribution of bees in Britain was not given much consideration until the late 1970s, when some work on 'humble' bees was carried out by the Bee Research Association (now the International Bee Research Association (IBRA)). However, it was not until the formation of the Bees, Wasps and Ants Recording Society (BWARS) in 1995 that work began to encompass all bees - nearly 270 species.

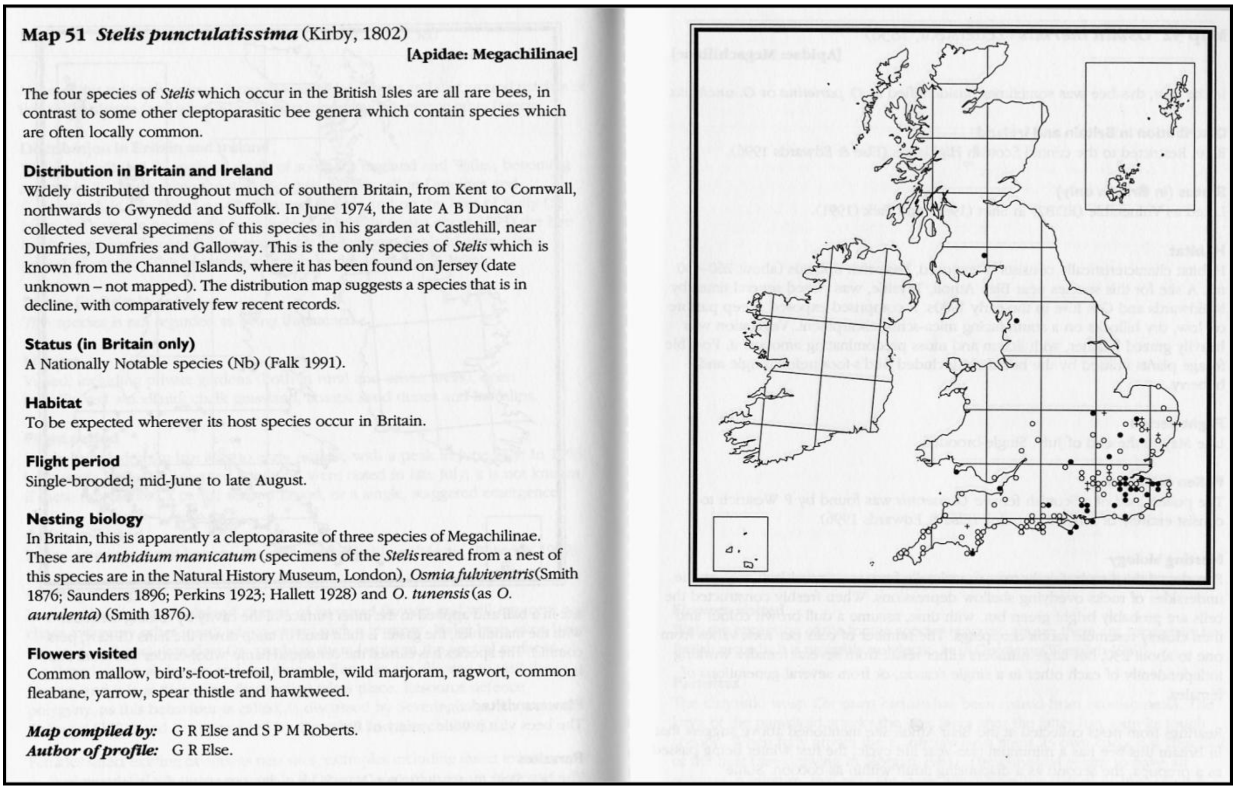
BWARS decided to map about 60 species of aculeates every two years, and the resulting "Provisional Atlases" made their first appearance in 1997 (Edwards, R.). The second part was published in 1998 (Edwards. R.), the third in 2001 (Edwards & Telfer), the fourth in 2002 (Edwards & Telfer) and the fifth in 2005 (Edwards & Broad). In those five parts, 97 species of bees have been mapped. Members are encouraged to contribute to the information used to produce the atlases and each receives a free copy.

Each Atlas entry contains a 'species profile' which gives information on the following:

- distribution in Britain and overseas.
- threat statuses (to show those species in need of conservation)
- habitat
- flight period
- pollen collected
- nesting biology
- flowers visited
- parasites and predators.

Each entry also includes a map of Britain and Ireland on which are shown recorded distributions in three date categories:

- before 1900,
- 1900 to 1969,
- 1970 to publishing date



Map 51 *Stelis punctulatissima* (Kirby, 1802)

[Apidae: Megachilinae]

The four species of *Stelis* which occur in the British Isles are all rare bees, in contrast to some other cleptoparasitic bee genera which contain species which are often locally common.

Distribution in Britain and Ireland
Widely distributed throughout much of southern Britain, from Kent to Cornwall, northwards to Gwynedd and Suffolk. In June 1974, the late A B Duncan collected several specimens of this species in his garden at Castlehill, near Dumfries, Dumfries and Galloway. This is the only species of *Stelis* which is known from the Channel Islands, where it has been found on Jersey (date unknown – not mapped). The distribution map suggests a species that is in decline, with comparatively few recent records.

Status (in Britain only)
A Nationally Notable species (Nb) (Falk 1991).

Habitat
To be expected wherever its host species occur in Britain.

Flight period
Single-brooded; mid-June to late August.

Nesting biology
In Britain, this is apparently a cleptoparasite of three species of Megachilinae. These are *Anthidium manicatum* (specimens of the *Stelis* reared from a nest of this species are in the Natural History Museum, London), *Osmia fulviventris* (Smith 1876; Saunders 1896; Perkins 1923; Hallett 1928) and *O. tunensis* (as *O. aurulenta*) (Smith 1876).

Flowers visited
Common mallow, bird's-foot-trefoil, bramble, wild marjoram, ragwort, common fleabane, yarrow, spear thistle and hawkweed.

Map compiled by: G R Else and S P M Roberts.
Author of profile: G R Else.

Individual Atlases contain a comprehensive bibliography, a list of plants (with their scientific names) and a cumulative index to aculeate species. Each is printed in A5 format, and has paper covers. Atlases are distributed free to BWARS members.

Gardening for bees (by Martin Jenner)

With over 250 wild bee species in Britain, it's not surprising that many visit gardens and, with the loss of many natural habitats, these gardens can sometimes be important places for foraging, or even nesting. Some gardeners may be unaware that they are actually helping to conserve wild bees; there are, however, a number of benefits to helping them along a bit more.

Most social and solitary bees are important pollinators of fruit trees and flowering plants. They are also attractive and fascinating insects; observing them can be enjoyable and fun, especially for children. This chapter shows you how you can attract them to your garden by providing suitable foraging plants and nesting sites.

There are a several things you can do to encourage bees. Any one of the following will be beneficial to bees and other insects.

- Ensure you introduce plants that provide useful pollen and nectar sources (see table 1.)
- Make a wildflower garden using appropriate plants (see table 2.)
- Provide suitable nesting habitats
- Try to avoid insecticides and weed killers; many of these can be toxic to animals and should be avoided if at all possible.
- Make sure suitable flowers are planted in areas where there is plenty of sun

Providing suitable garden plants for wild bees

Bumble bees and solitary bees feed on nectar and collect pollen for provisioning their nests. Whilst they appear to nectar from a wide variety of plants; most species are more selective when collecting pollen and some have very specialised requirements, utilising specific plants or plant groups.

In certain areas some bee species are more likely to be found in the garden than in the wild. *Anthophora quadrimaculata* for example collects pollen from Catmint and is also found on Lavender. If you have Lambs-ear in your garden (a plant with beautiful silver foliage), females of *Anthidium manicatum* (one of our most attractive solitary bees) will almost certainly arrive to collect the hairy parts of the plant for nest construction and males will also hover around waiting for them. Bees such as *Chelostoma campanularum* and *Anthophora quadrimaculata* are strongly associated with Campanulas and labiates respectively. Removing such plants or cutting them at an inappropriate time may be catastrophic for some bee species and providing a continuing supply of flowers is important for all bees. A few bees will only forage on one species of plant and providing flowers of this plant may encourage these into your garden. If Yellow loosestrife (make sure it's the wild version) is planted around a damp <u>and</u> sunny spot *Macropis europea*, an attractive, shiny black bee, may come to visit. I recently had this bee visit our garden within one year of planting this at the edge of our pond!

There are some plant groups that are especially good for bees, the table below lists below some of the most useful.

<u>Table 1. Bee garden plants for all seasons</u>
Common Name, Botanical Name, Star plant
(star plants are particularly effective in attracting bumble bees)

March – April

Bluebell	*Hyacinthoides*
Barberry	*Berberis* *
Bugle	*Ajuga*
Cowslip	*Primula*
Crocus	*Crocus*
Dead-nettle	*Lamium* *

Flowering currant	*Ribes* *
Forget-me-not	*Myosotis*
Gorse	*Ulex*
Heathers	*Erica*
Lungwort	*Pulmonaria* *
Mexican orange	*Choisya*
Plum	*Prunus* *
Rhododendron	*Rhododendron* *
Rosemary	*Rosmarinus* *
Creeping comfrey	*Symphytum grandiflorum*

May – June

Anchusa	*Anchusa*
Apple	*Malus*
Bellflower	*Campanula*
Borage	*Borago*
Ceaonothus	*Ceaonothus*
Chives	*Allium*
Colombine	*Aquilegia* *
Comfrey	*Symphytum* *
Crab apple	*Malus*
Crane's-bill	*Geranium* *
Everlasting pea	*Lathyrus* *
Fleabane	*Erigeron*
Foxglove	*Digitalis* *
Hawthorn	*Crataegus* *
Honeysuckle	*Lonicera*
Lamb's-tongue	*Stachys*
Poppy	*Papaver*
Perennial cornflower	*Centaurea*
Thyme	*Thymus* *

July – August

Apple blossom	*Escallonia*
Alpine aster	*Aster Alpinus*
Cornflower	*Centaurea* *
Delphinium	*Delphinium* *
Fennel	*Foeniculum*
Firethorn	*Pyracantha*
Globe thistle	*Echinops* *
Hebe	*Hebe* *
Jasmine (summer)	*Jasminum*
Lavender	*Lavandula* *
Marjoram	*Origanum* *
Masterwort	*Astrantia*
Cat Mint	*Nepeta*
Rock-rose	*Helianthemum* *
Sage	*Salvia*
Scabious	*Scabiosa* *
Sea holly	*Eryngium* *
Verbena	*Verbena*

***Tables** adapted with kind permission from '**Field Guide to the Bumblebees of Great Britain and Ireland'**. Mike Edwards/ Martin Jenner, Ocelli Ltd.

Fruit trees need insects to pollinate their flowers to produce fruit. Interestingly, some wild bees are much more efficient pollinators than the domesticated honey bee the hives of which are often introduced to orchards for that purpose. *Osmia bicornis*, a common mason bee, can pollinate fruit tree flowers up to five times faster than a honey bee while bumble bees forage earlier in the year than honey bees.

Most garden plants originate from the wild, although not necessarily from the UK. Whilst we like to introduce unusual plants to the garden; perhaps collected originally from Europe and other continents, there are many wild flowers from Britain which can provide a showy display throughout the year. In fact, some of them have traditionally been grown in the garden for many years such as the Deptford pink, Jacob's ladder, *Campanula glomerata*, Foxgloves, Aquilegia and Spiked speedwell. It is therefore possible to create flower beds with wild plants quite easily or even intersperse traditional garden plants with some wild ones, which helps prolong the flowering period of your garden.

Table 1:2 lists wild flowers which are beneficial to bees and that will attract them and other insects to your garden. These can be planted in traditional flowerbeds, wild flower meadows and pond margins. The most attractive to bees and other insects are highlighted in the table as star plants. When situating them it is important to remember that bees are sun-loving insects.

Table 2. Bee wild flowers for all seasons
Common Name, Scientific Name, Star plant

March – April	
Alexanders	*Smyrnium olusatum* *
Barren strawberry	*Potentilla sterilis* *
Blackthorn	*Prunus spinosa*
Bluebell	*Hyacinthoides non-scripta*
Bulbous buttercup	*Ranunculus bulbosus*
Bush vetch	*Vicia sepium*
Cowslip	*Primula veris*
Dandelion	*Teraxacum officinale*
Germander speedwell	*Veronica chaemadedrys* *
Gorse	*Ulex europaeus*
Ground ivy	*Glechoma hederacea* *
Pussy willow	*Salix caprea* *
White dead-nettle	*Lamium album* *
Wild strawberry	*Fragaria vesca*
Yellow archangel	*Lamiastrum galeobdolon* *
May – June	
Autumn hawkbit	*Leontondon autumnalis*
Bilberry	*Vaccinium myrtilis* *
Bird's-foot-trefoil	*Lotus corniculatus* *
Bush vetch	*Vicia sepium* *
Bugle	*Ajuga reptans* *
Broom	*Cytisus scoparius*
Clary	*Salvia verbenaca*
Comfrey	*Symphytum officinale*
Common mallow	*Malva sylvestris*
Common melilot	*Melilotus officinalis*
Common vetch	*Vicia sativa*
Common wild thyme	*Thymus praecox*
Creeping cinquefoil	*Potentilla reptans*
Figwort	*Scrophularia nodosa*
Foxglove	*Digitalis purpurea* *
Hawthorn	*Crataegus monogyna*
Hedge woundwort	*Stachys sylvatica*

Hogweed	*Heracleum sphonylium*
Horseshoe vetch	*Hippocrepis comosa*
Meadow cranesbill	*Geranium pratense* *
Meadow vetchling	*Lathyrus pratense* *
Mouse-ear hawkweed	*Pilosella officinarum*
Musk mallow	*Malva moschata*
Musk thistle	*Carduus nutans*
Petty whin	*Genista angelica*
Rasberry	*Rubus idaeus*
Red clover	*Trifolium pratense* *
Rough hawkbit	*Leontondon hispidus*
Smooth hawk's-beard	*Crepis capillaris*
White bryony	*Bryonia cretica* *
Wild carrot	*Daucus carota*
White clover	*Trifolium repens* *
Wild crab apple	*Malus sylvestris*
Yellow archangel	*Lamiastrum galeobdolon*
Yellow flag	*Iris pseudacorus*
Yellow rattle	*Rhinanthus minor* *
Zigzag clover	*Trifolium medium*

July – August

Bell Heather	*Erica cinerea*
Betony	*Stachys officinalis*
Burdock	*Arctium minus*
Clustered bellflower	*Campanula glomerata*
Cross-leaved heath	*Erica tetralix*
Dyer's greenweed	*Genista tinctoria*
Field scabious	*Knautia arvensis* *
Greater knapweed	*Centaurea scabiosa* *
Hawkweed	*Heiraceum vagum*
Harebell	*Campanula rotundifolia*
Hedge woundwort	*Stachys sylvatica* *
Honeysuckle	*Lonicera pericyclymenum*
Ivy	*Hedera helix*
Lesser knapweed	*Centaurea nigra* *
Lucerne	*Medicago sativa* *
Ox-eye daisy	*Leucanthemum vulgare*
Lucerne	*Medicago sativa*
Marjoram	*Origanum vulgare* *
Marsh thistle	*Cirsium palustre*
Marsh woundwort	*Stachys palustris* *
Meadow crane's-bill	*Geranium pratense* *
Melilot	*Melilotus species* *
Musk thistle	*Carduus nutans* *
Nettle-leaved bellflower	*Campanula trachelium*
Purple Loosestrife	*Lythrum salicaria*
Red Clover	*Trifolium pratense* *
Restharrow	*Ononis repens*
Sainfoin	*Onbrychis viciifolia*
Sea aster	*Aster tripolium*
Self-heal	*Prunella vulgaris*
Small scabious	*Scabiosa columbaria*
Spear thistle	*Cirsium vulgare*
Stemless thistle	*Cirsium acaule*

Tansy	*Tanacetum vulgare*
Tufted vetch	*Vicia cracca* *
Viper's bugloss	*Echium vulgare* *
White clover	*Trifolium repens* *
Water mint	*Mentha aquatica*
Wild chives	*Allium schoenoprasum*
Yellow loosestrife	*Lysimachia vulgaris*

Providing nesting sites for bees

Solitary bees nest in a variety of different habitats, all of which can be created. Some are cavity nesters and use or make holes in walls, cliffs, trees or any dead wood situation. Mining bees nest in the ground by digging holes in a number of different substrates. These may also nest in colonies and sometime a good habitat can maintain many species and several hundreds, or even thousands, of insects.

Bumble bees nest in a variety of situations, some are surface nesters and some below ground nesters. Nesting habitats for both are in great demand and it is therefore possible to provide suitable substitutes. Bumble bees often nest in old vole nests and you can make substitutes for these by using Kapok, a plant based toy stuffing material, mixed with moss – do not use artificial fibres, they can be harmful to bumble bees. Place these in the bottom of grass tussocks or in bank holes. You can also encourage voles by leaving areas of tall grass by hedge bottoms.

Creating nesting habitats for bees in your garden is not difficult (providing you have suitable space). Here are some tips:

Cavity nesters.

This is covered in depth in the chapter on trap-nesting.

Ground nesting bees

Different species will use flat surfaces, banks or cliffs, most species preferring little or no vegetation present. These situations can be created within the garden. Different species of mining bees have preferences for different soil types and situations, but generally prefer sandier soils. Creating a sand bank is simple enough; depending, of course, on how ambitious you are! It is possible to purchase a ten-ton load of un-graded sand, straight from the pit, which is much cheaper than buying building sand. This can then be formed into a variety of differently shaped banks with varying heights and angles, or may be mixed with clay or cement to form vertical banks. A 100 to 1, sand to cement, mix is often used for Kingfisher nests. Make sure it's not any stronger than this or the bees will have a job to create burrows.

Any created sand bank needs to be situated in a sunny position; those in the shade will attract fewer species. Early morning sun or afternoon sun locations are fine; in fact it is good to have both.

The finished result

By creating such friendly habitats in your garden you will, in time, notice an increase in the number of species that appear and sometimes take up residence. You will be providing an environment that will help other insects, such as butterflies and moths, as well as birds, mammals, slow worms, frogs and toads and generally increase the number of different animals in your garden.

Photographing bees in the wild (by Robin Williams)

Introduction

A quick look through this book reflects the importance of photography in enjoying bees and their often-strange behaviour. The variety of bees makes for some extraordinarily photogenic images; while capturing the moment is crucial, together with the memories this will bring back.

Prejudice exists against using pictures for identification but, provided a number of different views have been taken, it should be possible to identify some bees, and be confident of the results. In other instances this may not be sufficient; however a record of the plant on which it is found, together with the date, may help complete a satisfactory identification. A picture, with a captured specimen, gives the perfect combination, though it requires rapid reactions and sleight of hand, which can only be gained with experience.

Photography in the field involves capturing images of wild, unconstrained insects, without resort to anaesthetising them, damaging the creatures or affecting their lives. Successful insect photography portrays the creatures as they appear in nature and may involve highly magnified close-ups.

A few ground-rules apply to photography in the field:

- Carry as small an amount of equipment as possible – it gets noticeably heavier as the day goes on,
- always be prepared for that once-in-a-lifetime opportunity,
- take lots of pictures as they present themselves – digital memory is virtually free.

The digital equivalent of 35mm is the accepted format for close-up photography in the field. Superb lenses are available from many makers; the ultimate in technological advances, lightness and reasonable cost make these systems the only real choice. However, it is not essential to invest in all the latest and most expensive equipment. I use a superb macro lens at least ten years old.

Digital cameras have come on enormously in the last few years and no doubt progress will continue apace. Single Lens Reflex (SLR) bodies made by major manufacturers are available with superb lenses and accessories, and have the resolution to more than match the finest slide films. Prints may be produced using widely available computers and printers, without any of the chemicals, smells and wizardry used in a darkroom. Perhaps most importantly, results may be seen immediately in camera, without waiting a couple of weeks for a film to come back.

The secret of success in close-up photography lies in the accuracy of the exposure system and the quality of the lens, together with focusing correctly and freezing the action. The latest auto-focus systems are first-class and may be relied on for even the most extreme circumstances, like insects in flight. If you want to take pictures easily and quickly, concentrating on the bee and on composition, there are two vital decisions:

- Use flash where possible, regardless of the strength of daylight and the brilliance of the sun.
- Use a monopod, or your knees, not a tripod**.**

It has long been given wisdom to set the camera up on a tripod and to use natural daylight where possible. But, if you want to take pictures of insects as you see them during the day, while out on a field trip, time will not allow the setting up of a tripod, nor will the majority of insects - opportunities have to be taken whenever they present themselves. Flash freezes the moment, regardless of weather conditions; while a monopod provides support with rigidity, giving flexibility and speed of operation.

While the highest quality, most versatile systems are heavy, with external flash sources and longer lenses; many people find the latest compact digital cameras, fitted with light, stabilised macro lenses, using the camera's built-in flash or natural daylight, are also suitable for photographing bees and fit in well with the other demands of entomology. Another route to follow is to use a so-called 'Bridge' camera, like a small

SLR but fitted with a fixed lens, giving good macro performance. These have come on amazingly in recent months and offer a real alternative to those who want to carry little extra equipment.

Weight

Many years of photography in the field confirm that weight is the enemy of the photographer. The minimum basic equipment is best carried in a rucksack - or in the hand. An excellent design has the lower part padded and sectionalised and is just large enough to carry the camera gear, while the top has a compartment for waterproofs, food and drink. A rucksack puts the least strain upon neck and other muscles and is comfortable if fitted properly. Photographers who have carried heavy bags over the shoulder for years often end up with permanent and serious damage to joints.

Stalking in the field

The assembled camera may be carried round in the hand, with flash switched on and the lens aperture set at f11 or f16 using the 'aperture priority' setting. Close-ups need all the depth of field that can be used. A set of re-chargeable batteries will last more than a day in the flash, while digital SLR Li-on batteries will last for well over a three hundred RAW pictures on a 4GB card.

When approaching insects move slowly, wait for the creature to settle and then wait a further moment for it to relax. However active, it will settle eventually, either to rest or to eat. A slow approach, preferably at or below the creature's level, should see you close enough for fine whole-insect shots.

Future studies - what we still do not know (by Geoff Allen)

The Western honey bee or hive bee, *Apis mellifera*, is one of the best studied insects and hence a great deal is known about it, ranging from information on its molecular biology and DNA to detailed parameters of behaviour, including foraging strategies. This has come about because it is easily domesticated and its sophisticated social behaviour has evoked comparisons with our own human societies. The honey bee is also economically important, even more so following the decline of many of our natural pollinators.

When we turn to our native bees, large gaps in our knowledge become apparent. Bumble bees are quite well studied but even here there are deficiencies. For example: once, when attempting to net a worker *Bombus muscorum* visiting red clover in long grass, an interesting example of behaviour was observed. The net narrowly failed to trawl the bee, just scraping it; the fortunate but ruffled creature took flight immediately and vanished. Within a few seconds, all of the *B. muscorum*, as well as other *Bombus* species in the immediate vicinity, also took to the wing and flew away. This was ascribed to the use of an alarm pheromone by the first bumble bee, which appeared to affect all species. *B. muscorum* is known to defend its nests with particular ferocity, perhaps initiated by the alarm pheromone. We know very little about alarm pheromones in the bumble bees, least of all their chemical compositions. Queen pheromones are not chemically identified either, although it is likely that all *Bombus* species have them; the exocrine glands which produce these pheromones have not been located with certainty. Observation of bumble bees in artificial nests may give a good indication of which species have which types of pheromones; amateur naturalists could carry this out, although any chemical analysis would have to be done in the laboratory.

Bumble bee foraging strategies are apparently fundamentally different to those of the honey bee, which has to maximise nectar foraging during the second half of the flying season, in order to produce enough honey to feed the colony over the winter. Bumble bees store little honey, as the colony does not normally survive over the winter; it is of a thin consistency and only has to last a few days or a week, if there is inclement weather. The sole aim of the bumble bee nest is to rear as many fertile new queens as possible to over-winter and carry on the next life cycle. The economy of bumble bee nests needs further investigation in this light.

When it comes to solitary bees, even detail on geographical distribution is not known for all species. Ascertaining this is a core function of BWARS, and the membership of the society, mainly amateurs, makes an enormous contribution through our recording scheme.

The synchronised emergence times for many solitary bee species, was a puzzle for a long time. It is now believed that the scent of the first opening host flowers in the vicinity may be one factor prompting a mass emergence. But in some species, like *Andrena nigroaenea*, it is normal for some specimens to make a delayed appearance. It is quite usual to find the first males flying in mid to late March, with females joining them a few days later. However, fresh examples can be found as late as June and females may fly occasionally into July, although by that time they appear quite sun-bleached and abraded. These bees all belong to one generation, so why do they not all appear at the same time? There must be further, so far unknown, factors at work.

In some bee genera, there are species complexes in which the sibling species appear very similar to one another, making identification even under the microscope difficult. The *Colletes succinctus* group is a good example. Advances in DNA analysis have made it possible to identify differences in the genetic material of such bees, which may help define ideas on what is a ‘good’ species. In *Andrena*, there are some complexes where one species is single brooded whilst another closely-related species has two generations. The scarce mining bee, *Andrena marginata*, appears to have two flight periods, each with a different single-species host plant visited for pollen. It has been tentatively suggested that there could be two cryptic sibling species confused under this one name. DNA analysis on these examples would be valuable. Gathering material in the field for this kind of work is something the amateur can carry out effectively, given that there is a specialist with the laboratory time to analyse the material.

For many bee species, the complete range of flowers used as pollen sources is unknown. Analysis of pollen from collected females produces good results, but observations of living bees in the field are also important. Some bees visit a variety of flowers and females of one species can often be seen gathering pollen on different species on the same day, in the same locality. The way each individual selects her pollen source is worth investigation; one could imagine that there is most competition for the best flowers and less-fit females would be displaced on to poorer forage species. Sometimes aggression by foraging solitary bees may to be observed, within a single species, but what makes some females more fit to compete than others? And anyway, what makes some flower species better potential forage than others, for a given species of bee?

Cleptoparasitic bees usually select a limited range of hosts when there may be several other apparently suitable species nesting at the time. What stimuli prompt the cuckoo female to use a particular host? Many host/parasite associations are known, especially where both cuckoo and hosts are common. In a few examples, however, even the host genus is not certain. *Sphecodes reticulatus* belongs to a genus which usually parasitises *Halictus* and *Lasioglossum*, whilst a few species of the genus obtain a living from *Andrena*; but the host genus of *S. reticulatus* remains unknown. Observations in the field could verify the hosts of several species of cuckoo bee where there are only tentative associations.

Several researchers have used behavioural patterns to try to elucidate or confirm evolutionary relatedness within aculeate groups. Bees have complex behaviour compared with many other insect groups, often to do with parental care. Most basically, in solitary species the female has to: find a mate, form a nest with a cell, provision it and lay an egg, seal the cell, probably repeat the cell production sequence more than once, then close the nest and possibly attempt to disguise it from parasites. There are usually subtle variations between closely related species in the way these instinctive behaviours are carried out and careful study of them may enable theoretical reconstruction of the evolution of whole blocks of patterns. This could shed light on the whole phylogeny of the bees. Some work in this field has been done but there is much remaining. Perhaps new doctoral theses await here.

The above are a few of many examples where amateur natural history observations can add to our knowledge of the bees, particularly if they are made within a common framework of reference. While much is known about the identification of bees, there are many gaps in our knowledge of why they behave in a certain manner, whether existing species are as we see them, or should be separated. With little or no work being carried out by professionals on the less economically important species, there is a great need for individual naturalists to get out there and find out further facts, to increase our knowledge – in the finest traditions of our Victorian forefathers.

Chapter 3 – Conservation

The Economic value of bees (by Michael Milton)

All ecosystems and human societies are dependent on a healthy and productive natural environment that contains diverse plant and animal species. The plants produce the air that we breathe. But this environment affects us more personally than the benefit of a pleasant place to live. Every third mouthful that we eat comes from plants pollinated by insects and by far the most important pollinators are bees. Pollination literally makes the world go round. Insect pollination is an essential step in the growth of most fruits and vegetables, in the production of many plants used in the pharmaceutical industry and in the regeneration of many forage crops used by animals. .

Einstein is reported to have said 'if bees were to become extinct, the civilised human race as we now know it would follow within twenty years'. And Einstein was a mathematician, not a naturalist.

This pollination process has been going on for millions of years. Over this time, plants have adapted their shapes, colours, scents and behaviour to best suit the physical characteristics of the insects which normally pollinate them and so assist the process. This complex natural phenomenon has come to be regarded as an automatic free service, part of the scenery that will just happen. With the great rise in world population, the need for increased food production has become more important and the availability of pollinators in the right place and at the right time is vital. But with the reduced numbers of both wild and managed pollinators the prospects of an "impending pollination crisis" has become a real possibility. As a result, scientists and economists are now attempting, for the first time, to evaluate the true economic and financial value of bees as pollinators. A 2001 Ministerial investigation estimates the annual value of bees as commercial crop pollinators in England at £120 million. This figure takes no account of the value of pollinated animal food crops, or of the immense value to the ecosystem of the pollination of plants in the wild environment.

However these figures, though considerable, are very small in relation to the world picture. In the United States it is estimated that the annual value of increased agricultural production due to insect pollination was $14.6 billion in the year 2000. As an indication of the magnitude of activities in this field, approximately one million colonies of honey bees, *Apis mellifera,* (more than 25 thousand million bees), are moved into central California each spring to pollinate the almond crop. When the value of legumes fed to animals is added, the total value of insect pollinated production in USA is estimated at $40 billion. No detailed analysis has ever been made of the world wide benefits, but on the assumption that these could be four or five times that of USA then the value of pollination to world agriculture could be $200 billion each year; a very large sum for a normally ignored resource.

Although most estimates of pollination focus on *Apis mellifera*, honey bees often receive credit for work carried out by other bee species. The perennial mode of the honey bee colony with a large spring population, the time when most commercial pollination is needed, and the ease with which they can be moved, ensures that the honey bee remains the most widely used commercial pollinator. However, recent research has, however, shown that some other species are more efficient. For instance, the mason bee, *Osmia bicornis*, has been found to be a very effective pollinator of orchard fruit. Some crops require certain characteristics of an insect to ensure proper pollination and seed set. Red clover, *Trifolium pratense*, has very long florets and is only visited by longer tongued bees. Bumble bees are excellent pollinators of these types of plants.

In recent years a very large industry has built up in the pollination of tomatoes in greenhouses; now, all commercially-grown tomatoes, in Western Europe, United States and Japan, are pollinated by bumble bees. Small colonies are maintained in the houses throughout the growing season and the bumble bee's ability to "buzz pollinate" renders it very effective. Since the 1990s, this industry is now estimated at more than $40 million per annum, and growing.

It will be seen, therefore, that bees play a very important part in the world economy and, in the future, may contribute even more. In fact, their essential role in ensuring that we continue to live in a pleasant and healthy environment is impossible to evaluate. At present, we are not doing a very good job of ensuring their future existence, particularly in the pollination of wild flowers.

Bees in our landscape (by Andrew Grace)

Bees are responsible for the pollination of the majority of the world's flowering plants. In return, they are supplied with pollen, nectar and floral oils which are used as food, as stores of nutrients for the immature stages, and as a source of chemicals for use in nest construction and biochemical processes of other sorts. Plants also supply leaf fragments for nest lining. Hairs are collected from plants by some bees, while the plant stems are used for nest sites, as are natural cavities or borings in the trunks of woody species.

The term 'keystone mutualist' has been used to describe the relationship bees have within the complex and vital ecological matrix of plants, soil, atmosphere and other animal species. Bees are also users of the natural resources of landscapes and, as such, are able to adapt and have co-evolved with flowering plants across the planet since at least the Cretaceous period.

Within Britain, there are a number of key aspects responsible for the presence of flower communities and the species of bees found. Firstly, Britain lies within the temperate Atlantic climatic region of Western Europe. Despite climatic changes, recent millennia have been characterized largely by both mild and wet winters, and summers. Many insects and flowering plants are adapted to generally hotter conditions than those found within Britain, although some groups of bees, such as the bumble bees, are generally warm-temperate species, which are able to cope with the cooler summers of the more Northern latitudes. A general feature affecting the presence of many bees in Britain is that the climate produces a constantly changing weather pattern, which fluctuates seasonally and year by year. Thus, British insects other than migratory species must be able to cope with the vagaries of the local weather. In the wild, flower species too need to be adapted to the cooler and wetter conditions, but also be generally resistant at the population level to periods of frost. In Britain especially, there is a marked contrast between upland regions of hill and mountain and the lowlands.

Two further historical features affect the distribution of bees and flowers, the first of these being the impact of the glacial periods. At the end of the most recent, much of Britain had become inhospitable to flowers and bees, due to the severity of the weather and the action of glaciers on soils and vegetation. This was followed by another significant event, the creation of a shallow sea following the retreat of the ice sheets. Britain was rendered an island before many plant species were able to return from lands to the south and east. This process has been repeated in the past on a number of occasions and influences the population biology of plants and insects surviving these periods of isolation.

By the modern period, the variety of flowers present in the British landscape had increased; some of this increase was due to the natural spread within Britain of plants that had survived in pockets of land or otherwise were adapted to upland Arctic and sub-arctic conditions. More plants arrived as seeds carried in the crops or plumage of migrating birds, while some coastal plants spread by seed carried along inshore waters. This amelioration and enrichment of species occurred very recently in geological terms. It was by no means the first such event, and many species had already evolved into their familiar forms aeons before. Even so, the extreme and complex pattern of isolation and change must have maintained significant effects on the genetic diversity and species distribution and evolution of both plants and animals.

The process of diversity was further assisted by the immigration of waves of human settlers who brought with them a variety of flowers, either as seeds mixed within stores of fodder or as arable crop seeds. There was also a deliberate import of flowers for medicinal, aesthetic, folklore, religious or other significance from their natal areas. The size and influence of these importations varied from small medicinal herbs to trees such as the English Elm, a cultivated form brought in by the Romans for use in Vineyards.

By 7000 BC, bees would have already re-colonised areas of Britain alongside the spread of pioneering plant species. Bees adapted to mountainous areas of rigorous climate may have already survived and then spread back into Scotland and Northern England; some of our northern bumble bees and *Osmias* would be examples. Other species of bee would have arrived naturally from the Scandinavian and Western Seaboard. Those flowers able to attract efficient pollinators would be able to establish viable populations and expand their distributions and firmly stamp their presence in the emerging plant communities. Bees constantly attended and moulded this development, the generalist species able to take advantage of new communities of flowers and types of flower structure. More adapted bees might have already an evolved dependency on a particular group or even single species of flower. Of course, bees vary enormously in the modes by which they gather and transport pollen, and the mix of bee species with scopal hairs of a particular pattern may have influenced the relative success of particular groups of flowering plants. Composites such as hawkbits would be able to cross-pollinate after depositing pollen onto those bees with a scopa on the underside of the abdomen; these bees crawling over composites, and feeding on nectar, would quickly transfer pollen from one plant to another. A long-tongued bee such as *Anthophora quadrimaculata*, on the other hand, may well have only been present around homesteads in Roman times, emerging in the summer to visit and pollinate a small range of flowers in the mint family which had been brought in to Britain by settlers, who wished to be accompanied by plants of the Mediterranean familiar to them from home.

Some species of bee would have journeyed back into Europe from the Steppe grasslands of Asia, while many others would have survived in the Mediterranean during the ages of severe frost, before spreading back, along with the trees and flowers which had also been provided with sanctuary.

Leafcutter bees nesting in dead wood sought out new homes in wooden fencing and in the timbers of small ships coming into port. As man and the surviving large herbivores maintained or extended heath clearings in the lowland wildwood, so flowers spread and bees with them.

Soil type is important for the distribution of flowers in Britain, and there are other general variables, which include aspect, height, underlying geology, rainfall, temperatures and latitude. Bee distribution is influenced by all of these factors; for instance, an upland moor in the North of Scotland has a very different fauna and flora to that of a lowland alluvial valley. In the North of Scotland there is a very interesting and important community of bumble bees, because these insects are adapted to cool temperate conditions and are able to take advantage of the rich botanical resources of low intensity meadows and heather moors.

Bees and flowers also occupy an important place in the structure of human health and aesthetic values. Floral properties, such as essential oils, are related to bee community diversity and have played a vital role in the history of medication, remedial and other treatments. Not only is honey an ancient resource, denoting man's domestication of the Honey bee, but all bees benefit from the mixtures of fructose, sucrose, glucose and amino acids produced from the nectaries of flowers.

Conserving bees and their habitats (by Martin Harvey)

Do bees need conserving?

If you are aged 50 or more, then during your lifetime 97% of Britain's lowland flower-rich grassland has been destroyed, along with half of the country's ancient woodland, 40% of lowland heathland, 60% of lowland raised bogs and 90% of fenland. Given this background, it is not surprising that many of our wild bees have also suffered losses of range and abundance. In fact, the surprise is that so many species have been able to survive.

As habitats have been lost or changed, bees have declined with them. Of the 250 or so British wild bees, nearly half are designated as Nationally Scarce or Red Data Book species, a higher proportion than for any other insect group. At least 19 bees are thought have become extinct over the last 200 years, which shows a rate of nearly one extinction for every decade.

This is not just a disappointment if you study bees; it represents a worrying loss of biodiversity that should concern everyone. Bees are important pollinators of wild and cultivated plants. One estimate has calculated that bees pollinate crops worldwide worth 1,590 million dollars every year and most of this is carried out by wild bees. Quite apart from helping produce food for humans, bees are themselves food for other wildlife, such as birds, badgers and whole range of other insects including parasitic wasps, bee-flies and species like oil beetles. Some of these predators and parasites are themselves becoming scarce.

The conservation needs of insects have become much more widely acknowledged in recent years, and there is now a better understanding of why insects such as bees have declined (although there is plenty left to learn about the life-histories and ecology of many species). Some bees are in serious trouble and continue to decline, but for others there has been success in maintaining their habitats, and populations have been able to recover. However, many challenges remain if we are to keep the full fauna of bee species across our fragmented countryside.

Sun, soil and structure

A habitat for a bee must provide at least two things: a suitable structure in which to build a nest, and plenty of food within a reasonable distance. Some bees have extra requirements - they may need a particularly warm and sheltered spot in which to warm up before they can go about their activities. Most adult bees can feed on nectar from a range of flowers, but other species require pollen from one or a few particular plant species to provide food for the larvae in their nest.

Ground-nesting bees construct a nest by burrowing into the soil, in which case their habitat must include suitable areas of bare ground that is neither too solid to burrow into, nor too frequently disturbed so that the nests get destroyed. Other species nest in holes in dead wood, often making use of the holes left by wood-boring beetles, or use the hollow stems of plants such as bramble.

Food sources, in the form of flowers, are also bound in with the structure of the habitat. A grassland may contain all the species of plant that a bee needs, but they have to be flowering in sufficient quantity to support a reasonably-sized population. If all the grassland in a vicinity is mown or grazed during the flowering season, even just for one year, then the bees may fail to breed successfully. Unless another population exists in the vicinity, it may take a very long time for the bees to return, even if the flowers are back the next year.

Over a quarter of British bee species do not provision their own nests, choosing instead to lay their eggs in the nest of other species. These 'cleptoparasitic' bees are of course still dependent on finding the correct habitats for their host species, and many of them are significantly rarer than their hosts.

The solitary bee *Hylaeus pectoralis* provides a good example of how a mix of habitat requirements fit together. It nests inside the 'cigar' galls found on Common Reed (*Phragmites australis*). The galls are caused by a fly, *Lipara lucens*, whose larvae live inside the stem of the reed and cause the plant to form a swollen gall around the stem. The adult fly emerges from the gall in the spring, leaving behind the hollowed out chamber which *Hylaeus pectoralis* can then use for nesting (and the bee's nest is in turn sometimes taken over by wasps of the genus *Gasteruption*, which parasitise the larvae there). So, habitat for *Hylaeus pectoralis* must include reed stems that are left uncut for at least two years, have the right species of fly present, and with nectar and pollen sources nearby for food and nest provisions. The bee is quite scarce, being found only in southern and eastern England, so it may have particular climatic requirements as well.

Bumble bees in trouble

The first atlas of British bumble bees was published in 1980, and it was already apparent that many species had been lost from areas in which they were previously found. Since 1980 the picture has worsened, with several species continuing to decline, and one, *Bombus subterraneus*, now thought to be extinct in Britain. Only six of the 20 British bumble bees are still widespread.

Why should bumble bees have suffered such a heavy decline? As for many other types of wildlife, habitat loss and change is the main cause, with alterations in systems of agriculture having had the biggest impact. Bumble bees live in colonies that are active from spring to autumn, with queens and later workers requiring access to plentiful supplies of flowering plants. In particular, flowers with long corolla tubes, matched to the length of the bumble bees' tongues, are an important food source. Plants such as Red clover and Black knapweed form the mainstay of nectar and pollen sources for bumble bees. Bumble bees also require nesting sites; for some species these are underground, e.g. in abandoned small mammal nests, or at ground level among undisturbed vegetation. Less is known about hibernation sites, but these are also likely to be in undisturbed areas of vegetation.

Mixed, low-input agricultural systems would once have provided these resources in good measure. Flower-filled meadows surrounded by hedgerows were a familiar feature of farms in the first half of the twentieth century, providing food and lodging for bumble bees. As agricultural production intensified after the second world war there were significant changes in farming practice, with many farm fields given over to arable production, or turned into permanent pasture, with heavy inputs of fertiliser to maintain grass productivity at the expense of flowering plants. Fewer fields are left undisturbed over winter, reducing the availability of potential hibernation sites.

Several bumble bee species are now listed as Priority species in the UK Biodiversity Action Plan (BAP - see below), and they have been the subject of much research over the last few years. Their habitat requirements are now much better understood, but providing for these requirements is not easy. It will involve changes in land use over large areas, having implications for agricultural policy at a national and international level. However, there are already some grant schemes available to help restore habitats suitable for bumble bees, and support for farming in the future is likely to extend these options.

Bees and Biodiversity Action Plans (BAP)

The UK Biodiversity Action Plan is now one of the main driving forces for conservation, setting out priorities for conserving species and habitats in the UK. A total of 17 species of bee are currently identified as priority species, each with its own national action plan. Many conservation organisations are working to carry out the actions listed in the BAP, and many other organisations now take BAP priorities into account to a greater or lesser extent, including local authorities, some businesses and other land-owning organisations. Although the BAP-listed species and habitats do not automatically have any greater legal protection, they are now receiving more attention in the planning process. While one can argue about exactly which species should or should not be listed in these plans there is no doubt that the BAP process has generated real action for threatened species, as well as an awful lot of paperwork!

Species action plans are being implemented with the help of funding from a variety of sources, including the government conservation agencies, World Wildlife Fund, Royal Society for the Protection of Birds, and the Wildlife Trusts. An aculeate conservation group, Hymettus Ltd, has been set up to coordinate work on the BAP-listed bees, wasps and ants. Members of the Bees, Wasps and Ants Recording Society work closely with this organisation, providing records and helping with detailed surveys. A number of research reports on particular species are now available, and recommendations for habitat management to favour bees and other invertebrates are being communicated widely, for example via the steering groups for the various habitat action plans, as well as through more traditional publications and societies.

There are also Local Biodiversity Action Plans (LBAPs) for many counties and other areas, and these too are achieving real actions for wildlife conservation. For example, the LBAP for Staffordshire highlights solitary bees and wasps as a group of special significance for the county, requiring action to survey and manage the best sites. Jon Webb of the Staffordshire Wildlife Trust was determined to do something practical to help provide habitat for these species. While out watching bees and wasps burrowing in the sand on one of his local heathlands, he began to consider what else was black and yellow and dug in the sand. The answer he came up with, after a bit of lateral thinking, was JCB digging machinery.

Jon approached JCB to see if they would help fund some habitat restoration work on Staffordshire's heathlands and, sure enough, they were able to contribute funds and machinery to a two-year project. As a result, Staffordshire Wildlife Trust was able to create new nesting habitat for bees and wasps by using the machines to scrape off the vegetation in small areas of heath, creating the warm bare ground that many species need to nest in. Follow-up surveys recorded positive breeding records for species such as *Nomada integra* and its host *Andrena humilis*.

Conservation of *Osmia* bees

Although the warmer climate of the south supports the greatest numbers of bee species in Britain, there is a small arctic/alpine element of our fauna that is confined to northern Britain. This includes three scarce *Osmia* mason bees, all of which are listed in the UK BAP: *O. inermis*, *O. parietina* and *O. uncinata*. The Aculeate Conservation Group has been carrying out some of the BAP actions for these.

Although these are northern species, they still like their warmth! *Osmia inermis*, for instance, nests under small stones and rocks on the sunnier slopes of grasslands in the central Scottish Highlands. It provisions its nests with pollen from bird's-foot-trefoil, a plant that is common enough where flower-rich grasslands have survived, but which is soon lost if the grasslands are ploughed and fertilised, or if they are abandoned or planted for forestry. Winter grazing by sheep or cattle maintains the open grasslands and allows the bird's-foot-trefoil to flower. Summer grazing will not wipe out the plant, but is likely to result in the flowerheads being grazed off, thus denying the bee its food sources.

The first stage of the BAP for this species was to undertake surveys to find out where *O. inermis* still survived, and to identify what types of habitat supported viable colonies. At the end of the 1990s the only known sites were in the Blair Atholl area. Surveys in 2001 found further colonies in Deeside. Several nests were found, providing evidence of breeding both for the bee and for a cleptoparasitic wasp, *Chrysura hirsuta*, itself a BAP-listed species that attacks the nests of *O. inermis*. At one site near Blair Atholl the grazier had been able to film *O. inermis* building its nest, showing the way in which its nest-cells are constructed and provisioned.

So, initial results from the BAP have added to our knowledge of the bee and its ecology, but what is being done to conserve it? Even during the course of the survey work problems have arisen, with one of the best sites for the bee coming under threat of being planted for forestry. Thanks to the publicity and concern that BAP species can attract, the threat seems to have been averted for now. On other sites the problems are to do with maintaining a suitable grazing regime, not easy given the pressures that farming is experiencing.

As a result of the work for the BAP, it may be possible to encourage targeted funding schemes to encourage farmers and other land managers to maintain suitable habitat for *O. inermis*. This is an important step forward, as the grasslands that support *O. inermis* had not always been recognised as important features in their own right. Although this type of grassland, with its abundance of plants such as bird's-foot-trefoil, has undoubtedly declined greatly, it had not previously been seen as a conservation priority.

A similar situation is causing concern for another northern *Osmia* species, *O. uncinata*, that usually nests in beetle holes in the bark of Scots pine trees. The bee has nesting colonies in several nature reserves that are recognised and protected for their native pine woodland, but as well as nest-sites it also needs flower-rich meadows with bird's-foot-trefoil. Such meadows were once widespread around the woodlands, but surveys by the Aculeate Conservation Group have found that although the woodlands remain suitable for the bee, many of the surrounding meadows are being lost.

Save your own bees

To conserve the full range of bee species we need to ensure that habitats are available for them. This means making sure that nature reserves with important bee habitats are managed sympathetically, taking bees into consideration alongside more 'popular' forms of wildlife. It means encouraging people to maintain their gardens in a way that is friendly to bees. And perhaps the biggest challenge is to influence policy in the wider countryside, in agriculture and planning, so that we bring a halt to the increasing fragmentation of natural habitats, and begin to reverse the declines that so many species have experienced.

There are many ways of helping to conserve bees. In practical terms you can help in your garden by providing nectar and pollen sources, and artificial nests. You can volunteer for conservation work on your local nature reserve, where you may be able to use your knowledge of bees to ensure that their habitats are looked after. Contact your local Wildlife Trust or other conservation organisation to find out what work is being carried out on nearby reserves.

If bees are to be taken seriously in developing action plans or legislation for conservation then we need to have reliable data on which to base our arguments. Most of this data is provided by volunteer recorders. By joining BWARS you can find out more about recording and identifying bees, and help to provide records for the atlases and reports that BWARS produces. Without this basic knowledge of where species are found it is impossible to conserve them or protect their habitats.

Habitats will not be conserved unless people realise their value, so we need to spread the message as widely as possible. Bees make challenging subjects for photography, and good images can be used to communicate their fascination to others. Attractive photos, not just of the bees themselves but also of their habitats and behaviour, are immensely helpful, perhaps used to illustrate articles, to give talks or to load onto a website.

In addition to practical work with bees and their habitats, a lot of background work for conservation is done indoors, in committee rooms and offices. Conservation charities depend on volunteers at all levels, from helping out with office administration to setting policy and acting as a Trustee. Societies such as BWARS are run entirely by volunteers. Although this side of conservation can seem remote from being out in the field watching bees, it is vital work, and if it helps change national policies for agriculture, planning or environmental legislation, it could be the most important thing you will ever do for wildlife.

Further reading

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box 1:

Conservation status of bees

Bees and other insects can be classified according to their rarity. One way of doing this is to use the 'official' conservation status terms that are ratified by a government agency, the Joint Nature Conservation Committee (JNCC). JNCC are responsible for maintaining **Red Data Books** (RDBs) that list the most endangered wildlife species in Britain. There are three main categories:

- RDB1 (Endangered) – these are species considered to be at highest risk of extinction, with just one or very few known populations, or existing in habitats which are especially at risk
- RDB2 (Vulnerable) – species that are not yet Endangered, but are at risk of moving into that category if the threats facing them continue to cause losses

- RDB3 (Rare) – species with small populations at few sites, not currently at risk but could easily become so.

Most RDB species are known from 15 or fewer of the approx. 2,800 ten-kilometre squares that cover Britain; in other words they have been recorded from less than half of 1% of Britain's land area. There are now new international criteria for allocating RDB categories to take declines much more into account, but as yet these have not been applied to bees.

Species that have been found in 16-100 ten-kilometre squares are classified as **Nationally Scarce** (formerly called Nationally Notable), and these are subdivided into "Na" species (16-30 ten-kilometre squares) and "Nb" (31-100 ten-kilometre squares), so that a Nationally Scarce species has been recorded from less than 4% of Britain's land area.

Bees were classified into RDB and Nationally Scarce categories in the 1980s/early 1990s, and the system is now somewhat out-of-date, due to changes in the distribution of the bees since then, as well as to increased knowledge for many species.

Biodiversity Action Plan (BAP) species were selected using somewhat different criteria, aimed at highlighting species that are declining, even if they are still quite widespread at the moment, and at species for which Britain holds especially important populations. There is a lot of overlap between BAP species and RDB species, but the two lists are not directly comparable. The BAP species list is due to be reassessed in the near future.
