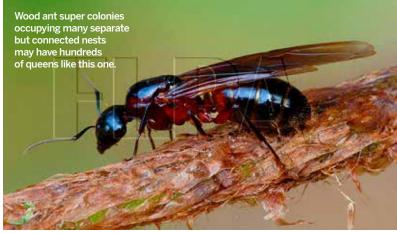


subterranean city, a labyrinth of tunnels and chambers, home to some 300,000 inhabitants. At its centre, an ageing queen surrounded by daughters; her protectors, foragers and nursemaids. Inside and out, plunderers and predators lurk. No, this isn't TV blockbuster *Game of Thrones*, but something even more extraordinary. It's the reality of life for some of our most fascinating insects.

Red wood ants are familiar to many of us, with six closely related species in Europe's *Formica rufa* group, four of which are native to Britain (though one may now be extinct here). Take a walk in a good bit of woodland that's home to these ants and you will be hard-pressed to miss them. They're often present in massive numbers and their nest mounds can be as much as 2m high. In Britain, some of the best examples can be seen in the Scottish Highlands.

Look closely at one of these mounds and around your feet you'll see thousands of scuttling ants. Many will have taken offence to your presence and be standing with jaws agape, or spraying formic acid in your general direction, lending the air the distinctive odour of these insects. Covering the mound is a seemingly untidy thatch of pine needles and other plant material, but it is actually constructed in such a way as to make the most of the sun's rays to warm the nest as well as protecting it from rain.

MANY WILL HAVE TAKEN OFFENCE TO YOUR PRESENCE AND WILL BE SPRAYING FORMIC ACID IN YOUR GENERAL DIRECTION.





The loose thatch of the mound also belies the complexity of the nest beneath, which is nothing less than a marvel of arthropod architecture. The subterranean part is often bigger than the mound you can see above ground, giving you a good idea of the size of these structures. Shielded by the thatch is the rotting tree stump in which the nest was established, chambers for the queen, nurseries for the brood in varying stages of development – all the way from egg to pupa – not to mention food stores and rubbish tips.

HIDDEN AWAY

Getting to grips with the nest's structure and tracing its every tunnel and chamber is next to impossible without disturbing it in some way. Indeed, the challenges of working out what's going on in a nest without upsetting it is one reason why we still have plenty to learn about wood ants. The internal architecture of the nest and the activity therein is one thing, but the over-arching social structure of these ants in the landscape is also remarkable.

The story of a nest can be acted out in a number of ways, but the beginning is always the same: young larvae in the darkness of a mature, healthy nest, destined to be queens, which are fed more, better quality food than the rest of the brood. Once adult, the young queens mate in the nest or leave it to mate nearby, either on the ground or in the air — a so-called nuptial flight.

Having mated, the queens have to establish a nest, and the place they often choose is a cosy retreat in a rotting tree stump. But the queens of many wood ant species are completely incapable of doing this on their own. A young red wood ant queen, for example, becomes a parasite in the nest of a related ant species, relying on the host workers to do all the hard work for her.

A queen that mates underground in her birth nest

employs a different strategy. Instead of turning parasite, she establishes her nest very close to the birth nest with the help of a splinter group of workers. This process, known as budding, is the reason why in some populations of these ants you find nests very close together forming a super-colony, while in other areas the nest mounds are more widely scattered.

These 'budded' colonies retain links to the 'mother' colony, and if they are too far from food sources they do not make any foraging trails, instead relying on food from other parts of the super-colony's empire. Some of these nonforaging nests may eventually form foraging trails and are then fully integrated into the super-colony, while others do not and are abandoned.

Establishing a nest depends on the queen being able to produce many daughters, which will maintain and expand the nest, tend to the brood, find food and repel enemies. This ability to produce an army of loyal daughters hinges on the mind-bending nature of reproduction in these animals. The queen ant can control the sex of her offspring by using the

of her offspring by using the sperm she stored from her single dalliance vary sparingly.

If a daughter is needed, the queen releases a tiny amount of sperm to fertilise the egg as it is being laid. If the queen withholds the sperm, the egg is not fertilised and it will develop into a son. This quirk is at the root of the success of ants because it means that a female worker is more closely related to her sisters than her own offspring, so it pays for her to look after her sisters and the nest rather than strike out on her own.

Above left: F. rufa milks black bean aphids, stroking them with its antennae to draw out a drop of honeydew. Above: a wood ant (F. rufa) carries a cocoon over a woodland floor. Why? Below: erect hairs on the head and mesosoma of F. polyctena are very sparse or absent.

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With a nest well and truly established, this sisterhood begins to exert a powerful influence on its habitat. The driving preoccupation of the multitude of ant workers is sourcing food for themselves and their nest-mates, including the brood, which are particularly ravenous. If you watch a nest – or a foraging trail leading to it – for any length of time, you'll see bits and pieces of various insects and spiders that have been butchered and are being transported back to the nest to be fed to the brood.

Any arthropods are fair game. Caterpillars, beetles or spiders that find themselves on the wrong side of a foraging party will be quickly subdued and dismembered. Although these ants are very capable predators and scavengers, their most important food source, making up 90 per cent of their diet, is the sweet liquid – honeydew – that oozes from the back-ends of aphids high in the trees that surround the nest.

SUPPLY AND DEMAND

An ant delicately strokes an aphid with its antennae to elicit a droplet of honeydew, which it greedily consumes – a process known as milking. Like miniature herders tending their livestock, the ants are very protective of the aphids and will drive off the many species for whom aphids are a favourite snack. They'll even move the aphids to better feeding grounds to increase the production of honeydew. Satisfied ants then head back to their nest and regurgitate the honeydew for the queen and other workers.

In tending and protecting aphids, these ants have a considerable impact on tree growth and the structure of the forest. They also play a crucial role in nutrient cycling, taking honeydew and arthropod prey from the canopy and surrounding forest down into their subterranean chambers. These outside nutrients, the waste material produced in the nest, and the constant digging and tweaking of the nest, together help to enrich the soil for further plant growth.

COLONIES AND **SUPER COLONIES**

Pain-staking research involving genetics and the marking of thousands of worker ants has shown that wood ant colonies can have a single queen (monogyny) or lots of queens (polygyny). A colony can also inhabit a single nest mound (monodomy) or multiple, connected nest mounds (polydomy) that form by 'budding'. In any given area, there might be a mix of these social structures.

1 THE THATCH

This outer layer of the nest consists mostly of pine needles arranged in a specific way to make the most of the sun's warming rays and to keep rain out.

→ NEST ENTRANCES

There are several of these all over the nest mound. They can be opened or closed to maintain optimal temperature and humidity within the nest.

TREE STUMP
The foundress of the colony often establishes the nest in an old tree stump, which might already be occupied by another ant species and so has ready-made chambers and tunnels. As this stump decays, it helps to keep the nest mound warm.

QUEEN CHAMBERIn the deepest part of the nest resides the queen, attended by workers and laying a stream of eggs. Deep down in the nest, she can live as long as 15-20 years.

5HOT ROOMEggs from the queen are taken by workers to the top of the nest mound, where temperatures can be higher, to hasten their development.

6 BROOD CHAMBER
Mature eggs are taken from the hot room to brood chambers deeper in the nest, where their every need is attended to by an army of nurse-maids – their older sisters.

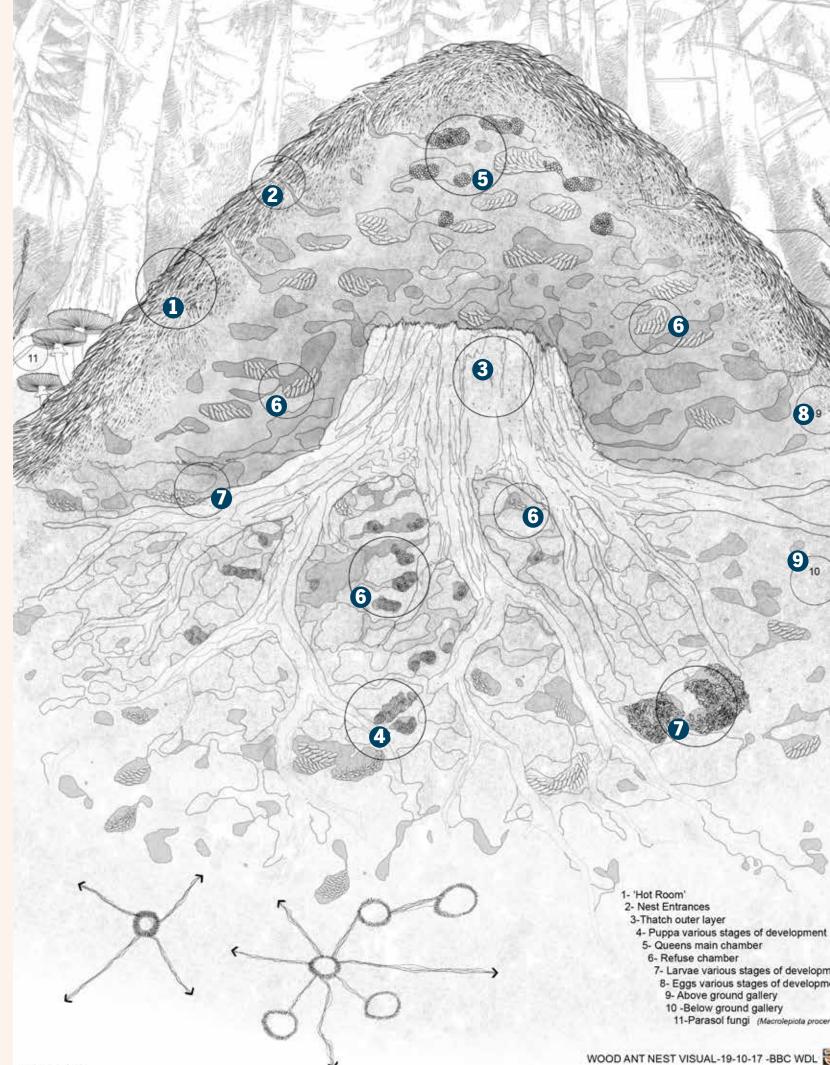
TREFUSE CHAMBER

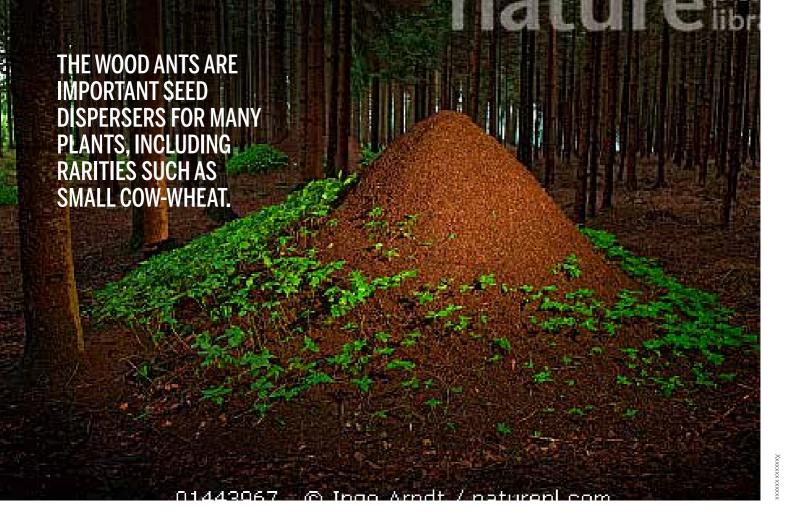
Ants are scrupulously tidy. They have to be, because conditions in the nest are perfect for harmful fungi and bacteria. Waste, spent workers and diseased or dead eggs and larvae are dumped here to be safely contained.

ABOVE GROUND GALLERY
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BELOW GROUND GALLERY Need copy here (2 to 3 lines)

Above: ants from the Formica rufa group are protected by law in many European countries. The insects play important ecological roles.





In constructing their elaborate nest mounds the ants move lots of plant material, including seeds: they've been shown to be important seed dispersers for many plants, including rarities such as small cow-wheat. Even though the nest mound is protected by hordes of fierce, acid-squirting workers, it is nothing more than a pile of food to many larger animals, such as badgers, capercaillies and green woodpeckers. To them, the brood deep in the nest are the real prize – they're less 'bitey' than the workers.

ECOSYSTEM ENGINEERS

The internal complexity of the nest, its benign conditions and the bounty of food and protection it offers, has also been a draw for a veritable menagerie of other species, some of which are completely dependent on the ants. As an entomologist, it is this aspect of life inside the nest that really excites me, as the biology of many of these ant-associates is shrouded in mystery.

One-hundred and twenty-five species of arthropod are known from in or around European red wood ant nests. There are 52 beetle species, as well as 28 mites, 15 other ants and wasps, 10 flies, eight true bugs, six spiders and even a moth. Some live in close proximity to a nest, others inside it, some are not tolerated if discovered and others fool the ants into accepting them. It is among the many beetle species where we see the most intriguing ant guests.

Take the rove beetle, *Lomechusa pubicollis*, which as a larva lives deep inside the nest of red wood ants and dupes its hosts into grooming, feeding and carrying it by tapping into their odour-dominated messaging system. In effect, the ants treat the beetle larva as one of their own brood. In return, the young beetle tucks into the developing siblings of its carers. After pupation,

Above: wood ants create ventilation holes in their nest in order to deal with the heat of summer. Below: a leaf beetle larva in its egg case.

the adult beetle begs it carers for food one more time and heads outside to seek the nest of another ant species in which to see out the winter. As the warmth of spring arrives, the beetle slips back into another red wood ant nest, where it will breed to complete its lifecycle.

A strange species of leaf beetle, *Clytra quadripunctata*, is another specialist in the nests of red wood ants. From a leafy perch, the female *Clytra* deftly encases each of her eggs in faeces before flicking them to the ground. Some of these eggs are picked up and carried by workers into the nest. The beetle larvae hatch but retain their egg case as a mobile retreat, recoiling into it at the first sign of danger, their tough little heads making a perfect plug. They add to the case with their own droppings and soil as they grow, eventually forming a perfect little pot.

Trundling around the ant's nest, these larvae feed on organic matter and detritus and are impervious to attack thanks to their protective pots. This is not the case for the adult beetle when it emerges, and it must run a gauntlet of angry worker ants to escape the nest.

We still have a huge amount to learn about the inner workings of these very familiar ants and their interactions with other species. We know they are a crucial element of forests around the world and that they're extremely vulnerable to human activities, which have caused the decline and extinction of some species. But only by studying them will we fully appreciate their ecological significance and fragility.



ROSS PIPER is an entomologist and author, and was a

presenter on the BBC Two series *Wild Burma*.

→ GET INVOLVED

Take part in Buglife's wood ant citizen-science survey at www.buglife.org.uk/nest-quest.