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# INTRODUCTION

I MIGHT BE BIASED, but insects are the most fascinating animals with which we share this planet. From my first tottering steps I was spellbound, which was bad news for the various small beasts in my yard and wider neighborhood. Small, grubby fingers ferreting unfortunate beetles and caterpillars from their hiding places and incarcerating them in plastic tubs, often together and often in pretty squalid conditions. In my defense, it was the early 1980s, I was young and I didn't know any better. My favorite was a violet ground beetle. At the time, I had no real idea what it was. All I knew was that it was big, metallic purple, and that it deserved a stint in a tub. This is probably how it begins for all insect-botherers.

When you take time to find and observe these animals, you begin to understand their fabulous diversity. Their appearance is so varied and often so strange that they make sci-fi monsters look a bit lame. Then there are the ways in which they live. From microscopic, incestuous wasps that live their whole life in the eggs of other insects, caterpillars that fool ants into believing they are their sisters, and beetles that lure flies to their doom using stinky secretions. If you want sex, violence, and intrigue, insects have all of this and much more besides.

Their lives are so juicy that you could easily fill ten meaty tomes with what insects get up to, yet we have only scratched the surface of understanding how they live. To date, just over one million species of insect have been described, but there are still millions more out there awaiting description. Our knowledge of even the described species is generally very poor. For the vast majority of insect species, we know next to nothing about the ins and outs of their lives. Insects tend to get overlooked because of their generally small size. As well as being overlooked, they are generally maligned animals because a few species nibble our crops, run amok in our homes, or transmit diseases to us, our pets, and livestock.

We are all familiar with insects, but what are they? Let's begin at the beginning. Insects are animals. You, a scuttling beetle, and a sea anemone all share a common ancestor that lived probably one billion years ago. I've lost count of the times I've read or heard "animals and insects." If you see or hear this then it is your duty to correct it. Within the animals, insects are a type of arthropod.

## What Is an Arthropod?

Arthropods are the animals we commonly call "bugs" or in even more derisory terms, "creepy crawlies." This is the largest group of animals by far (1.25 million known species and counting), way bigger than all the other animal groups

✓ This phylogenetic tree shows how the different groups of arthropods are related. This reveals that insects are crustaceans.



combined. The arthropods are the insects, springtails, and their relatives, crustaceans, arachnids, horseshoe crabs, sea spiders, centipedes, millipedes, and their relatives. This is a mind-bogglingly diverse group of animals, but they all share the following features:

- Jointed limbs
- An exoskeleton made of chitin, often reinforced with calcium carbonate
- The exoskeleton must be periodically shed for the animal to grow
- A segmented body; each segment often has a pair of appendages.

From an evolutionary point of view, the insects are terrestrial crustaceans. Their closest living relatives are two enigmatic groups of crustaceans—the remipedes and the cephalocarids. The former are rarely seen denizens of flooded caves and the latter are tiny animals that inhabit marine sediments. Insects also go back a very, very long way, with their likely origins some 480 million years ago in the early Ordovician Period. Between then and now planet Earth has been many different worlds, but the insects took to a life on land and made it their own.



# What Is an Insect?

In insects, the general arthropod body-plan has been tweaked and they all share the following features:

- A three-part body: head, thorax, and abdomen
- Compound eyes and often simple eyes, too
- One pair of antennae
- Wings (secondarily lost in some insects).

During the long history of these animals, this form has been fine tuned by time and the environment into the extraordinary diversity of forms we see in living insects today.

By any measure, insects are among the most successful land animals there have ever been. They exist in such numbers and live in such bewildering ways that they pull at every single thread of the terrestrial domain. What are the secrets to this success?



< Aquatic insects have a smooth exoskeleton and paddle-like limbs.

> Top: Adapting to life among running water has led to the evolution of flattened, hydrodynamic forms, such as this mayfly nymph shown here.

Bottom: *Halobates* water striders live on the surface of the open ocean. Their exoskeleton is exceedingly water repellent.

#### Exoskeleton

First, is the exoskeleton. This is so much more than a suit of strong, light armor. It is the insect's skeleton, composed of chitin, and so it must provide anchor points for all the animal's muscles, which it does via tiny, inward projections. It must keep the insides in and the outside out. Crucially, it needs to prevent undue water loss as dehydration is the ultimate challenge for all terrestrial beings. A waxy layer prevents the insect from becoming a dried-out husk. Insect exoskeletons range from the incredibly delicate, such as that sported by ephemeral beings like mayflies, to the almost impregnable, such as those of the aptly named ironclad beetles and some weevils. The exoskeleton and the efficient musculature beneath made life on land possible for the first insects, but it also has one major flaw. It's not very elastic. So, when an insect needs to grow it has to escape its old exoskeleton and make a new one. This sounds rather straightforward, a bit like a snake shedding its skin, but it is so much more complicated. For starters, the

✓ The earwig on the left has just shed its exoskeleton. The new exoskeleton is pale and soft.











The limbs of insects come in a bewildering array of forms, such as the rear legs of *Calodromus mellyi*, which are used in defense and perhaps courtship.  $\wedge\,$  The exoskeleton is most armor-like in the beetles, such as this Leptochirus rove beetle.

exoskeleton extends down the insect's throat to line its foregut and up through the anus to line the hindgut. The exoskeleton also lines the vanishingly tiny tubes that transport gases to and from all the insect's tissues. All this has to be replaced too for the insect to grow. The whole process is a remarkable natural phenomenon precisely controlled by a symphony of hormones. The new exoskeleton has to be synthesized and ready before the old one is cast off, and the physical process of leaving the old exoskeleton is fraught with danger. Not only that, but when the insect is finally free of its old covering, the new one is still soft and pliable, leaving the animal acutely vulnerable. Considering all of this, it's a wonder that any animal with an outer layer like this could ever be more than just a footnote in the history of life on Earth, but its downsides are more than made up for by the protection and opportunities it provides an insect.

If you have a good look at a range of insects you'll be struck by their colors. They come in a staggering variety of hues, from the vivid red of a lily beetle to the deep, metallic iridescence of a

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long-legged fly. These colors can be formed by pigments, but in those insects with metallic iridescence the colors are due to the scattering of light by the crystalline structure of the exoskeleton. To our eyes, lots of insects look like living jewels.

The exoskeleton is also festooned with all manner of outgrowths that appear as hairs, bristles, and scales. These structures are multifunctional. The wings of butterflies are covered in huge numbers of scales that give the wings their colors and patterns. These scales can be rather fur-like providing their owners with insulation and protection from predators. Many beetles are dusted with scales of every hue that are easily dislodged.

The exoskeleton also sheathes the jointed appendages of the insect, which come in every shape and size. The appendages of the head have been modified into all manner of shears, syringes, and saws for making short work of food. Alongside these mouthparts are delicate little limbs called palps that mainly taste and manipulate food. Emanating from the head are a single pair of antennae. In some insects these are almost invisible, but in others they're fantastically elaborate and bristling with sensory pits for detecting food and members of the opposite sex. The limbs of insects have the same basic structure, the segments of which are named after the structures of vertebrate legs, so they have a coxa, trochanter,

✓ Outgrowths on the exoskeleton include all manner of bristles and scales, such as the fur-like covering of many moths (*Deilephila elpenor*).



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11.2

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C The mandibles of this nut weevil are at the tip of its long snout-like rostrum (*Curculio nucum*).

femur, tibia, and tarsus. The tarsus is normally tipped with a pair of claws. Natural selection has worked wonders on this basic limb form. For example, you can see lots of unrelated insects equipped with raptorial legs for snatching prey.

In others, such as the mole crickets, the legs are beautifully adapted for digging, while others have beefy rear legs that power prodigious jumping abilities. Some leaf hoppers are even equipped with cogs on the upper parts of their legs that keep the legs perfectly in time when they jump. If you've ever seen a flea beetle or one of these leaf hoppers in action you'll understand that insects are the undisputed champions of jumping.

# Wings and Flight

The most significant extension of the insect exoskeleton and the innovation that makes these animals so remarkable is the wing. Have a good look at an insect wing—under a microscope if you can. They're one of the most elegant structures in nature. Watch a hoverfly in the summer months and marvel at what they do with these wings—they make other flying animals look a bit clumsy. The level of precision that goes into their flying far outstrips that of most larger flying animals.

Wings appeared very early in the evolution of the insects, probably around 400 million years ago, which is at least 170 million years before vertebrates ever took to the air. The origins of the insect wing are hotly debated, although recent research suggests they evolved from legs. Regardless of their origin, this innovation completely transformed the fortunes of the insects. As the wings and their musculature became ever more fine tuned it opened up all sorts of possibilities. Flight enabled insects to better evade their enemies, to hunt prey, and to seek out mates and new areas of habitat. The ability to fly long distances is not something we normally attribute to the insects, but lots of butterflies, moths, hoverflies, beetles, and many more insects undertake enormous migrations every year—borne aloft on their wings—a true wonder of nature.

The singular flying abilities of insects, such as hoverflies, relies on an extremely efficient, ingenious system that combines the brute force of the wing muscles with the elasticity of the wing and that of the thorax that houses the muscles. In the most proficient flying insects, when the muscles in the thorax contract to bring up the wings, the thorax is distorted. Muscles that join the front and back of the thorax then contract, the springy thorax goes back to its original shape and the wings pivot downward.



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S The delicate hind wings of an earwig are normally out of sight—intricately folded beneath the short, tough first pair of wings.

∧ True flies owe much of their aeronautical abilities to their halteres—one of which can be seen here (circled).

Insects that can beat their wings extremely rapidly also have a special type of muscle that is unique to insects—the so-called asynchronous muscle. Normal muscles need an electrical signal from the nerves for every contraction, but asynchronous muscle can contract multiple times with each nerve signal. This allows extremely rapid wing beats. In some midges this can be more than 1,000 beats per second! Indeed, true flies, such as hoverflies and midges, are the real experts when it comes to flying. In these insects, the second pair of wings has been reduced to mere stubs—the halteres. These tiny, inconspicuous structures are crucial to the flying abilities of the true flies as they beat along with the wings and act like tiny gyroscopes. The fly uses the information from the halteres to fine tune its position in flight and precisely control the muscles that power the wings and stabilize the head.

In beetles it is the first pair of wings that have been greatly modified to form a tough, protective shield over the abdomen, called the elytra. Elytra are key to the success of beetles, since they allow the otherwise soft abdomen to be better protected, and they enable beetles to live in places where soft-bodied animals would otherwise be squashed, such as the tight spaces between tree bark.

# Miniaturization

We overlook insects because they're generally tiny animals, but this small stature is another reason they are so successful. A smaller body is less "expensive" to produce and maintain, especially in terms of the various systems that are needed to get around the problems of ventilation, nutrient distribution, and excretion. Small animals can also exploit niches that are completely inaccessible to larger animals.

Insects might be small, but they are also incredibly complex. Remember that these animals have tissues, organs, and organ systems. The brain of a honey bee has around 850,000 neurons and it is capable of complex behaviors, so we mustn't equate small with simple.

Insects, like few other animals, have embraced miniaturization by squeezing enormous biological complexity into a tiny space. The champions of miniaturization have to be the staggeringly varied parasitoid wasps. These wasps are probably the most diverse of all the insects, but it's difficult to estimate just how many species there might be because they're so poorly studied. Some of them are so tiny—much smaller than some single-celled beings—that the full stop at the end of the last sentence could comfortably contain several of them. How is this possible? How can a body of tens of thousands of cells be so tiny? Inside the head of a fairy wasp there is a brain, which reaches out to the rest of the body via nerve cords and nerves. In some of the smallest wasps, this brain is composed of only 4,600 neurons, but they process the information streaming in from the senses to control complex behaviors, such as flying, walking, finding a mate, and seeking out hosts. In addition, these microscopic bodies contain muscles, a complex gut, the insect equivalent of kidneys, and lots more besides.

To become very small, these microscopic insects have simplified some of their organ systems, but a cell can only get so small until more drastic modifications are needed. One way of shrinking cells is to get rid of the nucleus. This happens in the central nervous system of these miniature marvels and allows more cells to fit in each space. The nerve fibers of these insects are so thin that they shouldn't be able to work in the normal way, and it has been suggested that their nervous system may in fact be mechanical rather than electrical.

The tiny size of these wasps enables them to exploit the smallest niches with many of them completing their development within the eggs of other insects. In the smallest fairy wasps, the eyeless, wingless males remain within the host egg and mate with all their sisters before they disperse.





∧ This fairy wasp (L) is about 0.03 in (0.8 mm) long, which is quite big compared to many of its relatives (*Mymar pulchellum*). In order to show just how tiny this wasp is, here it is photographed next to a one pence coin for scale (R).

## Metamorphosis

There can be few phenomena in nature that are as marvelous as metamorphosis. To see an insect change from a larva into a pupa and finally into an adult takes some beating. When you look at a caterpillar or a maggot and then the moth, butterfly, or bluebottle fly that they become, it is difficult to grasp how these wildly different animals are related at all, let alone the same animal. The process of metamorphosis has captivated people for thousands of years and is another reason these animals are so successful. The most diverse groups of insects—the beetles, flies, wasps, bees, ants, butterflies, and moths—all go through metamorphosis. Some even go through what is known as hypermetamorphosis, where an active, hatchling larva turns into a grub-like larva that grows and pupates into the adult.

Generally, insect larvae look like soft targets. They're mainly soft-bodied and slow moving. It's true to say that a good proportion of insect larva get picked off by pathogens, parasitoids, and predators, but these shortcomings are more than compensated for by the very process of change from one form into another. Crucially, a separate larval stage and adult stage allow a division of labor in the life of an insect. The larval stage is an eating machine—dedicated solely to growth—while the adult gets all the fun and can spend its time mating and finding new areas of habitat. The other masterstroke of this strategy is that because the larva and adult are so different and typically live in different places they won't compete for resources.

The pupa was once thought to be a resting stage in the life cycle of insects, but it is anything but. The pupa's calm exterior belies an incredible amount of activity. In a series of beautifully choreographed, hormone-controlled steps, the body of the larva is dismantled and the adult form assembled.



There's still a huge amount to learn about this remarkable phenomenon. It was once thought that all the larva's tissues were broken down during pupation to create a "soup," but new research has shown this is not the case. Some of the tissue is broken down and new structures develop from clusters of cells known as imaginal discs, (for example, the muscles), but others are retained and remodeled (for example, the gut, trachea, and some parts of the nervous system). The imaginal discs can even be active before pupation. Indeed, memories formed by the larva (yes, insects have memories) are retained in the adult insect, so the connections between nerve cells must be maintained during this transformation.

### Senses

The senses of insects are as refined as those of much larger animals, but their small size means that we overlook their complexity. The sensory structures of insects are often invisible to the naked eye. Look closely at an insect, perhaps through a microscope and you'll see it's furnished with an array of senses—the acuity of which contributes to their success.

There are sensory cells on the surface and within their body that sense stretching, bending, compression, and vibration. Many of these are used to sense the environment, such as the minuscule movements of air that might indicate the proximity of prey or predator, while others provide information on the position or orientation of the body. In cave-dwelling insects where eyes are of no use because of the darkness, they often have long sensory setae (sensory, hair-like structures) for detecting the movement of prey. In some beetles and true bugs, sensory cells have even been modified to detect infrared. The offspring of these insects can only develop in the wood of burnt trees, and their remarkable heat sensors enable them to find freshly charred trees.

> Insects have sensory "hairs" on their body. These are at their most elaborate in eyeless cave insects, such as this beetle, Arctaphaenops muellneri.

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Not all insects can detect sounds in the way that mammals do, i.e. by picking up movements of the air via a drum-like membrane. Receptors that pick up the tiniest vibrations traveling through the substrate are common. Some insects do have organs with a drum-like membrane and they provide some of the sharpest hearing in the animal world. In some true bugs these ears are located on the thorax. Grasshoppers, cicadas, and moths have ears on their abdomen, whereas you must look to the front legs to find the ears of crickets and katydids.

The most sensitive known ears among the insects belong to a parasitoid fly (*Ormia ochracea*) that has to pinpoint the location of its hosts—crickets—by their song. Depending on where the sound of the singing male cricket is emanating from, the tiny ear drums will reverberate at slightly different times. This difference may be as little as 50 billionths of a second, but it is enough to allow the fly to directly home in on a singing male cricket. It doesn't have to stop and cup its ears; it just precisely identifies the source of the sound. Even if the cricket stops singing, mid-homing, the fly can approximate its position from the last sound it made.

The ability to detect chemicals, i.e. taste and smell, is extremely acute in insects. You won't find a nose on an insect, well not one that you see on the face of a mammal, but they are bristling with all manner of receptors for detecting chemicals. These are normally concentrated on the mouthparts, but they can also be found on the antennae of some insects, as well as the feet and ovipositor of others. The life cycle of many insects hinges on being able to detect mates and food from afar, so their ability to sense individual molecules in the air is remarkable. Flies and beetles that need decaying animal remains for their larvae can detect the chemical signatures of death from many miles away. The adult lives of insects are often very fleeting (sometimes a couple of hours) and the window in which to detect a receptive mate is tiny, so males must be able to detect the

> The antennae of this male glowworm are able to detect tiny quantities of female pheromone to lead him to a mate (*Calyptocephalus* sp.)

> Many insects have very sensitive ears. Bush cricket's ears are on their front legs (circled).

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merest whiff of a female on the breeze. For this reason, male insects often have elaborate antennae for just this job. The ornate, often branching antennae of male insects are effectively molecular sieves able to screen individual molecules from the air. By following the increasing concentration of these molecules, the male will eventually be led to a potential mate, unless he's beaten to it.

Insects have very snazzy eyes. Often, they have more than one type of eye compound eyes and so-called simple eyes. Simple eyes aren't exactly simple. They're exquisite, tiny structures for sensing light, and one type—the lateral ocellus—can probably resolve outlines of nearby objects. The other type of simple eye—the dorsal ocellus—is only ever found with compound eyes and it is thought they may be important in tweaking the sensitivity of the compound eyes to light intensity.

Compound eyes can be relatively enormous and in some insects the head is little more than eye. Every compound eye is made of individual, tightly packed units called ommatidia. Each ommatidium has a lens and associated cells that detect light, so each ommatidium captures an image that is relayed to the brain. Up until recently it was assumed that this arrangement could only provide relatively low-resolution images. However, the photoreceptor cells underneath the lenses of the compound eye move rapidly and automatically in and out of focus, which © Copyright Princeton University Press. No part of this book may be



∧ Owlfly compound eyes are split into two parts. The top part is exclusively UV sensitive. The lower part has more sensitivity in the blue-green wavelength range. This probably helps them to pick out prey against the sky.

provides a view of the world that is much sharper than previously thought. As well as giving insects a sharp view of the world, these compound eyes also have a very wide angle of view and are second to none when it comes to detecting movement. Many insects can also detect light that is invisible to humans.

#### **Reproductive Potential**

Phrases such as "to breed like flies" do have a basis. Indeed, insects generally are synonymous with fecundity. Many female insects lay lots of eggs, often hundreds. Insects such as oil beetles, which have strange, convoluted life cycles, must produce thousands of eggs to off-set the low chances of any one offspring reaching adulthood. Some of the supreme egg layers though are the queen ants and termites. A termite queen may produce more than ten million offspring in her long life, but even this is meager compared with some leafcutter ant queens who can produce 150 million young in their lifetime.

Most of the eggs laid by a female insect will hatch, and in several types of insect the generation time is very short. Aphids in particular are renowned for the short generation times and in some species, this is as little as five days. Unbound and in

perfect conditions the populations of the most fecund insects can explode. Large numbers of eggs and short generation times are not the only secrets to the reproductive success of these animals. Female insects can store sperm from a single mating and make it last a lifetime—enough to fertilize all the eggs they will ever produce. In any given population of an insect, females often outnumber the males, as a few of the latter can more than meet the sperm demands of the females. In aphids, thrips, stick insects and many other insects, this trend has reached its ultimate conclusion, as males only feature in part of the life cycle, are very rare or have been erased completely leaving parthenogenetic females pumping out clones of themselves. This is how mass gatherings of aphids can appear on plants, seemingly out of nowhere.

All these factors combined mean that, as a rule, insects are very good at making more insects. Perhaps the most important aspect of this rampant reproduction is that it churns out mutations, a tiny proportion of which will be beneficial and allow the owners to adapt to a continually changing world. This is perhaps most easily understood when we think about insecticide resistance in the insects that we want to get rid of. When we douse the environment with a new insecticide the initial results are dramatic. The targets are seemingly vanquished, but there will

✓ Without the need for sexual reproduction for part of their life cycle, aphids can establish enormous populations with alarming speed.





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The ability of a caddisfly larva to construct this case from silk, snail shells, and plant debris is completely innate. ∧ A female spider-hunting wasp with her prey. The ability to find and dispatch prey in a very specific way and provision a nest for her offspring is hard wired in her brain (Auplopus carbonarius).

always be some survivors, a small proportion of individuals that have a chance mutation that renders them immune to the insecticide. These resistant individuals go on to breed, passing this resistance to their offspring. In a relatively short amount of time, all the insects in a population will be resistant to the insecticide. This is evolution in action and the same process applies to every aspect of an insect's life. There will always be the genetic resources out there that allow adaptation to the challenges that life throws their way.

## **Complex Behaviors**

The behavioral repertoire of insects is immense. From the intricacies of their life cycles, through to the finding of food and mates, and the evasion of their many enemies, insects do some remarkable things. Much of what they do is innate, in other words the behavior we see is encoded in their DNA. This includes very elaborate actions. When we watch a caddisfly making its remarkable case or a hunting wasp diligently snipping the legs from its spider prey before it transports the victim back to its nest, it's hard to believe that these complex actions aren't learned. The truth is that the caddisfly and the wasp don't need to learn these things—they're hard wired—somehow this knowledge is encoded in their DNA.

Although innate behaviors account for much of what we see insects doing, some of them can change their behavior because of experience. In other words, they can learn. As an example of how elaborate this learning can be you only need to look at honey bees. When returning from a successful foraging sortie, a worker honey bee will do a strange dance—the waggle dance. This has been known about for a long time, probably for as long as people have been keeping bees, but it took the genius of the ethologist Karl von Frisch (1886–1982) to figure out what it meant. Far from being a celebratory jig, this "dance" is the worker using symbolic language to teach her sisters about the location of food, water, and new nesting spots. The fact that these small animals can memorize and relay this information to others of their kind to learn is something to marvel at.



Other more recent studies on insects have found that bees can count and that they can discern whether two symbols are the same or different. Not only that, but social wasps have also been shown to recognize the faces of other wasps. These examples show that some insects are capable of impressive cognitive feats.

There's still an awful lot to discover about the learning ability of insects and we've only just scratched the surface. Of the more than one million species of insects that have been described, only a handful have been studied to test whether they are capable of learning. Most of the insights so far come from social insects and it's not really a surprise these animals are capable of learning because they live in large, complex groups where there's ceaseless interaction between individuals conveying information about many things, such as food and threats.

# About this Book

In this book we explore the lives of insects. Within the confines of 40,000 words I had to be very selective in what examples I used in each chapter, and I have focused on the bizarre and remarkable. Bear in mind that the insects are an enormous group of animals, with many more species than all the other animal groups combined. Even though only a small proportion of insect species are well studied, these "known" ways of life are still stunningly diverse. Even among the well-known species there are still discoveries to be made and just think about all the other insect species out there. The ones that have been described by taxonomists, but the lives of which are a mystery, and the millions of species that are still to be collected and described. It would take an army of biologists thousands of years to understand exactly how all these insects live. You can reflect on all those species, the ways in which they might live, and the web of interactions they have with other living things. The complexity is mind-bending.

The facts in this book about how certain species live and why they do the things they do, were gleaned by patient observation, often over many years and sometimes over whole careers. The curiosity, patience, and dedication of these naturalists and scientists is sometimes as remarkable as the insights to which they led. The drive to ask questions, and understand more about life on Earth, is what makes us who we are, and it's something we should all celebrate and nurture. The great thing is that anyone can help to fill in these blanks—there's enormous scope for exploration and discovery within entomology. Watching and studying insects can take you to some amazing places, but equally, discoveries can be made in your own backyard. All you need to do is get out there and look. Hopefully, this book will give you a taste of the remarkable lives of insects, help you to make sense of some of the things you might see if you watch them, and encourage you to look more closely at these endlessly fascinating animals.

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You can find more about my work and the incredible lives of insects at: https://www.rosspiper.net/

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