© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

CONTENTS

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

THE MANY FORMS AND FUNCTIONS OF A TREE'S COMPANIONS

1

THE COMPLEX WEB

You can tell a lot about a tree from the company it keeps—the birds that fly, the mammals that climb, the snakes that slither, and the frogs that hop among its branches and call trees their homes. Squirrels, monkeys, porcupines, bats, sloths, songbirds, owls, hawks, geckos, and tree frogs are all familiar residents of trees. Some, like sloths and tree frogs, settle down in one tree, almost never leaving their one arboreal home, but most travel from tree to tree in search of the food, shelter, and lookout posts that trees offer. They have forged lasting relationships with trees. These relatively large and conspicuous vertebrate companions of trees eat their leaves and fruits, disperse their seeds, chew their bark, pollinate their flowers, and control their insects. The destinies of trees are interwoven with the fates of these familiar animals that keep them company (fig. 2).

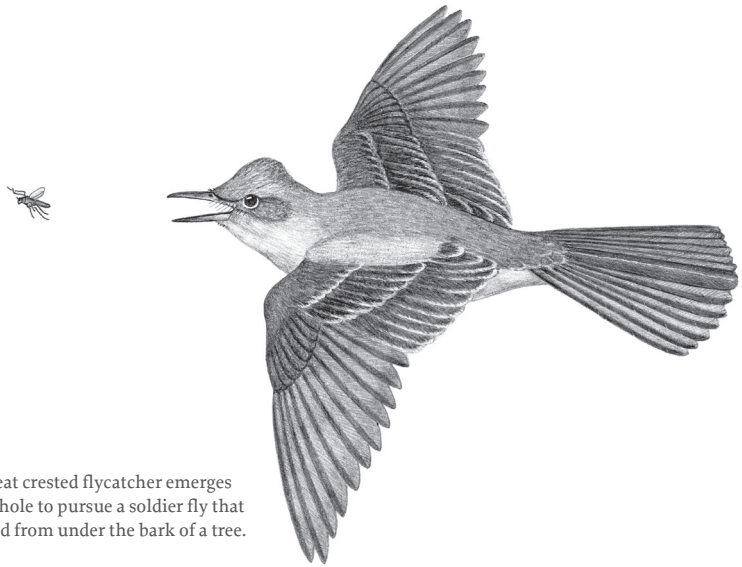


FIG. 2 A great crested flycatcher emerges from a tree hole to pursue a soldier fly that just emerged from under the bark of a tree.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

All the birds, mammals, frogs, lizards, and snakes whose lives come together on a tree during its lifetime can be easily tallied, but all the smaller creatures that establish their lives on that tree are countless. The small hidden creatures among the trees' leaves, limbs, and roots are not only the ones that have the greatest impacts on the lives of trees but also the ones about which we often know the least. Among them are those that nurture each generation of nestling birds, those that satisfy the appetites of tree frogs, and those that supplement the vegetarian diets of many mammals. Trees may simply tolerate their company or may actively entice and welcome their company, but sometimes trees must aggressively defend themselves from certain uninvited companions.

Every tree, whether rooted in a great forest, city park, or backyard, has a unique story to tell about the creatures that share its company. The following pages focus on trees of Earth's temperate zones. However, the creatures that keep company with these trees have different species as their counterparts in other parts of the world. Looking closely at a tree reveals that it is a busy crossroads of activity where innumerable lives arrive, depart, or just carry on. We can think of each tree as a community where creatures are caught in a web of interactions that links them to each other and to the tree in which they live. They all share two essential needs: energy and nutrients. This web of interactions involves coexistence, cooperation, and competition among members of the community. And even though individual creatures may fall prey to predators and trees may have their leaves devoured, the members of the web manage to transact their business—giving and taking energy and nutrients—and usually balance their accounts so that few, if any, species gain or lose too much. Each species has its job to do and does it. One tree can thus support—directly or indirectly—many lives. The destiny of each tree is tied to these myriad connections with its companions (fig. 3).

Partnerships among trees and other creatures began when green plants attained the ability to capture the energy of sunlight with molecules of chlorophyll. With the energy they captured, plants began to produce nourishment and oxygen not only for themselves but also for countless other creatures. This process is known as photosynthesis, a word that means "to put together with light." Trees "put together" sugars and oxygen from the simple raw materials of carbon dioxide from the air and water from the soil, using the energy that their chlorophyll molecules capture from sunlight. This energy from the sun is transferred to the sugars that the tree produces, to the creatures that feed on the sugars, and to the creatures that feed on the creatures that have fed on the sugars of the tree. Each life form uses this energy of sunlight—directly or indirectly—to survive. When one creature eats another or eats part of the tree, it obtains energy and nutrients from the meal. This is true whether that meal is alive or dead, plant or animal or fungus. Without contributions from certain partners that supply them with mineral nutrients such as magnesium for each chlorophyll molecule and calcium for every cell wall, however, trees could not survive, even though they can perform the astounding feat of capturing the energy of sunlight.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

These contributing partners include microbes and all the other creatures larger than microbes that provide recycled mineral nutrients for a tree by consuming the remains of creatures that once lived on the tree as well as dead or discarded parts of the tree itself. In other words, the tree and its many partners, including other decomposers, provide the raw materials for the recycling efforts of the decomposers. These other partners are (1) herbivores and pollinators that consume the nutrients of the tree's living tissues, as well as plants such as lichens and mosses that live on the tree; (2) fungivores that consume the tree's fungal pathogens, its fungal decomposers underneath it, and its fungal partners known as mycorrhizae and endophytes; and (3) predators, parasitoids, and parasites that survive by feeding on living animals of the tree (fig. 3).

By far the most numerous inhabitants of trees are also the tiniest. These are the microbes—fungi, protists (*protist* = very first) such as slime molds and protozoa,

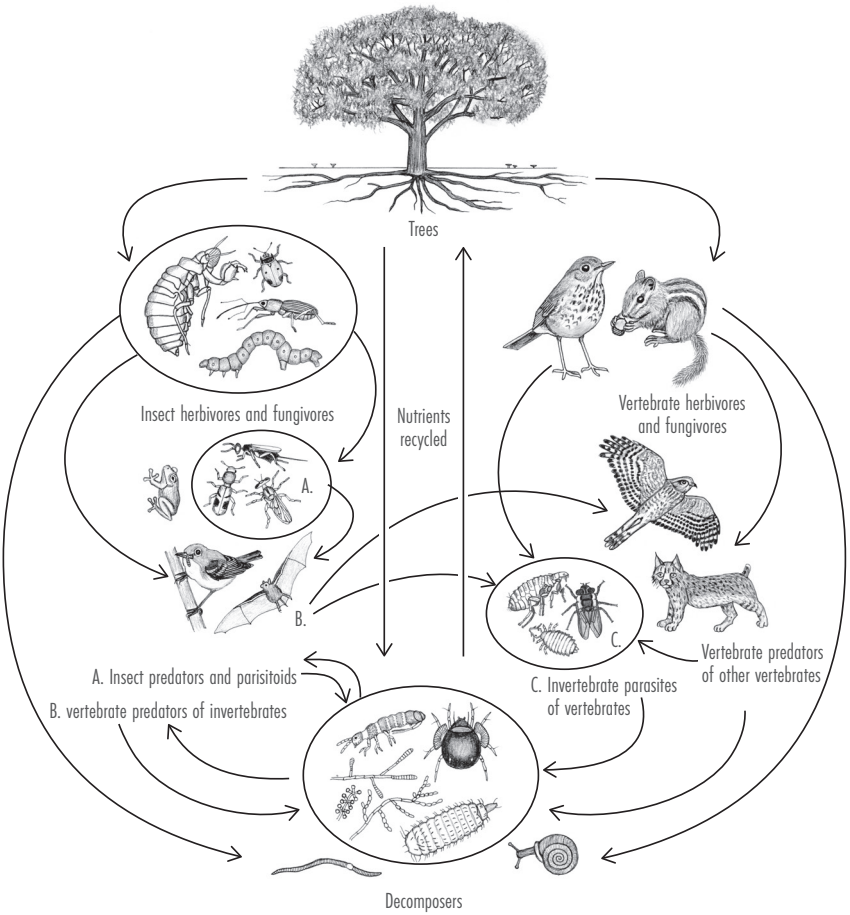


FIG. 3 The companions of a tree exchange energy and nutrients.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

and prokaryotes (*pro* = before; *kary* = nucleus) such as bacteria and archaea—that intimately associate with the tissues and cells of a tree and form what is known as the tree's microbiome. Trees are not unique in having microbiomes; microbial associates also have intimate partnerships with the tree's animal companions. Bacteria and archaea are known to reside in fungal tissues, so even fungi have microbiomes (Bonfante and Anca 2009). The network of interactions in a tree extends across all kingdoms—archaea, bacteria, fungi, plants, animals, and protists. Microbes clearly touch the lives of everyone in a tree in ways that remain bewildering.

Except for microbes, arthropods are always the most numerous creatures on all parts of a tree aboveground as well as underground. Arthropods—animals with jointed legs—include the familiar insects, mites, spiders, woodlice, centipedes, and millipedes as well as the unfamiliar proturans, pauropods, diplurans, and symphylans. As a group, arthropods make up a phylum, a taxonomic group comparable to our own animal phylum—the Chordata, animals with backbones. In their forms and in number of species, arthropods are by far the most diverse animals of our planet. Eighty percent of animals are arthropods. At last count, arthropods boasted over a million species distributed among 10 classes. One of the 10 arthropod classes is the Insecta, and insects make up about 82 percent of the arthropods. Ranking second and third in number of species are the class Arachnida and the class Crustacea, representing respectively about 8 percent and 3 percent of the arthropods. All 10 arthropod classes associate with trees in some way. Many of the species that live in the litter and soil under trees live nowhere else on Earth; representatives of the remaining seven arthropod classes—Collembola, Protura, Pauropoda, Chilopoda, Diplopoda, Symphyla, and Diplura—are wed to lives underground and rarely venture far beyond its dampness and darkness.

The vertebrates to which we humans belong represent a subphylum within the phylum Chordata. Vertebrates number 57,000 of the 60,030 species in their phylum. Compared with this number of species distributed among the five classes of vertebrates—from fishes to mammals—arthropod species outnumber vertebrate species by a factor of 22. The number of new arthropod species described each year always vastly exceeds the number of new vertebrate species described.

We can appreciate the complexity of interactions among these countless creatures, but no one can know all the creatures involved and all the ways they relate to each other. This mystery is especially profound for the groups of small creatures, many of whose species are still undiscovered and unnamed. For those that we know by name, many accomplish seemingly unimaginable, Herculean feats. For others, we often know little, if anything, about how they spend their days and how their obscure lives mold the life of their tree, their forest, and beyond.

Many of these creatures, even though they are often smaller than the periods in this book, are formed from molecules, cells, and tissues like ours and are made up of organ systems like ours—hearts, nerve cords, brains, intestines. The forms of their organs may differ from those of our own organs such as brain, gut, liver, heart, and lung, but they function like our organs and share similar proteins, and

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

all have been molded over geological time by their environments. Their body surfaces are covered with sensory bristles of all lengths and widths that touch, taste, smell, hear, and see from many angles and on many sides. Their survival depends on being acutely aware of their surroundings. At the base of each of these sensory bristles lie one or more nerve cells that convey sensations to their brains and nerve cords. Processing of sensory information in the central nervous system determines which muscles are excited and how the creatures ultimately respond. Despite their minuscule forms, insects, spiders, and mites can exquisitely monitor their environment. The beauty and exemplary functioning of their myriad forms often inspire better designs for our own instruments and machines.

No one expressed our disparate as well as shared heritage with these fellow creatures in more lyrical and moving terms than the writer-naturalist Henry Beston (1928):

> *In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear.*

THE GIVING TREES: GIFTS FROM TREES TO THEIR COMPANIONS

We often take for granted the many gifts of trees. With light energy captured from the sun, trees provide chemical energy and nourishment for their companions. All members of a tree's community, including the tree, at the end of their lives provide energy and nutrients as raw materials for the countless decomposers. The decomposers then liberate and recycle these mineral nutrients into forms that the tree can obtain from the soil. The cycle continues unabated; each tree takes up these nutrients from the soil for its own tissues and takes up more energy from the sun so it can share its energy and mineral nutrients with countless companions (fig. 4).

Trees are gracious and neighborly. Their forms muffle noises as well as add cheer and beauty to a landscape. They hold moisture in the soil, and they also protect it from erosion. With their roots, trees pull up mineral nutrients from deep in the soil that will be shared with other creatures in their communities. They absorb carbon dioxide and many pollutants from air. Each year when they shed their leaves, trees return many nutrients to the soil to replenish the fertility of the land. Trees offer nourishment and refuge to all visitors and companions. In the cold of winter, they block icy winds (fig. 5). In the heat of summer, they provide coolness and shade (fig. 6). Saving trees and planting trees invests in the integrity and beauty of the Earth.

Urban trees can reduce summer temperatures as much as 6.5˚F (3.6˚C) (McDonald 2016). When the collective transpiration of trees in a forest condenses as clouds, air containing the transpired vapor condenses and decreases in volume, resulting in reduction of air pressure. As the air pressure drops, air with less

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

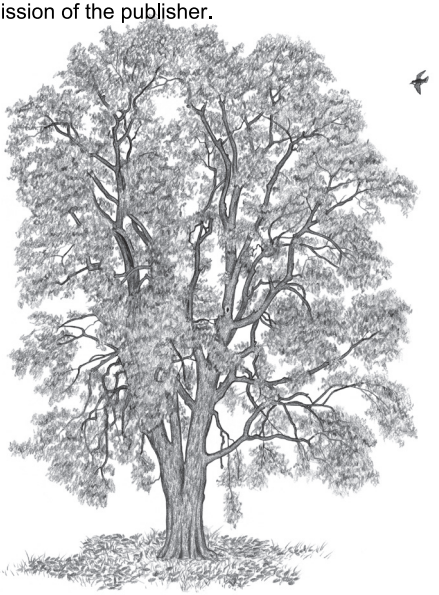


FIG. 4 Trees create a welcoming environment for their companions and visitors.

FIG. 5 A tree sparrow huddles among the branches of a spruce tree during a winter storm.

moisture is horizontally drawn in and generates winds that cool the landscape (Pearse 2020). Thoreau, in deploring the rampant cutting of America's trees in the nineteenth century, mistakenly noted with relief, "Thank heaven, men cannot cut down the clouds." "Aye, but they can!" presciently observed the naturalist Gene Stratton-Porter in *Music of the Wild* (1910). "I never told a sadder truth, but the truth is that man can 'cut down the clouds.'" And the latest research on how trees influence temperature, cloud formation, and climate confirms her sad truth.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

FIG. 6 A fox squirrel relaxes in the shade of walnut leaves.

From treetop to root tips, wherever trees grow, each tree—in life and in death—hosts its own community of creatures. Some creatures choose a particular tree for its fruits or leaves, its flowers, or its decaying hollow limbs; the tree's insect life attracts others (fig. 7). Each creature seems to find what it needs somewhere on the tree and manages to repay the tree in some way for its generosity. All these creatures share in the gifts offered by trees, and trees are accepting of all sorts of companions, some of which even devour their leaves, eat their fruits, or bore into their wood. Many companions of trees turn out to be trusted allies in defending them and ensuring that harmony and balance is maintained among trees and their myriad companions.

HOW TREES RESPOND TO COMPANY AND DEFEND THEMSELVES WHEN NECESSARY

Within the cells and tissues of trees, the synthetic reactions of photosynthesis and the breakdown reactions of respiration continually fuel the chemical reactions that occur during the life of trees. During photosynthesis, energy-rich sugar molecules are generated with energy from the sun, water, and carbon dioxide; and during respiration, the energy of those sugar molecules is released as carbon dioxide and water, which are again recycled by photosynthesis. The compounds generated by these chemical reactions combine to form the myriad chemicals that make up the metabolites of the tree. Trees are continually producing primary metabolites that are essential for their proper growth and physiology; these include the substances that make photosynthesis and respiration possible and the

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

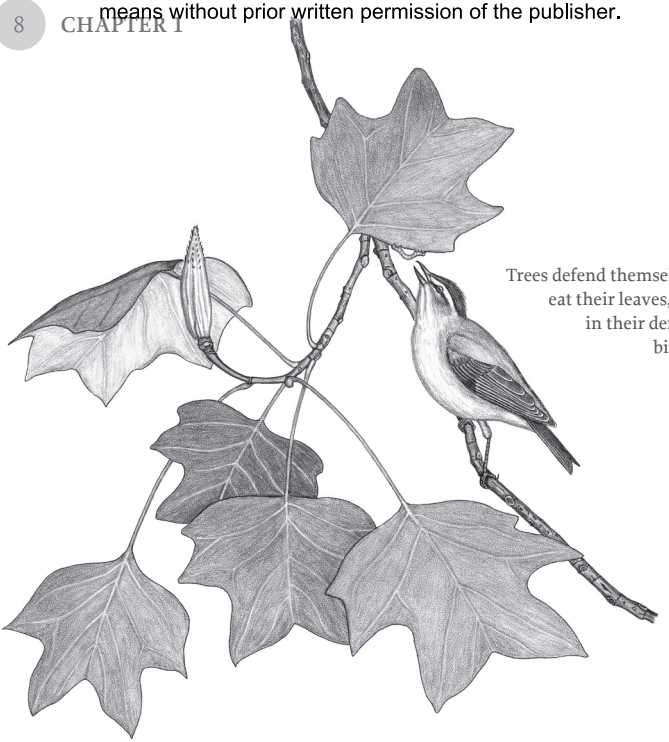


FIG. 7
Trees defend themselves from insects that eat their leaves, and they are assisted in their defense by insect-eating birds such as this vireo.

variety of hormones that orchestrate the formation and functioning of each part of the tree. Secondary metabolites are compounds that are not essential for the tree's survival but that certainly influence how trees interact with other creatures in their environments. Plants are estimated to produce an astonishing 200,000 different secondary metabolites. Plant cells constantly produce these chemicals, some of which repel or sicken many insects. But there are always some insects that relish the flavors that are so repellent to others. Not only do these insects have means to detoxify these compounds, but some have even adopted these chemicals for their own defense against insect and vertebrate predators. The colors, flavors, and scents of trees can not only repel but also entice the company they keep.

In the face of insect and microbial attacks, plants superficially appear placid and passive, but under the surface of their leaves and bark, plant cells promptly recognize an attack from a foreign agent and mount a robust defense. Although Willa Cather noted that "I like trees because they seem more resigned to the way they have to live than other things do," she had no idea how assertive a tree can be when facing challenges from herbivores and pathogens. The lack of flight or any other evasive movement by trees belies their highly effective ability to circumvent attacks with their arsenal of evasive chemistry. The defensive chemicals of trees can repel, intoxicate, or disrupt digestion of their herbivore attackers.

Trees release volatile defense compounds whenever they experience mechanical damage to their tissues. Trees that are battling intruders alert their tree neighbors of dangers and threats by releasing a variety of volatile compounds that waft

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

through the air and elicit the production of additional defenses in preparation for their own possible upcoming battles. Over a thousand different volatile compounds are known to be released by different plants as their first defensive response to invaders (Dudareva et al. 2004), and these compounds prompt a tree to release a cascade of new defense chemicals that travel to other parts of the tree, sounding the alarm from branch to branch and root to root. These volatile chemicals carried through the air recruit not only other trees but also predatory and parasitic insects as allies in battles with plant-feeding insects (fig. 8).

Just as our immune systems can distinguish self from nonself, rejecting any objects recognized as foreign—from bacteria to tissue grafts—plants also respond to foreign invasions of their tissues. After encounters with microbial pathogens, insect mandibles, insect beaks, insect ovipositors, or even the pressure exerted by

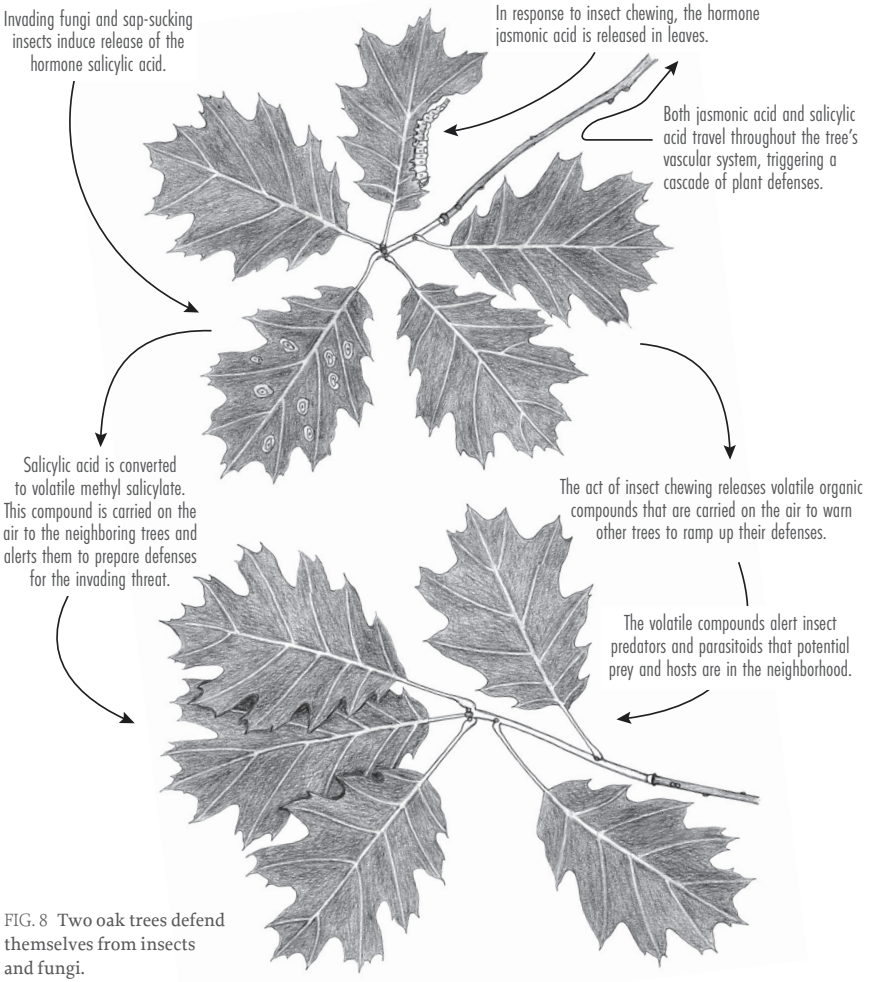


FIG. 8 Two oak trees defend themselves from insects and fungi.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

insect tarsi, the levels of the two master hormonal regulators of a tree's immune response—jasmonic acid and salicylic acid—almost invariably increase in the tree's tissues. Insect saliva often contains substances that boost these two master regulators of the initial wound response, but in some instances, the herbivores secrete chemicals that can tamp down the normal defense response to mechanical damage (Musser et al. 2002).

After a fungal or insect attack, the tree hormone salicylic acid is converted to methyl salicylate, which vaporizes and wafts to other leaves and other trees where it triggers the release of other defensive compounds. The release of these key compounds alerts tree cells to send out reserves from their repertoire of thousands of defensive secondary metabolites (Fürstenberg-Hägg et al. 2013).

Hormones such as jasmonic acid and salicylic acid govern all aspects of a tree's life—its birth and eventual death, its leaf sprouting and flowering in the spring, its leaf fall in the autumn, and all its growth between birth and death.

WHAT HAPPENS AFTER AN INSECT BITES?

The very first response of a tree to an insect bite is comparable to our response to a mosquito bite. Nerves immediately send a long-distance signal to the brain that a mosquito has landed and is taking a blood meal. In our bodies the signal is induced at the site of the bite by the chemical glutamate, which mobilizes the calcium that then carries the signal all the way to the brain.

To communicate that damage has been inflicted at one location on the tree to more far-flung locations on the tree, an insect bite on a leaf likewise induces the release of glutamate. Glutamate is the positively charged form of the amino acid glutamic acid, a simple compound found throughout living cells that travels from the wound throughout the plant at about 1 mm/second. As it moves through the tree, glutamate binds to receptors on surfaces of plant and animal cells. Receptors are proteins of cells whose forms perfectly complement the forms of the proteins that bind to them, in the same way that only a specific key will perfectly match a specific lock. These surface receptors represent channels in cell membranes that allow the influx of calcium into plant cells in the same manner that glutamate opens ion channels and acts as the most abundant neurotransmitter in our animal nervous systems, rapidly sending signals from cell to cell. Binding of glutamate to its receptors opens the ion channels for calcium (Muday and Brown-Harding 2018).

The sudden release of calcium activates special enzymes that cleave fragments or peptides (PEPs = plant elicitor peptides) from one or more large proteins referred to as precursors of plant elicitor peptides (PROPEPs) (Haner et al. 2019). These newly generated peptides diffuse to nearby cells, where they bind to receptors on their surfaces and by the act of binding activate and elicit the tree's master regulators of the immune system—jasmonic acid and salicylic acid or their derivatives (collectively referred to as jasmonates) in the cells of the vascular tissues. The presence of jasmonic acid exerts a ripple effect on the expression of many genes referred to as jasmonic-responsive genes. After being induced by herbivores and pathogens, these key hormones set off a cascade of defense compounds to ward off attacks from insects and fungi (Ramirez at al. 2009). In the years ahead, more details will be added to this complex story.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

TREES AND THEIR ALLIES

Herbivores and microbes seem to find ways to counter or circumvent even the best defensive strategies of trees. Trees have come to rely not only on their own multiple chemical defenses but also on the ingenuity and aid of their microbe, arthropod, and vertebrate companions. Trees do not have to fight their battles alone; they can count on help from these allies in confrontations with insects and pathogens. In addition to pollinating their flowers and dispersing their seeds, allies of trees keep the numbers of invasive microbes as well as leaf-chewing, wood-boring, and sap-sucking insects in check. Trees in turn reward their allies with an all-you-can-eat buffet.

By enticing creatures to live on their leaves, bark, and flowers, trees also attract the predators that keep the numbers of these other creatures in check. Different wasps and predatory bugs stalk and eat insects that feed on leaves and wood. Many songbirds flit from branch to branch in search of their six-legged meals and the telltale signs that insects leave behind—leaf rolls, leaf mines, bored wood, and well-chewed leaves. Nuthatches and woodpeckers constantly inspect the recesses of bark for any insects that may be sheltered there (fig. 9). Hawks and owls keep

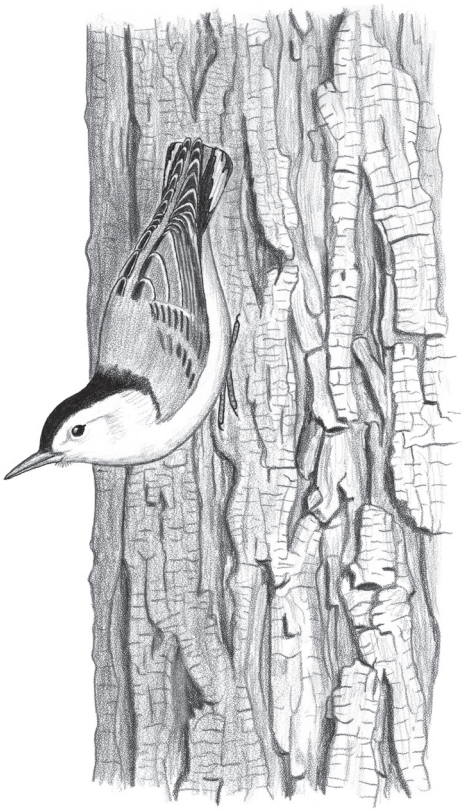


FIG. 9 By providing many hideouts for insects, the shaggy bark of shagbark hickory also provides a rich hunting ground for nuthatches.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

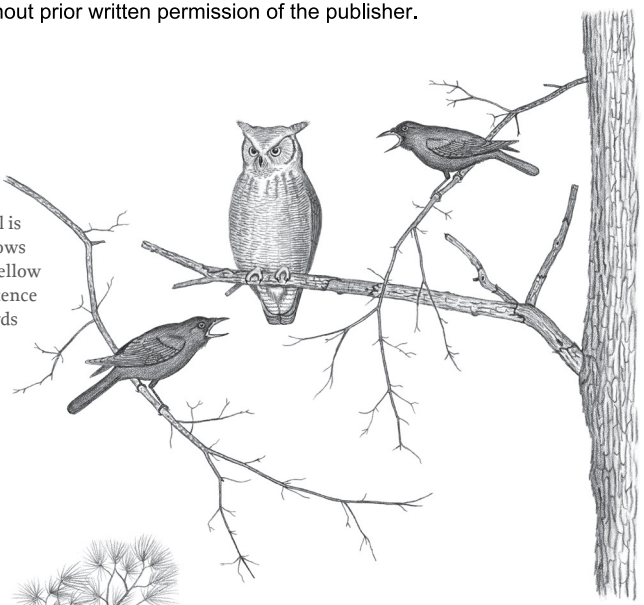


FIG. 10 A great horned owl is scolded and mobbed by crows for attacking one of their fellow crows. The owl's very existence depends on its meals of birds and mammals that have been nourished by the countless insects, fruits, wood, and leaves of trees.

FIG. 11 Porcupines do not seem to have met many trees whose bark they do not relish, and the fisher is one of the very few predators that can evade the formidable quills of this big, furry herbivore and keep its population in check.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

a sharp lookout for movements of birds and squirrels (fig. 10). Fishers search evergreens of the north woods for signs and scents of porcupines (fig. 11). The hunters and the hunted hold together the intricate web of life in a tree community.

Vertebrate Allies and Their Deceptive Insect Prey

The birds, frogs, and mammals that perch, climb, hop, flit, and ramble among a tree's leaves and branches are the least numerous of its allies but certainly the largest and most conspicuous. Many are predators of insects and purveyors of microbial allies that colonize tree tissues.

Birds and other vertebrate predators of insects, however, must deal with the deceptive tactics of the insects they stalk and eat. Insects can masquerade as any part of a tree, including lichens on bark and bird droppings on leaves, and their disguises are surprisingly deceptive (fig. 12; chapters 2 and 4). Green is always a popular color for insects that live among green leaves; green caterpillars blend well with green leaves and green twigs. Brown and gray caterpillars intermingle with brown bark and gray twigs.

As immobile pupae, moths and butterflies are even more vulnerable to attack than they are as wandering larvae. As a prelude to pupation, many caterpillars spin cocoons as shelters in which to undergo their transformations; some burrow into the soil beneath a tree, hide in leaf rolls, or crawl under loose bark or into clefts in the bark. However, birds such as nuthatches and woodpeckers patrol tree trunks and routinely dig out insects from the recesses of the bark. Migrants such as warblers and vireos have an uncanny ability to uncover pupae and caterpillars tucked away in leaf rolls. The pupa or chrysalis of the hackberry butterfly, however, has a mottled color pattern that blends not only with the green of the

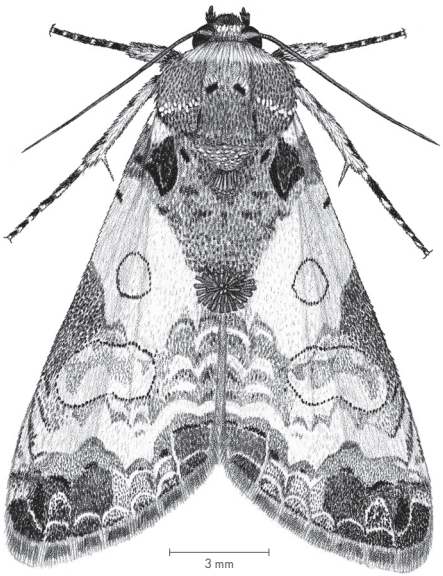


FIG. 12 A dagger moth called the tufted bird-dropping moth has all-purpose camouflage patches of blue, brown, lichen green, and white and can be as easily mistaken for a bird dropping as it can for a patch of lichen.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

FIG. 13 The markings on the surface of a hackberry butterfly pupa blend with the pattern of veins in the hackberry leaf.

hackberry leaf but also with the cream color of the leaf veins (fig. 13). Those pupae with naturally camouflaged cuticles can rest exposed and unnoticed as they masquerade as part of the tree on the surfaces of leaves, twigs, and bark.

Birds assiduously search trees for their favorite caterpillars. They leave no leaf unturned as they scour the canopy for food. While so many caterpillars blend in with their surroundings (fig. 14), they still leave chewed leaves as telltale traces of their whereabouts. Birds use these signs to locate their prey as they scour foliage and branches. Even well-camouflaged caterpillars cannot be too careful about deceiving their predators. After their leaf-feeding sessions, caterpillars go so far as to eliminate all the partially eaten leaves by chomping through the petioles of these leaves and letting them fall to the forest floor, far from the caterpillars' dining area. These deceptive caterpillars leave few clues for any clever and hungry birds that attempt to track them down (Heinrich 2019; Heinrich and Collins 1983).

Rather than resorting to deception and camouflage to avoid predators, however, some insects use just the opposite strategy of being ostentatious and blatantly calling attention to themselves. These insects sport bright, often garish colors to announce attributes that make any close encounters with them unpleasantly memorable and preferably avoided. These attributes can include painful stings, foul-smelling secretions, irritating hairs, or toxic blood. The word soon gets out that these insects should be kept at a respectful distance (chapters 2 and 4).

Harmless mimics often imitate these insects with bad reputations for successfully intimidating predators; the mimics gain protection simply by virtue of superficial appearances without having to invest in any weaponry. Other harmless insects shock and startle anyone who threatens them with their sudden, unexpected changes in form or color (fig. 15).

For all the defenses insects have mounted against their vertebrate predators, a few predators remain unimpressed and undeterred by what these caterpillars have to offer. How can caterpillars covered in annoying, fuzzy coats possibly be appetizing to any bird? However, the cuckoos of North America seem to have a fondness for fuzzy caterpillars and can dispatch great numbers in a short time (fig. 64; chapter 2). Cuckoos are endowed with thick linings of mucus in their

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

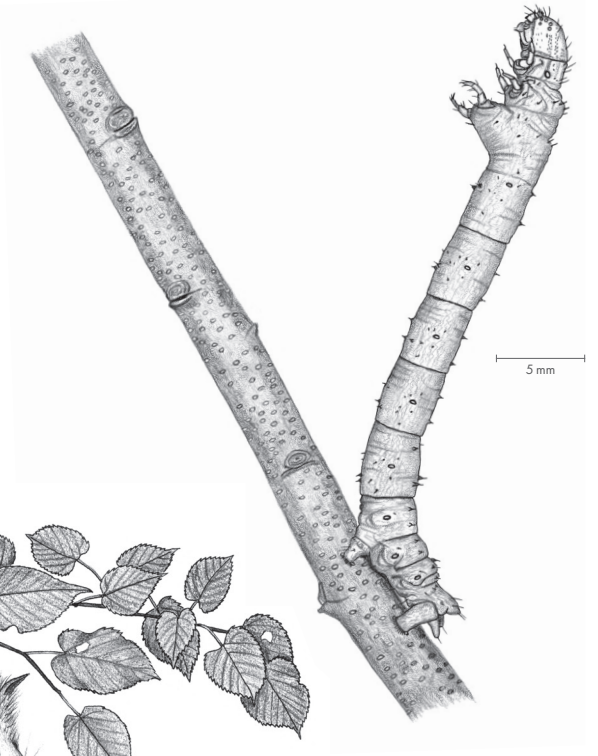


FIG. 14 An inchworm poses as a branch of a wild cherry twig.

FIG. 15
When an underwing moth (chapter 4) takes flight, its flash of striking color suddenly startles a foraging possum.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

stomachs that absorb the fuzz, which the birds simply regurgitate as a fuzz ball in the same way that cats cough up fur balls.

You would suspect that wasps with their painful stings would have few enemies, if any, but even these insect hunters of other insects are also hunted. Certain songbirds not only share caterpillar prey with wasps but also feed on the wasps themselves. Somehow birds such as tanagers can snatch and dispatch wasps and bees in midair without ever getting stung (fig. 16).

Arthropod Allies: Parasites and Predators

The insect predators and insect parasite companions of trees safeguard the trees by keeping in check the damage inflicted by insect herbivores. The antennae of parasitic and predatory insects pick up some of the airborne defensive chemicals released by plants attacked by herbivores. The scents of plants in distress recruit and guide parasites and predators to aid the besieged plants (Ananthakrishnan 1999). The olfactory sensors of predators and parasites are finely attuned to detecting the odors emitted by damaged plants and by the digested plant fragments of caterpillar droppings. Predators such as ground beetles and rove beetles patrol mostly under trees, but some species also search leaves and branches for insects, mites, and fungi that threaten trees' well-being. Hornets and wasps, lacewings and ladybird beetles, robber flies and long-legged flies, assassin bugs and beetle predators survey trees from the air, under their bark, and over their surfaces for insects that

FIG. 16 Tanagers are some of the few birds that have expanded their insect meals to include wasps, bees, and hornets.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

become meals before they become devastating pests. Insects whose larvae are parasites on other insects are just as thorough in their surveillance. These insect parasites and predators control populations of insects that feed on trees, but they, along with the insect herbivores, also convey beneficent microbes to and from trees for the benefit of all parties—trees, insects, and microbes (Arnold et al. 2003).

Parasitic Insects

Parasitic insects exert an unheralded influence on the harmony and integrity of a tree's food web. Many carry out their early work as larvae and pupae hidden within the bodies of their hosts (endoparasites). At metamorphosis, however, parasitic insects forsake their secluded carnivorous lives for lives outdoors where they placidly sip nectar and munch on pollen grains. Parasitic insects make up around 10 percent of all animal species. Parasitic wasps are estimated to number well over 130,000 species, possibly even more species than beetles, which for so long have been claimed to be the animal order with the greatest number of species. An estimated 15 percent of all insects are parasitic on other arthropods (Forbes et al. 2018; Feener and Brown 1997; Askew 1971), and no arthropod—herbivore, fungivore, decomposer, predator, or even another parasite—seems to be spared from being a host for some parasite.

Each parasite prefers hosts of a particular developmental stage, and each developmental stage—from egg to adult—has its share of parasites. The few parasitic beetles and moths feed as ectoparasites on the outer surfaces of their hosts. Some parasitic insects are parasites of parasites—hyperparasites. The caterpillars of about 50 species of moths and the larvae of 5,000 species of beetles live as external parasites. Most of the thousands of species of wasp and fly parasites (at least 130,000 species and 16,000 species, respectively), however, feed within the bodies of their hosts surrounded by their blood cells and have developed elaborate tactics to evade the blood's immune system. The influence of so many different parasitic insects—some with broad, wide-ranging preferences for their hosts, others with very narrow, finicky preferences—ripples throughout the food web. Strands of the food web radiate from predators and parasites to practically all living animal members of a tree's food web—its decomposers, herbivores, even other predators and parasites.

The hosts of parasitic insects are often shared as the prey of predatory insects. Parasites can subdue far larger creatures for their hosts than predators can overpower as their prey. Locating a host or the general vicinity of a host is the responsibility of the parasitic insect's mother. Each time predators feast they must use energy to chase down and overpower their prey. However, once parasitic insects settle down with a host or hosts, they can conserve a great deal of energy by staying in one place and growing at the expense of the host, which continues to provide shelter and nourishment until the parasite no longer needs its still-living, but doomed, host. Because hosts of most insect parasites eventually die, the parasites are generally referred to as parasitoids to distinguish their lifestyles from those of insects or other parasites that live at the expense of their hosts but do not kill them.

For general queries, contact webmaster@press.princeton.edu

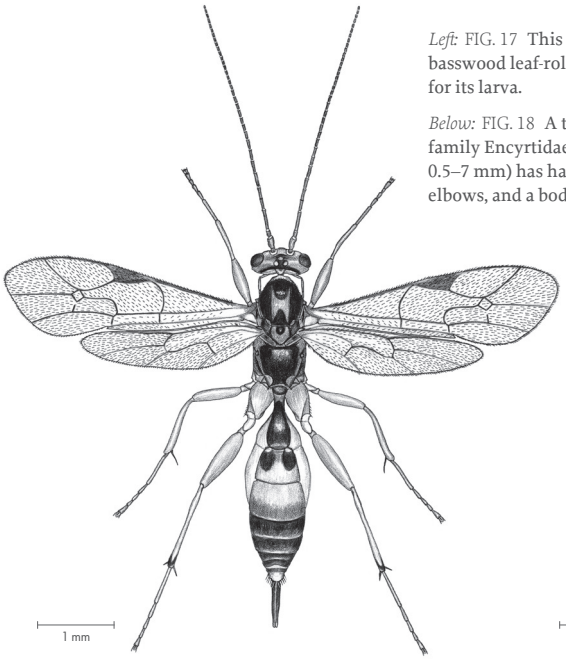
© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

The many families of parasitic wasps boast species whose hosts range from insect eggs and embryos to large beetle grubs and hefty caterpillars. Many wasps are very particular about their hosts and will parasitize only specific families or species of insects. Caterpillars are certainly favorite hosts. In the following pages, we will encounter a number of parasitic wasps that parasitize hosts found on tree leaves, under bark, underground, or inside galls. They employ their ultrasensitive antennae to track down the scent and the slightest movements of even the best-concealed hosts. As an introduction to these incredibly diverse insects, we feature an ichneumonoid wasp that is known to parasitize leaf-rolling caterpillars, and a tiny chalcidoid wasp from the leaf litter under a tree. These two wasps are members of the two most species-rich superfamilies of parasitic insects—Ichneumonoidea and Chalcidoidea (figs. 17 and 18). Other parasitic insects will be introduced as their specific habitats on trees are discussed in upcoming chapters, but the parasitic wasps in other superfamilies are neither as common nor as diverse as the wasps in these two superfamilies.

— ICHNEUMONOID WASPS, SUPERFAMILY ICHNEUMONOIDEA, include two large families of parasitic wasps: Ichneumonidae and Braconidae.

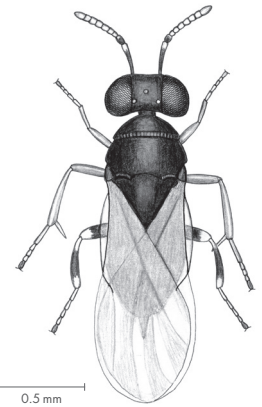
— **Ichneumon Wasps, family Ichneumonidae** (*ichneumon* = tracker) (25,000 described species, estimated 60,000–100,000 species; 5,000 described species NA; 3–40 mm).

— **Braconid Wasps, family Braconidae** (*brachy* = short, referring to their usually small size) (17,000 species; 1,900 species NA; 1–15 mm, many 1–3 mm). Many thousands of species, possibly as many as 30,000, remain undescribed.



Left: FIG. 17 This ichneumon wasp chooses the basswood leaf-roller caterpillar (fig. 114) as a host for its larva.

Below: FIG. 18 A typical chalcidoid wasp in the family Encyrtidae (3,800 species; 480 species NA; 0.5–7 mm) has hardly any wing veins, antennae with elbows, and a body with a stout, iridescent cuticle.



For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

— CHALCIDOID WASPS, SUPERFAMILY CHALCIDOIDEA, include 19 families (*chalkos* = bronze, copper, referring to their metallic colors) (22,000 described species but at least 500,000 species estimated; 2,000 species NA; 0.1–20 mm). As we explore different parts of trees, we will encounter members of several of these chalcidoid families.

Many parasitic wasps are capable of the Herculean task of subduing hosts hundreds of times their size. There are at least three secrets of success that enable these parasitic wasps to subjugate the immune responses of their larger hosts—polyembryony, teratocytes, and symbiotic viruses (fig. 19).

POLYEMBRYONY OF PARASITIC WASPS One lone wasp can accomplish a feat worthy of hundreds of wasps: polyembryony. The infrequent appearance of identical human twins, triplets, or even octuplets is accompanied by equal partitioning of a single fertilized egg to generate respectively two, three, or eight identical embryos. Insect parasitoids are capable of consistently accomplishing even more remarkable reproductive achievements. From a single fertilized egg laid in a host insect, as many as several hundred identical eggs can arise, and all can develop and eventually emerge as adults from the remains of their host. From a small maternal investment, a massive return is achieved. A tiny parasitic wasp mother makes up for her diminutive size by contributing up to 500 offspring from a single egg deposited in a single host that is far larger than she is. Thanks to polyembryony, the collective contribution of each mother wasp to the control of host populations far outweighs her minuscule size.

TERATOCYTES OF PARASITIC WASPS As every animal embryo begins its life, cells segregate into two distinct lineages—those cells destined to form all the parts of the

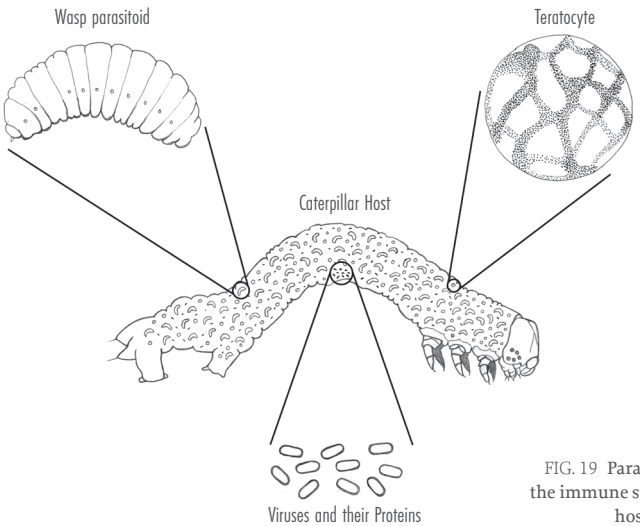


FIG. 19 Parasitoid wasps can suppress the immune systems of their caterpillar hosts in three different ways.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

embryo proper, and those extraembryonic cells that form the protective membranes encompassing the embryo. The extraembryonic cells of certain parasitoids separate from newly hatched larvae and take on a new role as they float free in the body cavity of the host. They begin avidly absorbing nutrients from the blood of the host insect and rapidly expanding. In their new role they are referred to as teratocytes (*terato* = monster; *cyte* = cell). While the cells of the embryonic lineage proliferate to produce hundreds of identical embryos during polyembryony, the production of teratocytes involves the proliferation and excessive growth of the extraembryonic cells as teratocytes. All parts of the perfectly spherical teratocyte grow. Its nucleus undergoes a dramatic increase in its DNA content, adopting a complex, arabesque topology, and the diameter of the cell expands twentyfold or more to about a tenth of a millimeter, while other cells by comparison are less than a hundredth of a millimeter. These massive, nutrient-rich teratocytes supplement the diet of a parasitoid larva as it approaches metamorphosis and probably also help suppress the immune response of its larger insect host.

SYMBIOTIC VIRUSES OF PARASITIC WASPS The genetic material of symbiotic viruses is integrated in the genetic material of the parasitoid, and as the mother parasitoid injects her eggs or egg into her host, she also releases viruses or protein particles of viral origin. These either coat the egg surfaces or in some cases multiply in the host's blood cells and suppress the host's immune response. With viral particles covering the eggs, the host's blood cells are fooled into mistaking these particles for self-proteins and thus do not mount an immune response and do not encapsulate what they do not recognize as foreign. However, if these particles are first removed from the newly laid eggs before these eggs are injected into the host, the treated eggs are quickly encapsulated by the hosts' blood cells. Here is a sinister example of mimicry at the protein level tricking the host into not recognizing its foreign invader.

Members of another family of parasitic wasps lead most improbable lives either as hyperparasitoids of parasitoids or as parasitoids of predatory hornets and wasps. These colorful black and yellow parasitic wasps are peculiar in so many ways that they are considered members of their own superfamily, which contains only one family (fig. 20).

— TRIGONALID WASPS, SUPERFAMILY TRIGONALOIDEA, FAMILY TRIGONALIDAE (*trigon* = triangular; *al* = wing) (90 species; 8 species NA; 3–15 mm).

Each mother trigonalid wasp lays several thousand tough, tiny eggs on tree leaves; the eggs can lie dormant for many months. Only after an egg passes through the gauntlet of caterpillar jaws and into the caterpillar's digestive tract does it hatch. The newly hatched parasitoid larva passes through the cells of the caterpillar's gut into the caterpillar's blood space. However, once again the wasp hatchling patiently lies dormant in the caterpillar's blood space until the caterpillar ends up as a meal for a predatory wasp larva or until the caterpillar is parasitized by either a parasitic fly or an ichneumonid wasp. Only a larva of one of these parasitic insects is acceptable as a host for this hyperparasitoid. However, if the

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

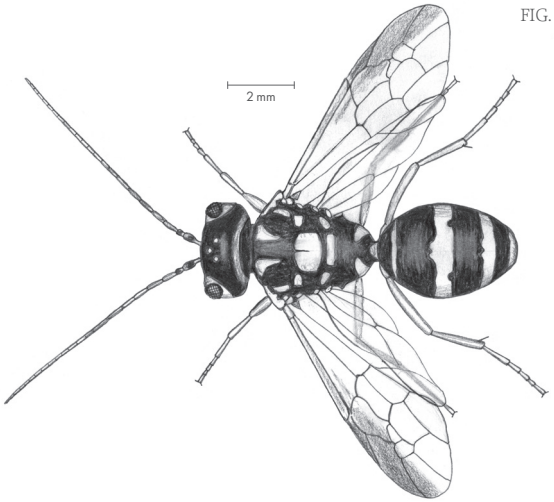


FIG. 20 Unusual life cycles seem to be commonplace among parasitoids, and trigonalid wasps lead remarkably improbable lives.

caterpillar becomes a meal for the larva of a hornet or yellowjacket, then the trigonalid larva ends its days as a parasitoid of a predatory wasp's larva.

Several families in the fly order Diptera are exclusively parasitic and usually very selective in their choices of hosts, but one family of flies, the Tachinidae, can claim the most species of parasitic fly larvae and the broadest range of host choices.

— TACHINID FLIES, FAMILY TACHINIDAE (*tachin* = swift) (> 10,000 species, with new species continually being described; 1,350 species NA; 2–18 mm).

The first impression one gets of tachinid flies is their "bristliness." Tachinids are renowned for the length and abundance of their sensory bristles (fig. 21; LeafScape, 9). Of all the flies that parasitize other insects, tachinid flies are by far the most diverse, and their choices of hosts are correspondingly diverse. While some tachinids are very choosy about their hosts, over 100 species of hosts are acceptable to other tachinid species, including such hosts as larval and adult beetles, stink bugs, moth and butterfly caterpillars, earwigs, centipedes, sawfly larvae, grasshoppers, scorpions, or larvae of other flies.

The variety of tachinid forms and colors is matched by the variety of ways in which mother tachinid flies can lay eggs or lay newly hatched larvae that are retained within an insect version of a uterus until the time of hatching. They can carefully place a few eggs on hosts, or they can scatter many eggs in an area frequented by hosts or on leaves being consumed by host larvae. These eggs have tough eggshells and can remain viable for many weeks until a suitable host finally ingests them, and the tachinid larvae hatch inside the host's gut. Other flies deposit newly hatched larvae on surfaces of leaves, logs, or soil where they are left on their own to search for a suitable host. These active larvae or planidia (*plano* = wandering) are covered with thick cuticles to prevent desiccation. Although no fly larvae have true legs, these specially adapted larvae have false legs and two long projections (cerci) at their tail ends that expedite their search for the right host (fig. 22). However, once

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

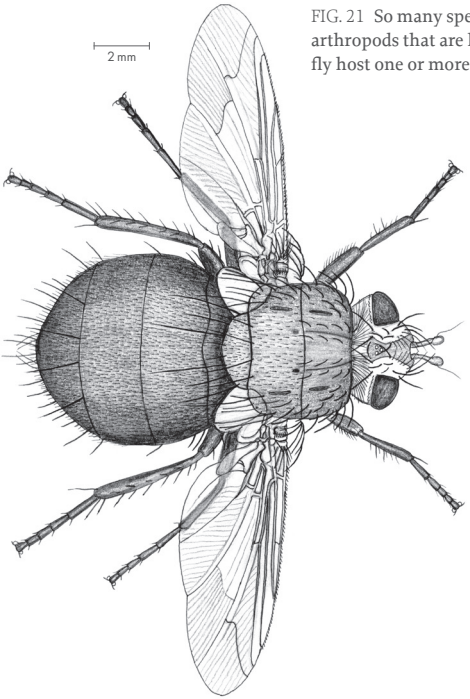


FIG. 21 So many species of tachinid flies exist that most arthropods that are large enough to host a larval tachinid fly host one or more species of these parasitoids.

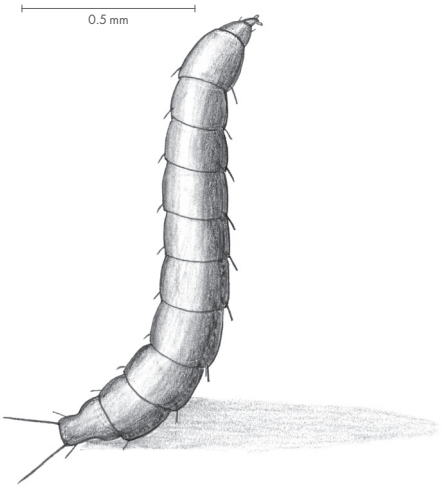


FIG. 22 A newly hatched tachinid larva actively searches for a host, often rearing up to scan the surrounding landscape.

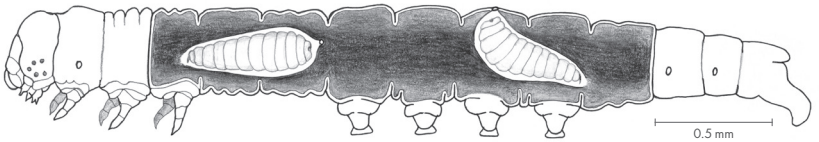


FIG. 23 A view inside a caterpillar parasitized by fly larvae: two larvae of a fly parasitoid avoid the immune response of their host by remaining encapsulated in a sheath that the host forms to seal off the intruders; however, the larvae still manage to maintain critical connections to nutrients from caterpillar blood at their front ends and to oxygen at their rear ends.

inside that host, these active larvae transform at their first molt to sedentary, legless larvae that grow inside the comfort and security of the host's body.

One group of tachinid flies that use adult beetles as hosts have elaborations of the mother flies' abdominal segments that enable them to snatch beetles in flight and pierce the firm beetle cuticles with a spine that guides the mother's short ovipositor to its exact destination. While almost all tachinid mothers lack the often long, penetrating, and impressive ovipositors of their parasitic wasp counterparts, they have adopted other strategies to ensure that their larvae begin life with certain advantages.

Once inside their insect hosts, tachinid larvae must face the onslaught of the host's immune response to their intrusion. These fly larvae do not resort to the tactics of parasitoid wasps that suppress and overwhelm the host's immune system; instead

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

they rely on the host's healing response to isolate them from host immune cells. The blood cells that normally engulf and suffocate intruders recognized as foreign now form an encapsulating sheath that seals off the parasitoid larva from the blood space of its host. Only the larva's mouth remains free to access nutrients from the host's body. At its rear end, each larva obtains oxygen by forming a snorkel connection to the exterior air, thereby maintaining a very narrow passageway through the host's integument or through one of the host's large air tubes (tracheae) (fig. 23).

Fly Predators

— ROBBER FLIES, FAMILY ASILIDAE (*asilus* = type of fly) (7,500 species; 1,000 species NA; 3–50 mm).

— LONG-LEGGED FLIES, FAMILY DOLICHOPODIDAE (*dolicho* = long; *poda* = legs) (7,400 species; 1,300 species NA; 1–9 mm).

After a larval lifetime of stalking other insects in the litter beneath trees (fig. 326), and in some cases beneath tree bark, larvae of these flies transform into adult robber flies and long-legged flies that stalk tree leaves and branches (fig. 24; LeafScape, 25). The larvae of one genus of long-legged flies, *Medetera* or woodpecker flies, specialize in preying on the abundant larvae of bark beetles. At metamorphosis the eyeless and legless larvae transform into adult flies with large, bulging eyes and keen eyesight. With their long, spiny legs, they move swiftly to capture and firmly grasp their prey.

Robber flies choose favorite perches from which they can scan their territories for passing prey. These swift flies can snatch prey as easily from the air as they can from the surface of a leaf or branch. Some of the fuzzier members of this family look and sound like bumblebees. Only a close inspection can establish whether the fuzzy insect is a fly or a bee. Flies, however, have two rather than four wings and do not have stingers. Nor do these predatory flies have jaws for chewing, but they do have sharp, penetrating beaks with which they impale their prey, inject digestive enzymes, and then suck their victims dry. Anyone who has attempted to hold a robber fly can attest that its bite is as painful as the sting of a bee.

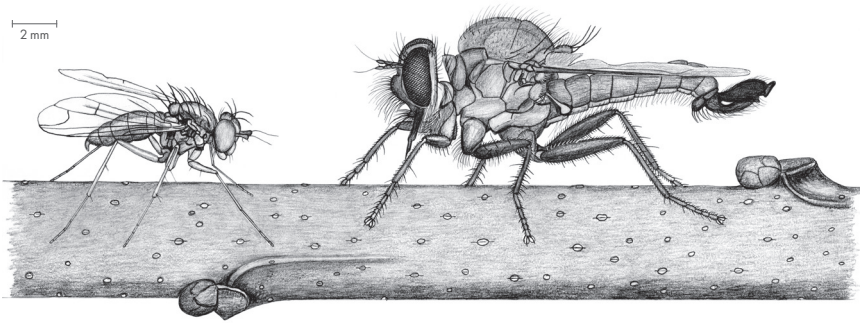


FIG. 24 Robber flies (*right*) and long-legged flies (*left*) begin life as larval predators in the soil or under bark, and as adults they patrol trees for insect prey aboveground.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

Long-legged flies perch high above the bark or a leaf on their long, slender legs and survey the landscape for small arthropods. The swift, fidgety movements of these iridescent green-blue flies, which are otherwise inconspicuous, make them stand out on sunlit leaves and twigs. During their courtship, the male flies are known for ostentatious displays of finery that can embellish their legs, antennae, face, or wings.

Wasp Predators

— HORNETS, YELLOWJACKETS, FAMILY VESPIDAE (*vespa* = wasp) (5,000 species; 300 species NA; 10–40 mm), SUBFAMILY VESPINAE (70 species; 22 species NA).

The success of a hornet (fig. 25) or yellowjacket (LeafScape, 11) colony and the well-being of its thousands of residents depend on the availability of a constant supply of insects to feed its growing population. Wasps catch caterpillars and other insects, chew them, and then feed them to their large broods. As many as 2,500 larvae and 500 workers can live in a single paper nest that the industrious hornets craft from chewed wood pulp (fig. 26). While hornets, such as the bald-faced hornet, establish their nests in conspicuous locations, yellowjacket nests are usually concealed underground, in hollow logs, or under bark. A yellowjacket colony can have as many as 5,000 workers and 15,000 brood chambers. With that many wasps bustling around a tree, whatever caterpillars are around will not likely strip many leaves from that tree.

The wasp queen and her daughters do all the insect collecting as well as the pulp and papermaking. Only at the end of summer do male wasps begin appearing in the colony along with newly hatched queens. After the young queens have mated with the males, each queen finds a protected spot under bark or in a hollow limb where she can pass the winter. In the spring she starts a new family and new nest alone, for none of the males or her worker daughters survive the winter. The queen uses her jaws to scrape off bits of wood from tree trunks and branches. She adds her saliva, chewing the wood to a pulpy texture and shaping it into the foundation for a new nest. After the queen has constructed several brood chambers, she lays a fertilized egg in each one and then begins to nurse daughter larvae that hatch from her eggs. Several weeks later all these larvae develop

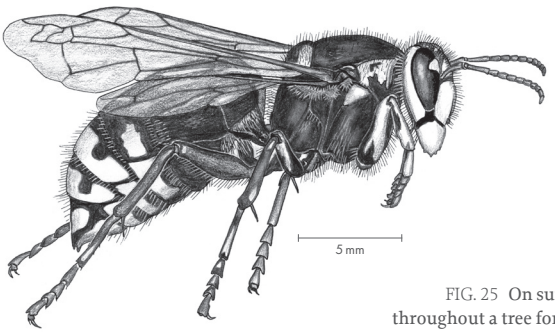


FIG. 25 On summer days bald-faced hornets search throughout a tree for insects to feed their growing colony.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

FIG. 26 The construction of a hornet nest from tree pulp represents a communal effort by the hornet queen and her many daughters.

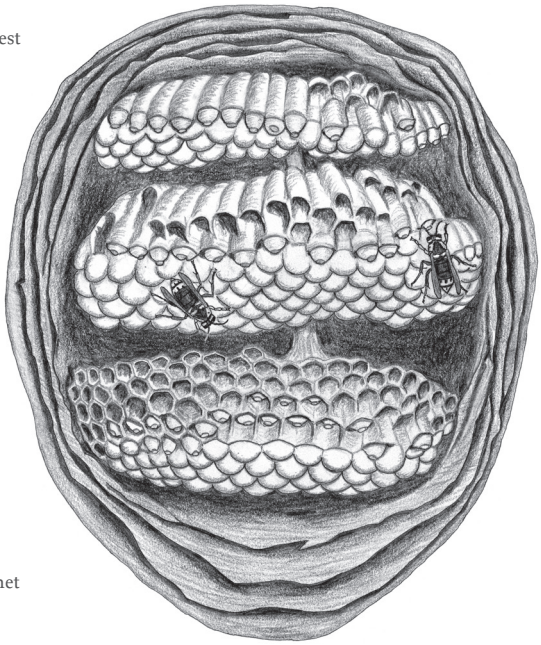


FIG. 27 The interior structure of a hornet nest is a testament to the architectural prowess of these creatures.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

into workers that will take over the job of building more brood chambers and nursing more larvae. But only the queen lays the eggs. Thanks to the assistance of her many daughters, the nest grows from the few paper chambers she first built to several thousand brood chambers by the end of the summer (fig. 27).

Bug Predators

— TRUE BUGS, ORDER HEMIPTERA, SUBORDER HETEROPTERA (*hetero* = different; *ptera* = wings, referring to their mosaic wings that are membranous at the tips but hardened at the bases) (42,000 species; 4,100 species NA; 1–110 mm).

All three suborders of true bugs have piercing-sucking mouthparts that are used not only for sucking sap from plants (chapters 3 and 6) but also for sucking blood and fluids from animals. Only the suborder Heteroptera, however, includes predatory bugs. True bugs that are predators have salivary glands that can deliver an extremely painful dose of venom to anyone who carelessly handles or molests them. These venoms and their multiple components prove very effective not only in subduing but also in digesting all but the cuticular skeletons of their insect prey (Walker et al. 2016).

— ASSASSIN BUGS, FAMILY REDUVIIDAE (*reduvia* = hangnail, perhaps referring to the ominous-looking beak [proboscis] hanging from the head) (7,000 species; 200 species NA; 4–40 mm).

Assassin bugs are striking insects—some of the largest and most conspicuous of our true bugs (fig. 28). They stalk the bark, leaves, and the ground beneath trees,

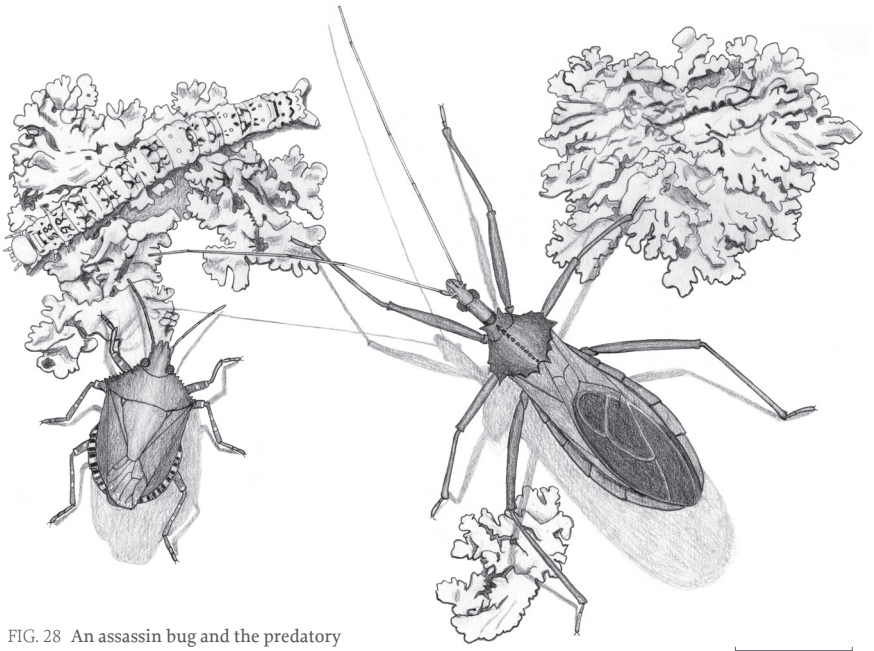


FIG. 28 An assassin bug and the predatory stink bug *Brochymena* face off over a caterpillar.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

tackling some of the larger insects by impaling them with their long, extended beaks. The potent salivary enzymes that pour into the impaled victim begin digesting and liquefying the internal tissues of their prey well before the predigested contents begin passing down the bug's digestive tract.

— STINK BUGS, FAMILY PENTATOMIDAE (*penta* = five; *tomos* = sections) (4,700 species; 230 species NA; 5–18 mm).

The few members of the stink bug family that suck insect blood rather than tree sap include the *Brochymena* stink bugs that patrol tree trunks and blend so well with their backgrounds of bark and lichens (fig. 28; BarkScape, 26).

Brochymena stink bugs roam tree trunks and branches in search of caterpillars and other insects. These stink bugs use their beaks to first stab their victims, then to inject them with digestive juices, and finally to suck out the body fluids of their prey. If these stink bugs are as inconspicuous to the eyes of other insects as they are to our eyes, they should be very successful at ambushing their unsuspecting victims.

Predatory Beetles and Mites

Many of the predatory beetles and mites are ground-based allies of trees. The predatory beetle and mite residents of the leaf litter and soil not only ward off attacks on tree roots but also eliminate many insects before they emerge from the soil to lay eggs or feed aboveground on leaves, twigs, and wood.

As larvae and as adults, ground beetles and rove beetles are known for their speed and sharp, powerful jaws. Their larvae are very similar in appearance, but at metamorphosis, the form and behavior of the two beetles visibly change. Adult ground beetles have wing covers, or elytra (*elytra* = sheath, cover), that restrict the movement of their abdomen, while adult rove beetles have elytra that leave the posterior end of their abdomen exposed. Adult rove beetles often raise their abdomen in a threatening pose even though they are incapable of stinging. The great diversity of forms in these two large families ensures that almost all invertebrate companions of trees are potential meals for these carnivorous beetles (fig. 29; chapter 6; figs. 327–329; RootScape, 5, 15, 21).

— ROVE BEETLES, FAMILY STAPHYLINIDAE (*staphylinus* = kind of beetle) (63,000 species; 5,000 species NA; 1–35 mm).

— GROUND BEETLES, FAMILY CARABIDAE (*carabus* = kind of beetle) (40,000 species; 2,440 species NA; 1–65 mm).

New mite species are constantly being discovered, and their number steadily grows. At least 45,000 species are known so far, but several times this number could be waiting to be named by acarologists, those who specialize in the study of mites. Mites are found in just about all habitats—soil, ponds, household dust, animal skin—so it should not be surprising that they are found on tree leaves, bark, and roots (figs. 30, 96, 109, 293, 294; LeafScape, 32; BarkScape, 30; RootScape, 42, 43). The soil and leaf litter inhabitants probably display the greatest range of forms and behaviors (chapter 6). Because many are so tiny, you need to inspect a tree closely and carefully to detect their presence. However, red velvet mites with their intense red cuticular coats stand out wherever they are found.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

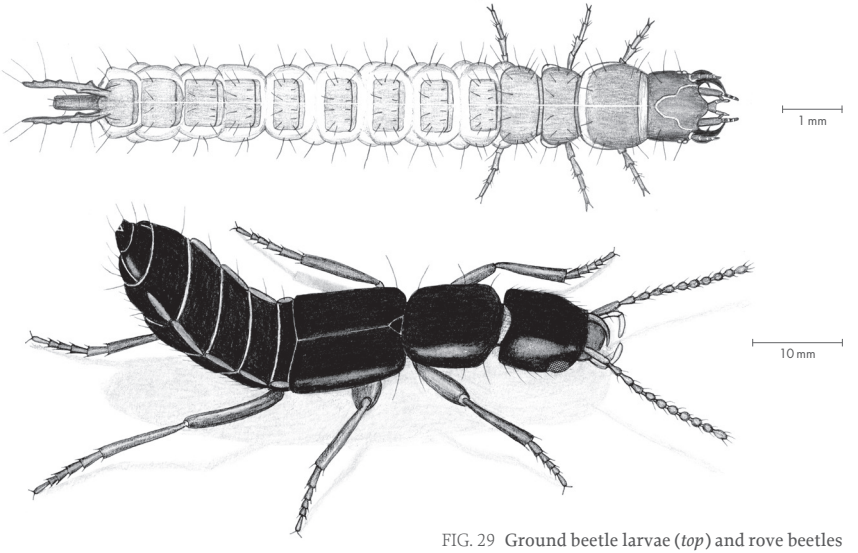


FIG. 29 Ground beetle larvae (*top*) and rove beetles (*bottom*) patrol hunting grounds under trees.

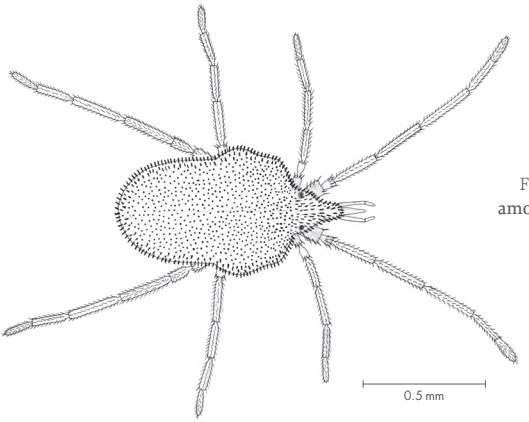


FIG. 30 This bright red mite that scurries among fallen leaves under trees is a parasite in its youth and a predator as an adult.

— RED VELVET MITES, CLASS ARACHNIDA, SUBCLASS ACARI, FAMILY TROMBIDIIDAE (*trombid* = little timid one) (~ 300 species; unknown number of species NA; 1–4 mm).

Lacewing Predators

The fragile, delicate appearance of adult lacewings (figs. 31 and 32; LeafScape, 13, 36) belies their ability to dispatch legions of aphids.

— GREEN LACEWINGS, FAMILY CHRYSOPIDAE (*chrys* = gold; *op* = face) (1,500 species; 85 species NA; forewing 4–32 mm).

Lacewing larvae have reputations as voracious and rapacious hunters. In his popular natural history book of 1902, *The Book of Bugs*, Harvey Sutherland wrote how the

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

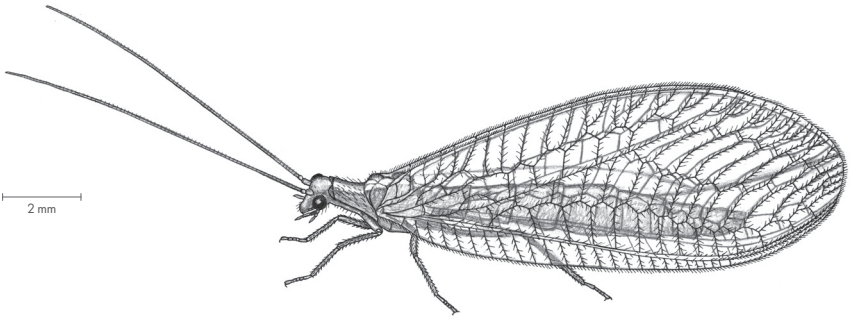


FIG. 31 Aphids seem to be the preferred food for larval and adult green lacewings.

mother green lacewing "dare not lay her eggs in one mass for the first one out would eat all the rest. She spins a lot of stalks of stiff silk and sticks one egg on the end of each, thereby giving each young one a chance for its life." Even though a female green lacewing places each of her eggs on top of a stalk stretching about 10 mm above the leaf's surface and out of reach of many small predators, her relatives the brown lacewings simply place their eggs directly on leaf surfaces, perhaps reflecting a difference in familial temperaments.

— BROWN LACEWINGS, FAMILY HEMEROBIIDAE (*hemera* = goddess of the day; *bio* = life) (600 species; 60 species NA; forewing 4–18 mm).

Larvae of a few of the approximately 1,500 species of green lacewings stake out hunting grounds on lichen-coated trunks and branches decked out in coats of lichens that they have sown together with silk threads. Lacewing silk is derived from an unusual source, their internal excretory organs—the counterparts of our kidneys known as Malpighian tubules. The tubules pour their contents into the larva's gut, and then silk is spun from the larva's anus. The spiny bristles covering its back impale and secure the lichen coats. Weighed down with its lichen attire, this camouflaged larva lumbers across the bark landscape, resorting to stealth rather than speed for its hunting success (chapter 4; fig. 195; BarkScape, 27). The

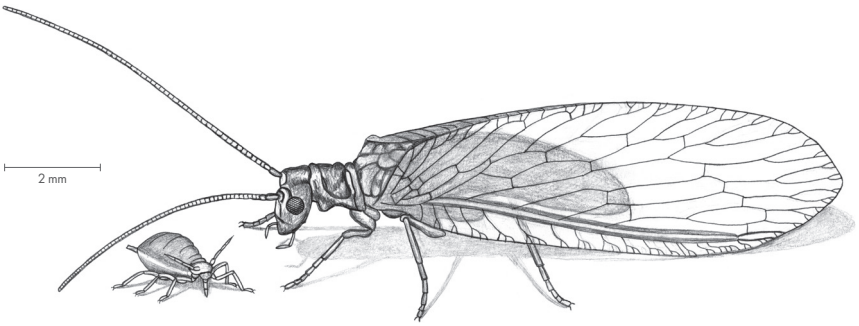


FIG. 32 The most obvious difference between brown lacewings and green lacewings is their color.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

larvae of other green lacewings and all brown lacewings are unencumbered by any such bulky attire and move rapidly over leaf surfaces, dispatching slow-moving aphids and sessile scale insects (chapter 3; fig. 145; LeafScape, 13).

With the approach of autumn, all these fierce-looking larvae use their silk to fashion almost perfectly spherical cocoons in which they transform into deceivingly delicate, ethereal adults. These surprisingly hardy adults nestle in the leaf litter under trees where they survive the winds and freezing temperatures of long winters. In the spring, unblemished by months of cold, they flutter forth to lay eggs on tree leaves.

These aphid predators, the lacewings, are not without their own predators: parasitoid wasps in the family Heloridae. This entire family of wasps—albeit a family with only 12 known species worldwide and only one species from North America—feeds exclusively as parasitoids on lacewing larvae. The infected larval lacewing survives the depredations of the helorid parasitoid long enough to spin its pupal cocoon, but only an adult helorid wasp emerges from the ill-fated lacewing cocoon.

Spider Predators

— SPIDERS, CLASS ARACHNIDA, ORDER ARANEAE (*arane* = spider) (50,000 species; 3,000 species NA; body length 0.4–90 mm).

All spiders are predators, and they have adopted a variety of hunting approaches, both on and under trees. Some spiders ambush, some pounce, some weave webs that trap their prey. The silks spun from their spinnerets can have various physical properties; different silks are used to weave webs of several forms for different purposes. Members of one spider family, the Thomisidae, can produce silk but choose not to spin webs to catch their prey.

— CRAB SPIDERS, FAMILY THOMISIDAE (*thomis* = whip) (2,100 species; 135 species NA; 2–11 mm).

Wherever insects are likely to land from the air or venture forth on foot, crab spiders most often stake out their hunting territory. Most species blend in beautifully with their surroundings on tree bark, leaves, or flowers. Other species stand out by mimicking bird droppings. These spiders take on poses crabs assume and scuttle

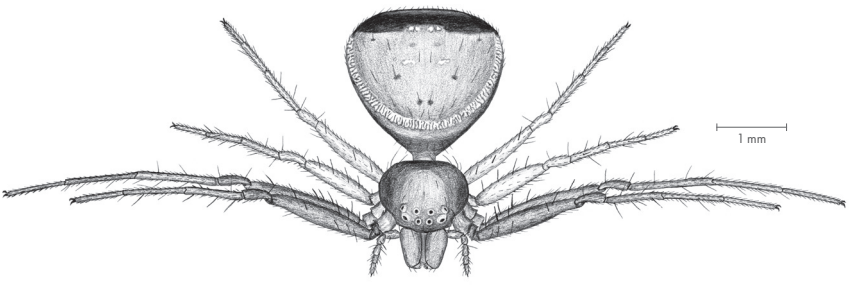


FIG. 33 A crab spider with legs outstretched prepares to ambush a fly that landed on its leaf.

(continued...)

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

INDEX

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

For general queries, contact webmaster@press.princeton.edu