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Why Insects Matter
Earth's Most Essential Species

Course Guidebook

Scott Solomon

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Scott Solomon is an Associate Teaching Professor at Rice University, where he teaches ecology, evolutionary biology, and scientific communication. He received his PhD in Ecology, Evolution, and Behavior from The University of Texas at Austin. He has also worked as a visiting researcher with the Smithsonian Institution in Washington DC and with São Paulo State University in Rio Claro, Brazil.

Scott has taught field biology courses at Rocky Mountain Biological Laboratory in Colorado and in the rainforests and coral reefs of Belize. He has also been a resident associate at Baker College, one of Rice's residential colleges, and served as a faculty fellow at Rice's Center for Teaching Excellence, where he acted as a liaison to other faculty. He received the George R. Brown Award for Superior Teaching and the Outstanding Undergraduate Research Mentor Award from Rice University as well as the Rising Star Award from the University of Illinois Laboratory High School.

Scott is a member of the American Association for the Advancement of Science and the Society for the Study of Evolution. He also serves as an associate editor for the *Journal of Tropical Ecology*. He regularly lectures on science topics at museums, schools, churches, and TEDx events. His writing and photography have appeared in such publications as *Aeon*, *Nautilus*, *Slate*, and *WIRED*. He is the author of *Future Humans: Inside the Science of Our Continuing Evolution*.

Scott is also the expert for the Great Course *What Darwin Didn't Know: The Modern Science of Evolution*.

Table of Contents

Introduction

Guides

Supplementary Material

Why Insects Matter: Earth's Most Essential Species

Life as you know it would not be possible without insects. This course introduces you to the many unappreciated, fascinating, and wholly relevant aspects of the world of insects. With a passion for the remarkably diverse and adaptable insect, your professor shares with you the many reasons we should study insects and helps you appreciate the scientific and aesthetic wonder of this awe-inspiring animal world.

The opening lecture explores insects you encounter every day—those that live in and around your home and gardens. Yet rather than regarding them as universally unwelcome pests, you'll consider their diversity in the world and the important contributions they make to natural ecosystems, to the ecosystem of your home, and to human endeavors. In the next four lectures, you'll gain a greater understanding of the biology of insects, including the structure and function of their bodies, how they grow and reproduce, some of their fascinating and important behaviors, and their evolutionary history. At the same time, you'll consider the many roles insects have played throughout human history. These include the practice of beekeeping as depicted in ancient Egyptian hieroglyphs as well as the role silkworm moths played in driving trade along the Silk Road while also spreading fleas that caused the Black Death and other plagues.

Lectures 6 through 15 guide you through the many vital services insects provide to the natural world and to people—some helpful and some harmful. On the one hand, you'll see how destructive some insects, like locusts and boll weevils, can be to crops and other plants. On the other hand, you'll gain a new appreciation for the benefits that many insects, like bees and ants, provide to plants as pollinators, seed dispersers, and protectors from herbivores. People spend more money per year on insect damage to their homes than they do on damage from earthquakes, hurricanes, and tornadoes, yet they often neglect the extremely helpful roles insects like blow flies and dung beetles play in recycling dead animals and their waste products. You'll see how important insects are in the web of life as food for other animals, like birds and bats. You'll also explore the many human cultures in which insects, from crickets to grubs, are an important part of the diet.

In the next section of the course, you'll consider the impressive abilities of insects and the ways they inspire human creativity and ingenuity. For example, you'll meet insects that can breathe underwater, such as the predaceous beetle, and winged insects with masterful flying abilities, such as the dragonfly. The sounds produced by crickets have made them popular pets in some parts of the world, yet the noise made by thousands of cicadas can be deafening. The success of some insects, such as ants and termites, that grow fungi for food informs practical solutions to human agricultural challenges. And much of what scientists know about genetics comes from studying insects like fruit flies, while other insect behaviors have inspired designs for robots, drones, and computer networks. You'll also learn about the ways that insects have inspired artists, writers, and filmmakers.

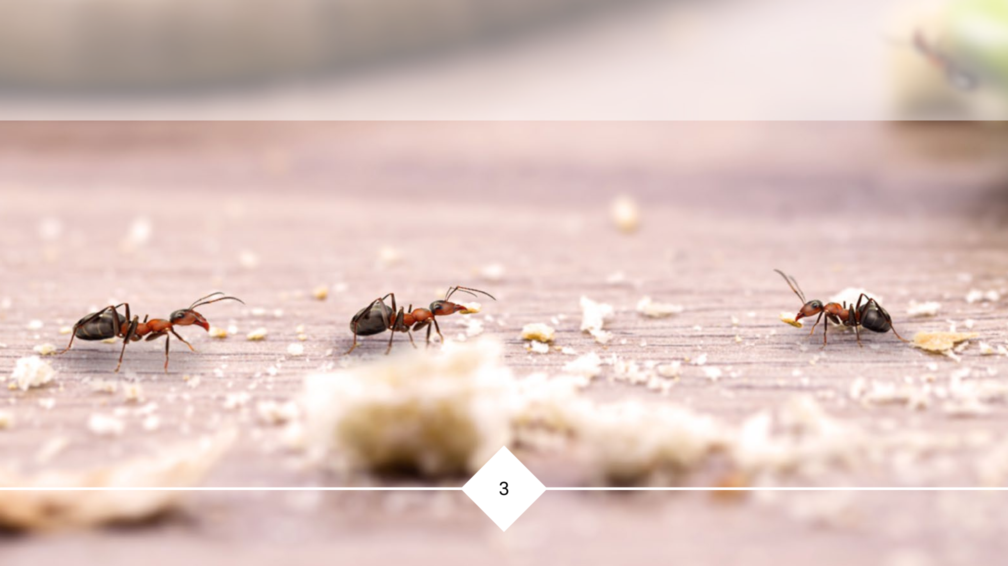
The final segment of the course begins with a practical lesson on how to start your own insect collection. You'll then learn about the many threats insects face and the declines that researchers have documented in some insect populations. You'll gain an appreciation for why so many people find these trends alarming. Your professor will take you behind the scenes in the efforts to document and formally describe the thousands of insect species that remain unknown to scientists. And in the final lecture, you'll consider human perceptions of insects. Why is it that many people love butterflies but hate cockroaches? This course will challenge you to reconsider your own views of insects—Earth's most essential species.

««« TABLE OF CONTENTS

LECTURE 1

Insects Living All around You!

We rarely consider the many different roles of insects—both positive and negative—in the natural world and in our own lives. Yet insects are among the most important of all living things. To begin to appreciate the diversity of insects and the many important roles they play, this lecture takes you on a tour through a typical house, looking carefully for some of the insects that share your living spaces.



Bed Bugs

- The tour begins in our beds, where there can be bed bugs. The term *bug* refers to a particular subgroup of insects classified in the order Hemiptera, or the true bugs. Like all true bugs, bed bugs have mouthparts that are sharp and pointy, which they use for poking into their food source to get a meal. In the case of bed bugs, that food source is human blood.

- Bed bugs have chemicals in their saliva that act as anesthetics so their hosts don't feel pain when the insect's mouthparts penetrate into their blood vessels. The saliva also contains chemicals that act as vasodilators and anticoagulants. Vasodilators cause the blood vessels to widen so more blood can be taken up by the insect. Anticoagulants ensure that the blood keeps flowing and doesn't quickly clot. These same chemicals also cause an immune reaction, making the bites itchy.


BED BUG

- Noticing itchy welts on your back when you wake up in the morning can be a sign of a bed bug infestation. Because bed bugs often disappear into your sheets when they aren't feeding, one of the best ways to be sure that you've got bed bugs is to look for rust-colored stains on sheets where the bed bugs have defecated after a blood meal. Like all insects, bed bugs must shed their exoskeletons as they grow, and their pale, yellow skins can be found left behind as well.

Silverfish and Earwigs

- The vast majority of insects in our homes are either harmless or helpful. An example of a mostly harmless species can probably be found in your sock drawer. A silverfish is a small, wingless insect with long antennae on its head and three long filaments that extend from the other end of its body. Silverfish belong to an ancient lineage of insects, the Zygentoma, that first appeared more than 400 million years ago—long before the first dinosaurs roamed the planet.

- The reclusive silverfish are joined in their hiding places by earwigs, which can be predators of silverfish. Earwigs are easily recognized by their long cerci—appendages that extend from the end of the abdomen and curve together at their tips. The cerci act like pincers for defense, to capture prey, and during mating. A common myth is that earwigs crawl into people's ears while they sleep to lay eggs, but this is simply not true.

Drain Flies

- As you make your way into the bathroom, you're likely to encounter drain flies. Like all true flies, which are classified in the insect order Diptera, drain flies have only one pair of wings. Lots of other insects that have the word *fly* as part of their common name—like dragonflies, butterflies, mayflies, sawflies, and scorpionflies—actually have two pairs of wings. Drain flies lay their eggs in drains, pipes, or corners of a shower where water accumulates. Their larvae feed on the bacteria that grow in these moist environments. Like the majority of insects that share our homes, drain flies are harmless.

Fruit Flies and Ants

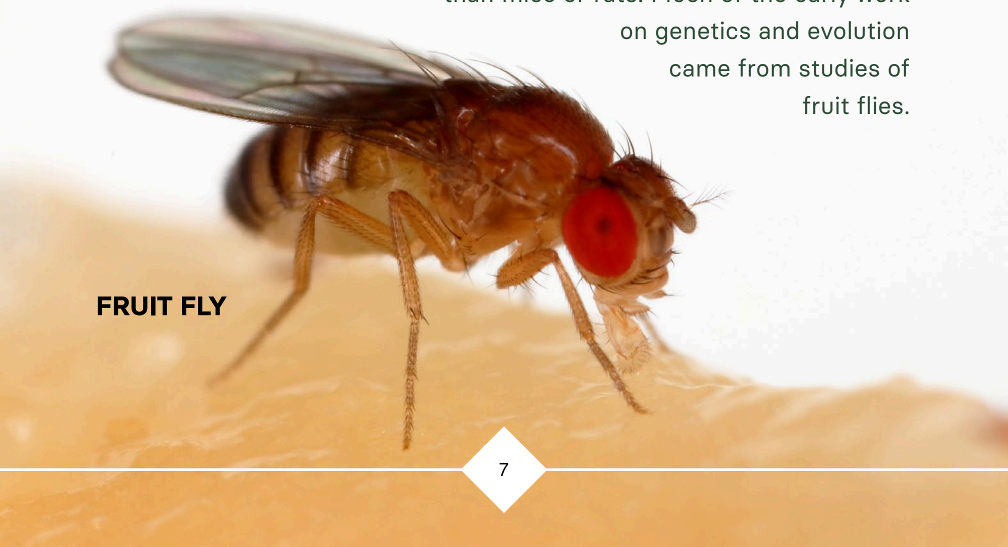
- Moving into the kitchen, you have a good chance of encountering another harmless insect—the fruit fly. These tiny flies gather around ripe fruit, vinegar, and wine. Their attraction to these particular items is tied to their reproductive biology. In the wild, fruit flies lay their eggs in rotting fruit. As the fruit decomposes, fermentation by yeasts produces ethanol as a by-product. Subsequent fermentation by bacteria produces acetic acid, one of the chemicals that gives vinegar its strong smell.

- Rotting fruit doesn't last long, so the fruit flies have to work quickly to lay their eggs so their larvae will have time to feed before all the nutrients are used up by microbes and other decomposers. Consequently, fruit flies have evolved a live-fast-die-young life cycle. A female fruit fly can lay 100 eggs, all of which can develop into adults that are capable of reproduction less than two weeks later. This is the reason why a fruit fly infestation can develop quickly if you leave bananas out too long past their prime.

- There are some insects that are much more social than others. The little ant crawling across the kitchen counter is part of a colony, which can contain hundreds, thousands, or even millions of individuals. The ants you most often see are workers. They perform tasks like finding food, building and maintaining their nests, and defending their nests from enemies. In some species, the workers divide their tasks based on the size of the ant. The largest individuals are soldiers specialized in defense, while the smallest stay inside and help rear the young. The queen's job is to lay eggs, and that's pretty much all she does.

- This division of labor makes an ant colony very efficient. Yet, amazingly, ants go about their business without a leadership hierarchy or any centralized control. This apparent paradox has led some people to look to ants as an inspiration for technological innovations. For example, some computer programs for finding the fastest route between two points are based on the efficient ways that ants find food.

Beginning in the early 20th century, biologists realized they could easily and cheaply keep cultures of the fruit fly *Drosophila melanogaster* in the lab and breed them much faster than mice or rats. Much of the early work on genetics and evolution came from studies of fruit flies.



FRUIT FLY

Flour Beetles and Cockroaches

- There's a good chance that if you have flour, rice, or other grains stored in your pantry, you've also got some insects. Flour beetles like *Tribolium castaneum* are among the world's most common pests of stored grains. If you judge them by the number of species, beetles are the most successful insects in the world. Beetles alone account for 23% of all described species of any group, including plants, animals, bacteria, and fungi.

- Another common resident of the pantry is the cockroach. The cockroaches in our homes are mostly just a nuisance; while they are capable of spreading germs, they really don't pose a threat to human health except for causing allergies in some people when they are found in very high numbers. Ironically, when we don't treat our homes with pesticides, we're much more likely to keep cockroach populations in check by not eliminating their enemies.

FLOUR BEETLE

Carpet Beetles and Houseflies

- If you have a wool rug in your living room, you may encounter carpet beetles. As larvae, carpet beetles can chew and destroy the wool fibers that are often used to make rugs. Wool comes from animal hair, which isn't a material that many insects can digest—but carpet beetles can. Outside of the home, these insects—which are also known as dermestid beetles—are most often found feeding on the bodies of dead animals. Natural history museums keep colonies of the effective dermestid beetles to help them clean and prepare animal bones for exhibits and research collections.

- In the living room and elsewhere, you might also be bothered by a housefly. Houseflies are among the most common insects found in homes—or at least the insects people are most likely to notice. And they also notice people. Anyone who's ever tried to swat a housefly knows they're incredibly good at seeing the flyswatter coming and quickly moving out of the way. Part of this ability comes from their exceptionally good vision.

- Like many insects, flies have two compound eyes on their heads. Each eye consists of 3,000 individual facets, called ommatidia, and each ommatidium functions like an individual eye. The thousands of ommatidia in a housefly's eye point in all directions, allowing the fly to see what's coming. The fly's evasive maneuvers also have to do with their agility in flight. Despite all our technological progress, we still haven't been able to design an aircraft or drone that can perform as well as a housefly.

CARPET BEETLE

Termites

- There can also be insects hidden inside the walls of your home. Termites are famous for their ability to eat wood. It's this ability that allows termites to cause some $40 billion in damage each year to buildings around the world. But termites themselves can't actually digest wood; they rely on microorganisms living in their guts to provide the enzymes needed to break down the tough lignin and cellulose in wood. Outside of your home, termites use this ability to feed on dead trees and other decaying vegetation. They play an important role in breaking down dead plant matter and returning the nutrients to the soil, where they become available for other plants.

Garden Insects

- Even more insects await you in the garden. If there are flowers blooming, then chances are there are bees. The most familiar are honeybees, a species introduced to North America from Europe to help pollinate our crops. The majority of all crop plants depend on bees and other insects as pollinators. Their services are worth about $195 billion each year. Yet bees and other pollinators are becoming rarer for reasons that have been hard to pinpoint.

- While most gardeners welcome bees, they don't feel so fondly about aphids. These tiny insects gather on tomatoes, roses, and other popular garden plants. Aphids drink plant sap and, though usually harmless in small numbers, can damage plants when they're present in large numbers. While resorting to pesticides is one way to treat aphids and other insect pests in your garden, another approach is to cultivate their natural enemies. Ladybugs, also known as ladybird beetles, are voracious predators of aphids. You can buy them online and introduce them to your garden, where they'll happily munch on as many aphids as they can find.

- If you're still outside when evening falls, you might find yourself itching from mosquito bites. Only female mosquitoes drink blood, and they do so to get energy for producing their eggs. A mosquito's mouthparts are a complex system of moving parts that work together to locate and extract a blood meal effectively and quickly. Like bed bugs, their saliva contains anesthetics and anticoagulants. Unfortunately, it can also contain parasites that cause a wide range of diseases.

- Once it's dark out, it's time for a different group of insects to appear. Take a look around any lights and you're almost certain to find some moths. Like their close relatives, the butterflies, moths have delicate scales on their wings that can fall off if you touch them. Moths serve as an important food for bats, and bats in turn help control the populations of many other insects, including some that are agricultural pests.

Two mosquito-borne diseases, malaria and yellow fever, have had an outsized effect on human affairs. They contributed to both the rise and fall of the Roman Empire and influenced the outcomes of the American Revolution, the Civil War, and World War II. Together, malaria and yellow fever kill hundreds of thousands of people each year.

- Before you head inside for the night, pause and listen. Chances are you can hear many of the insects that you're unlikely to see, like crickets and katydids. The sounds made by crickets have made them popular as pets in China since the 7th century. Hearing a cricket's song is considered good luck in many cultures. In other cultures, they're a popular food. In fact, insects are eaten by more than 2 billion people worldwide and are considered by some to be the animal protein of the future.

Reading

Dunn, *Never Home Alone*.

United States Environmental Protection Agency, "How to Find Bed Bugs." https://www.epa.gov/bedbugs/how-find-bed-bugs.

Questions

1. True or false: Most of the insects commonly found in homes are dangerous pests.

2. How have human efforts to eradicate cockroaches made them harder to kill?

ANSWERS CAN BE FOUND ON PAGE 222.

<<< TABLE OF CONTENTS

LECTURE 2

Insect Bodies and Human History

In 2019, crop plants in Yemen were decimated. The damage spread from the Arabian Peninsula to East Africa and as far east as Iran, India, and Pakistan. The culprit in all places was the same: the desert locust, or *Schistocerca gregaria*. Locusts and other large grasshoppers in the order Orthoptera are a helpful starting point for learning about the basic body plan of insects. This lecture also looks at the roles of honeybees, dung beetles, and fleas throughout human history.

The desert locust has probably been a pest for people since the dawn of agriculture in the Fertile Crescent about 10,000 years ago. Plagues of locusts are mentioned in the Qur'an and the *Iliad*, and in the Old Testament, locusts were one of 10 plagues that befell the Egyptians.

Classification System

- Locusts are a type of grasshopper, which are classified in the order Orthoptera. In the system of classification used by scientists to categorize all living things based on shared features, an order is a subset of a class, which is a subset of a phylum, which is a subset of a kingdom. Each order is divided into families, and within a family are the different genera.

- Insects belong to the kingdom Animalia, the phylum Arthropoda, and the class Hexapoda. Within the class Hexapoda, which means "six legs," scientists recognize about 29 different insect orders. About 93% of described insect species fall into one of six orders:

  - **Orthoptera** includes grasshoppers, crickets, and katydids. It has about 20,000 described species.

  - **Hemiptera**, or the true bugs, consists of approximately 70,000 described species.

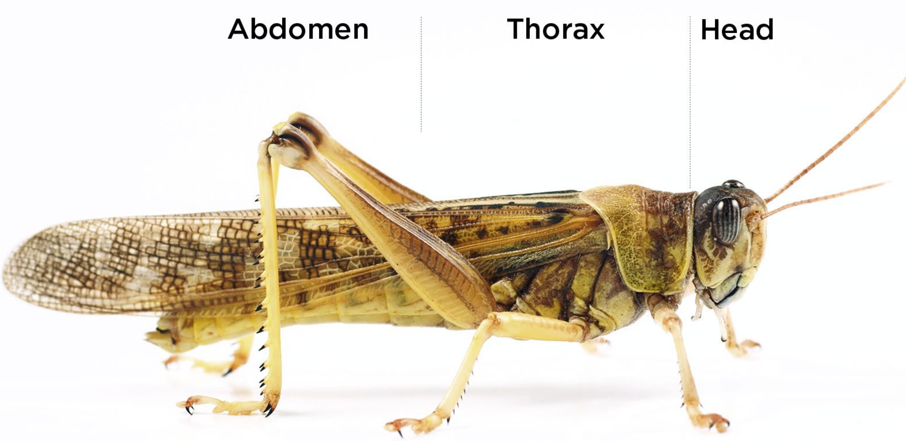
  - **Hymenoptera** includes ants, bees, and wasps. There are about 150,000 described species.

- **Diptera**, or the true flies, has 153,000 described species.
- **Lepidoptera**, which includes butterflies and moths, contains roughly 180,000 described species.
- **Coleoptera**, or beetles, is the most diverse insect order, consisting of some 400,000 described species.

The Exoskeleton

- The exoskeleton is the hard body wall that all insects share—even those that are soft and squishy like caterpillars. It has several layers, much like human skin. The outermost layer, the cuticle, is the hardest part and is made of a substance called chitin that gives it its strength. Having an exoskeleton with a tough cuticle protects insects from predators, helps them avoid excess water loss, and gives their muscles something rigid to attach to.

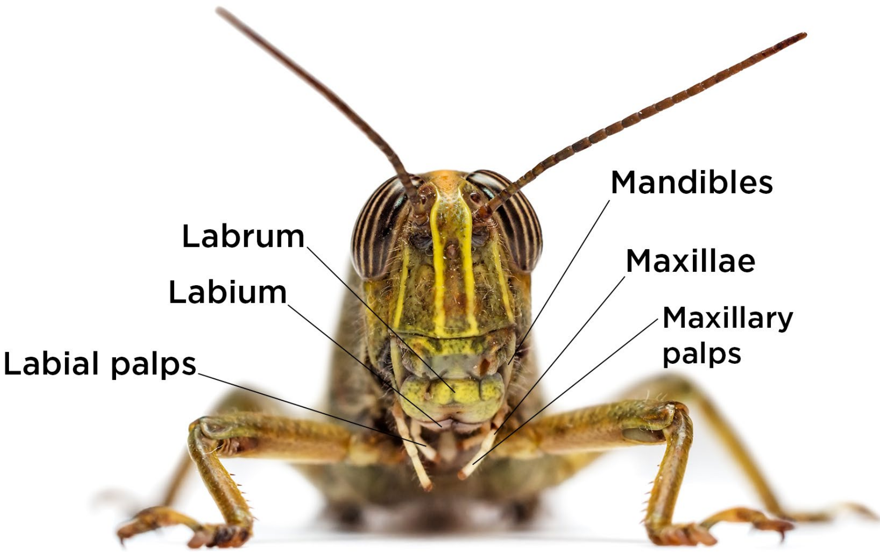
- If you look carefully at a locust, you can see lines, or sutures, separating different sections of the exoskeleton. These are sclerites. Groups of sclerites form the larger body regions of an insect. Like all insects, the desert locust's body has three main segments: the head, the thorax, and the abdomen.



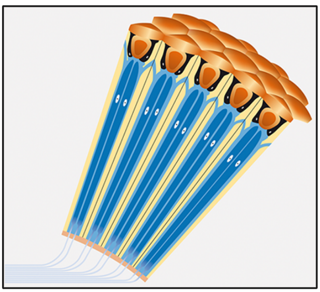
The Head

- The majority of a desert locust's sensory organs are located on its head. Like all orthopterans, the desert locust has mouthparts specialized for chewing. A pair of mandibles with serrated edges provide a powerful cutting apparatus, allowing the locust to quickly slice through vegetation. Behind the mandibles are a second set of paired structures called maxillae that have pointed tips and help the locust hold its food and move it toward the mouth.

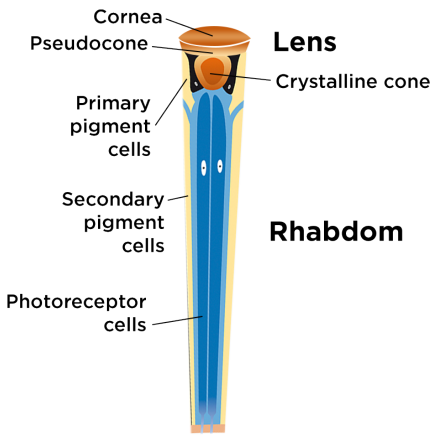
- Above the mandibles is the labrum, which extends over and protects the mouth and prevents food from falling out. And below the mouth is the labium, which acts like a bottom lip and performs a similar function as the labrum. Surrounding the mouth are two pairs of jointed appendages, the labial palps and maxillary palps. Both pairs of palps look like miniature antennae and are used to feel and taste food.



- Locusts and other orthopterans have large compound eyes that consist of hundreds of individual eye facets, or ommatidia. Each ommatidium is like a miniature eye—it has its own lens and photoreceptors, with nerves that connect to the brain. Some of the ommatidia in the dorsal rim area have specialized photoreceptor cells that allow desert locusts to detect differences in the polarity of light. Desert locusts are thought to use the plane of polarized light as a navigation tool as they fly from one location to another searching for new sources of food.



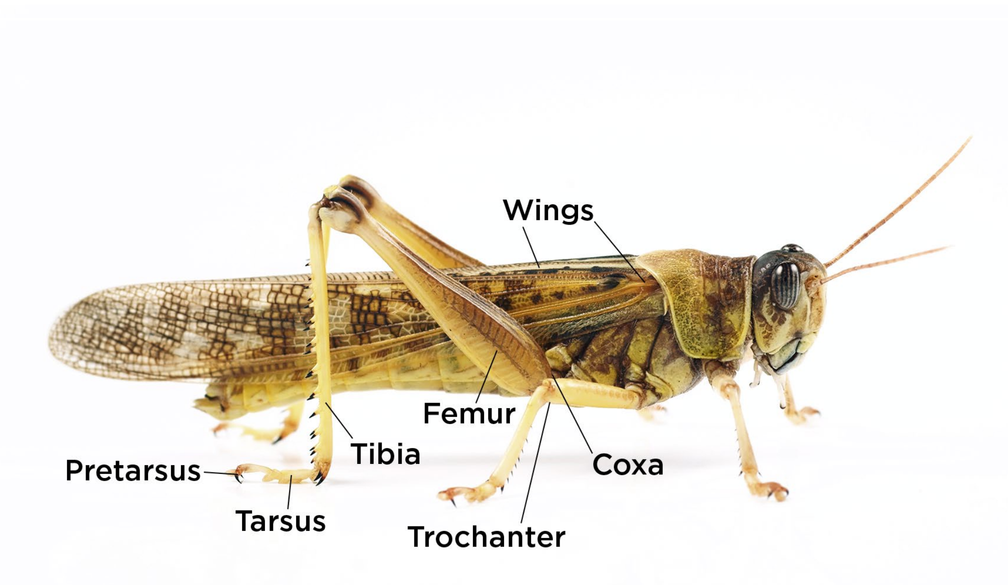
Compound eye structure



Ommatidium

The Thorax

- The desert locust holds the record for the fastest recorded flight speed of any insect at 20.5 miles per hour. By making their wing movements more efficient, they are able to fly not only at high speeds but also over long distances. The wings are controlled by muscles in the thorax, the middle segment of an insect's body. The main function of the thorax is locomotion.



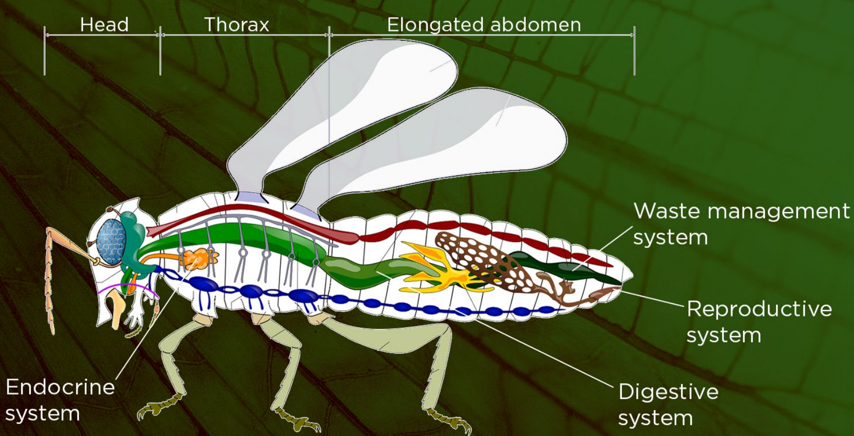
- The thorax itself is divided into three segments. Most insects have two pairs of wings, with the front pair attached to the middle segment of the thorax and the second pair attached to the third thoracic segment, closest to the rear of the insect. Each of the three segments also has a pair of legs, giving insects six legs in total—one of the easiest ways to tell insects apart from other arthropods.

- Locusts, like other members of the order Orthoptera, have enlarged hind legs with powerful muscles for jumping. The legs themselves are made up of five distinct segments. The coxa is the segment of the leg that attaches to the thorax. The next segment is the trochanter, followed by the femur and the tibia, which are typically the longest segments of the leg. The final segment is the tarsus, which is made up of five subsegments, including two at the tip that act as claws.

The Abdomen

- The third major body segment of an insect is its abdomen, which houses many of the internal organs. The digestive, respiratory, waste management, endocrine, and reproductive systems are all housed mostly within the abdomen. The abdomen of the desert locust is elongated and subdivided into 11 segments.

- Small holes called spiracles form the entrance to the respiratory system, which provides oxygen to all the tissues of the body. Insects don't have lungs; instead, air enters the spiracles and travels through a system of branched tubes called tracheae. Air sacs located along the tracheae are compressed by contracting muscles in the abdomen, which pushes air through the respiratory system. When locusts fly, they contract their abdomens more rapidly, pumping more oxygen to their flight muscles.



Honeybees

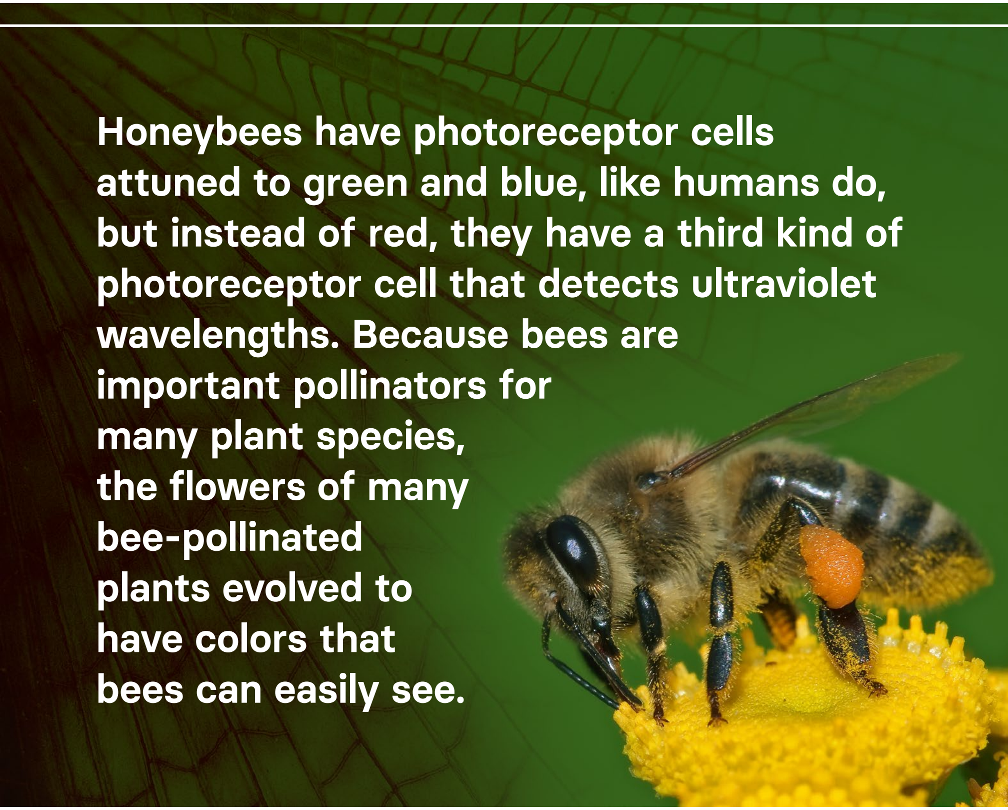
- Remnants of beeswax in pottery fragments from 9,000 years ago in Turkey suggest that beekeeping has a long history going back to the very start of agriculture. Honey was one of the only available sweeteners in the ancient Near East, and beeswax also had medicinal and practical uses.

- Bees are relatively easy to work with. Unlike many other stinging insects, the European honeybee—*Apis mellifera*—is relatively reluctant to sting. That's especially true when a bee fills up with honey, which honeybees do instinctively when they smell smoke.

- The anatomical feature that allows honeybees to fill up on honey is the crop. The crop is the frontmost section of an insect's gut that, in honeybees and some other insects, functions like an expandable sack. Bees use their crop to fill up with nectar when visiting flowers. Later, they regurgitate the nectar inside the hive and fan it with their wings to reduce the water content through evaporation, turning it into honey.

- Despite their importance as pollinators and honey producers, some people are afraid of bees because they can sting. But for most people, a bee sting is unpleasant but not dangerous. And honeybees are usually reluctant to sting because doing so is fatal to the bee.

- When a bee stings, it inserts its syringe-like stinger into the skin of its perceived enemy and injects venom from a gland located near the base of the stinger. The stinger itself is actually a modified ovipositor, the organ used by female insects to lay their eggs. Because the stinger is derived from the ovipositor, which only females have, male bees cannot sting.



Honeybees have photoreceptor cells attuned to green and blue, like humans do, but instead of red, they have a third kind of photoreceptor cell that detects ultraviolet wavelengths. Because bees are important pollinators for many plant species, the flowers of many bee-pollinated plants evolved to have colors that bees can easily see.

- The venom is produced in the venom gland, which is surrounded by muscles that contract to push venom through the stinger. The venom gland and its associated muscles remain attached to the stinger when the bee flies away after stinging an enemy, and the muscles around the venom gland continue to contract even once detached from the rest of the bee's body.

Dung Beetles

- By the 1960s, the waste produced by Australian cattle herds was accumulating, leaving fields of cow patties where the grass became fouled and inedible. As much as 20% of cattle pastures were rendered unusable each year, and because it could take years for an individual dung pile to decompose, the problem was getting worse each year. The solution was to import dung beetles.

- Elsewhere in the world, the accumulation of cattle dung was much less of a problem, thanks in large part to the activities of dung beetles. These insects belong to the Scarabaeidae family, commonly known as scarabs, one of the most diverse families of beetles. Dung beetles feed on animal dung, and the females lay their eggs in balls of dung that they bury underground, creating a safe place for their larvae to emerge and feed until they grow into adults.

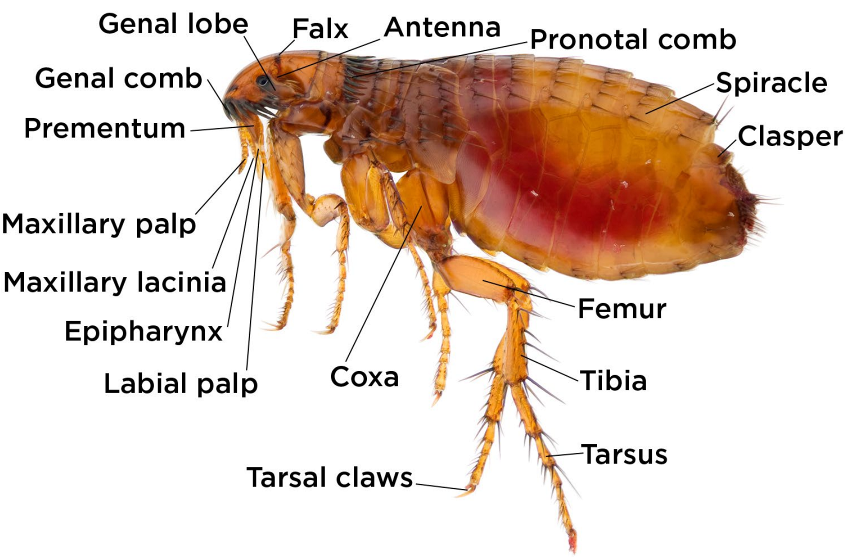
- Dung beetles have several anatomical features that make them well suited to their role as waste recyclers. The faces of scarab beetles are broad and flat due to an enlarged clypeus, located just above the mouth. The clypeus protects the mandibles and has a jagged lower edge that serves as a digging tool for scraping and sorting through dung.

DUNG BEETLE

- The tibiae on the front pair of legs are enlarged and serrated in many scarab species to serve as an additional pair of digging tools. The dung beetle uses these front legs to scrape dung under its body, where the other pairs of legs form it into a ball. The hind legs have pointed tarsi that are used for holding the ball as it is rolled away to be buried.

Fleas

- Fleas are supremely well adapted as parasites. The two maxillae, along with a specialized structure called the epipharynx, form three stylets that puncture the skin. The epipharynx is then inserted into a capillary and acts like a straw to suck up blood. Saliva containing anticoagulants is produced in the flea's salivary glands, which are connected by a short tube to its mouth and excreted into the wound to keep the blood flowing while the flea feeds.



- Many fleas have comb-like spines that help keep the flea on its host by allowing hair or fur to get caught between the grooves. They also have compressed bodies and reinforced exoskeletons that make it difficult to squish a flea even if you do manage to dislodge it. Fleas do not have wings, but they are able to jump long distances—as high as 8 inches, the equivalent of 66 times their body length. This jumping ability serves as a way of making a sudden escape but also can be used to jump up onto a host as it passes by.

- Being such an effective blood-sucking parasite has made fleas ideal vectors of disease. The most infamous disease transmitted by fleas is plague. Today, plague is treatable with antibiotics, but outbreaks were a common part of life throughout much of human history. The Black Death, which killed millions of people in Europe and Asia between 1346 and 1353, was caused by an outbreak of bubonic plague that began in China and made its way to Europe as rats, along with their fleas, traveled along the Silk Road trade routes.

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Questions

1 The insect exoskeleton contains which of the following substances?

- **a** keratin
- **b** chitin
- **c** propolis
- **d** silicon

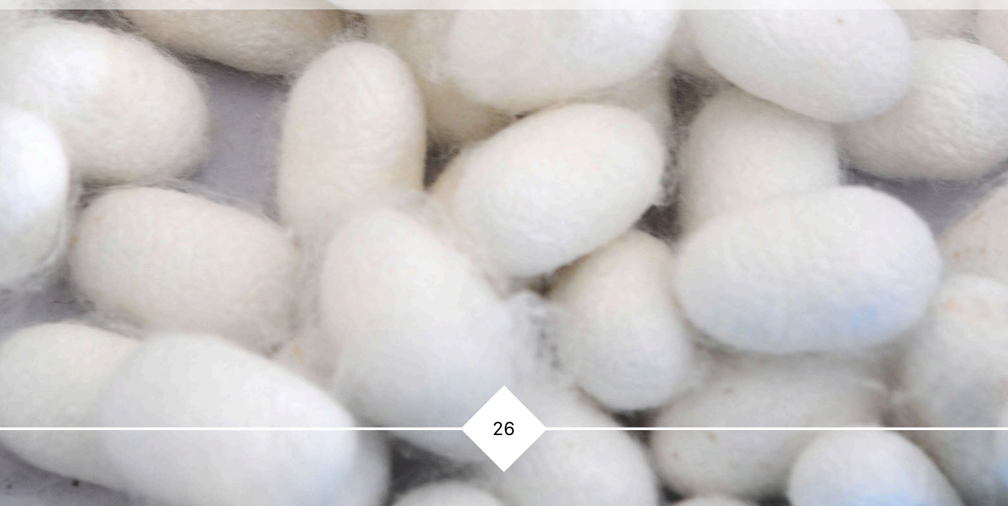
2 Some insects, like bees, have photoreceptor cells that enable them to see ______ light.

ANSWERS CAN BE FOUND ON PAGE 222.

LECTURE 3

Insect Life Cycles and Reproduction

According to legend, the use of silk began in China in the 27th century BCE, when the empress Leizu noticed a silkworm cocoon that fell in her tea. As she removed it, the heat from the tea caused it to unravel. The thread of silk is said to have stretched all the way across her garden by the time it was done. Whether or not the legend is true, silk production has played an important role in world history and is a great example of why insect life cycles matter.



Silkworm Moths

- Silk is made by the silkworm moth, *Bombyx mori*. Like all moths and butterflies, which are classified in the order Lepidoptera, the silkworm life cycle includes a larval stage commonly known as a caterpillar or worm. Once the caterpillar reaches a critical size—about 2 ¾ inches long—it enters the pupal stage, where the insect's body undergoes a complete metamorphosis before emerging as a winged adult.

A single silk thread from one silkworm cocoon can be half a mile long.

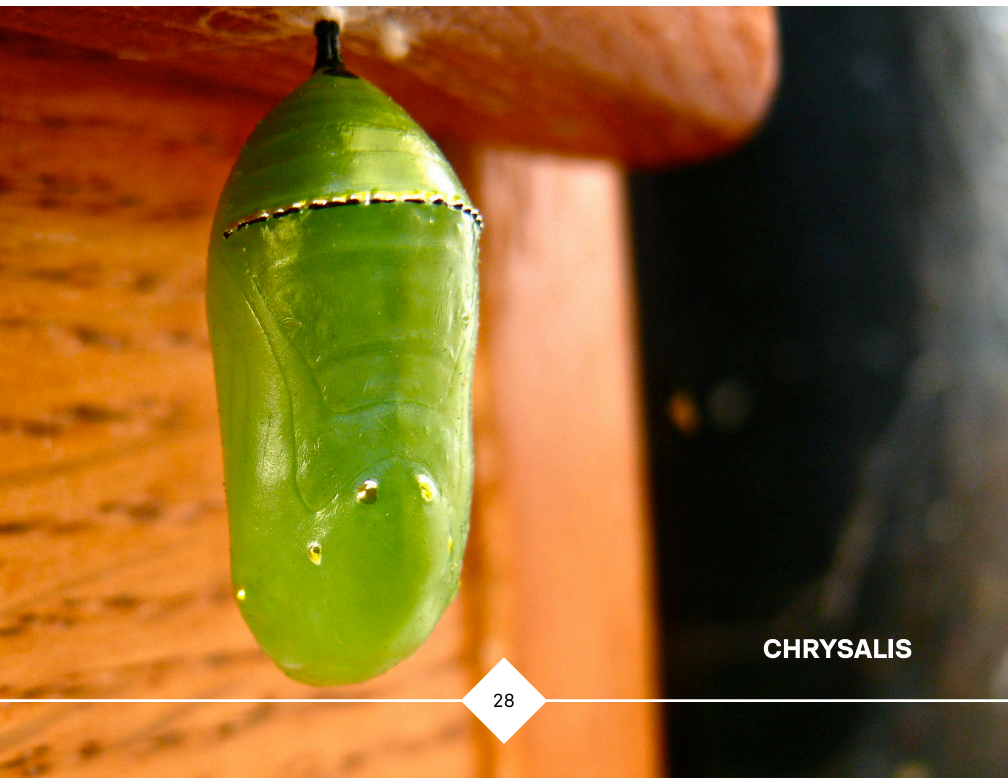
- The silkworm moth's pupal case, or cocoon, is unusual in that it's made of one continuous thread of silk. The silk made by silkworms is one of the strongest, most durable materials found in nature. It's even tougher than synthetic materials like the polyethylene used in helmets or the Kevlar used to make bulletproof vests. The silken cocoon provides natural protection for the pupa as it develops into a mature, adult moth.

- As adults, silkworm moths show many of the characteristics typical of moths and butterflies, but with some interesting exceptions. Like most moths and butterflies, they have two pairs of wings covered in tiny scales. But domesticated silkworm moths have lost the ability to fly after so many generations of being cared for by humans. Since their sole purpose is to reproduce, adult silkworm moths have no mouthparts and get all their energy from the feeding they do as caterpillars.

- By the time of the Han dynasty in the 2nd century BCE, Chinese silk production was already an established part of its economy. The silk trade expanded west to the Roman Empire, and thus was born the Silk Road, a system of trade routes that connected Europe and Asia. Silk production continues to be a major industry today, particularly in China and India. But silkworms aren't raised only for their silk—they're also raised for food.

The Chrysalis

- You may have learned that butterflies make cocoons, but only moths make a true cocoon. A butterfly's pupal stage is a chrysalis. Butterflies typically spend about a week inside the chrysalis, transforming from legless larvae into adult butterflies with legs, wings, antennae, and reproductive organs.



CHRYSALIS

- Surprisingly, the transition from larva to adult actually begins before the pupal stage. Inside a caterpillar's body are clusters of cells called imaginal discs. Each one corresponds to a different adult body part. As the caterpillar grows, the imaginal disc cells divide, forming buds that extend inward from the cuticle.

- To grow larger, the caterpillar must shed its exoskeleton several times. This process is controlled by hormones. The ecdysteroid hormones cause the epidermal cells beneath the exoskeleton to make proteins that will form the new exoskeleton. When it's time to moult, the epidermal cells secrete enzymes that dissolve the current exoskeleton, which weakens until it splits. Some components of the old exoskeleton are reabsorbed, but the hard, outer shell, called an exuvium, is left behind.

- Another hormone, called juvenile hormone, prevents the development of adult characteristics by shutting off the genes needed for adult development. As long as juvenile hormone is present in high levels, each moult leads to a larger larva. Without juvenile hormone, genes in the epidermal cells of a caterpillar produce the proteins that will form the thick, protective outer case of the chrysalis.

- Inside the chrysalis, enzymes begin to break down most of the tissues that made up the body and internal organs of the caterpillar. The only cells that are not degraded during the pupal stage are those that made up the tracheal system and the imaginal discs. The tracheal system that allows the insect to breath has already formed and remains intact. The little buds that formed in the imaginal discs during the larval stage now continue developing into legs, antennae, eyes, and wings.

- Once fully developed, the adult butterfly emerges in a process known as eclosion. But it isn't yet ready to fly. It must first extend its wings by pumping hemolymph into them, which typically takes between 30 minutes and two hours.

Monarch Butterfly Migration

- Adult butterflies can live for a few months or as long as a year. They tend to live longer in captivity because they don't have to worry about being eaten by predators. Adult monarch butterflies usually live up to six weeks, but the population of monarchs in the eastern half of North America lives longer. That's because these monarchs undergo one of the most epic migrations of any animal.

- Each fall, monarch butterflies in the parts of Canada and the United States east of the Rocky Mountains begin flying south. Much like migrating birds, these butterflies seek warmer weather as winter approaches. But unlike migrating birds, the monarch butterflies that begin the southward migration will never complete the round trip.

- These monarch butterflies travel up to 3,000 miles to reach a particular area in central Mexico where they'll spend the winter. They navigate in part by using the position of the Sun in the sky, calibrated with an internal circadian clock that tracks the time of day. Monarch butterflies can also detect differences in magnetic fields, so they can keep track of where they are and in which direction they need to fly to reach their overwintering grounds.

- The sites where they overwinter are located on 14 forest-covered mountaintops in central Mexico in an area smaller than New York City. The monarchs cluster together on oyamel fir trees, which grow only in the cool conditions at elevations above 6,900 feet. Most monarch colonies are found at around 10,000 feet on somewhat warmer, southwest-facing slopes. A single congregation can have as many as 300 million butterflies.

MONARCH BUTTERFLY

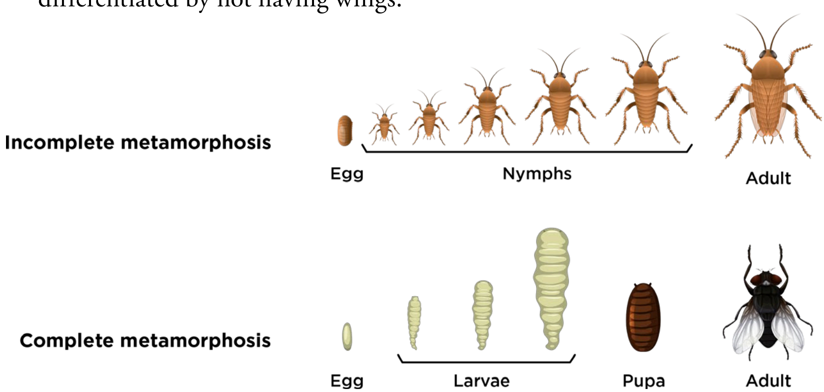
- By February, as temperatures warm and days get longer, the monarchs are ready to begin heading back north. They have already been adults for about six months, but their reproductive development has been put on hold in order to complete the migration south and survive the winter. With their reproductive development complete, the butterflies mate and females lay eggs on milkweed plants they find along their northward journey. While these adult butterflies will not live much longer, the eggs they lay will hatch and grow into caterpillars, which will pupate and then eclose as adults who will continue flying north. In total, it will take four or five generations to complete the round-trip journey.

Incomplete Metamorphosis

- From an ecological perspective, having such a different body and lifestyle means that the adults of the species do not compete with their young. Most caterpillars eat leaves, while most adult butterflies and moths eat nectar or pollen. Entomologists refer to this type of life cycle, in which the young look very different from adults, as complete metamorphosis.

- Today, about 90% of all insect species have complete metamorphosis. But that wasn't always the case. The first insects to evolve about 480 million years ago had a simpler life cycle in which young individuals looked like small versions of adults and got gradually larger with each moult. Most insects have wings as adults, which requires more of a transformation from the wingless juvenile state. But there are a lot of insects that are wingless when young that don't undergo the total transformation of the pupal stage like in butterflies and moths. This type of development is called incomplete metamorphosis.

- Mayflies are a great example of an insect with incomplete metamorphosis. Immature insects with incomplete metamorphosis are nymphs, which distinguishes them from larvae, the term for insects with complete metamorphosis. Nymphs look a lot like adults but can usually be differentiated by not having wings.



- Mayflies hatch from eggs laid on the surface of freshwater lakes or streams. The nymphs emerge and live underwater for months or years, eating algae and organic debris. When the time is right, they crawl out of the water onto a rock or a piece of vegetation and moult into a winged form. But they aren't adults quite yet. Mayflies are the only insects that can have wings before they are reproductively mature, which is when they are technically considered adults. They will need to go through one more moult before their wings are fully formed and they are capable of flying off to find a mate.

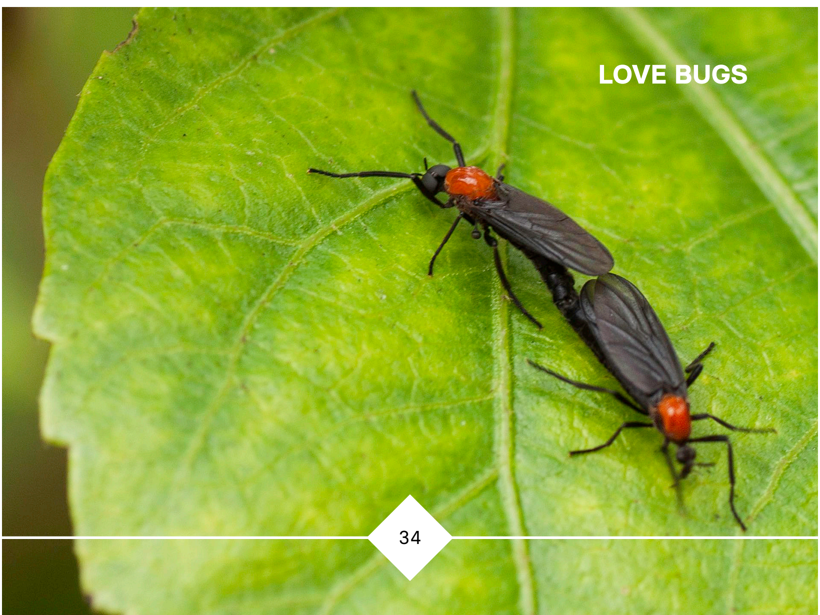
- The sole purpose of the adult stage is reproduction. Adult mayflies do not even have functional mouthparts or digestive tracts—they don't live long enough to need them. Relying on stored energy from their underwater nymph stage, the male mayflies flutter up into the air above the water and then drop down low, repeating this pattern again and again to attract females. Mating is brief and takes place in the air. Females then search for a place to deposit their eggs.

Mayflies belong to the insect order Ephemeroptera, named for the ephemeral nature of their adults, which typically live for only a few days or even hours.

Mating Practices

- The reproductive habits of insects often involve even more elaborate courtship rituals and mating practices. Fireflies, which are actually a type of beetle in the family Lampyridae, use flashing light produced in their abdomens to attract mates. Males flash to attract females, who respond with a flash of their own to indicate their location and interest. The rate and pattern of flashing is different in each species, providing a way to ensure mating happens between males and females of the same species.

- Love bugs are a type of fly in the family Bibionidae. They get their name from their mating behavior, in which males and females remain physically attached to one another for two to three days. Once mating has begun, other males may attempt to interfere and remove the first male. The female, which is larger, can continue to fly, and she may choose to leave the swarm when she is satisfied with the mate she has chosen. The pair continues to fly around, each facing the opposite direction but connected at the end of their abdomens, until fertilization is complete.



While the prolonged mating of love bugs may be surprising, the mating practice of bed bugs is even more extreme. It involves the male using his genitals—which have evolved into a sharp, needlelike organ—to pierce the female's exoskeleton. The sperm are then injected into her body cavity and travel through the hemolymph to the ovaries. This process is called traumatic insemination, and it creates a wound in the female's body that can lead to an infection. This violent method seems to benefit the male by making it harder for the female to resist mating.

For aphids, it's the females that seem to have the advantage. When aphids hatch from eggs, they are all female. Each female aphid can reproduce by making a genetically identical copy of itself, which will also be female. Aphids also give birth to live young, making their reproduction even faster. But they can also switch their reproductive strategy if conditions become less favorable. Instead of just producing genetically identical female offspring, they will also make some male offspring. By producing males, the next generation of aphids can reproduce sexually or asexually.

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Yong, "3-D Scans Reveal Caterpillars Turning into Butterflies." https://www.nationalgeographic.com/science/phenomena/2013/05/14/3-d-scans-caterpillars-transforming-butterflies-metamorphosis/.

Questions

1 Which of the following is the correct term for the pupal stage of a butterfly?

- **a** cocoon
- **b** exuvium
- **c** nymph
- **d** chrysalis

2 In all insects except ______, wings are found only in the adult stage.

ANSWERS CAN BE FOUND ON PAGE 222.

TABLE OF CONTENTS

LECTURE 4

Insect Behaviors and Communication

In the summer of 1945, an Austrian-born professor named Karl von Frisch made a discovery that would later earn him a Nobel Prize. Through a series of clever experiments, he showed that bees can communicate with one another through a type of interpretive dance.

Communicating about Food

- Von Frisch noticed that foraging honeybees repeatedly shake their abdomens in consistent patterns once they return to the hive. He believed the shaking, which became known as the waggle dance, communicated some sort of information about sources of food the foraging bees had encountered.

- To test this, he marked individual bees with different colors of paint. He then placed baits with different types of food, like flowers or solutions of scented sugar water, in different locations and made note of which bees visited which bait. He observed that the bees changed their waggle dance depending on which food source they visited, but it wasn't the type of food that mattered but rather the location of the food source.

- A bee performing a waggle dance moves in a figure eight, waggling its abdomen where the two loops that make the figure eight come together. By carefully adjusting the location of each food source, von Frisch figured out that the further away the food is from the colony, the longer the bee waggles before turning either right or left to complete the figure eight. One second of waggling indicates a food source that is about 1 km away from the hive.

- But if a bee wants to visit that food source, it needs to know not only how far to fly but also in what direction. Von Frisch's experiments showed that the angle at which the bees perform their waggle dance tells the other bees which way to fly when they leave the hive entrance. Specifically, the angle with respect to the vertical axis of the honeycomb corresponds to the angle with respect to the Sun that the bee should fly to find the food. Knowing the direction and the distance, the other bees in the hive have all the information they need to find the food.

Locating Hive Sites

- The size of the hive is an important factor for bees to survive the winter. They need enough space to accommodate all the worker bees as well as the honeycomb and the combs that the bees use to raise their larvae. But if the space is too large, it won't be possible to keep it warm with their vibrating wings. An average sized bee colony, with its 44 pounds of honey, will need about four gallons of space. Each year, the bees must find a new, slightly larger hive site to accommodate the growing colony.

- The way they locate these sites involves another remarkable example of complex communication. The first person to notice this aspect of honeybee communication was Martin Lindauer, a student of Karl von Frisch. One afternoon in 1949, Lindauer noticed a swarm of bees performing waggle dances. But these bees were outside of the hive, which happens when the queen and a group of workers are in search of a new home.

Beekeepers use artificial hives that are larger than what the bees need. Bees tend to fill the hive with as much honeycomb as they can, meaning there is extra that can be harvested. A single colony kept in a 36-gallon hive can make more than 220 pounds of honey in one summer.

- Looking more carefully, Lindauer noticed that some of the bees looked dirty. He suspected that the bees he saw dancing had been inspecting new nest sites. By marking individual bees with dots of colored paint, deciphering the location information contained in the waggle dance they were performing, and chasing after the swarm as it flew toward the site the colony had selected, Lindauer discovered that the bees were indeed dancing to report the location of potential new homes.

- Certain worker bees, called scouts, visit different possible home sites and evaluate them using the criteria that bees care most about—entrance size, location, and volume. The scouts then return to the swarm and perform a waggle dance to indicate the location of the potential new home. Because there are numerous scout bees—typically a few hundred—many of them are likely to have found different potential homes. That means there are multiple different waggle dances being performed at the same time, representing different options for the colony to choose from.

- The other scout bees observe the dances by feeling the vibrations with their antennae. Scout bees advertising particularly good nest sites will dance faster and for a longer time. After watching a scout advertise a potential home with its waggle dance, the other scouts then go to the site to assess it for themselves. Eventually, a consensus is reached in which all the scout bees are dancing for the same site.

Pheromones

- One of the most common ways that insects communicate with one another is through the use of chemicals called pheromones. Whereas hormones have an effect somewhere in the body of the organism that produced the hormone, pheromones are produced by one individual and have an effect on another individual.

- The French naturalist Jean-Henri Fabre discovered the power of pheromones by accident. After capturing a female moth and keeping it alive in a small enclosure in his home in southern France, he was shocked to later find his house filled with male moths that had flown in through an open window. Noting that they had arrived when it was dark outside, Fabre suspected that the male moths were attracted by a chemical cue given off by the female.

- To test this idea, he put female moths in different types of enclosures—some of which were tightly sealed and some of which had small openings. No males arrived at the enclosures of females kept in tightly sealed containers, but females kept in enclosures with even the slightest opening were swarmed by males.

- In another experiment, Fabre kept a female moth in a wire mesh container overnight and then transferred her to a glass container the next day. The male moths swarmed around the open container where the female moth used to be but ignored the container where she could be seen but not smelled. Fabre concluded that there must indeed be a chemical that attracts the male moths to the female.

- Fabre's idea that moths use chemicals to find mates remained unproven until 1959, when a German biochemist isolated a substance called bombykol from female silkworm moths. Male moths that were presented with a pure solution of bombykol began rapidly flapping their wings, performing what's known as a flutter dance—an indication of their interest in mating.

Ant Behavior

- In 1958, an American naturalist named Edward Osborne Wilson reported a discovery of another way that chemicals control insect behavior. One behavior that Wilson was curious about was the way that dead worker ants are removed from the colony and deposited in a refuse pile. Removing dead ants from the nest makes sense, as they could spread disease, but he wondered what cues the ants used to determine that an ant had died.

- Wilson soaked pieces of paper in an extract made from different chemicals isolated from dead ants and gave each piece of paper to live ants. He found that the live ants treated the paper soaked in one particular chemical, oleic acid, as if it were a dead ant. Other items, like food, were also treated as dead ants if they were soaked in oleic acid. Even live ants soaked in oleic acid were carried off to the refuse pile.

- Wilson and colleagues soon found other chemicals that act as pheromones and play important roles in ant behavior. Alarm pheromones are used to signal an emergency, like a predator digging into the nest. Some ants also use trail pheromones to let their nestmates know where they've been, making it easier for foraging ants to find their way home.

- Trail pheromones can also make finding food more efficient by helping foraging workers to take the shortest path from their nest to a source of food. Ants generally follow the path with the strongest pheromone trail, so even if they choose their path randomly at first, ants following behind them will end up choosing the shortest path because more workers will have traveled along it, causing it to accumulate the most pheromones.

A class of computer programs called ant colony optimization uses virtual ants and pheromones to explore different possible routes between points. Ant colony optimization programs can quickly calculate the fastest delivery routes or the most effective design for a wireless network.

Conflicts between Nests

- Ants can usually tell whether another ant belongs to its nest by the way it smells. Chemicals called cuticular hydrocarbons that make up part of the insect exoskeleton serve as identity markers, making it easy to determine whether an ant is a nestmate or an enemy—unless one of the ants has a particular mutation that makes it lose the ability to recognize nestmates from non-nestmates.

- The mutation affects a part of the genome known as the social chromosome, which includes a gene called *Gp-9* that makes a protein involved in the ability to detect smells. The mutated version of *Gp-9* causes ants to lose the ability to smell cuticular hydrocarbon cues. The result is that fire ants with the mutated form of *Gp-9* treat all other fire ants they meet as if they are nestmates.

- The mutated *Gp-9* gene is one of the factors that has allowed red imported fire ants to spread across much of the southern United States. This species, whose scientific name is *Solenopsis invicta*, is native to Brazil and Argentina but was introduced to North America accidentally as stowaways in soil or vegetation. Fire ants have painful stings, and some people are allergic to their venom.

- For fire ants, avoiding conflicts between nests has been a successful evolutionary strategy. Yet, pacifists are rare among insects, especially ants. While most ant species act aggressively toward any other ants they encounter, especially those of the same species, the desert honeypot ant, *Myrmecocystus mimicus*, evolved a way to determine the outcome of such encounters while minimizing casualties.

- When workers from rival colonies of desert honeypot ants encounter one another, they release alarm pheromones to call for backup, much like other ants. But rather than attacking one another, the workers line up and extend their legs, making them look as if they are walking on stilts. This is a way of figuring out which colony would win if they did fight by using the number of workers on each side as a proxy for the total size of the colony. The tournaments can go on for days, but eventually a winner is determined based on which colony recruits more ants to the tournament site.

If the victorious colony is much bigger, then the losing colony is in serious trouble. Workers from the larger colony will raid the nest of the smaller colony, kill its queen, and carry the workers, larvae, and pupae back to their nest. The worker ants of the raided nest will spend the rest of their lives working inside the nest of the raiders.

Reading

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O'Malley, *The Wisdom of Bees*.
Seeley, *Honeybee Democracy*.
———, *The Lives of Bees*.

Questions

1 In the waggle dance used by bees to communicate the location of a food source, which of the following indicates how far the food is from the hive?

- **a** the angle that the bee dances
- **b** the distance the bee dances
- **c** the number of vibrations per second of the bee's abdomen
- **d** the number of bees dancing

2 Ants use ______ to mark the path to and from the nest.

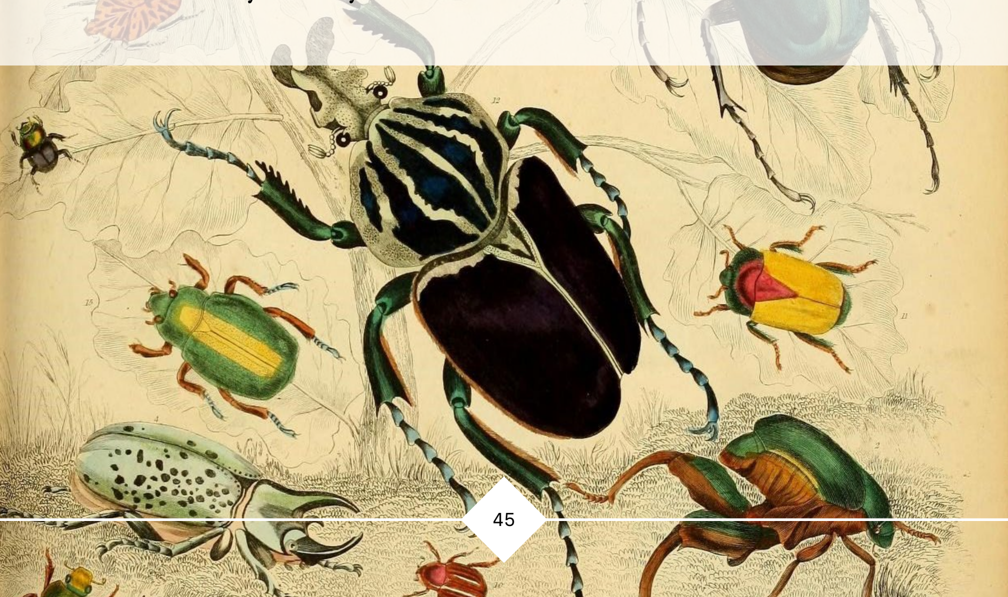
ANSWERS CAN BE FOUND ON PAGE 223.

<<< TABLE OF CONTENTS

LECTURE 5

Why So Many Beetles?

Beetles are the world champions when it comes to diversity. There are more than 350,000 living species of beetles that have been formally described by scientists, meaning beetles account for 35% of all known insect species and 23% of all living species. For comparison, there are about as many species of beetles as there are species of plants. To explore why are there so many beetles, this lecture looks at the many different types of beetles and traces their evolutionary history.



Colorful Beetles

- Buprestids, also known as the jewel beetles, often have a metallic sheen. These beetles have been used to make jewelry and to decorate textiles, paintings, and other works of art. The impressive coloration in buprestid beetles is the result of the structure of their exoskeletons. Reflective surfaces are stacked in layers within the exoskeleton, with the thickness of each layer affecting the wavelength of light—and therefore the color—that is reflected. Many buprestids are metallic green, which is thought to serve primarily as a form of camouflage. Some metallic gold buprestids use their unique coloration as a way to find mates of the same species.


JEWEL BEETLE

- Another group that contains colorful species is the tiger beetles, in the family Carabidae and the subfamily Cicindelinae. As their common name suggests, tiger beetles are ferocious predators. They have large compound eyes that help them spot their prey and long legs that help them achieve running speeds of up to 125 body lengths per second. For comparison, the fastest human sprinters can run only about 5.6 body lengths per second. In fact, tiger beetles run so fast that they have to slow down to see where they are going—their eyes cannot process visual information fast enough to keep up with their bodies.

Beetle Defenses

- In some beetles, bright coloration evolved as a way to warn predators to stay away. Blister beetles in the family Meloidae, many of which are metallic or have bright spots, produce a toxic chemical called cantharidin. Male blister beetles get cantharidin from their diets and store it in glands inside their mouths and reproductive tracts.

- When courting females, they excrete a small amount of it from their mouths, which the females use as a way of determining whether or not to mate with that male. If they do decide to mate, the male deposits a package known as a spermatophore, which contains sperm and cantharidin, into the female's reproductive tract. After her eggs are fertilized, the female then uses the cantharidin she received from her mate to protect the eggs she lays from potential predators.

- Cantharidin works well as a defense for blister beetle eggs because it is a potent toxin. If ingested by humans or animals, it causes blood vessels to dilate, leading to blistering or even organ failure and death. Yet historically it has been used as a medication and even as an aphrodisiac, known by the common name Spanish fly. The efficacy of cantharidin as a medication has mostly been discredited in modern times, although it continues to be used today as a treatment for warts and other skin conditions.

- As defenses go, the bombardier beetles are among the most impressive. These beetles shoot boiling-hot noxious chemicals at high speeds out of their abdomens. They do this by initiating a chemical reaction when they feel threatened. It's about as effective as a defense can be—it burns, it stinks, it tastes bad, and it irritates the skin, eyes, and digestive tract. Predators like toads often regurgitate bombardier beetles after getting an unpleasant surprise when eating them.

- Sometimes it's enough to just surprise a predator, like the click beetles do. Click beetles, in the family Elateridae, have a hinge-like structure where the thorax meets the abdomen. The hinge is made up of a peg formed by an extension of the bottom of the thorax and a lip that extends over the peg from the abdomen. When the beetle arches its body, lifting its thorax relative to its abdomen, the peg pushes against the lip. But the lip keeps the peg in place until a sudden release, causing such a rapid motion that the beetle can be launched about a foot into the air—more than 25 times its body length. It also makes a loud clicking sound, which is probably the main way it scares potential predators.

Weevils

- No discussion of beetle diversity would be complete without including the most diverse group of beetles, the weevils. Weevils are an entire superfamily called the Curculionoidea, which is divided into 11 different families. Altogether, there are more than 97,000 species of weevils. By comparison, all of the vertebrates—including all known fish, amphibians, reptiles, birds, and mammals—have about 70,000 species.

ACORN WEEVIL

To figure out whether an acorn has an acorn weevil growing inside it, place the acorn in water. If it floats, then the chances are good that there is an acorn weevil larva growing inside. If you want to find out for sure, just keep it in a small container with air holes and wait a few weeks to see if a long-snouted weevil emerges.

- Despite having mouthparts that look a bit like the long, pointed proboscis of mosquitoes and other insects with piercing/sucking mouthparts, weevils are actually chewers. Weevils are herbivores, and some species are major plant pests. Others specialize in eating seeds, like the acorn weevil with its impressively long snout. The acorn weevil uses this snout to penetrate into acorns to feed, but it is also used by females to make a hole in the acorn, where she will lay her eggs. Inside the acorn, the larvae have plenty of food to sustain them as they grow.

- In some years, for reasons that aren't yet fully understood, oak trees will produce unusually large numbers of acorns. Biologists refer to this as a mast year. One theory is that they do this to overwhelm the predators—such as acorn weevils and squirrels—that like to make a meal out of their seeds. By producing so many acorns all at once and with unpredictable timing, the oak trees can ensure that at least some of the acorns will survive long enough to grow into a new tree.

The Carboniferous Period

- Reconstructing the evolutionary history of beetles using DNA sequences of living species along with molecular clocks calibrated by fossils suggests that beetles may be even older than the earliest fossils that have been discovered. According to a study published in 2019 that compared DNA from 4,818 genes from 146 species of beetles and their close relatives, the common ancestor of all beetles may have lived about 327 million years ago. That's about 47 million years before the earliest known fossils. This suggests that beetles first evolved during the Carboniferous period.

- The Carboniferous period is famous for its coal deposits, which are formed when plants die and decay, creating deposits of peat rich in carbon. Over time, they get buried by additional layers of soil and rock that are deposited on top of them. Much of the surface of the land was covered by forests of early plants like ferns and horsetails, which were among the first plants with the ability to grow tall to compete for sunlight. To do so, these plants used chemicals that give wood its durability, like lignin and cellulose.

- In addition to giving plants structural support, lignin and cellulose are difficult for animals to digest. In fact, during the Carboniferous period, this ability had not yet evolved among animals—including insects—so there were very few herbivores. Not many organisms could break down wood, even once a plant had died, like thousands of insect species do today. That made it more likely for plants to grow large and then get buried once they died, rather than be eaten or turned into soil like tree trunks do in modern forests.

The Carboniferous period featured some of the largest insects that ever lived. Meganeura, an early relative of dragonflies, was flying around with a wingspan of 28 inches—more than 2 feet!

- The evolution of woody plant tissues may have been responsible for the evolution of the first beetles. The beetle body plan is well adapted for living in tight spaces, like under tree bark. Indeed, some of the earliest fossil beetles appear to be specialized for boring into wood. Being well protected while still having the ability to fly may have been one of the first advantages that set beetles up for evolutionary success.

- Another innovation that may have helped beetles flourish was the ability to digest the lignin and cellulose in plant cells thanks to the evolution of specialized enzymes. These enzymes are rare in animals, and many that consume plant matter, like termites, are only able to do so because they have microorganisms living in their guts that produce these enzymes. That's true of many beetles, too, but beetles also evolved the ability to make these digestive enzymes themselves.

- Once beetles had the ability to break down the tough cell walls of plants, they began to really flourish, with many species becoming specialized herbivores in the Jurassic and Cretaceous periods. Bursts of new species came into existence and expanded into new niches. And as new types of plants came into existence, the beetles were able to take advantage of them. Beetles may have been among the first insect pollinators since bees, butterflies, and moths did not yet exist when flowering plants first appeared.

Beetle Survival

- A comparison of speciation rates—the rates at which new species come into existence—between beetles and other insects suggests beetles have not diversified faster than other groups. So, we can't say that there are so many beetle species because they multiplied faster than other groups. But it may be that beetle species have been more likely than other groups to survive. The fact that beetles have existed since at least the Permian period means that beetles have survived three of the five major mass extinction events in Earth's history.

- The mass extinction event that marked the end of the Permian period 252 million years ago was the most devastating event in the history of life. Around 96% of all living species disappeared in less than 500,000 years, coming close to the complete elimination of all life on Earth. We don't yet know what caused it, but one of the leading hypotheses is that a supervolcano erupted around this time. This would have released carbon dioxide and methane into the atmosphere, causing a greenhouse effect great enough to increase temperatures by more than 10° Fahrenheit. Yet somehow beetles survived.

- At the end of the Triassic period, another major mass extinction occurred, this time in two or three phases over a much larger span of about 18 million years. Again, the beetles survived. The most famous mass extinction occurred 66 million years ago, when an asteroid crashed into the Earth. The dinosaurs became extinct, but the beetles once again survived.

- The ability of beetles to live in concealed spaces, including inside living and dead plants, may have been an advantage during times of such devastation and death. The fact that beetles have such diverse lifestyles, including the ability to live in a wide range of habitats and consume many different types of foods, has probably been a hedge against changing conditions.

Reading

National Geographic, "Bombardier Beetles." https://www.nationalgeographic.com/animals/invertebrates/facts/bombardier-beetle.

Questions

1. Which of the following is closest to the number of described species of beetles?

   a 350
   b 3,500
   c 35,000
   d 350,000

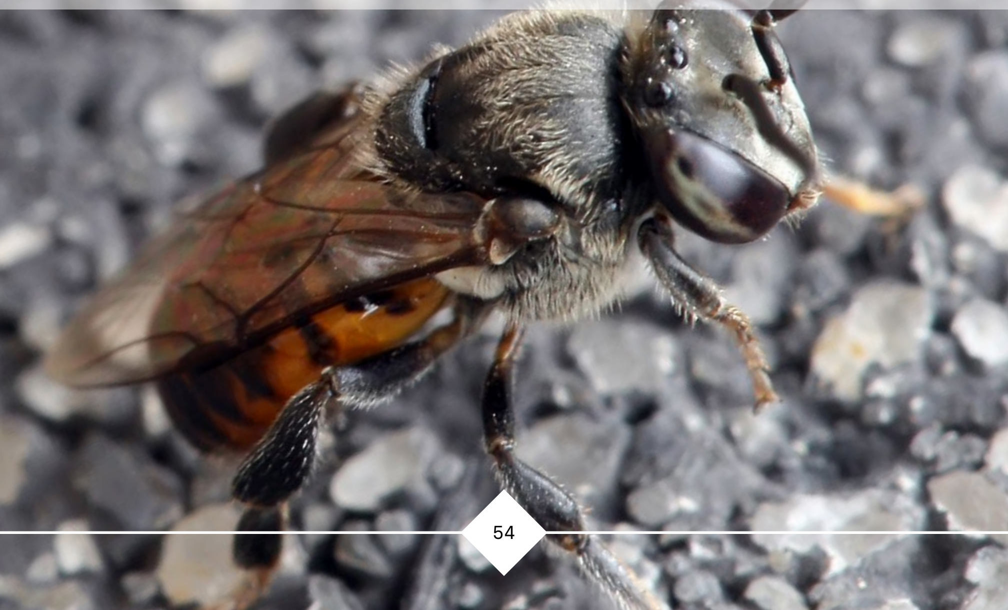
2. A distinctive feature of beetles is a hardened pair of forewings called ______ that come together at rest to form a straight line down the center of the abdomen.

ANSWERS CAN BE FOUND ON PAGE 223.

LECTURE 6

Pollinators We Cannot Live Without

About two-thirds of North American crops depend on insects for pollination. Worldwide, the numbers are even higher: Out of the 94 most important crop plants grown around the world, 75 of them—that's 80%—are pollinated by insects. Altogether, insect pollinators contribute about $195 billion dollars to the global economy.



Honeybees

- Pollination is all about moving pollen grains, which contain sperm, to the female part of the flower so that fertilization can occur. In some types of plants, like many grasses, pollen is blown by the wind from one flower to another, so the only thing needed for pollination is a good breeze. But a lot of the pollen that blows in the wind never makes it to another flower. As many seasonal allergy sufferers are well aware, the air can be filled with pollen during certain times of year. That's because wind-pollinated species have to make a ton of pollen to ensure that at least some of it makes it to another flower.

- On the other hand, plants that are pollinated by animals, like bees, are much less likely to waste pollen because the same bee often visits many different flowers from the same species as it's out collecting food. Beekeepers refer to this quality as the flower constancy. The flower constancy of the honeybee is about 90% or higher, meaning that when a honeybee is flying around, 90% of the pollen it's carrying is from a single species of flower.

- Another reason that honeybees are great pollinators is that they're fuzzy. A honeybee's exoskeleton is covered in hairs, or setae, which are branched, like feathers. In addition to making them endearing to humans, these branched hairs are what makes pollen stick to a honeybee's body after it visits a flower.

- When a bee visits a flower, the pollen is released from the anther and attaches to the branched hairs on the bee's body. Sometimes this happens unintentionally—if, for example, a bee visits a flower to collect nectar. But sometimes the bees are after the pollen itself, which is rich in protein, fat, vitamins, and minerals. Honeybees mix pollen with honey and saliva, creating a substance known as bee bread, or ambrosia, which they store in cells inside the hive.

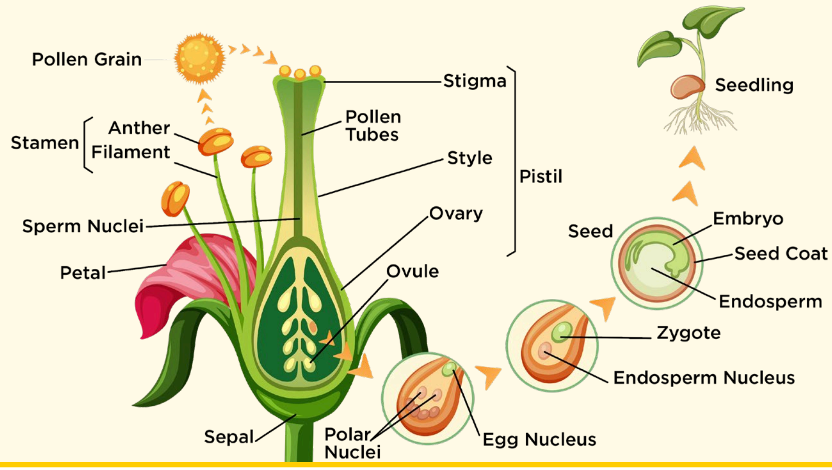
- To get as much pollen back to the nest as possible, honeybees have evolved specialized structures on their hind legs called pollen baskets. The pollen basket is a cavity on the tibia surrounded by long hairs that make it possible for a honeybee to transport as much as 29 milligrams of pollen on each trip—almost a third of its body weight.

- Bees typically visit many flowers on a single outing—anywhere from 50 to 100—adding up to about 1,000 with multiple trips in one day. The pollen attached to a bee's branched hairs can become dislodged if it comes into contact with another flower, especially the sticky top of the female part of a flower called the stigma. Once the pollen reaches the stigma, pollination has occurred.

Encouraging Pollination

- But fertilization is not yet complete. For the plant to reproduce, the pollen grain needs to grow into a pollen tube that will travel from the stigma down through the style to the ovule, which is located near the base of the flower. Within the pollen tube are two genetically identical sperm formed from the pollen grain. One sperm will fertilize the egg, forming a zygote that will then develop into an embryo. The other sperm fertilizes the central cell within the ovule, forming the endospore. Together, the embryo and the endospore make up a seed, which—if all goes well—will germinate and grow into a new plant.

- Plants are generally capable of completing these last few steps on their own, but for many species, transporting pollen from the anther of one flower to the stigma of another flower is a critical step that relies on pollinators like bees. Because this step is necessary for the species to reproduce, many species of plants have evolved strategies to encourage pollination.

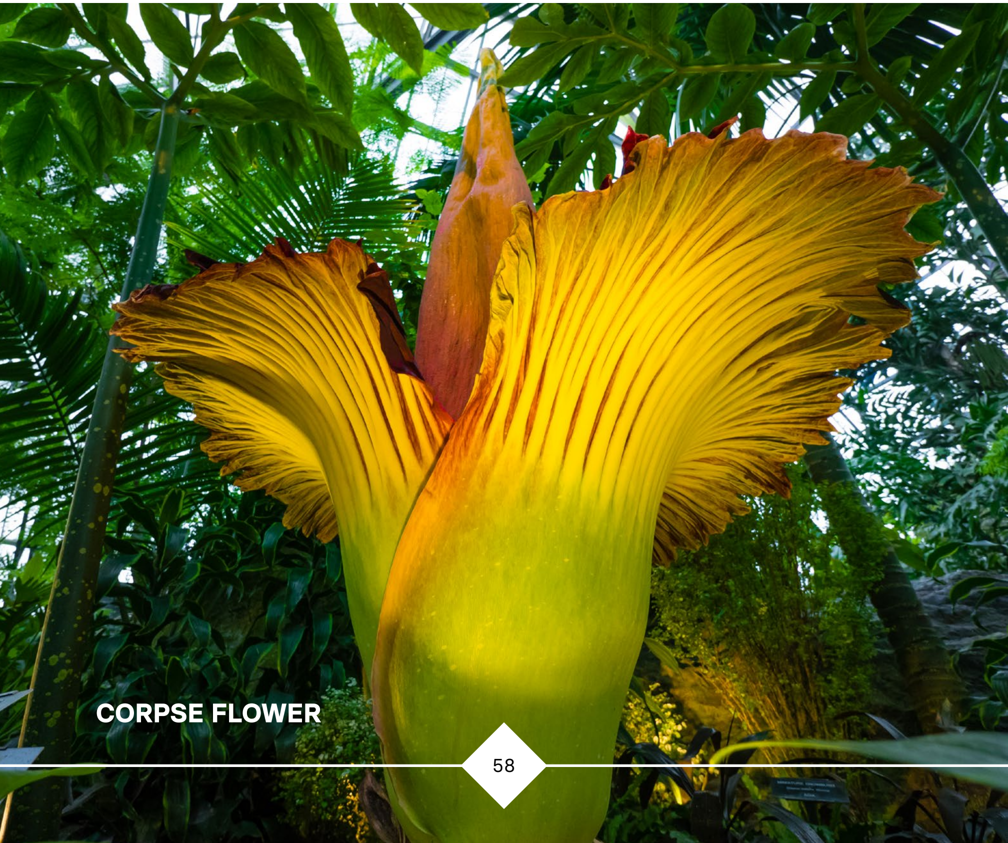


- One common strategy is to entice pollinators by rewarding them with nectar. In fact, the only reason that plants produce nectar, which is made of two of the most precious substances to a plant—sugar and water—is to encourage pollinators to visit. Two German naturalists, Joseph Gottlieb Kölreuter and Christian Konrad Sprengel, figured out in the 18th century that the function of many flowers is to attract pollinators. But it was Charles Darwin's painstaking work in the 19th century that showed the often extreme lengths that plants go to get pollinators to visit and to effectively transfer pollen between flowers.

- Darwin observed, for example, that the stamens of some flowers, like rhododendrons, are curved in such a way that the pollen-covered anthers are directly in the path that a bee must take to reach the nectar. Other flowers, like barberries, have a spring-loaded mechanism by which the weight of an insect on the flower causes the stamen to act like a catapult, launching pollen directly toward the visiting insect.

- Some plants evolved less generous ways to attract pollinators. The bee orchid *Ophrys apifera* has flowers that look and smell like female bees. Male bees visit these flowers thinking they are courting a female bee, and in their efforts to fertilize her, they instead get covered with pollen. The same bee often moves from flower to flower, helping the orchids' reproduction rather than his own.

- Deceiving insect pollinators is a widespread strategy among flowering plants. One of the largest, and most bizarre, flowers in the world is *Amorphophallus titanum*, known as a corpse flower because of the putrid smell of their flowers. The fact the titan arum smells like rotting flesh is no coincidence—it attracts carrion beetles and blowflies that act as pollinators.



CORPSE FLOWER

Bumblebees

- Like honeybees, bumblebees feed on both nectar and pollen and collect these from a wide variety of flowers. Unlike honeybees, bumblebees have small colonies, with at most a few hundred bees, compared to tens of thousands in a honeybee colony. With fewer mouths to feed, and because individual colonies don't persist through winter, bumblebees don't need to store nearly as much food. Instead of making honey, they store small amounts of nectar that isn't thickened through dehydration the way that honeybee honey is.

- The way that bumblebees visit flowers makes them more effective at pollinating some flowers. Bumblebees perform what's known as buzz pollination. When a bumblebee visits a flower, it grasps the base of the anthers with its mandibles and curls its abdomen around the other side. It then decouples the indirect flight muscles from the wings, allowing the muscles to contract without the wings moving. These muscles then contract and relax in rapid succession, creating vibrations that resonate through the bumblebee's body. Because the bee is in direct contact with the anthers, the vibrations are transferred from the bumblebee to the anthers, shaking them rapidly and causing pollen to be released.

- As many as 20,000 different species of plants have flowers that require buzz pollination. If you take a close look at a tomato flower, you can see why buzz pollination works. The petals are often pointed backward, with a cone projected forward encasing the anthers inside. There is a small opening at the tip of this cone, along with the stigma. When a bumblebee lands on the flower and starts buzzing, the pollen grains are released and fall out of the opening in the tip of the cone.

If you're having trouble growing tomatoes in your garden, gently shake the blossoms to release the pollen from the stigmas, allowing it to attach to the stigma right next to it. Some gardeners even use automatic toothbrushes or tuning forks to simulate the vibrations of bumblebees.

- Tomatoes have been bred to be able to self-fertilize without requiring pollinators, but sometimes the plants don't produce tomatoes, or they produce smaller tomatoes, if they haven't been visited by a buzzing bumblebee. So, why would plants that benefit from pollinators evolve ways to make it harder for insects to reach their pollen? Part of the answer seems to be that not all insects follow the rules.

- Some insects, including many bees, are nectar and pollen robbers. They chew a hole through the base of the flower and drink nectar or collect pollen without coming into contact with the flower's stigma, meaning that they don't contribute to the transfer of pollen between flowers. One of the advantages of buzz-pollinated flowers is that it's harder for thieves to steal their pollen because the anthers are enclosed and the pollen isn't easily released. And these flowers typically don't produce nectar, so they're less attractive to nectar robbers.

Colony Collapse Disorder

- Bumblebees aren't the only insects that can buzz pollinate. Many other bees can, too, although honeybees are a notable exception. The fact that honeybees cannot buzz pollinate means that, despite being the most commonly used commercial pollinators, honeybees are not able to pollinate all crops.

- Still, honeybees remain the most important pollinators for crop plants in North America. This reliance on honeybees as commercial pollinators is why there has been so much concern about a recent phenomenon known as colony collapse disorder, in which almost all honeybee workers within a seemingly healthy colony suddenly disappear. The causes for colony collapse disorder have been debated, but several factors seem to be associated with it.

- One factor is the widespread use of pesticides known as neonicotinoids, which have a neurotoxic effect on insects. These pesticides are effective at killing pest insects that eat leaves and other parts of crop plants. But neonicotinoids accumulate in all parts of a plant, including nectar and pollen, meaning that insects that collect large amounts of nectar and pollen for food are especially vulnerable to their effects.

- Another factor is a parasitic mite called *Varroa destructor*, which lives inside honeybee colonies and can spread viruses and fungal diseases. The movement of managed honeybee hives across long distances to serve as pollinators for different crops in different regions and seasons makes it easier for diseases to spread between hives. And sudden temperature fluctuations can weaken bees' immune systems.

We still don't know which of these factors is most responsible for colony collapse disorder. Fortunately, the phenomenon has been widely publicized, which has led to a growing awareness of the plight of honeybees—as well as native pollinators—and a reminder of how important they are to us as pollinators.

Reading

McAlister, "The Unexpected Pollinator of the Cocoa Tree." https://www.sciencefriday.com/articles/meet-the-flies-that-pollinate-cocoa-trees/.

Pearson, "You're Worrying about the Wrong Bees." https://www.wired.com/2015/04/youre-worrying-wrong-bees/.

United States Department of Agriculture, "Insects and Pollinators." https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/plantsanimals/pollinate/.

Questions

1. True or false: Pollen can become attached to a bee without the bee ever touching a flower.

2. Which of the following plants is incorrectly matched with its insect pollinator?

   a cacao (chocolate) / midges
   b vanilla / stingless bees
   c figs / fig wasps
   d titan arum / bumblebees

ANSWERS CAN BE FOUND ON PAGE 223.

<<< TABLE OF CONTENTS

LECTURE 7

Insect Herbivores

Worldwide, insects are the most important herbivores. They collectively have a greater impact on plant populations than mammalian herbivores do because of the sheer number of herbivorous insects. About half of all known insect species—about 450,000 species—are herbivores. By comparison, there are only about 6,451 species of mammals. And because many herbivorous insects have enormous numbers of individuals, their impact on plants is tremendous.

Herbivore Strategies

- The ability to feed on and digest plants evolved fairly early on in insect evolution, with a proliferation of herbivorous insect species coming into existence between 345 and 280 million years ago. This coincides with the rise of the first forests, consisting of horsetails, ferns, and conifers whose decayed organic matter became coal. These plants offered reliable sources of energy and nutrients to those species that could find a way to access them.

- Insects evolved a wide range of strategies to feed on different parts of plants. Cochineal bugs have piercing-sucking mouthparts they use to penetrate plant tissues and suck out their fluids. The *Cactoblastis* moth larvae, on the other hand, use their mandibles to chew and eat plant tissues from the outside in. Both strategies have evolved numerous times and are common among insect species.

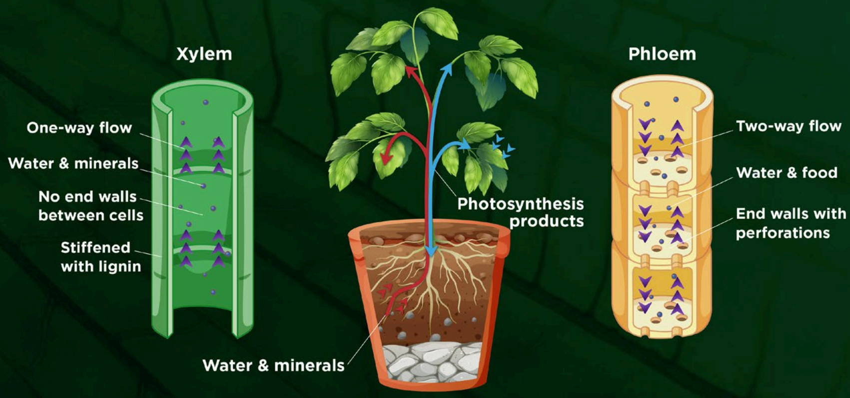
- Cochineal bugs belong to the order Hemiptera, which contains more than 93,000 species. All hemipterans have piercing-sucking mouthparts called a proboscis, and many of them feed on plant fluids. The proboscis is formed by the mandibles and maxillae that have been modified to form stylets that function like needles.

- The stylets form a bundle, and inside are two tubes. One of the tubes allows saliva to flow from the salivary glands in the insect's head through the proboscis and to the plant tissue. This aids in digestion and keeps the fluid flowing. The other tube allows the plant sap to flow up the proboscis and into the insect's digestive system.

- The plant fluids that insects like cochineal bugs feed on are used by plants for transporting water and nutrients to different parts of the plant. Plants have a system of tubes to transport these fluids around. One type of tube, called xylem, transports water from the roots up to the stems and leaves. The other, called phloem, transports sugars made in the leaves to the rest of the plant.

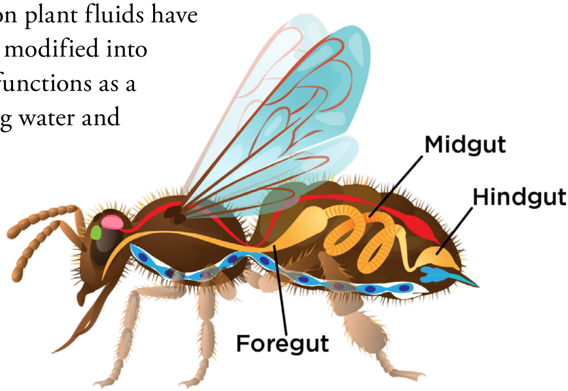
- The phloem, being more nutritious, is the fluid most insects are after. Phloem contains about 30% nutrients and 70% water, so insects still need to consume a lot of it to get the nutrients they need. But that's not hard to do, because phloem is under pressure and readily flows out of any wound.

- In contrast, insects that feed on xylem, like cicadas, have to suck the fluid out of the plant. That's because xylem makes its way from the roots of a plant up to the stems and leaves through a combination of capillary action and negative pressure created by the loss of water from small pores in leaves through the process of transpiration. For this reason, xylem feeders have a pump in their heads at the base of the proboscis that contains muscles that contract to create negative pressure to suck out the xylem.



The Insect Digestive System

- Once the fluid enters the insect's body, it needs to be processed. The insect digestive system is divided into three parts: the foregut, the midgut, and the hindgut. In most insects, the midgut is where most digestion and absorption of nutrients takes place. But hemipterans that feed on plant fluids have a midgut that has been modified into a coiled structure that functions as a filter chamber, directing water and sugars to the hindgut. Most of the sugar is then absorbed, and the excess water is eliminated from the anus.



- The digestive tracts of insects that feed on plant juices have evolved to allow them to handle large volumes of dilute liquid. Because these insects have to consume large quantities of dilute liquids to get enough energy and nutrients, they end up excreting a lot of liquid waste. While the insect's digestive systems absorb much of the sugar, some of it remains in the liquid waste, known as honeydew.

- While rich in carbohydrates, plant fluids are low in other important nutrients, such as some essential amino acids. To compensate, many insects that feed exclusively on plant fluids have symbiotic microorganisms like bacteria living within their bodies. These microbes contribute the missing nutrients to their hosts in exchange for a safe environment and access to carbohydrates.

Ants love to eat honeydew. Many species use fluid-feeding insects like aphids and mealybugs as livestock, guiding them toward good places to feed, protecting them from predators, and milking them when they get hungry for a sweet treat.

- In contrast to the many species of herbivorous insects that rely on microbes to supplement their fluid diets, caterpillars like *Cactoblastis* don't seem to have many resident microorganisms. That's probably because many caterpillars feed on leaves and other parts of plants that contain a more complete set of nutrients than do plant fluids.

- Other insects have adopted a different way to use microorganisms to help them eat plants. Leafcutter ants are among the most voracious insect herbivores, but they can't digest leaves themselves because they don't produce the right kinds of enzymes to break down the lignin and cellulose. Instead, they rely on fungi that do produce the necessary enzymes as a sort of external digestive system.

- Leafcutter ants are very good at cutting leaves, thanks to mandibles with extremely sharp edges that contain zinc. Once a leaf fragment has been cut, the leafcutter ant workers carry them back to their nests, where they are cut into even smaller pieces. The tiny leaf bits are then carefully placed on the fungus garden to allow the fungus to break it down. A single colony of leafcutter ants can consume as much vegetation as an adult cow. And if you add up the weight of the 5 million or so ants that live in a colony as well as all the fungi they grow in the nest, the combined weight of this superorganism would weigh about the same as a cow.

Plant Defenses

- Not surprisingly, plants have evolved different ways to defend themselves against the hordes of insects out to eat them. The defenses come in many different forms, including physical barriers that make it hard for insects to crawl along a plant and toxic chemicals that poison anything that consumes them.

- Many plants, like milkweed, use more than one defense. Milkweed gets its name from the thick, white sap that oozes from any wound inflicted on its leaves or stems, such as might be made by a chewing or sucking insect. The sap, or latex, is under pressure within the plant's tissues, so any damage to those tissues causes the latex to gush out and spread around the wounded area. The latex is extremely sticky, and insects can become entangled and permanently trapped by it as it dries in just a matter of minutes.

- The leaves and stems are also covered in a carpet of fine, white hairs called trichomes that make it difficult for insects, especially small ones, to feed on the edible tissues beneath them. But the most formidable defense against herbivores that milkweeds possess is the chemical composition of their milky latex. Milkweed latex contains a cocktail of toxic chemicals including cardenolides, a type of steroid that interferes with the function of animal cells and is lethal in high doses.

- Given the triple threat of defenses that milkweeds possess, you might think that it is well protected from herbivorous insects. Indeed, there are only a handful of species that have evolved to be able to bypass all three defenses and feed on milkweed. Interestingly, these species have become specialized in eating milkweed.

Milkweed and Monarchs

- The most famous of the insects that evolved to be able to eat milkweed is the monarch butterfly, *Danaus plexippus*. While adult monarchs can feed on nectar from the flowers of a wide range of different types of plants, the caterpillars have a much more particular diet—they can only eat milkweed.

- Not all caterpillars are able to overcome all of the defenses that milkweed evolved. Many baby monarch caterpillars—about 60% in one study—succumb to the sticky latex after their first nibble of milkweed. Those that survive clear an area of its trichomes—those fuzzy hairs that coat the surface of milkweed leaves and stems—by cutting them near the base with their mandibles. They don't eat the trichomes, but removing them from an entire area makes it much easier to feed on the tissues below.

- The next step is often to create what monarch biologist Anurag Agrawal calls a circle trench. By cutting into the milkweed and turning its body and cutting again, the monarch caterpillar creates a circle that quickly turns white as the latex oozes out. This leaves the area inside the circle with only a limited source of latex with which to defend itself. This strategy has the added benefit of making it hard for predators to reach the caterpillar, as it is surrounded by sticky latex.

- But the caterpillar still has to get past the last and most challenging of the milkweed's defenses: its toxic cardenolides. Monarchs' ability to feed on milkweed without being poisoned can be traced to a mutation in a gene that makes part of the sodium-potassium pump found in the cell walls of all animals. A mutation involving just a single DNA base change was enough to make it difficult for cardenolides to bind to the sodium pump, thereby minimizing its toxicity.

- Monarchs also manage to use these toxins to their advantage. The reason that both monarch butterflies and their caterpillars are so brightly colored is to serve as a warning to potential predators that they are toxic. They get their toxins from the cardenolides in the milkweed they eat as larvae, which are retained in the adult. Predators learn to associate the color patterns of monarchs with the unpleasant, bitter taste of cardenolides, which often make them vomit.

- The cardenolides that monarchs sequester from the milkweeds they eat can also be used to protect themselves from enemies on the inside. Protozoan parasites called *Ophryocystis elektroscirrha*, or OE, can make monarch butterflies sick and reduce their reproductive output. Biologist Jaap de Roode discovered that monarchs infected with OE tend to lay their eggs on milkweeds with higher concentrations of cardenolides, giving their offspring the ability to develop higher cardenolide levels in their bodies. And having higher cardenolide levels reduces the number of OE spores in monarch caterpillars.

> Many of the chemical defenses that plants evolved to protect themselves from insect herbivores can be used medicinally. About 40% of our medicines—including opiates, quinine, and aspirin—are derived from plants, and many of these evolved as defenses against hungry insects.

Monarchs and milkweeds have been coevolving for millions of years. As milkweeds evolved more effective defenses, monarchs evolved ways to get around them, prompting even stronger milkweed defenses. Similar dynamics between plants and herbivorous insects have played out for hundreds of millions of years, resulting in an astounding diversity of both plant defenses and insects specialized to get around them.

Reading

Agrawal, *Monarchs and Milkweed*.
Greenfield, *A Perfect Red*.

Questions

1. A red dye called ______ that is made by scale insects was produced by the Aztecs and became a valuable commodity in the Spanish colonial empire.

2. True or false: A mature leafcutter ant colony consumes as much vegetation as an adult cow.

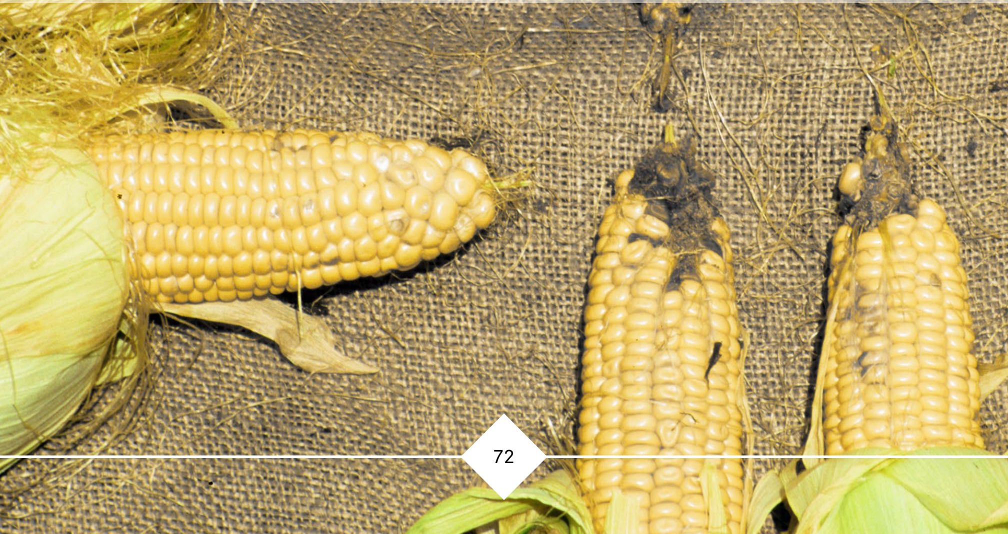
ANSWERS CAN BE FOUND ON PAGE 223.

<<< TABLE OF CONTENTS

LECTURE 8

Insect Pests

Each year, American farmers plant more than 90 million acres of corn—an area about the size of New Mexico—producing some 350 million tons of corn. That corn feeds both people and livestock. It's used to produce the ethanol that fuels our vehicles. Corn is even used in products like toothpaste, shampoo, cosmetics, diapers, paper, cardboard, tires, batteries, and bioplastics. Overall, the US corn industry is worth more than $60 billion. It's easy to understand why pests that attack corn are cause for serious concern.



Corn Rootworms

- Corn rootworms are the larval stage of several species of beetle in the family Chrysomelidae. As their name suggests, these beetle larvae, commonly known as grubs, feed on the roots of the corn plant. The western corn rootworm, *Diabrotica virgifera*, has an association with corn that may go back to teosinte, the ancestral plant from which corn was domesticated in Mesoamerica some 4,000 years ago. As corn cultivation by Native Americans spread into North America, the western corn rootworm spread with it.

- In the area that is now the midwestern United States, corn crops encountered another species: *Diabrotica barberi*, the northern corn rootworm. Northern corn rootworm larvae fed on the roots of native prairie grasses, but as corn became more abundant—especially after the arrival of European settlers who planted corn across much of the midwestern prairies—they switched hosts and became another corn pest.

- The larvae pupate in midsummer and typically emerge as adults in July or August. After a few weeks of feeding on the leaves and flowers of the corn plant, females mate and lay eggs in the soil near the base of the plant. The eggs will remain there in a dormant state known as diapause through the fall and winter. When the eggs finally hatch in the spring, the larvae need to start feeding on corn plants right away.

NORTHERN CORN ROOTWORM

- Luckily, the life cycle of these beetles made it relatively simple to minimize their damage to corn crops. Corn is an annual plant, meaning it has to be planted again each year. By rotating crops, farmers could avoid corn rootworm damage simply by not planting corn in the same place two years in a row. If the corn rootworm larvae emerge and find another crop, like alfalfa or soybeans, the grubs will starve.

- But in the middle of the 20th century, some of the northern corn rootworms began diapausing longer, emerging after two winters had passed. Farmers that planted corn in a particular field every other year once again found their corn crops infested with rootworm. The extended diapause strategy was successful for the beetles, and it began to spread. By the 1990s, crop rotation was no longer a solution to the northern corn rootworm problem.

- Western corn rootworms also found a way to get around crop rotation. In the 1980s, female beetles began laying their eggs near soybean plants rather than corn plants. Because farmers were alternating corn and soybeans every other year, eggs that were laid near soybeans in the fall would emerge as larvae the following spring surrounded by corn plants.

Moth Pests

- Corn farmers face other insect pests, too. *Helicoverpa zea* is a moth in the family Noctuidae whose larvae are known as corn earworms. The female moths lay their eggs on the silky tassels that stretch from the corn kernels out the tip of the ear, where the sticky silk captures pollen blown by the wind. The eggs hatch in just a few days, and the larvae—small, light yellow caterpillars—emerge. The caterpillars feed on the corn silk and then crawl into the ear, where they eat the corn kernels.

- Unlike corn rootworms, the corn earworm isn't restricted to eating only corn. They also feed on tomato, cotton, soybeans, and tobacco, among other crop plants. But corn earworms are nevertheless one of the most damaging pests of corn crops, infesting as much as 98% of the ears in some cornfields. Infestations of corn earworm are untreatable once established.

- Another type of moth that attacks corn is *Ostrinia nubilalis*, known as the European corn borer. As the name suggests, it arrived in North America from Europe in the early 20th century. This moth belongs to the family Crambidae. The larvae chew holes in the stalks of corn plants and sometimes into the ears as well.

- Unlike the corn earworm and corn rootworm, the European corn borer can survive through the winter as a fully grown caterpillar by going through diapause inside the plant tissue. This life cycle gives them a head start in the spring, and they develop quickly enough that they can complete two entire generations each year. In addition to lower yield caused by caterpillars that feed directly on corn kernels, damage to the stalks can weaken plants, increase disease prevalence, and destroy plants by causing them to collapse.

DDT

- Beginning in the 1940s, synthetic chemical pesticides that killed insects and appeared to have minimal effects on humans and other animals were discovered. Among the exciting new chemicals was DDT, or dichloro-diphenyl-trichloroethane. DDT disables the proteins that form sodium channels in the cell membranes of insects. Without functional sodium channels, nerve cells can't send signals. So, DDT kills insects on contact by disabling their nervous system.

- Due to its effectiveness on many types of insects and the fact that it persists in the environment long after it has been applied, DDT was used to control a wide range of agricultural pests, including corn rootworm, corn earworm, and the European corn borer. By 1959, 80 million pounds of DDT was being used per year, mostly to control agricultural pests. Yet there were concerns that DDT could harm beneficial insects, like bees, and that it might be toxic to people in high quantities.

- These concerns became widely known in 1962 thanks to the publication of the book *Silent Spring* by marine biologist and writer Rachel Carson. Many of the features of DDT that made it attractive as a pesticide turned out to also make it particularly harmful to other species. DDT lasts for decades in soil and is not water soluble, so rainfall causes it to accumulate in streams and rivers. Small amounts of DDT get taken up by plants, which are eaten by animals, which are eaten by larger animals. Through this process of bioaccumulation, animals near the top of the food chain, like bald eagles, were consuming very large doses of DDT.

- In addition to concerns about the safety of DDT, there were also indications that it was becoming less effective. The widespread use of DDT to control household pests led to the evolution of houseflies resistant to DDT as early as 1947. Soon after, DDT resistance began showing up among agricultural pest insects. The more often DDT was used, the greater the advantage became for any individual insects that happened to have genes that made them less susceptible to DDT. Those individuals were more likely to survive and reproduce, passing on their genes to the next generation. The same process is likely to play out for any pesticide.

> *Silent Spring* contributed to the growth of the environmental movement in the 1960s, which led to the establishment of the Environmental Protection Agency in 1970 and the ban of DDT in the United States in 1972.

Genetically Modified Crops

- As the science of genetics and biotechnology developed in the late 20th century, it became possible to insert genes from one organism into another. Through this copy-and-paste approach to genetic engineering, useful properties of one organism could be transferred into a different organism. An organism of one species that contains genes from a different species is known as transgenic. Another term that has become widely used is "genetically modified organism," or GMO.

- In the case of controlling insect pests, a soil bacterium called *Bacillus thuringiensis* was identified. It produces proteins called delta endotoxins that are toxic to insects when ingested. Different versions of the delta endotoxin proteins are toxic to particular types of insects, like flies or beetles. The genes that *Bacillus thuringiensis* bacteria use to make these delta endotoxins have been inserted into some crop plants, allowing the plants to produce their own insecticides. These genetically modified, or GM, crop varieties go by the name Bt, from the initials of the species from which the genes were taken.

- Bt corn can produce different types of delta endotoxins that target its primary insect pests, including corn rootworm, European corn borers, and corn earworms. Any of these insects that feed on Bt corn will die before they can mature, minimizing the damage to the crop. Many farmers like GM crops because they can keep their crop free from insect damage without having to apply any additional pesticides.

- Yet in much the same way that insects evolved resistance to chemical pesticides like DDT, some pest insects began to evolve resistance to the Bt toxins once they became widely used. And there have also been concerns about the safety of genetically modified crops for both humans and the environment. There is a lot of debate about whether there are any risks to people who eat food made from genetically modified crops, and some countries have imposed restrictions on their use.

Integrated Pest Management

- The lesson that has emerged from efforts to control pest insects is that no single strategy is perfect. Technologies like chemical pesticides or genetic modification of crop plants can work well, but their overuse leads to the evolution of resistant insects. There can also be unintended consequences for human health and the health of ecosystems.

- Rather than relying exclusively on a single way to control pest insects, farmers have increasingly adopted a multifaceted approach known as Integrated Pest Management. This system can include the judicious use of chemical pesticides in addition to a variety of other ways to deal with pest insects. An important aspect of this approach is scouting, or keeping an eye out for pest insects in the early stages of an infestation.

- Integrated Pest Management can include choosing the most appropriate strains of crops, which may include genetically engineered varieties. It can also involve crop rotation and timing planting and harvesting to take into account the life cycles of pest insects. The effective use of Integrated Pest Management requires a thorough understanding of not only the crop plants but also the biology of the pest insects.

- For example, the boll weevil, *Anthonomus grandis*, is a beetle in the family Curculionidae that attacks cotton plants. The first attempts to control boll weevils with pesticides were not effective. Likewise, Bt cotton quickly lost its efficacy as boll weevils evolved Bt resistance. But as researchers learned more about the biology of boll weevils, new approaches to control them became possible.

BOLL WEEVIL

Growing varieties of cotton that mature more quickly gave boll weevils less time to complete their life cycle and reproduce. Because boll weevil adults survive through the entire winter in a state of diapause among the cotton stalks, destroying the remains of cotton plants after harvest helped to cut the weevil's life cycle short. But the most important development was that the pheromones produced by boll weevils can be used to lure them into traps. These approaches have been successful at eradicating boll weevils from much of the Cotton Belt and minimizing the use of pesticides in areas where they are still present.

Reading

Conis, "Beyond *Silent Spring*." https://www.sciencehistory.org/distillations/beyond-silent-spring-an-alternate-history-of-ddt#:~:te.

Featured Creatures, "Southern Pine Beetle." https://entnemdept.ufl.edu/creatures/trees/southern_pine_beetle.htm.

United States Environmental Protection Agency, "Integrated Pest Management (IPM) Principles." https://www.epa.gov/safepestcontrol/integrated-pest-management-ipm-principles.

Questions

1 Why was the pesticide DDT discontinued in the United States in 1972?

a It was becoming less effective.
b There were concerns about its harmful effects on wildlife.
c There were concerns about its harmful effects on people.
d All of the above

2 A modern approach to pest control that embraces a combination of older techniques, like crop rotation, as well as newer techniques, such as genetic engineering, is knows as ______.

ANSWERS CAN BE FOUND ON PAGE 223.

LECTURE 9

Insect-Borne Disease

One of the most profound ways that insects have affected people throughout history is through the diseases that they can transmit to humans. While many types of insects can be vectors for infectious disease, the insect that has had by far the greatest impact on human affairs is the mosquito. Mosquitoes are capable of transmitting a wide range of diseases, but yellow fever and malaria stand out as having influenced the course of history in the most significant—and often surprising—ways.

Malaria in the Ancient World

- The historical record is filled with examples of the roles that yellow fever and malaria have played, beginning in the ancient world. The Egyptian pharaoh Tutankhamun suffered from malaria, and it may have contributed to his death in 1323 BCE. One thousand years later, malaria was also the likely cause of Alexander the Great's premature death in 323 BCE, at the age of just 32.

- The inability of Hannibal to conquer Rome led to its establishment as the dominant culture in the Mediterranean, Europe, and the Middle East, lasting for about 700 years. Rome's longevity was possible thanks in part to the protective moat of malarial mosquitoes surrounding the city that helped keep out successive waves of would-be invaders, including the Visigoths, Huns, and Vandals.

- While the Italian countryside around ancient Rome was filled with mosquitoes, malaria was common within Rome as well. This was probably due in part to their fondness for aqueducts, ponds, and fountains that provided additional places for mosquitoes to breed. Emperors Vespasian, Titus, and Hadrian are all thought to have died from malaria. Malaria was a constant drain on human resources in Rome, and, along with bubonic plague, it contributed to the eventual fall of the Western Roman Empire.

Disease in the Americas

- Beginning in 1647, mosquitoes carrying yellow fever accompanied slave ships from West Africa to the Americas. Both the slaves and the crew were often infected by yellow fever en route, but the enslaved Africans were less susceptible to yellow fever than the European crew members because many of the Africans had acquired resistance to it from having survived the disease as children.

- Both the virus that causes yellow fever and the mosquito that vectors it, *Aedes aegypti*, became established in the Americas by the late 17th century. They first arrived on the tropical islands of the Caribbean and from there were carried to mainland North and Central America. Along with other diseases brought by Europeans, like measles and smallpox, yellow fever decimated Native American populations and paved the way for European conquests.

- Summer outbreaks of yellow fever became a regular part of life in newly established North American cities like Philadelphia, New York, and Boston, reaching as far north as Quebec City. Yellow fever wreaked particular havoc in cities further south, like Charleston and New Orleans, where milder climates allowed *Aedes aegypti* to survive the winter. With mosquitoes thriving throughout the countryside, the American South became a hotbed of yellow fever.

Quinine became an important commodity for European nations during the colonial era. Cinchona trees were exported to establish plantations in other tropical regions, especially the Dutch East Indies, where they were grown on a much larger scale. Armed with plentiful quinine, European powers began their push to establish colonies throughout the African continent, where the risk of malaria had previously made European exploitation too costly.

- Mosquitoes and their diseases also played a role in the Civil War. Soldiers in both the Confederate and the Union armies faced hordes of biting mosquitoes, but the Union troops had a ready supply of quinine, a drug that can both prevent and treat malaria infections. The Union's blockade of the South kept the Confederacy from accessing the life-saving drug, which comes from cinchona trees native to South America. The impact of this discrepancy in quinine access contributed to the manpower shortage that ultimately led to the defeat of the Confederacy and the end of the Civil War.

Mosquitoes

- For much of history, the actual cause of diseases like yellow fever and malaria remained a mystery. The word *malaria* comes from Italian and means "bad air." The Greek word *miasma*, meaning "pollution," was used to describe the mysterious vapors that were thought to bring disease when inhaled. Malaria was known to be associated with swampy places with stagnant water. Swamps also tend to harbor microorganisms that produce methane gas as a smelly by-product of their metabolism, which we now know is the source of the bad air. It wasn't until the end of the 19th century that mosquitoes, which breed in stagnant water, were identified as the actual source of malaria as well as many other diseases.

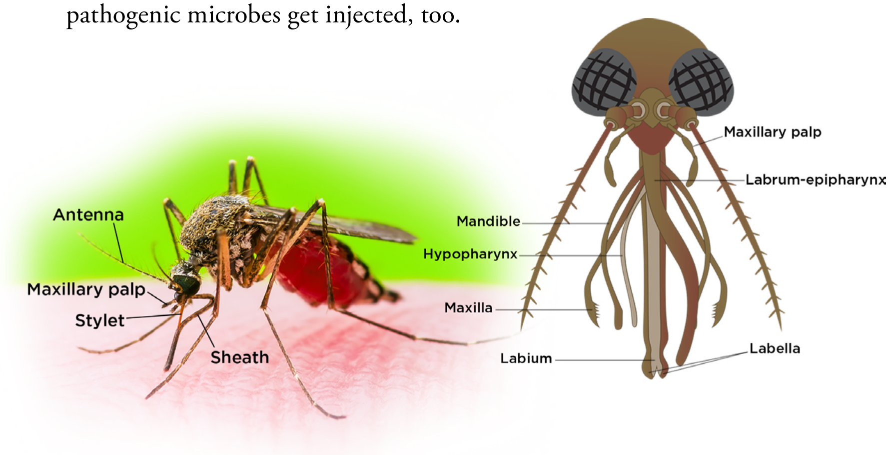
- Adult mosquitoes don't all feed on blood. In fact, the males never do—they get their energy from nectar or honeydew excreted by plant-sucking insects like aphids. Female mosquitoes supplement their diets with blood meals when they can to provide essential protein for their eggs. The time of day when female mosquitoes search for blood meals varies by species. *Anopheles* species, the vectors for malaria, are active at dawn and dusk.

- The mosquito's feeding biology makes it ideal as a disease vector. Once a female mosquito finds a host, it uses its specialized mouthparts to access and retrieve the blood. Two pairs of sharp stylets in the fascicle—part of the proboscis—penetrate the skin. One pair is formed by the maxillae and has a jagged edge that cuts like a serrated knife. Another pair, formed by the mandibles, opens the tiny wound created by the maxillae.

- Meanwhile, the labium, which forms a sheath that surrounds the fascicle, retracts as the fascicle pushes deeper into the skin. A hollow tube called the hypopharynx channels the flow of saliva and contains anticoagulants from the salivary glands to prevent clotting. Another hollow tube, the labrum, acts like a straw to suck blood into the mosquito's digestive system.

- The itchiness of mosquito bites comes from a reaction to a cocktail of proteins contained in the saliva. The proteins differ by species, but they function in similar ways to help the mosquito feed. They keep blood flowing by preventing blood vessels from constricting and they prevent the blood from clotting or coagulating. They also reduce the perception of pain to avoid getting swatted.

- In addition to making their bites itchy, a mosquito's saliva is also the delivery vehicle for the viruses and parasites that cause mosquito-borne disease. These microbes accumulate in the salivary glands. When a mosquito injects saliva into a wound to keep the blood flowing, the pathogenic microbes get injected, too.



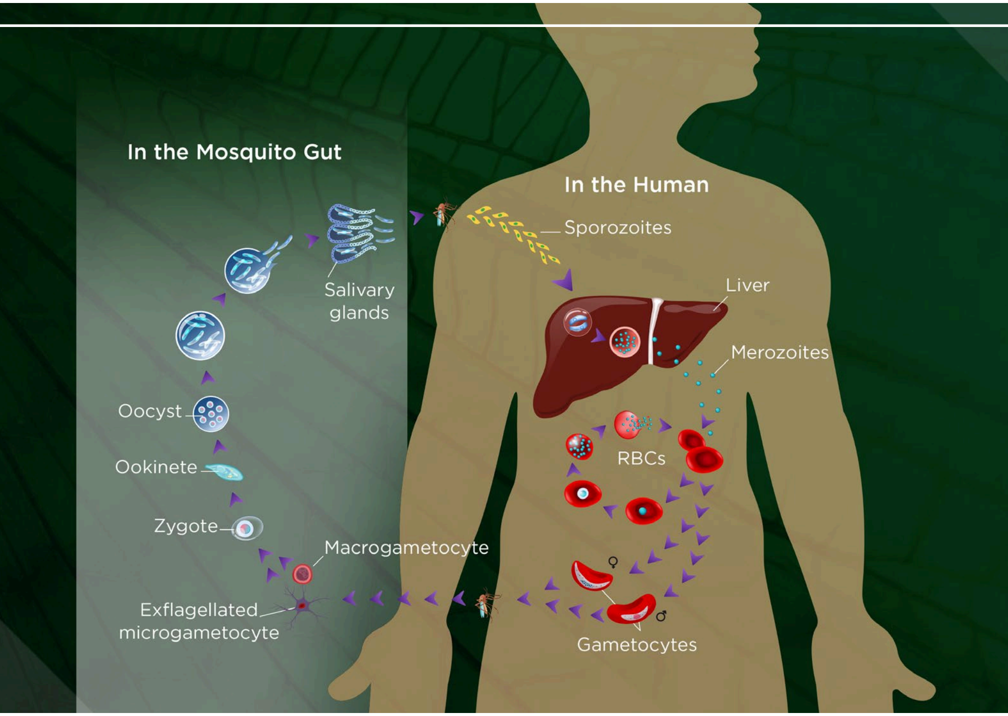
The *Plasmodium* Parasite

- Italian physician Giovanni Grassi was the first to work out the complex life cycle of the organism that causes human malaria—a parasite in the phylum Apicomplexa and the genus *Plasmodium*.

- *Plasmodium* enters a person's body through the bite of an infected *Anopheles* mosquito in the form of small cells called sporozoites that travel first to the liver. After multiplying inside liver cells, the parasite emerges in a new form called merozoites that have specialized structures that allow them to penetrate red blood cells. The merozoites further divide inside the red blood cells, and large numbers of merozoites eventually burst out of the red blood cells, causing the fever and chills that are characteristic of malaria.

- At this point, there are large numbers of merozoites circulating in the bloodstream. They develop into yet another stage called gametocytes, which are either male or female. At this time, if another mosquito bites the person and takes a blood meal, chances are good that the mosquito will ingest some male and female gametocytes along with the blood. The *Plasmodium* parasite completes its life cycle inside the mosquito.

- Fertilization, in which the male and female gametocytes come together to form a zygote, takes place in the mosquito's midgut. The zygote then develops into a form that is capable of moving around and penetrating the tissue that forms the lining of the mosquito's gut. Embedded within the gut lining, the parasite forms a round structure called an oocyst. Within the oocyst, thousands of sporozoites are formed, and they are eventually released into the mosquito's body cavity.



Like all insects, mosquitoes have an open circulatory system in which the circulatory fluid, called hemolymph, transports nutrients, hormones, and energy to all the organs of the body. Once the *Plasmodium* sporozoites are released into the hemolymph, they, too, can travel to all the mosquito's organs. But the one organ they target is the salivary gland. Once they enter the salivary gland, the sporozoites are ready to be injected with the mosquito's saliva into the blood of whoever is unlucky enough to be the mosquito's next host.

Combatting Mosquito-Borne Diseases

- It was clear by 1897 that the *Plasmodium* parasite causes malaria and that it's transmitted by mosquitoes. But knowing that mosquitoes spread the disease didn't necessarily mean people could stop it. In yet another 1897 discovery, Robert Koch was able to confirm that quinine kills the *Plasmodium* parasite.

- During World War II, as the Japanese expanded to occupy much of the Pacific, they gained control over some 90% of the global raw quinine supply. As the war progressed in regions with endemic malaria, Allied troops were at risk of being set back by the disease. By some estimates, 60% of all the American troops who saw action in the Pacific theater contracted malaria.

- With the source of the only drug known to be effective against malaria largely controlled by the Japanese, a secret malaria project became part of the American war effort. Out of this project came a new drug called atabrine that was somewhat effective against malaria. Another outcome of the effort to control malaria during World War II was the discovery in 1939 by Paul Hermann Müller that the chemical DDT can kill mosquitoes on contact.

While Benito Mussolini had attempted to eradicate malaria from Italy in the 1930s by draining the Pontine Marshes and improving infrastructure, the Nazis intentionally undid this progress by flooding the marshes in 1944 to encourage *Anopheles* mosquitoes to proliferate.

- In the postwar years, it looked like an end to humanity's war against mosquito-borne diseases might be within reach. Malaria rates plummeted around the world. By 1951, thanks in large part to DDT, malaria had been eliminated from the United States. But widespread use of DDT led to health concerns for both people and wildlife, and it was banned in the United States in 1972. Nevertheless, DDT is still used in some countries to control malaria and other diseases spread by insects.

- Aside from concerns about its toxicity, DDT was becoming less effective as mosquitoes evolved resistance to it. In much the same way, new drugs like chloroquine and mefloquine became ineffective as resistance evolved. It's clear that any chemical approach to try to kill either the mosquito or the pathogens it spreads will ultimately fail because resistant strains will inevitably develop.

- Unfortunately, diseases spread by insects, including malaria and yellow fever, continue to be a major problem worldwide. Yellow fever affects about 200,000 people each year and leads to about 30,000 deaths. About half of the world's population is at risk of contracting malaria, which infects more than 200 million people each year and kills about 400,000. Climate change is expected to allow mosquitoes to expand into previously unsuitable regions, exposing even more people to malaria and other diseases.

- Even as we look toward more sophisticated techniques to combat mosquitoes and their diseases, some of the simplest approaches remain the most effective. Preventing mosquitoes from breeding by eliminating standing water is one of the best ways to control the spread of mosquito-borne disease. The use of window screens and bed nets is also effective and much less expensive than drugs or pesticides. If you can, avoid being outside during the times when mosquitoes are most active. Wear long sleeves and pants or apply insect repellent.

Reading

Spielman and D'Antonio, *Mosquito*.
Winegard, *The Mosquito*.

Questions

1. How did insects contribute to both the rise and fall of the Roman Empire?

2. True or false: The majority of human deaths from malaria are children.

ANSWERS CAN BE FOUND ON PAGE 224.

<<< TABLE OF CONTENTS

LECTURE 10

Plants That Partner with Insects

Insects and plants have a complicated relationship. Insects can be some of the most important enemies of plants, but not all relationships between the two are antagonistic. Many plants rely on insects for pollination. In fact, some insects and plants have evolved to depend on one another in intricate ways. The insects that have developed the most peaceful relationships with plants are ants. While some ants—notably the leafcutters—are plant enemies, many other species of ants have become plant allies.

Extrafloral Nectar

- Because ants are social—meaning that they live in colonies that can contain thousands, or even millions, of individuals—they are a formidable ally. Their social structure depends on workers bringing a constant supply of food back to the nest to feed the larvae, so ants are always on the lookout for food. Most ants are carnivores that will kill and consume any form of animal protein they can get their mandibles on, including other types of insects. If an ant is walking around on a leaf and comes across a caterpillar busily munching away, the ant is likely to attack and kill the caterpillar. That's a win for the plant.

- One of the most common strategies that plants have developed to encourage visits by ants is to offer them a reward in the form of nectar. People usually think of nectar as being produced in flowers to attract pollinators, but many plants make nectar in other places, too. Nectar that comes from outside of a flower is referred to as extrafloral nectar. More than 3,940 species of plants are known to have extrafloral nectaries, which can be found almost anywhere on a plant.

- Nectar is rich in carbohydrates, making it an excellent source of energy for ants. And the fact that extrafloral nectar has a lot of carbohydrates but not much protein only enhances the effect. To get a well-rounded diet, ants need protein, making them even more eager to attack any animal herbivores they encounter. And ants tend to defend any source of food against potential threats, so any other insect that shows up on a plant that is providing the ants with food is treated as an enemy.

- Plants can even adjust the amount of extrafloral nectar they offer based on the threat posed by herbivores. Once their leaves start being damaged by herbivores, the plant can respond by increasing the amount of nectar being released in each extrafloral nectary. The plant may also increase the concentration of sugar in the nectar, making it more enticing to ants. In essence, the plants are sending out a distress signal to summon ants to come to their defense.

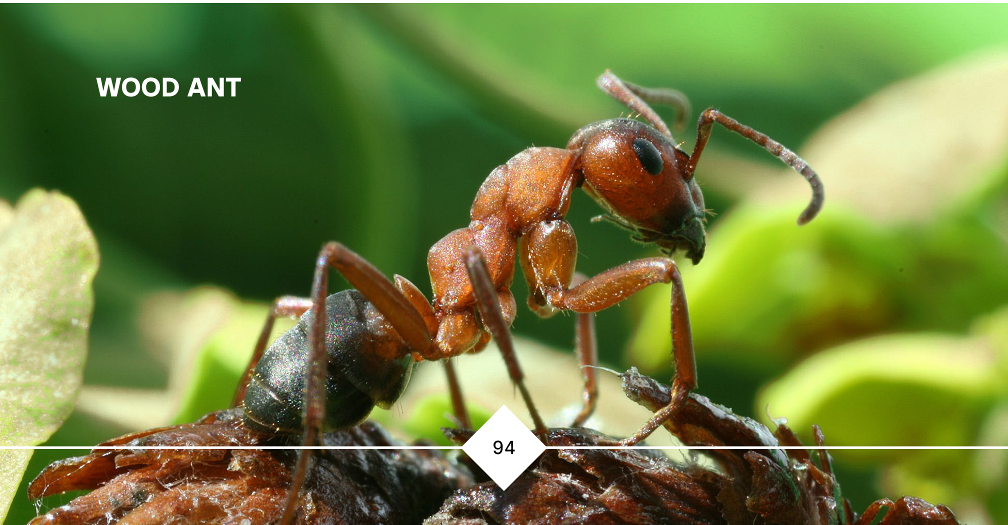
As early as 304 CE, Chinese farmers placed nests of weaver ants on their citrus trees to protect them from insect pests. This is the earliest known example of biological control—the use of one organism to control another.

Wood Ants

- People have often taken advantage of the role that ants can play in protecting plants from herbivores. Wood ants in the genus *Formica* have long been recognized as a natural form of pest control in Europe. By consuming large numbers of insect prey, wood ants protect trees from damage by forest pests.

- In Finland, large outbreaks of moth larvae can devastate entire forests of mountain birch trees. But small patches of healthy forest that measure about 130 feet across remain like green islands in a sea of dead trees. In the center of each patch is a mound of wood ants. By feeding on the moth larvae, the wood ants protect the forest. For this reason, wood ants are protected by law in some European countries.

- Wood ant nests are built in the ground, forming enormous mounds covered in small sticks. These mounds allow wood ants to survive the cold winters by moderating the temperature inside. The nests are tall, extending up to six feet above the ground. Their height allows the mounds to absorb more



WOOD ANT

solar energy. The ants also tend to build their mounds with a greater slope on the side facing south, maximizing their ability to absorb heat. For this reason, people in the Alps sometimes use wood ant nests like a compass.

- Wood ant nests also generate their own heat. As the sticks and leaves that form a thatch on the surface of the mound decompose, heat is given off, much like in a compost pile. In the cold winter months, it can be 20° warmer inside the nest than outside. The large mounds also retain the heat given off by the metabolism of the ants, acting like a giant blanket.

- With such large, climate-controlled nests, wood ants are able to house large numbers of workers. Some species of wood ants also tolerate having multiple queens within the same colony, increasing the rate at which new workers are produced. These adaptations benefit the plants near the nests because the ants reduce the number of herbivores, even during the colder months.

Bullhorn Acacia

- Some plants go to great lengths to encourage ants to defend them. The bullhorn acacia tree, with its intimidating spines, doesn't look like it needs much help keeping herbivores away. But while the spines might help deter large animals, they're no use against smaller herbivores, like caterpillars or beetles. The spines also serve a second purpose: Their hollow interiors are ideal nesting sites for ants.

- The bullhorn acacia has evolved a special relationship with ants in the genus *Pseudomyrmex*. After mating, a *Pseudomyrmex* queen will chew a hole in one of the spines of an acacia tree and lay her eggs inside the spine. When the eggs develop into workers, they treat the entire tree as their nest. And as the colony grows, the workers will carry eggs, larvae, and pupae into other spines. Extrafloral nectaries at the base of the acacia's leaves also provide a rich source of carbohydrates.

- Acacia trees have evolved a chemical trick that makes their extrafloral nectar especially attractive to *Pseudomyrmex* ants and somewhat less appealing to other ants. Most nectar contains the sugar sucrose, which is a composite of two other sugars—glucose and fructose—linked together by a chemical bond. Sucrose is attractive to many insects, but the ability to digest it requires an enzyme called invertase. Many insects that feed on plants make invertase, but the species of *Pseudomyrmex* ants that live symbiotically with acacia trees lose the ability to make invertase as adults.

- As part of their coevolution with *Pseudomyrmex* ants, acacia trees started producing invertase. Because they could get it from their food, the *Pseudomyrmex* ants no longer needed to produce invertase themselves. This further strengthened the mutual dependence between acacias and *Pseudomyrmex* ants because other types of ants find the acacia nectar less attractive. At the same time, for the *Pseudomyrmex* ants, the acacia nectar became an even more important part of their diets.

- Not only do the acacia trees with ants avoid being damaged by insects, but they also have less competition from neighboring plants. *Pseudomyrmex* ants living in an acacia bite any other plants that come into contact with the acacia and even those that grow immediately adjacent to it. Because plants compete with one another for access to sunlight, water, and nutrients from the soil, the ants give their host plant a significant advantage over others.

Devil's Gardens

- A similar type of relationship between ants and plants helped solve a mystery that long perplexed visitors to the Amazon Rainforest. In *supay chacras*, or "devil's gardens," just a single species of tree can be found growing. Some devil's gardens have as many as 600 of the same species of tree, *Duroia hirsuta*. Given that a single plot of land the same size normally houses anywhere from a dozen to 100 different species of tree, these bizarre places reminded local people of farms or orchards, which led them to speculate that they were created by supernatural beings.

- Instead, researchers found that the devil's gardens were created by ants. The ants were identified as *Myrmelachista schumanni*, known as lemon ants, which live inside the hollow stems of the *Duroia hirsuta* trees. Lemon ants get their common name from the formic acid they expel from their acidopores, located where the stinger would be in other ants. The formic acid gives these ants a citrusy smell, and, like lemon juice, its acidity is potent. To defend their homes, lemon ants inject formic acid into the tissues of any plants other than *Duroia hirsuta* that grow nearby. The result is a large area inhabited by only lemon ants and their host trees.

- Interestingly, there does appear to be a cost to the competitive advantage the devil's garden trees get from their ant defenders. Even though the lemon ants defend their host trees as best they can from other insects, having so many of the same tree in one area makes it a very attractive target for herbivores. Even though the trees are defended, a large concentration of the same type of tree attracts so many hungry insects that the ants just can't keep up. This is probably the reason why the whole Amazon Rainforest hasn't become one giant devil's garden. Trees tend to be better at hiding from their enemies when they are scattered and surrounded by other types of trees.

Ant Gardens

- Another possible example of a mutually beneficial relationship between ants and plants involves so-called ant gardens, which are suspended in the trees in some tropical rainforests. The gardens look like balls made of paper-mache nestled within the branches of a tree, with other types of plants, known as epiphytes, growing out in different directions. Epiphytes are plants that live on other plants rather than being rooted in the ground.

- The paper-mache-like ball at the center of an ant garden is a nest made out of carton, which is a combination of soil and degraded plant matter combined with ant saliva. Ants of several genera make ant gardens, including the carpenter ant genus *Camponotus* and others common in rainforest canopies, like *Crematogaster*. Ants have been observed carrying epiphyte seeds into these nest structures, suggesting that this may be the primary way the epiphytes begin to grow there.


CARPENTER ANT

- As the epiphytes grow, they provide structural support for the nest. Some also provide food in the form of extrafloral nectar or through phloem-feeding insects that are kept in the gardens by the ants. In return, the ants help the plants retain moisture by surrounding the roots with their carton nests and providing fertilizer from their waste. The fertilizer is especially valuable given that these plants don't grow in soil.

Ants that nest underground provide a more general benefit to plants that grow near their nests by bringing organic matter underground and by aerating the soil through the construction of tunnels and chambers. We often think of earthworms as providing this service, but on a global scale, ants actually serve a more important role in fertilizing and aerating soils.

Seed Dispersal

- Ants can also help plants by spreading their seeds. Harvester ants feed on seeds and accumulate them inside their underground nests. Because they don't eat all the seeds they collect, some germinate. Thus, harvester ants help spread seeds in much the same way that squirrels do when they forget the locations of some of the seeds they bury.

- Seed dispersal is important for plants because seeds that fall directly beneath a parent plant are often at a disadvantage. The seedling would be competing with the larger parent plant for nutrients, water, and sunlight. It's also easier for plant enemies, like herbivores or disease-causing microbes, to target an accumulation of many individuals of the same species. This is why plants have evolved so many ways to spread their seeds. Some, like dandelions, evolved to be blown by the wind. Others evolved fruits as a way to encourage animals to eat them and spread their seeds through their droppings.

- Some plants evolved ways to specifically attract ants to spread their seeds by attaching fleshy appendages called elaiosomes to their seeds. Elaiosomes are rich in carbohydrates, proteins, lipids, and vitamins. Ants collect the entire seed, carry it into their nest, and then harvest the nutritious elaiosome. They typically discard the rest of the seed in their refuse piles, which can be underground or at the surface. This leaves them free to germinate and also provides them with a compost to fertilize them. This strategy, called myrmecochory, is so effective that it has evolved in a wide range of plants.

Reading

Hölldobler and Wilson, *Journey to the Ants*.
Wilson, *Tales from the Ant World*.

Questions

1 Many plants encourage visits by ants by offering them which of the following?

- **a** carbohydrates in the form of extrafloral nectar
- **b** a protected place to live
- **c** structures rich in proteins and lipids
- **d** all of the above

2 True or false: *Oecophylla* weaver ants make nests by using silk made by the queen to bind leaves together.

ANSWERS CAN BE FOUND ON PAGE 224.

‹‹‹ TABLE OF CONTENTS

LECTURE 11

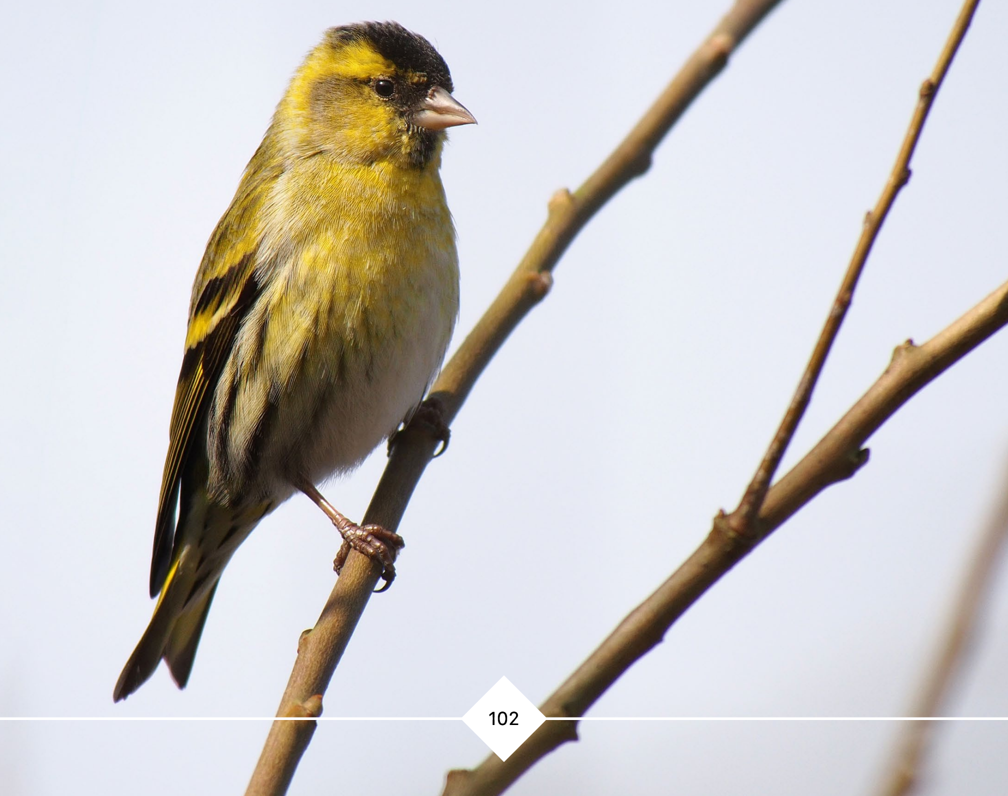
Insects as Food for Animals and Plants

Without insects, most ecosystems would collapse. That's because so many animals rely on insects as food, and many of the animals that eat insects are eaten by other animals, and so on. This lecture explores the critical role that insects play in providing sustenance to other organisms.

Birds

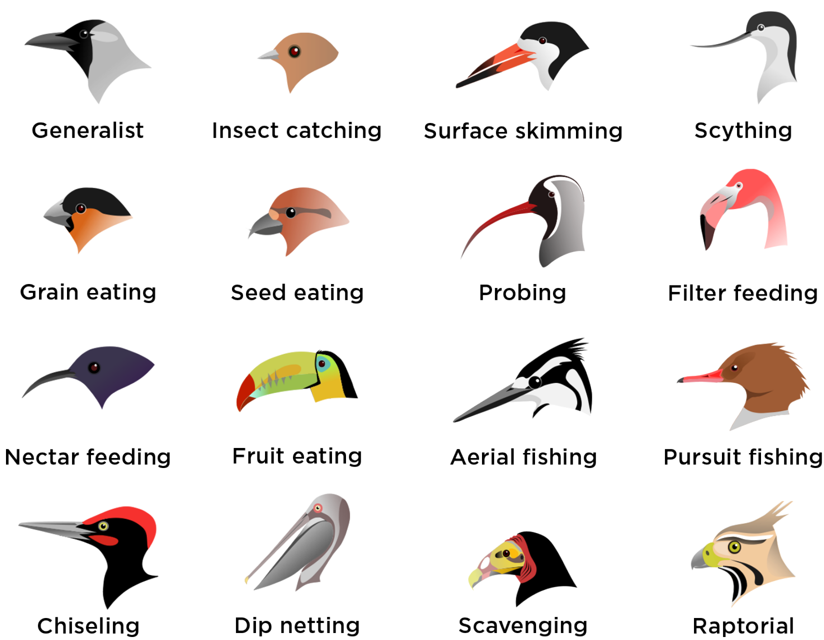
- Many types of birds—like robins, flycatchers, blue jays, warblers, and crows—include insects in their diets. In fact, about half of all bird species eat insects as well as other arthropods, like spiders. The majority of insectivorous birds belong to the passerines, or the perching birds.

- You can tell a lot about what a bird eats by looking at its beak. For example, birds that specialize in cracking open seeds, like some finches, have thick beaks that allow them to apply enough pressure to open the tough seed coats. Flamingoes have downward curving beaks with an internal filter for straining tiny crustaceans out of the water. Most birds that eat insects have straight, pointed beaks that work like a pair of tweezers for picking up insects.



- Some birds, like swallows and swifts, use their agility to feed on flying insects in midair. Others, like wrens and woodcreepers, pick insects off of branches and leaves. The black-capped chickadee can be seen hanging upside down from a tree branch as it looks for insects hiding on the underside. And woodpeckers use their reinforced beaks and long tongues to access insects living inside tree trunks and branches.

- Some birds use other animals to help them eat insects. Ant birds follow swarms of army ants and feed on the insects that hop and fly away to escape from the ants. Similarly, cattle egrets eat the insects that are flushed out of the grass by cattle as they walk around. Oxpeckers feed on ticks and flies that feed on cattle, water buffalo, and other large mammals. And honeyguides sometimes lead people to a nest of bees to help them get access to the bee larvae and wax honeycomb they like to eat.



Amphibians and Reptiles

- Amphibians like frogs also eat a lot of insects. Most are generalists, consuming any bugs they can get their sticky tongues on. But some, like certain species of poison dart frog, specialize on eating ants and mites. In fact, the highly toxic alkaloids in their skin—which have been used by Native Americans to make poison darts—come from the insects in their diet. In captivity, when they're fed a diet of fruit flies or other insects, the frogs lose their toxicity.

- Many reptiles feed on insects as well. Like amphibians, most lizards eat a range of different types of insects, including flies, beetles, ants, and true bugs. Some have adaptations that make them especially good predators of insects. Chameleons have long, sticky tongues that they can quickly extend to capture insect prey.

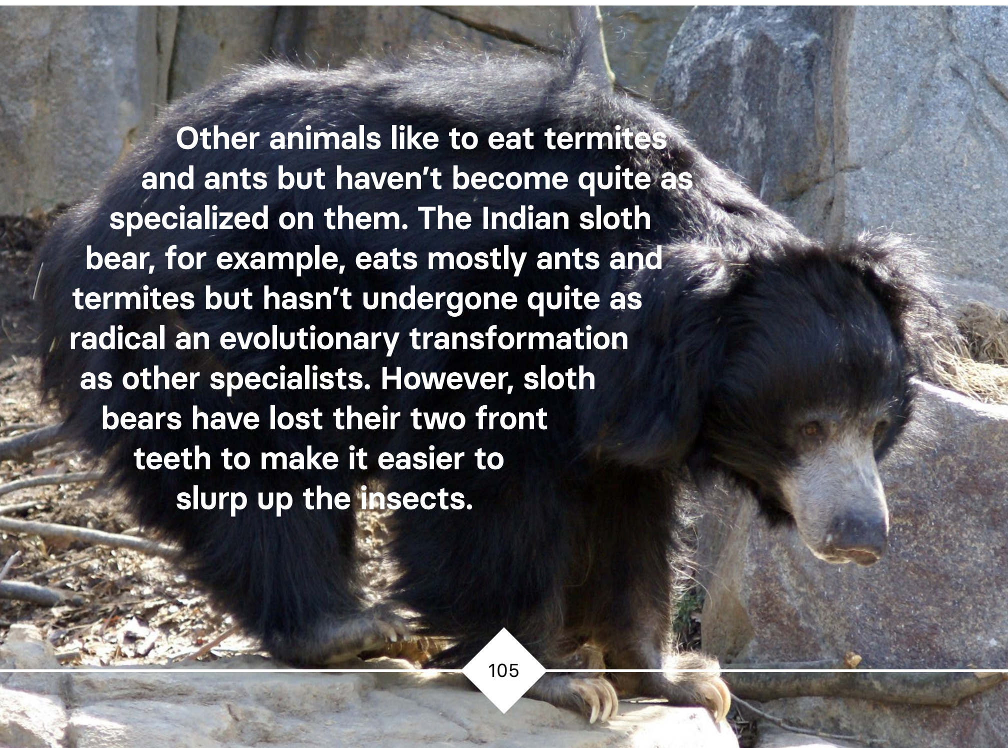
- Other lizards have become specialized to eat a particular type of insect. Because ants live in colonies, they make good prey. Horned lizards evolved large stomachs so they can eat and digest a lot of ants when they find them. Having a big belly makes it harder for them to be quick like most lizards, so horned lizards also had to evolve a different way to defend themselves from predators. Their strategy was to become both camouflaged and spiky.

Ant and Termite Specialists

- The horned lizard isn't the only animal to figure out that ants are a reliable source of food. Australia is home to the echidna, also known as the spiny anteater, which eats termites in addition to ants. Echidnas are monotremes, a branch of primitive mammals that have pouches like marsupials but also lay eggs. They have very small mouths at the end of a pointed snout, but they don't have teeth. They use a long, sticky tongue to lap up ants and termites from their nests, which they dig into with their strong claws.

- Other ant and termite specialists include the true anteaters of Central and South America. The giant anteater gets quite large, weighing up to 100 pounds. They have an elongated snout with a small mouth, no teeth, and a very long tongue. Unlike echidnas, anteaters don't have spines to protect themselves. Instead, they rely on their long, sharp claws for defense.

- Aardvarks are another termite specialist. They have long snouts and long, sticky tongues. Another animal, the pangolin, has the features you'd expect for an ant and termite specialist—powerful claws, no teeth, and a long tongue—but they have a different type of defense. Pangolins are covered in armored plates made of keratin, and they can curl up into a ball when they feel threatened.



Other animals like to eat termites and ants but haven't become quite as specialized on them. The Indian sloth bear, for example, eats mostly ants and termites but hasn't undergone quite as radical an evolutionary transformation as other specialists. However, sloth bears have lost their two front teeth to make it easier to slurp up the insects.

Bats

- Many bats are exclusive insect eaters. Because bats are small, warm-blooded, and use a lot of energy to fly, they have to consume a lot of food to meet their energy needs. To do so, insectivorous bats often have to eat their body weight, or more, in insects. This makes bats important for controlling populations of insects that are agricultural pests or disease vectors.

- Bats also play important roles in many cave ecosystems. While sunlight is the energy source for almost every ecosystem on Earth, caves are one exception. Without sunlight, there is no way for plants to grow. Yet there are many animal species that live deep inside caves, including some, called troglobites, that never venture outside. They rely on other species, like bats, that go outside the cave to find food.

- The Brazilian free-tailed bats of Carlsbad Caverns are a great example. The bats spend the night hunting moths and beetles and then return to the cave around dawn. They digest their nocturnal meal while hanging from the cave roof and then defecate onto the cave floor. The waste, called guano, that accumulates beneath the bat roosts provides energy and nutrients to millipedes, springtails, cave crickets, flies, and other invertebrates. These in turn are prey for cave spiders, carabid beetles, and centipedes.

Carnivorous Plants

- More than 600 species of carnivorous plants get nutrients from insects. Most carnivorous plants live in places with poor soil. They make up for a lack of nutrients in the soil by trapping insects, digesting them, and absorbing the nutrients from their bodies.

- Pitcher plants work like pitfall traps, using leaves that are shaped like cylinders to trap insects in the fluid that accumulates at the base. The smell of sweet nectar lures insects toward the edge at the top of the cylinder. The sloping rim has a thin layer of liquid made of extrafloral nectar and condensation that makes it slippery and causes insects to hydroplane and fall into the trap. The inside walls of the leaf are coated in downward-pointing hairs or wax crystals that make them too slippery for most insects to climb. A lip at the top of the cylinder adds an additional barrier.


PITCHER PLANT

- The water at the base of the pitfall trap contains microorganisms like bacteria, fungi, and protists that thrive in the nutrient-rich broth created by the decaying insects. Some of these microbes produce enzymes that help the insects decompose, so the microbes and pitcher plants have a mutually beneficial relationship. Ants are the most common prey for most pitcher plants. But many other insects—including termites, beetles, and wasps—can be trapped and consumed by pitcher plants.

- Some insects take advantage of the protected, nutrient-rich environment inside pitcher plants. In Borneo, one ant species, *Camponotus schmitzi*, steals prey from the pitcher plants by diving into the fluid and retrieving prey items before they can be digested by the plant. The ants have evolved not only to be good swimmers but also to be able to walk along the slippery surface of the pitcher without falling in and also to be able to climb out of the trap. These ants make their nests inside the pitcher plant's swollen tendrils, which usually attract ants to plants.

- Why would a pitcher plant want to encourage a species that steals its food? It turns out that the ants help the pitcher plants by grooming the rim of the plant, which keeps it clean and slick and makes it more effective at capturing prey. This benefits the ants, of course, because it ensures a steady supply of prey for them to steal. But experiments have shown that pitcher plants with *Camponotus schmitzi* ants do better than those without resident ants.

Avoiding Predators

- Although insects are important as prey items for animals and some specialized plants, they aren't without any defense against these predators. One of the ways that many insects avoid being eaten is to avoid being seen. Insects have evolved some of the most remarkable examples of camouflage.

- One master of disguise is the stick insect, a member of the order Phasmatodea. As their common name suggests, stick insects look like sticks. They generally have elongated bodies, and many also have long legs and antennae. The world's longest insect is a species of stick insect from southern China that is two feet long.

- If you can't avoid being noticed by a predator, the next best strategy is to try to get away. Insects were the first animals to be able to fly, and the evolution of wings may have begun as a way to avoid predators. Other insects evolved enlarged hind legs that make them good jumpers. The most remarkable jumpers are froghoppers, which can leap more than two feet high—more than 100 times their body length.

- Insects that can't hide or escape from predators often fight back. Stinging insects like bees, wasps, and ants use venom for both offense and defense. Many ants and wasps subdue their prey by stinging it and injecting venom that quickly kills or immobilizes the victim. But the pain of an insect sting is also an effective deterrent. Other insects use poison as a defense. Poison differs from venom in that venom is injected, whereas poison only has an effect if it's eaten.

- The monarch butterfly is one of the most famous of the poisonous insects. Monarchs let potential predators know that they're dangerous with their bold, bright colors. This is known as aposematism, or warning coloration. It works because predators that eat a monarch quickly learn to associate the orange, black, and white patterns on the monarch's wings with the unpleasant taste of cardenolides.

- Yet another strategy that many insects use to avoid predators is to pretend they're dangerous when they're not. The viceroy butterfly has orange, black, and white patterns on their wings that make them look remarkably like a monarch butterfly. But unlike the poisonous monarch, the viceroy is harmless and would make a good meal for a hungry bird. This type of mimicry is known as Batesian mimicry, named for British naturalist Henry Walter Bates.

Reading

Jiggens, "Mimicry." https://www.heliconius.org/biology/mimicry/.

Schmidt, *The Sting of the Wild*.

Yong, "Lies, Damned Lies, and Honey Badgers." https://www.discovermagazine.com/planet-earth/lies-damned-lies-and-honey-badgers.

Questions

1 Which of the following does not consume a diet rich in ants?

- **a** horned lizards
- **b** pangolins
- **c** pitcher plants
- **d** chameleons

2 True or false: The first animals to evolve the ability to fly were insects.

ANSWERS CAN BE FOUND ON PAGE 224.

‹‹‹ TABLE OF CONTENTS

LECTURE 12

Insects as Food for People

Insects are an important food source for many different animals, but they're also important as food for people. For people from North America or Europe, the idea of eating insects may seem strange or even objectionable. But for more than 2 billion people around the world, insects are simply part of their diets.

Early Human Diets

- Insects have been a part of many cuisines for centuries, and they may have even played an important role in the evolution of our species. One of the most important steps in the evolution of humans was an increase in brain size. Because brains demand a lot of energy, our ancestors required more calories in their diet.

- Animal protein is a rich source of energy, but hunting game isn't always reliable. Foraging for fruits, nuts, and other edible plant parts is a more reliable way to find food, but plants aren't as rich in energy and often lack essential nutrients like protein and iron. Insects may have provided the ideal solution to the energy and nutrient needs of early humans. Insects are abundant, especially in tropical regions like the African savannas, where most of human evolution occurred.

- Early humans probably ate many different types of insects, from beetle larvae to locusts. But social insects like ants and termites were likely among the most important insects in their diets. Because they live in nests that can contain thousands of individuals, ants or termites can be a very reliable source of food concentrated into a small area.

- Tools thought to have been used by early humans for collecting termites have been found in South Africa. The tools, which are 1.8 million years old, were made by a species of hominin called *Paranthropus robustus*, a member of the group known as Australopithecines. The tools are made of animal bone and are worn down at one end, suggesting that they had been repeatedly stuck into termite nests the same way that modern chimpanzees use sticks.

- Another reason to believe that early humans ate termites comes from chemical analyses of fossilized teeth. Analyses of the hominin teeth found at the same site in South Africa where the bone tools were found showed that 35%–40% of their diet had a chemical signature of grasses or sedges.

Grasses and sedges weren't commonly eaten by early humans because they're hard to digest. It's possible that the hominins were eating insects that had eaten grass, which would give their teeth the same chemical signature as if they had eaten grass directly.

- Our species, *Homo sapiens*, evolved about 200,000 to 300,000 years ago. Until about 10,000 years ago, all humans were hunter-gatherers and would have regularly eaten insects. And many modern hunter-gatherers continue to eat insects today. The San people of the Kalahari Desert collect termites, hawk moth caterpillars, grasshoppers, ants, and buprestid beetle larvae. And Australian aboriginal tribes in the Northern Territory eat termites, ants, and beetle larvae.

Insect-Based Dishes

- Hunter-gatherers are by no means the only people that eat insects today. Many traditional cuisines include insects as important ingredients. And as interest in traditional foods has grown, insect-based dishes are making a comeback.

- The best-known insect food is honey. When you eat honey, you're eating some of the bees' saliva. But bees themselves are edible, especially the larvae, which are a prized delicacy in many places. In Laos and Cambodia, honeybee larvae are eaten while still in their wax honeycomb cells. The honeycomb is wrapped in banana leaves, roasted over hot coals, and then eaten whole.

- Weaver ant larvae and pupae are eaten in China, India, the Philippines, and Papua New Guinea. The largest larvae and pupae are those that would develop into queens, and these are considered the most desirable. The worker ants aren't often eaten because the formic acid they produce makes them taste sour, but they're sometimes used as a condiment to provide a citrus-like flavor.

- Mexican cuisine is rich in insects, especially in Oaxaca. One of the most popular Oaxacan insect dishes is chapulines—fried grasshoppers seasoned with lime and chiles. They are usually eaten on a corn tortilla topped with salsa or guacamole.

- Another insect common in traditional Mexican cuisine is the maguey worm, which is actually the larva of a butterfly known as the tequila giant skipper. This is the famous "worm" sometimes found at the bottom of a bottle of tequila—or, more precisely, tequila's smokier cousin, mezcal. The original purpose of including a maguey worm in a bottle of mezcal was to prove that the liquor was strong enough to preserve the larva, which would quickly decompose if there wasn't enough alcohol. Maguey worms are also fried and eaten as tacos.

- Many insect foods are becoming increasingly popular in the United States and Europe. Insects provide an exciting and diverse opportunity for chefs looking to explore new flavors, and high-end restaurants around the world are increasingly featuring insects on their menus. The surge in interest in insects as ingredients has led to new insect farms popping up in the United States and Europe, and you can now find roasted crickets at some American grocery stores.

Insect Nutrition

- In addition to being tasty, one of the reasons why insects are such a valuable source of food for people is that they're very nutritious. In general, insects are high in protein and rich in vitamins and minerals like calcium, iron, and zinc. To get an idea of how nutritious insects are, you can compare the nutritional content of mealworms to that of beef.

- If you discard how much of the weight comes from water, the remaining weight of beef is 55% protein, whereas mealworms are about 49% protein. Mealworms and crickets also have proteins made of different combinations of amino acids. Isoleucine is an example of an essential amino acid that is more abundant in mealworms than beef (42 grams per kilogram in mealworms versus 16 in beef). On the other hand, some other essential amino acids, like lysine and methionine, are more abundant in beef than in mealworms.

- Mealworms have less fat—only 35%—compared to 41% for beef. Yet mealworms are rich in the essential fatty acids our bodies need. Mealworms are comparable to beef in terms of omega-3 fatty acids, but mealworms have nine times more omega-6 fatty acids than beef.

- Beef is often considered a valuable source of minerals like iron, potassium, and zinc. But mealworms have just as much of these minerals, and they have more vitamins than beef, with the exception of vitamin B_{12}. Because they're so nutritious, some people see a lot of potential in using insects as nutritional supplements. Cricket powder is very high in protein and can be used like whey protein to fortify smoothies and other foods.

Insects in Our Food

- If the idea of having insects in your food seems strange or upsetting, you may be surprised to learn that insects are already in many of the foods we eat. Many foods that are red, like strawberry ice cream or red velvet cake, get their color from a red dye called carmine that's made from cochineal bugs. Cochineal bugs feed on cactus, and the carminic acid they produce has been used for centuries as a natural red dye for textiles and ceramics.

- Candies like jelly beans, candy corn, and some chocolates are coated in a substance called confectioner's glaze, which makes them shiny. Confectioner's glaze is made from shellac, a resin produced by larvae of the lac insect, *Kerria lacca*. Lac insects produce a waxy resin as a way to protect themselves from predators as they feed on plant phloem. The resin secreted by lac insects forms a protective sheath around a tree branch, and this material is harvested and purified into shellac, which is sold and used as a food glaze.

- In addition to being used to coat candies, shellac is also used as a shiny wax on citrus fruits and as a coating on some medications. Having shellac on a pill slows the release of the medication so that it can be absorbed by the body over a longer period of time. Shellac can also be found on the lanes of bowling alleys, the outer coating of billiard balls, and playing cards. While it may seem surprising that the same substance used for all these purposes can also be edible, shellac is natural, nontoxic, tasteless, odorless, and biodegradable.

- Another way you may already be eating insects without realizing it is in processed foods, produce, and spices, many of which unintentionally contain parts of insects. The USDA puts limits on how many insect parts there can be in different types of foods, but the amounts that are allowable may surprise you.

- A typical chocolate bar can have about 24 tiny bug bits hidden inside. A jar of ground cinnamon can have around 400 insect parts. Ten grams of ground oregano can have up to 1,250 insect fragments. And in just 10 grams of hops—an ingredient in beer—there can be as many as 2,500 individual aphids. While these numbers may sound alarming, having small amounts of insects in our food doesn't do us any harm.

Benefits of Raising Insects for Food

- One of the reasons that some people consider insects to be the food of the future is that they require much less space and far fewer resources to grow. Rearing livestock like cattle, pigs, and chickens takes a lot of space. Currently, more than 70% of all agricultural land is used to raise livestock, and additional space is hard to come by. In contrast, raising insects requires very little space. And it can be done indoors, which makes it possible to raise insects as livestock in urban areas.

- Cattle, pigs, and chicken also need water to drink. About 40% of the water used goes to livestock, either for them to drink or to water the plants raised to feed them. And animals raised as livestock have to be fed a lot. To get 1 kg of chicken, you need 2.5 kg of feed. Beef is the most resource-demanding animal protein: To get 1 kg of beef, you need 10 kg of feed. By comparison, 1 kg of crickets requires just 1.7 kg of feed.

- Another benefit of raising insects for food is that insects produce far fewer greenhouse gases than other animal livestock. Cattle produce enormous amounts of methane as a by-product of the microorganisms that help them digest their food. Methane is a more potent greenhouse gas than carbon dioxide, so raising cattle is the greatest contributor to greenhouse gas emissions of all agricultural activity. Altogether, livestock contribute 18% of all greenhouse gas emissions, which is even more than transportation.

- Most insects do not produce methane—the exceptions being termites and some cockroaches. Crickets produce minute amounts of other greenhouse gases, like ammonia. But compared to cattle and pigs, crickets produce about 100 times less greenhouse gases. Furthermore, forests don't have to be cut down to make space for them.

- Altogether, the small space requirements, minimal water and feed requirements, and comparatively small greenhouse gas emissions make insects perhaps the most sustainable animal protein we currently have available.

Reading

Gates, *Insects: An Edible Field Guide*.
Gordon, *The Eat-a-Bug Cookbook*.
Lesnik, *Edible Insects and Human Evolution*.
Martin, *Edible: An Adventure into the World of Eating Insects*.

Questions

1. True or false: Insects are comparable in protein content to beef and are rich in vitamins, minerals, and omega-6 fatty acids.

2. ______, which comes from scale insects, is an edible coating used on many candies, citrus fruits, and medications.

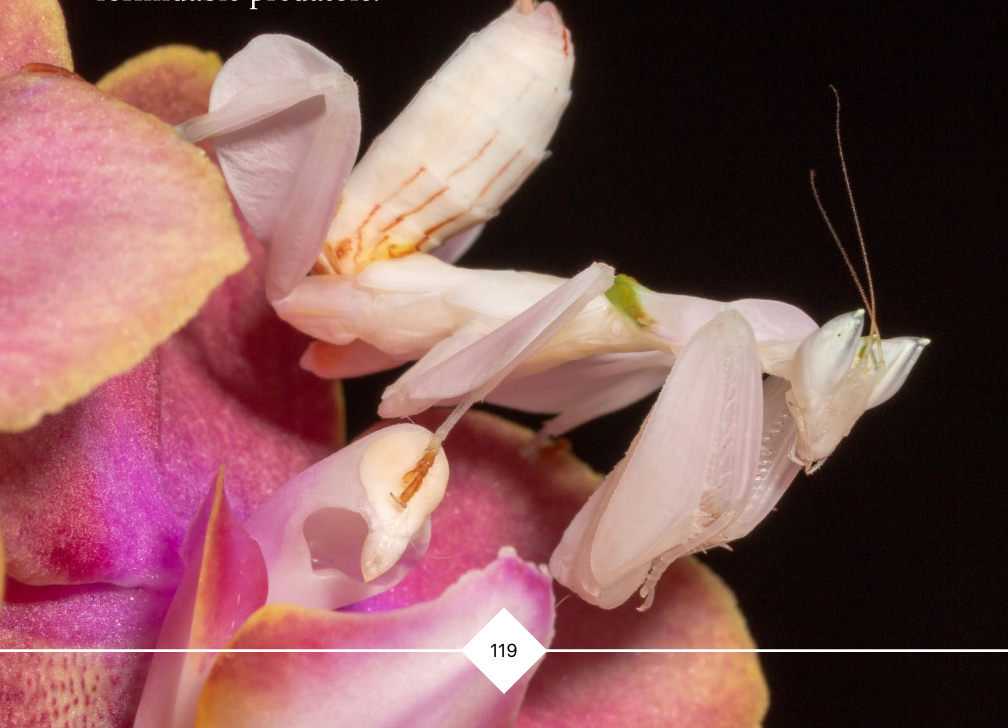
ANSWERS CAN BE FOUND ON PAGE 224.

‹‹‹ TABLE OF CONTENTS

LECTURE 13

Insects as Predators

Insects are an important source of food for animals, carnivorous plants, and people. But in addition to being prey, many insects are also predators. Insects have evolved some amazing strategies—from enhanced vision to lightning-fast jaws and elaborate traps—that make them formidable predators.



Mantids

- Among the most famous of predatory insects are the mantids. They are recognizable by distinctive front legs that are raptorial, or specialized for capturing prey. Each front leg has an elongated coxa—the segment closest to the body—which gives the mantids a longer reach. The next segment, the femur, has spines along its lower margin. It also has a groove that creates a space for the spines on the subsequent section to fit snugly into.

- Together, the spines on the femur and the tibia resemble an alligator's teeth, which fit side by side when it snaps its jaws shut. And the effect is exactly the same: Mantids strike quickly, snatching their prey in as little as 50 milliseconds. They will attack just about any type of insect and even a small lizard or mouse. The prey is impaled and immobilized by the spiny forelegs, giving the mantid time to consume it with its mandibles.

- The common name praying mantis comes from the way the forelegs of some mantids are held in front of the body, with the femur and tibia folded together like hands folded in prayer. Because the forelegs are so modified for capturing prey, they don't work well for walking. But, like all insects, mantids have six legs, and the other two pairs work perfectly well for moving around.

- Mantids are ambush predators, so rather than stalking their prey, they use a sit-and-wait approach. Some mantids are camouflaged with green or brown coloration and long, thin bodies that resemble leaves or twigs. Orchid mantises have bodies that match the white and pink petals of orchids, allowing them to stake out a flower and wait for a visitor to come in search of nectar or pollen. Their camouflage is so effective that pollinators are actually attracted to the mantises themselves, even if they aren't hiding inside a flower.

- Another adaptation that makes mantids such adept predators is their ability to turn their heads in any direction. To be effective in an ambush, they remain as still as possible. Instead of turning their bodies to look at an approaching bee or butterfly, the mantis can turn just its head a full 360°. Mantids also have large compound eyes and a unique form of vision that allows them to see in 3-D only those objects that are moving. That makes them very effective at judging the distance of potential prey without having to process unnecessary visual information.

Assassin Bugs

- Another fearsome group of insect predators are the assassin bugs. Like all hemipterans, assassin bugs have piercing-sucking mouthparts in the form of a proboscis, or beak. The proboscis is used to impale prey and to deliver enzymes that digest the prey's tissues, which are liquified and then sucked up. By killing and digesting prey outside of their own bodies, assassin bugs can feed on larger prey.

ASSASSIN BUG

- One type of assassin bug, the masked bed bug hunters, may be lurking in your home. The nymphs of the masked bed bug hunter are small and wingless and excrete a sticky substance that causes them to become covered in tiny particles of whatever's around. In the wild, they get covered by dirt or sand. In your home, they're more likely covered in dust, hair, and crumbs. So disguised, these assassin bugs stalk their prey, which may include bed bugs or whatever else is crawling around your home.

- The termite-eating assassin bug, *Salyavata variegata*, also disguises itself. It covers its body with tiny pieces of debris that form the outer structure of the termite's nest. The assassin bug then takes advantage of natural termite behavior in two ways. First, any hole made in the nest gets quickly repaired by the worker termites. The disguised predator lurks just outside the opening of a hole and snatches one of the workers that comes to help with the repair.

- Termites collect any dead colony members and bury them away from the living termites to minimize the chances of spreading disease. Taking advantage of this behavior, the assassin bug dangles the dead termite over the entrance hole and waits for another termite to come retrieve it. In essence, the assassin bug is fishing for termites using other termites as bait.

Dragonflies

- Dragonflies are one of the oldest groups of predatory insects. As immature nymphs, they're ferocious underwater predators. They feed on other aquatic insects, like water beetles, mosquito larvae, and even tadpoles or small fish. Some dragonfly larvae are ambush predators that hide in the muck at the bottom of a pond with just their eyes sticking up to watch for a potential meal. Others use aquatic plants or various structures as a base as they wait for prey to come within striking range.

- To capture its prey, the dragonfly pumps hemolymph into its labium, or lower lip. At rest, part of the labium covers the face while the rest of it is folded beneath the head. When it fills with hemolymph, the labium quickly extends forward, shooting out in front of the dragonfly's face. The end of the labium is a grasping mechanism made from the two labial palps that have been modified to resemble mandibles. Removing hemolymph from the labium causes it to contract, bringing the captured prey to the mouth. The whole sequence of extension, capture, and retrieval takes only about 187 milliseconds.

- Adult dragonflies are equally adept predators, patrolling the skies for flying prey like mosquitoes, flies, and butterflies. With enormous compound eyes and very small antennae, they rely mostly on vision to pursue their prey. Dragonflies anticipate where their prey will be and fly toward that point. The head can turn almost 360°, allowing their gaze to stay fixed on the prey while the rest of its body can change orientation as it flies.

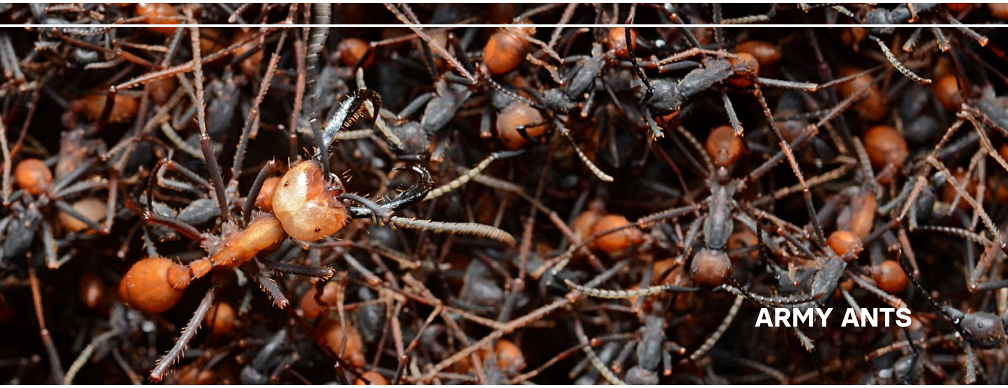
- Unlike the aquatic nymphs, which use extendible mouthparts, adult dragonflies capture their prey with their legs. The front pair of legs are held forward, acting like a basket that scoops up the prey once it has been intercepted. Studies have found that their success rate in capturing prey in midair ranges from 75% to 97%.

Trap-Jaw Ants

- While many ants are predators, some have evolved mouthparts that work like a mousetrap to capture prey at lightning-fast speeds. Amazingly, trap jaws have evolved independently in at least four different groups of ants, but the mechanism is similar for each.

- The mandibles are longer than in most other ants and can be held open at a wide angle. A latch holds the mandibles in the open position, setting the trap. Muscles that control the jaws are stretched, acting like a rubber band that will recoil as soon as the latch is released. The latch is controlled by trigger hairs located at the front of the face. If the trigger hairs are touched, the latch is released and the jaws quickly snap shut. The speed of trap jaws closing has been measured at 134 miles per hour in *Odontomachus* ants.

- *Mystrium camillae*, also known as Dracula ants, have jaws that have been clocked closing at 200 miles per hour—and they reach that speed in 0.000015 seconds. Dracula ants use a different mechanism, working much like the way you snap your fingers. Their mandibles curve inward and meet at a point in front of the face. One mandible, called the loading mandible, acts like the thumb, preventing the slip of the striking mandible. They push against one another, but friction and flexibility keep them from slipping. Then, the striking mandible suddenly slips and is propelled toward the ant's head, closing the jaws.



Army Ants

- The most ferocious ant predators are without a doubt the army ants. A hunting strategy called a swarm raid is used by just a few species of army ants, including *Eciton burchellii*. The ants follow one another in a tight formation called a base column. At some point, the workers begin to fan out into a network of columns, which further divides into smaller and smaller swarms along the front of the raid.

- The overall structure of the raid looks like a broom, with the long broomstick representing the base column and the brush at the end representing the swarm front. And in much the same way that a brush can sweep up almost all of the dust on a floor, and army ant swarm can attack, kill, and consume just about every creature it encounters.

- Army ants from the Americas are armed with both powerful mandibles and a venomous sting. *Eciton burchellii* workers come in a range of sizes, the largest of which are known as soldiers and have formidable, curved mandibles that resemble a sickle. When these mandibles sink into your skin, it takes a lot of prying to pull them off. This gives the soldiers time to deliver a painful sting. The bite-and-sting approach works well as an offense, too, allowing army ants to take in tens of thousands of individual prey items each day.

Ant Lions

- There are many types of predators that specialize in eating ants, including the ant lion. Adult ant lions feed on nectar and pollen, but the larvae, which are also known as doodlebugs, are predators that have an amazing way of catching their prey. The ant lion larva builds a cone trap in loose soil or sand by digging with its flattened abdomen, flinging away the excavated bits of loose sand with its head. The larva walks backward in a downward spiral that gets smaller the deeper it goes. Once the pit has been prepared, the ant lion larva buries itself at the bottom and waits.

- If an ant crosses the rim of the pit, the loose sand will make it slide down toward the bottom, where the ant lion is ready with its large, pointy mandibles open wide. To make it even harder for the ant to escape, the ant lion larva flings loose sand toward the ant, causing the sides of the pit to collapse. When the ant reaches the bottom, the ant lion's jaws snap shut. Digestive enzymes are injected through channels in the mandibles that are also used to suck up the ant's tissues once they've been liquified.

Glowworms

- To see one of the most magical insect predators, you'll have to travel deep inside New Zealand's Waitomo caves. Blue-green lights adorn the cave ceiling in what would otherwise be complete darkness. The lights are produced by the larvae of fungus gnats, known as glowworms.

- The larvae make nests out of silk that they attach to the cave ceiling. Up to 70 threads of silk hang down from the nest, and they're adorned with regularly spaced sticky blobs. These can be up to 16 inches long. They act as fishing lines, trapping flying insects as well as spiders and other small invertebrates. The light produced by glowworms attracts insects into the trap.

Reading

Kronauer, *Army Ants*.
McAlister, *The Secret Life of Flies*.

Questions

1. True or false: Dragonfly larvae are predators that can feed on small fish.

2. ______ are the larvae of fungus gnats, and they produce light to attract prey into their sticky silk threads.

ANSWERS CAN BE FOUND ON PAGE 224.

<<< TABLE OF CONTENTS

LECTURE 14

Insects as Parasites and Parasitoids

Many insects make a living as predators, and others are herbivores. Parasitism is another lifestyle used by many insects. A parasite is an organism that gets its energy from another organism without immediately killing it, although some parasites do eventually kill their hosts or at least make them more likely to die. The parasitic lifestyle may seem cruel or unpleasant, but it has been a successful strategy for many different types of insects.

Galls

- Plants often have structures on them called galls. They can look like swollen nodules or bumps, and some are spiky or fuzzy. Galls are places where plant tissue has grown around a foreign body. It could be a fungus, bacterium, or virus, but more often than not, galls are formed around insects.

- The gall begins to grow when an egg is deposited inside a plant's tissue. This triggers the plant's cells to begin growing larger and dividing rapidly, like a tumor. The plant cells closest to the developing insect are rich in carbohydrates and proteins. As the egg develops into a larva, it will feed on these nutritious plant tissues. Outside of this layer are cells with thick walls made of lignin and tannins. These cells form a tough, protective shield around the insect as it grows. After completing its metamorphosis, the adult will chew its way out of the gall and emerge to complete the rest of its life cycle.

- The relationship between gall-forming insects and their host plants is complicated. The insect clearly seems to benefit from the energy and nutrients it derives from eating the plant's tissues as well as from the protection it gets from being inside the gall as it develops. But why does the plant seemingly encourage the insect by building it a shelter and providing it with food? It's unclear whether the insects have tricked the plants into helping them or if the plants are actually acting to defend themselves as best they can.

- Only certain types of plants make galls. Likewise, only certain types of insects can induce the formation of galls. But the insects that induce gall formation can do so only in particular types of plants, which suggests a history of coevolution. Oaks are especially prone to galls. Live oak trees are host to at least 12 different types of gall-forming cynipid wasps. In each case, the insect has evolved a way to manipulate the plant into growing a characteristic structure that will provide it with food and protection.

- We still don't understand exactly how this manipulation works, but it seems to be triggered by substances injected when the insect lays its egg in the plant tissue or by the chewing activity of larvae. And because the gall will not continue to form if the insect dies early in development, its continued growth appears to be induced by substances released by the developing insect inside the gall.

Gall-forming insects are different than most herbivorous insects because they don't just eat their host plants; they cause changes to the plants that can affect the plant's growth and reproduction.

The Crypt-Keeper Wasp

- Aside from their own life cycles, cynipid wasps and the galls they induce on oak trees are the foundation of a complex set of interactions among a number of different species. Very often, the insect that emerges from an oak gall is not the insect that induced the gall to form in the first place. Rather, it is a different species of wasp—a parasite of a parasite—that develops inside the body of the gall wasp and feeds on its tissues while the gall wasp is still alive.

- Consider the cynipid wasp *Bassettia pallida*, which forms a gall in a live oak tree that causes the stem to swell. Inside the swollen stem is a small cavity, or crypt, where the wasp larva develops. In 2017, Scott Egan, Kelly Weinersmith, and their team announced the discovery of a new species of wasp in the superfamily Chalcidoidea that also develops inside these crypts. They informally dubbed the new species the crypt-keeper wasp. For its formal, scientific name, they chose *Euderus set*, named after the nefarious Egyptian god Set, who trapped his brother Osiris inside a crypt and then gruesomely murdered him.

- The crypt-keeper wasp develops inside the body of the larva that formed the gall and manipulates the host wasp's behavior to serve its own needs. The host wasp normally chews a large escape hole when it has developed into an adult and is ready to emerge. But when infected by the crypt-keeper wasp, the host wasp chews a smaller hole that's only big enough for its head to fit through. The host wasp gets stuck with its head in the hole and dies there.

- Remarkably, this is exactly what the crypt-keeper wasp needs to happen in order to complete its own development. Experiments showed that the crypt-keeper wasp isn't very good at chewing its own holes when developing inside galls. They were three times less likely to emerge. Once the hole has been made and then plugged by the host wasp, the crypt-keeper wasp completes its development by feeding on the internal tissues of the host wasp. After it's fully developed, the crypt-keeper wasp chews through the host's head and emerges as an adult.

Parasitoid Wasps

- Insects that live inside the body of their host and eventually kill it as they emerge are given a special name: parasitoids. This life cycle is unique to insects, and there are many species of parasitoids. One parasitoid wasp is *Cotesia congregata*, which belongs to the family Braconidae.

- The adult female wasp finds a host by following the smell of chemicals released by plant leaves that are being consumed by caterpillars. She then uses her ovipositor to lay about 65 eggs inside the caterpillar's body. The larvae will live and grow inside the caterpillar's body, feeding on its hemolymph, for about two weeks before chewing their way through its exoskeleton.

- The pupal stage takes place on the outside of the caterpillar's body, where it will spin a cocoon. Three to eight days later, the adult wasp will emerge and head out in search of a new host. A single caterpillar can be host to as many as 300 wasps. The host caterpillar stays alive long enough for the parasitoid wasps to complete their development into adults. Then, its metabolism typically shuts down just as the adult wasps emerge, or shortly thereafter. The host caterpillar won't survive long enough to mature into an adult.

- How do the parasitoids avoid being attacked by the host's immune system? Amazingly, when the female wasp injects her eggs into a host, she also injects a polydnavirus that has incorporated her own genes into the genome of the wasp. The virus uses its genes to produce viral particles inside specialized cells in the moth's ovaries. Once the viral particles are inside the caterpillar host, they act to suppress the host's immune system so that the wasp larvae can survive and grow.

> Every order of insect is parasitized by other insects, and many species of insects are hosts for multiple species of parasitoids. One study examined the parasitoids of 158 different genera spanning five insect orders. Researchers found that each insect species was host to, on average, between 2.6 and 9.4 species of parasitoids, which were mostly wasps.

- Polydnaviruses can also manipulate the plants that the caterpillar feeds on. By infecting cells in the caterpillar's salivary glands, the virus can reduce the production of particular enzymes that normally are recognized by the plants and used to increase the production of chemical defenses. Without these defenses, the caterpillar can feed and complete its development more rapidly. That's good for the parasitoid wasp and for the virus that lives within the wasp.

- As if that weren't complex enough, virus particles released in the caterpillar's saliva can also be detected by the plant. This results in the plant producing a different type of chemical that catches the attention of another species of wasp, *Lysibia nana*. This second wasp, a member of the family Ichneumonidae, lays its eggs inside the pupae of the wasps that are attached to the caterpillar. So, the second wasp is a parasitoid of a parasitoid, or a hyperparasitoid.

Bot Flies

- To be considered a parasitoid, an insect must live inside its host, feed on the host's tissues, and kill the host. Some insects, like bot flies, feed on their hosts from the inside but don't kill the host. These are classified as parasites rather than parasitoids.

- Bot flies are parasites of mammals. The horse bot fly, *Gasterophilus intestinalis*, lays up to 1,000 eggs that stick to the horse's hair. Larvae emerge about a week later and crawl toward the horse's mouth, where they dig into the lining of the mouth, tongue, or gums. They remain there for four weeks and then moult into the next larval stage. Then, they move down the horse's throat to its stomach, where they insert themselves into the stomach's lining.

- Thanks to rings of spines around each body segment as well as hooked maxillae that form part of their mouths, the larvae remain securely embedded in the tissue. They feed on the host's tissue by scraping at it with their mandibles. Once the larvae grow large enough, they detach from the stomach and pass through the rest of the digestive system, exiting the horse's body with its feces. The bot fly then forms a pupa in the horse's feces or in the nearby soil and emerges several weeks later as an adult.

- While bot flies don't kill horses, they can cause them a lot of irritation. Horses with a lot of bot fly larvae might not feed normally, and in rare cases, stomach ulcers and severe tissue damage can be caused by infestations.

- There's also a species of bot fly that can parasitize humans. While the species, *Dermatobia hominis*, is known as the human bot fly, its normal host is cattle or deer. Unlike the horse bot fly, the human bot fly completes its life cycle in its host's skin. The adults lay their eggs on a mosquito, and the larva enters the host through the hole made by the mosquito when it feeds. While being infested by a bot fly isn't common, the greatest chances occur in parts of Central and South America, where both cattle and mosquitoes are common.

Parasitic Ants

- Another form of parasitism involves taking advantage of social insects like ants. Some socially parasitic ants, like *Aphaenogaster tennesseensis*, infiltrate the nests of other species and rely on the host colony to provide them with food and shelter. The strategy works because the host is duped into treating the parasites as if they were part of the family.

- In ants, this deception often involves chemical camouflage. Young queens of some parasitic species are able to infiltrate a host's colony by having none of the hydrocarbons in the cuticle of its exoskeleton that ants use to recognize other ants as nestmates. Having none of these cuticular hydrocarbons makes the parasitic queen essentially invisible. After the parasite queen has been allowed inside the nest, it adopts the cuticular hydrocarbons of its host. And once the parasite smells like it belongs, the host workers will treat it like any other nestmate—not only allowing it to stay but also feeding it.

- Another version of social parasitism involves the reverse situation: One colony of ants steals workers from another colony, takes them back to their nest, and gets the captives to do all the work. This behavior is formally known as dulosis. Some ant species, like *Polyergus lucidus*, have become completely dependent on the labor of captive workers of other species, like *Formica incerta*. The *Polyergus* workers have evolved long, curved mandibles that are well suited for carrying pupae back to their nests, but they cannot be used to feed themselves or to care for their own young. Instead, they rely on the captive *Formica incerta* workers to feed them and their brood.

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Questions

1. Plant structures called ______ protect insect larvae as they grow and develop.

2. True or false: The parasitoid life cycle, in which a parasite lives inside the body of its host and eventually kills the host as it emerges, is unique to insects.

ANSWERS CAN BE FOUND ON PAGE 225.

<<< TABLE OF CONTENTS

LECTURE 15

Insect Recyclers

Organisms that consume the remains of plants and animals and their waste products are known as detritivores. By feeding on dead organisms, they recycle chemicals and make them available for other organisms. Although microbes like fungi and bacteria play important roles as detritivores and are essential for decomposition, they could not do so as effectively—or as quickly—without the aid of insects.

Termite Colonies

- One of the most important groups of detritivores are the termites. In tropical and subtropical regions, the collective biomass, or dry weight, of all termites exceeds that of all the vertebrate animals living in the same area. The total worldwide biomass of termites is about the same as that of humans.

- Part of the reason termites are so abundant is that, like ants and some bees and wasps, they live in colonies. Such colonies can consist of thousands or even millions of individuals. But the structure of a termite colony is quite different from that of ants, bees, or wasps.

- For one thing, a termite colony has not only a queen but also a king. The king and queen establish a colony together and continue to mate throughout their lives. The queen can live for 20 years or longer and lays an egg about every three seconds. Uniquely, the workers can be male or female, in contrast to the exclusively female worker castes found in nests of ants, bees, and wasps.

- Young termites aren't as helpless as the larvae and pupae of ants, bees, and wasps. Because termites have incomplete metamorphosis, immature termites, called nymphs, are capable of moving around and feeding themselves. That means that young termites can act as workers, performing important tasks like maintaining the nest, tending to the eggs and the queen, and foraging for food.

- The ability of termites to digest wood comes from the symbiotic microorganisms that live in their gut. These include bacteria and protozoans that produce enzymes that can break down the cellulose and lignin that give wood its rigidity. Cellulose is the most abundant organic compound on Earth. Having symbiotic microbes that help termites to digest cellulose has given them access to a resource that very few other insects can make use of.

One of the by-products of the metabolism of cellulose by microbes in the termite gut is methane gas. Altogether, termites contribute between 1% and 3% of all methane emissions worldwide. They would contribute even more, but their nests help absorb much of the methane.

- Termites acquire these microbes from their nestmates by feeding on their anal secretions. Every time a termite moults, it sheds not only its exoskeleton but also its digestive tract, which means it loses its symbiotic microbes. So, termites must continually reinoculate their guts with microbes from their nestmates' secretions after each moult. This reliance on sharing microbes may have contributed to the evolution of sociality in the first termites.

Termite Habitats

- Termites have thin exoskeletons that make them more vulnerable to drying out than most insects. Because most termites have to travel outside their nests to find food, they construct covered tunnels made of soil or wood pulp mixed with their saliva and feces. The undersides of tree branches in tropical forests often have networks of these tunnels. If you scrape away a small section, the termites will quickly repair the damage.

- Nests are built to protect the entire colony and in some species can be quite large. These impressive structures are built with tunnels that allow air to flow through them so that the termites don't suffocate. As temperatures fluctuate between day and night, warm air is driven up through chimney-like shafts. These shafts split into progressively narrower tunnels and eventually reach the thin outer wall through which the air diffuses. As the wind blows, it drives fresh air into the nest, which circulates until it reaches the termites deep inside.

- The termites can control the flow of air by adjusting the location and size of tunnels as well as the height of the mound. Controlling air flow also allows the termites to adjust the temperature and humidity inside the nest. This allows them to live in environments that would otherwise be inhospitable, such as deserts and dry grasslands, where termites play important roles in turning over and fertilizing the soil by bringing nutrients into their underground nests. In dry ecosystems, these are essential services that make it possible for plants to grow.

- Of course, termites are also capable of living in more mundane habitats, like inside the walls of your house. In addition to homes and buildings more generally, termites also damage furniture, fences, wooden bridges, boats, paper products, and even some plastic and rubber products, including the insulation on underground cables and pipes. In the United States, termite damage costs an estimated $2 to $3 billion annually. Worldwide, termites cause as much as $40 billion in damage.

Recycling Dead Animals

- Just as termites are important for recycling dead plant matter, other insects play valuable roles in recycling dead animals. Most of these are beetles and flies. Blowflies are often the first insects to arrive at a dead animal's carcass—often just a few minutes after death. They are attracted to particular chemicals that are released as microorganisms like bacteria begin to break down the proteins in the animal's flesh.

- Because dead animals are an unpredictable resource, insects that depend on them have to be especially good at locating carcasses and taking advantage of them before they rot away. Adult blowflies feed on the flesh of the carcass, and each female lays some 250 eggs inside it. Blowfly eggs

Some moths also feed on dead animals as larvae. The most familiar are known as clothes moths because they can also feed on animal products used in clothing, like leather, wool, silk, and fur. The common clothes moth, *Tineola bisselliella*, and the case-bearing clothes moth, *Tinea pellionella*, are among the few insects that can digest keratin, the protein found in hair and fur.

hatch within 24 hours, and the larvae immediately begin to feed. The entire developmental process is accelerated, with adult blowflies emerging 10 to 14 days after the eggs are laid.

- Flesh flies also arrive soon after an animal dies. In their race to feed on the carcass before others do, some flesh flies jump-start the developmental process by depositing larvae into a carcass. In these species, the eggs hatch inside the female's body, so they essentially give live birth.

- Competition for carcasses is intense. The larvae of flesh flies often attack and kill blowfly larvae. Another type of fly, *Dryomyza anilis*, attacks any member of the same species that attempts to lay eggs on a carcass where it has already laid eggs. Burying beetles in the family Silfidae try to monopolize carcasses by burying them underground before other insects can find them.

- The appearance of insects in rotting meat is so predictable that since at least the time of Aristotle, it was assumed that fly larvae, or maggots, were spontaneously generated from decaying meat. In 1668, the Italian physician Francesco Redi published the results of a series of experiments that disproved this idea. Redi put some meat in open jars and some in jars that were covered with gauze, allowing air to pass through but not flies. He found that maggots only appeared in the open jars, which flies were able to access.

- Not only is the sudden appearance of insects in a carcass fairly predictable, but so is the sequence in which particular types of insects appear. This predictability has some practical benefits. By identifying which insects are present—and at what developmental stage—it's possible to determine how long ago a person died. Forensic entomologists can often help reconstruct details about the cause of death, how long ago death occurred, and where the body has been.

Dermestid Beetles

- In addition to decomposing dead animals and plants and helping solve crimes, the insect detritivores also play another important role. Specimens of human and animal bones are important for research and education. But before they can be used in a museum collection, laboratory, or classroom, bones must be completely cleaned of any soft tissue. That's not so easy, especially for bones that have small cavities that can't be accessed by tools.

- The standard way that bones are prepared for research and teaching collections is to use dermestid beetles, another insect detritivore. A large colony of dermestid beetles can clean the skeleton of a small bird overnight. Larger skeletons, like that of a pig or a deer, can take a week or longer. When they have finished, there is nothing left but cleaned bones.

- Dermestid beetles typically arrive at a carcass later in the stage of decomposition, after the blowflies, flesh flies, and clothes moths. By this time, the soft tissue has usually dried and hardened. While the adult beetles do feed on soft tissues, it's the larvae that are especially voracious. Dermestid beetle larvae have lots of long setae, or hairs, that give them a fuzzy appearance. They are narrow in shape and taper to a point at both the head and the rear. This shape helps them fit into very narrow spaces, like the sinuses inside a skull.

- If you're interested in starting a collection of animal bones, you can easily keep your own colony of dermestid beetles. You can order them from suppliers that will ship a small number—maybe 25 to 50 individuals—to get you started. You can grow your starter colony by feeding them leftover meat. If fed well, the colony will grow substantially within a few weeks, and they'll be ready for the first skeleton you want them to clean.

- You can keep the colony in an aquarium with a screen on top. They aren't good at climbing or flying, but you'll want to make sure the lid fits snugly just in case. It's also a good idea to scrape away the silicone at the bottom of each corner, since they can sometimes climb up the corners. The smell of the colony can be a problem, so keep them outdoors and away from your living quarters. They do need to stay warm—between about 65° and 80°—so if you live in a colder climate, you'll want to put a heater nearby.

DERMESTID BEETLES

- In terms of where to get skeletons for your dermestids to clean, there are lots of options. Sometimes butchers or taxidermists have extra material they're willing to give away. If you're a hunter or you know someone who hunts, then you can probably get your hands on some carcasses. Roadkill is another option, although you'll want to check your local regulations about collecting roadkill. Be aware that some species, including many birds, are often illegal to have in your possession.

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Questions

1 True or false: Termite colonies contain both a queen and a king.

2 Which of the following are important for decomposition of animal carcasses and are also used to prepare skeletons for museum collections?

a blowfly maggots
b termites
c dermestid beetles
d clothes moths

ANSWERS CAN BE FOUND ON PAGE 225.

TABLE OF CONTENTS

LECTURE 16

Insects That Fly

Insects were the very first animals to evolve the ability to fly. Evidence from fossils and DNA suggests that flight first evolved in the Late Silurian or Early Devonian period, around 400 million years ago. The origin of flight may be the single most important event in the evolutionary history of insects and in the history of all life on Earth.

The Evolution of Flight

- The ability to fly gives insects a lot of advantages over other animals, including a way to escape predators. Flying also allows insects to access resources that would require much more effort to reach by walking or climbing. It's probably not a coincidence that the evolution of flying insects happened around the same time that plants began to grow taller and the first forests appeared. Reaching edible leaves and other edible parts at the tops of plants would have been much easier for insects that could fly.

- Flight can also make it easier to find a mate, especially one that isn't a close relative. Genetic diversity is critical for adaptation. Natural selection acts like a filter to sort through the variation available in any one generation, and only the traits that are a good fit for the current environment are passed on to the next generation. Being able to access a diverse pool of potential mates gave flying insects a greater ability to adapt to changing conditions. These advantages made winged insects extremely successful, and they quickly diversified into different species.

- There is considerable debate among experts on how the very first flying insects came into existence. There aren't a lot of fossils from the exact time when insects first evolved wings, but we can make some inferences based on fossils from before and after the very first flying insects appeared. We can also make inferences from observations of living insects and from what we know about the evolution of flight in other animals.

- It's likely that the structures that ultimately became insect wings first evolved for a different purpose. This happens all the time in evolution. For example, the ancestors of birds didn't evolve feathers because they're helpful for flying. Instead, feathers first appeared in dinosaurs that could not fly, possibly to help them stay warm.

- One hypothesis is that wings evolved from extensions of the thorax that were used for gliding. This gliding-first idea is similar to how scientists think other animals—birds, bats, and pterosaurs—first evolved flight. In fact, fossils with just this kind of structure on the thorax, called paranotal lobes, have been found from the Upper Carboniferous period. The Palaeodictyopterida had two fully formed pairs of wings as well as an additional pair of smaller paranotal lobes on the first segment of the thorax. These lobes didn't act as functional wings, but they may provide a clue about the type of structure that may have given rise to wings.

- It's worth noting that insect wings evolved not by modifying existing appendages, like legs, but from a completely independent part of the body. In all other animals that have evolved flight, the wings are modified limbs. Having limbs modified into wings certainly works well for flying, but it means that those limbs are no longer useful for other purposes. Insects, on the other hand, gained the ability to fly but retained all six of their legs. This is another factor that has contributed to the tremendous success of insects.

Almost all flying insects have two pairs of wings, but flies have just one. Instead of a second pair of wings, flies have structures called halteres on their last thoracic segment, where their hind wings would be. The halteres act as sensory organs that provide feedback during flight. If its halteres are amputated, a fly cannot fly.

Controlling Wings

- Going from gliding to flying required not only functional wings but also developing muscles and nerves to control the wings as well as several other physical changes.

- Dragonflies are some of the most ancient flying insects and also some of the most capable fliers. They are some of the only living insects that control the movement of their wings directly with their muscles. When the flight muscles contract, the wing moves upward. A parallel set of muscles contract to pull the wing back down again. The only other living insects with direct muscle control of their wings are the mayflies and the damselflies. Together, these form a group known as the Paleoptera, a name that means "old wing."

- All other flying insects use a different system to control their wings. They're collectively known as the Neoptera, or "new wing" insects. Neopteran insects have flight muscles that connect to the exoskeleton


DRAGONFLY

rather than the wings. One set of muscles runs vertically from the top to the bottom of the insect's thorax. When these muscles contract, the exoskeleton bends, causing the wing to move upward. Another set of flight muscles runs horizontally through the thorax. When these muscles contract, they pull on the exoskeleton and bend the thorax to make it slightly shorter. The top of the thorax bulges upward and causes the wing to be pulled downward.

- It may seem odd to control wings by deforming the exoskeleton rather than manipulating the wings directly, but there is an advantage to doing it this way. The exoskeleton is made of a protein called chitin, which is not very flexible. When the exoskeleton is deformed by the flight muscles pulling on it, it creates an elastic force. As soon as the muscle relaxes, the elastic force causes the exoskeleton to spring back to its previous shape. So, the movement of the wing is aided by this elasticity, allowing the insect to conserve more energy when it flies.

How Insects Fly

- One thing that all flying insects have in common is the motion of the wings that is used for flight. For any object to fly, it has to achieve a balance of four different forces. Weight is the force that pushes the object toward the ground, thanks to gravity. The opposite force is lift, the force that pushes an object upward. To fly forward requires thrust, which is acting against the opposite force, drag.

- Airplanes fly by first generating forward speed along the ground—that's the thrust—and then using the shape of their wings to generate lift. An airplane's wing, if viewed as a cross section, is shaped like a teardrop. The wing is thicker toward the front and tapers toward the back. Air travels faster as it flows over the top of the wing compared to the flow of air below the wing. That difference in speed creates lower pressure on the top surface of the wing, generating lift.

- Using these principles, French scientist August Magnan noted in 1934 that bumblebees should not be capable of flying since their wings appear to be too small to generate enough lift to balance their weight. We now know that the secret to how bumblebees and other insects fly has to do with the way they move their wings. Unlike bats and most birds, insects don't just flap their wings up and down to fly. Instead, they move their wings in a figure-eight motion.

- Biologist Charles Ellington was the first to describe this motion. He observed that as the wing moves downward, it also moves forward, with the leading edge slightly lower than the trailing edge. Air moves faster over the upper surface of the wing compared to the lower surface, generating lift. And drag is created when the flow of air catches the underside of the wing, pushing the wing upward. The insect then pulls the wing down and backward, generating thrust to propel the insect forward through the air. By tilting the forward edge of the wing downward again and lifting it, the wing rises and the next downstroke begins.

- The small size of insects means that the viscosity of air affects them more than it does larger objects, like airplanes or even most birds and bats. This allows insects to use a higher angle of attack—the angle of the wing relative to the direction of motion. If an airplane were to use an angle of attack greater than 15°, it would stall and begin to fall because its weight would exceed the lift being generated. But insects, being small, can generate a lot of lift by using an angle of attack as high as 30° to 45°.

Engineers have successfully designed drones with wings that move just like an insect's wing, using the figure-eight motion to create a vortex of air above the wing to generate lift. By using flexible wings like those of insects, these drones are better at recovering from collisions than drones with rigid propellers.

- The figure-eight motion of an insect's wing also creates a vortex of air above the wing, which acts like a miniature tornado and pulls upward, generating even more lift. Insects have to keep moving their wings rapidly to make this vortex stable and to continue generating both lift and thrust. The insects with the smallest wings have to beat their wings especially fast to fly. Some tiny flies called midges beat their wings more than 1,000 times per second. Insects with larger wings, like some butterflies, can beat their wings more slowly because each wing beat generates a lot of lift. Swallowtail butterflies are among the slowest, beating their wings just five times per second.

Gliding Insects

- There are some insects that maneuver through the air without any wings at all. While working up in the canopy of the Amazon Rainforest, biologist Steve Yanoviak discovered that some ants are able to glide from the high branches of trees down to the trunks. Most gliding animals have structures that function like a wing or parachute, but Yanoviak's ants didn't have any such structures.

- In subsequent experiments, Yanoviak and his colleagues figured out how canopy ants glide. They hold all six of their legs up and out, and they lower their abdomen. This body configuration slows their descent and causes the ant to move backward through the air. By changing the position of their legs and abdomen, the ants can steer left or right. Incredibly, these ants are able to identify the trunk of the tree they fell from and steer toward it. They then use the claws at the tips of their tarsi to grab onto the tree trunk.

- We now know that this behavior evolved many times independently among different groups of tree-dwelling ants. Natural selection has led to the evolution of gliding abilities because ants that can glide back to their tree trunk are more likely to survive than those that can't. Because ants live in colonies and cannot survive on their own, an ant that gets lost is a dead ant. Falling from a tree branch to the forest floor would make it very difficult for an ant that nests in the treetops to find its way back home.

- Yanoviak and his colleagues found that several other species in the rainforest canopy could also glide. These include some spiders and wingless insects called jumping bristletails. Jumping bristletails evolved before the earliest flying insects, so the fact that they are able to glide may offer clues about the evolutionary origins of flight in insects.

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Questions

1. Insects in the order _______, which includes dragonflies and damselflies, are among the most ancient flying insects.

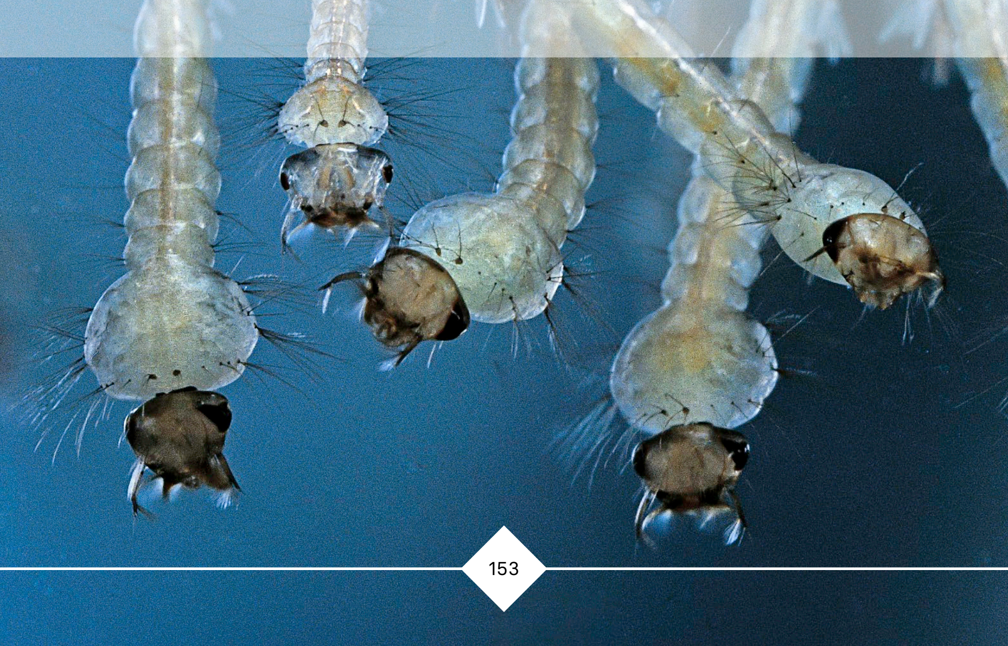
2. True or false: How bumblebees can fly despite their relatively heavy bodies and small wings has not yet been explained by science.

ANSWERS CAN BE FOUND ON PAGE 225.

LECTURE 17

Insects Adapted to Aquatic Life

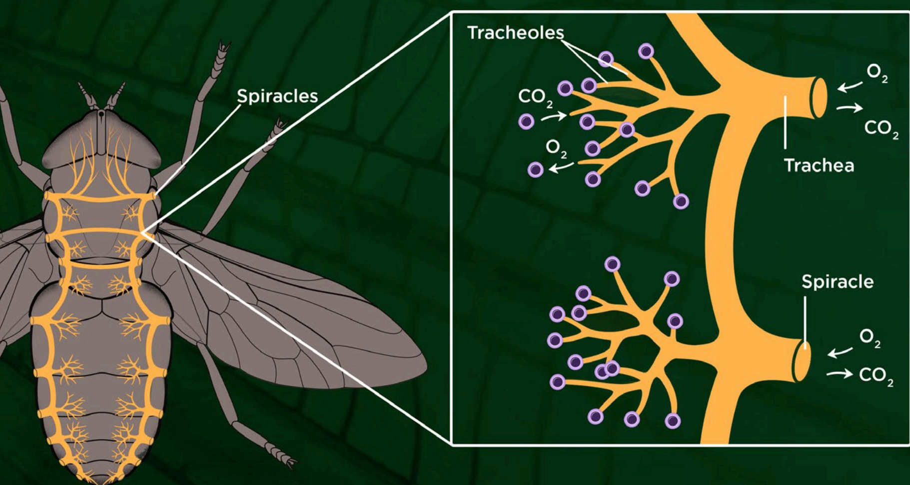
Insects have come to dominate many terrestrial ecosystems across the planet, but many species spend part or all of their lives in the water. Indeed, in many aquatic ecosystems, insects form important roles in the balance of life. And the presence of aquatic insects can be used as an indication of the overall health of an ecosystem.



The Insect Respiratory System

- One of the greatest challenges of underwater life is how to breathe. Insects have small openings called spiracles distributed across their bodies. When air passes through a spiracle, it enters a tube called a trachea. The trachea splits into various narrower tubes, which further divide until they become very fine tubes known as tracheoles.

- Each of the cells in an insect's body is close to one or more tracheoles. Oxygen from the outside air can reach these cells by passing through the tracheal system and diffusing out of the tracheole. The oxygen diffuses into the cell, where it's used as fuel for the metabolic demands of the insect's physiology.



O_2 diffuses 300,000× faster in air than in fluid
CO_2 diffuses 10,000× faster in air than in fluid

- In some ways, the insect's tracheal system is reminiscent of the system that's present in all vertebrates, including humans. We, too, have a branching system of tubes that takes oxygen around the body to individual cells, where the oxygen diffuses out of the tube—an artery, in our case—and into the cell. But there are some important differences between the respiratory system of insects and that of vertebrates.

- We have to inhale to fill our lungs with air so that oxygen transfers to the blood and makes its way around the body. In contrast, insects don't have lungs. Air can enter any spiracle that's open, although insects often push air through their tracheal system when doing activities that require a lot of energy, like flying. Airflow can be regulated by closing some spiracles and opening others to create a one-way flow through the system or by expanding and contracting the abdomen or thorax in a way that resembles the movements of our chests as we inhale and exhale.

- In vertebrates, oxygen is ferried through the blood by a specialized carrier molecule called hemoglobin. Most insects don't have hemoglobin—or any carrier molecules—to transport oxygen to their cells. They rely instead on diffusion, the physical process by which molecules naturally move from higher to lower concentrations.

- Because the concentration of oxygen is lower inside a cell than in the air that enters the trachea, oxygen molecules will naturally diffuse toward the lower concentration inside the cell. At the same time, carbon dioxide made as a by-product of metabolism diffuses from the relatively higher concentration inside the cell to the lower concentration in the tracheole. As air moves through the insect's tracheal system, the carbon dioxide makes its way out through one of the spiracles.

- These two major differences between insect and vertebrate respiratory systems put some limitations on what insects can do. Insects can't grow very large because the diffusion of oxygen from the outside air through the tracheal system and into the cells only works over relatively short distances.

- But there are also advantages to the insect respiratory system. You can't suffocate an insect by covering its mouth, and an insect can't choke to death on its food. Another advantage to the insect respiratory system is that it's filled with air, not fluid. Oxygen diffuses 300,000 times faster in air than in fluid, and carbon dioxide diffuses 10,000 times faster in air. So, insects are far more efficient than vertebrates in getting oxygen into their cells and carbon dioxide out.

Siphons

- Aquatic insects have modified their respiratory systems in different ways. One solution to the problem of breathing underwater used by some insects is to breathe air from the surface. Insects that use this approach often have a breathing tube that functions like a snorkel, allowing the insect to be underwater while still getting air from above the surface.

- Water scorpions—aquatic insects in the order Hemiptera and family Nepidae—have long breathing tubes called siphons at the end of their abdomens. Many flies that have aquatic larvae, including mosquitoes, also use siphons as breathing tubes. Mosquito larvae can often be seen just below the water's surface with their breathing tubes sticking out.

- At the tip of the siphon is a spiracle where air enters and leaves the tracheal system. Mosquito larvae have five flat lobes surrounding the spiracle that fold together to form a hollow cone. The cone covers the spiracle like a tent and keeps water out when the larva is underwater. When it comes to the surface, the lobes fold open to allow air to enter the spiracle.

- Advanced snorkelers can hold their breath and swim well below the water's surface, coming up to breathe through their snorkels when they can't hold their breath any longer. In much the same way, insects that breath through siphons aren't confined to the surface but still must return to it periodically to replenish their supply of oxygen and get rid of excess carbon dioxide.

A few species occasionally get air from aquatic plants by using a siphon to suck air out of bubbles trapped by underwater leaves. Others, like reed beetles in the subfamily Donaciinae, have aquatic larvae that chew directly into plant stems and roots, insert their spiracles to spaces within the plant tissues where air is trapped, and get oxygen by breathing directly from this trapped air.

Air Bubbles

- Scuba divers, on the other hand, can stay much longer underwater because they bring a supply of air with them as they swim. Some aquatic insects, like predaceous diving beetles, use a similar approach. They bring a bubble of air with them from the surface, holding it in place through surface tension between the hind wings and the elytra.

- When you watch a predaceous diving beetle swimming underwater, you can see the air bubble at the tip of its abdomen, where the wings come together. Spiracles on the abdomen allow oxygen to diffuse into the tracheal system. Eventually, the oxygen supply in the bubble is depleted as it's replaced by carbon dioxide, which diffuses out of the tracheal system. When this happens, the beetle releases the bubble and returns to the surface to get a new one.

- Some other aquatic beetles, like riffle beetles in the family Elmidae, keep a thin air bubble attached to the entire underside of their bodies. They have a dense coat of tiny hairs, or setae, that are hydrophobic, meaning they repel water. By having so many hairs—up to 2.5 million hairs per square millimeter—the surface tension of water traps a bubble as a thin film of air. This structure is called a plastron.

- Just like the air bubble at the tip of the predaceous diving beetle's body, the plastron is connected to the riffle beetle's tracheal system, allowing gas exchange to occur. But unlike the predaceous diving beetle, which has to return to the surface when the oxygen supply is depleted, the riffle beetle's plastron gets constantly replenished. As the oxygen supply decreases, oxygen from the water diffuses into the air in the plastron. Likewise, as the plastron fills with carbon dioxide, the carbon dioxide diffuses from the higher partial pressure in the plastron to the lower partial pressure in the surrounding water.

In places with sufficient amounts of dissolved oxygen, many species that have aquatic larvae or nymphs, like damselflies and dragonflies, have gills that allow dissolved oxygen to be taken directly from the water.

- Riffle beetles have an effectively inexhaustible supply of oxygen and can stay underwater without having to return to the surface to breathe. But for their breathing system to work, there has to be a lot of dissolved oxygen in the water. The presence of aquatic insects that get oxygen directly from the water is a good indicator of how much oxygen is in the water. The amount of dissolved oxygen is a critical factor in many aquatic ecosystems because other animals, like fish, need dissolved oxygen to survive.

Marine Insects

- In addition to living under the surface of the water, some insects live just above its surface. Water striders—true bugs in the order Hemiptera and family Gerridae—have elongated legs lined with hydrophobic hairs that repel water. Along with their relatively small size, these adaptations allow water striders to take advantage of the surface tension of water to skim along its surface.

- Some species of water striders in the genus *Halobates* live on the surface of the ocean hundreds of miles from shore. Known as sea skaters, these insects coat themselves with a waxy secretion that makes them especially waterproof. Sea skaters feed on plankton and dead creatures that float at or just below the water's surface. They lay their eggs on floating objects, too, like bird feathers. Sea skaters escape being eaten by fish and other predators by using the surface tension of the water like a trampoline, launching themselves into the air at a rate of acceleration of 400 m/s^2.

- There are very few insects that live in the ocean. Most that do live in the ocean live on the periphery of the sea—either just above its surface, like the sea skaters, or at its edge, along coastlines. Midges in the family Chironomidae are common in some coastal environments, like shallow lagoons and rocky tidepools. Another type of fly, the species *Oedoparena glauca*, are predators that feed on barnacles.

- These marine insects have found ways to make a living at the edge of the sea, but there aren't any insects that live entirely within the world's oceans. One reason why may be that the ocean is already filled with so many types of organisms that there just hasn't been room for insects. For an insect to eke out an existence in the sea, it would have to find a way of life—including a place to live and a way to feed—that another species isn't already using.

- Another possible explanation for why insects aren't found in the ocean is that their respiratory systems won't work well deep below the water's surface. Aquatic insects have found ways to get oxygen into their tracheal systems, either by getting it from the surface or directly from the water. But the deeper you go, the greater the pressure becomes, and the increased air in the tracheal system would be compressed into a smaller volume as the pressure rises. For insects at depths below about 300 feet, the pressure would shrink the air in their tracheal system to a volume so small that it would interfere with the process of diffusion that they depend on to get oxygen into their cells. Likewise, plastrons fail at depths of around 100 feet.

- An apparent exception to the rule that no insects are found in the deep sea are lice that feed on marine mammals. These lice attach themselves to the bodies of seals, and they stay attached even as the seals dive deep underwater. In one experiment, researchers exposed lice collected from seals to pressures comparable to what they would experience at a depth of more than 6,500 feet. Amazingly, most of the lice survived. One possible explanation is that the seals are diving to such depths only briefly, and the lice may be able to slow their metabolism enough that they can survive without much oxygen until the seal resurfaces.

Reading

Amateur Entomologists' Society, "Insect Respiration." https://www.amentsoc.org/insects/fact-files/respiration.html.

Goforth, "Mayflies, Damselflies, and Stoneflies." https://thedragonflywoman.com/2011/01/17/may-damsel-stone/.

Mahadik, "Sea Skaters Are a Super Source of Inspiration." https://discovery.kaust.edu.sa/en/article/975/sea-skaters-are-a-super-source-of-inspiration.

Questions

1. True or false: Insects that live underwater must return to the surface to breathe.

2. True or false: While some insects live at the edge of the sea or at its surface, none live in the ocean.

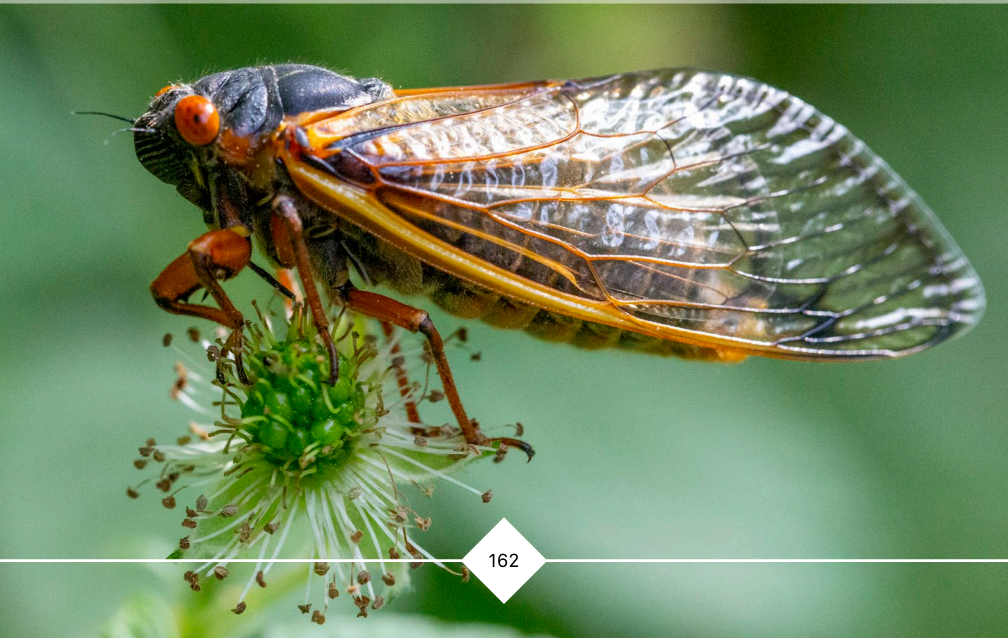
ANSWERS CAN BE FOUND ON PAGE 225.

<<< TABLE OF CONTENTS

LECTURE 18

Insect Songs and Sounds

In many places, chirping crickets, chorusing cicadas, and rhythmically pulsing katydids are an iconic part of the natural soundscape. Insects produce sounds in many ways and use them for a variety of purposes, from finding mates to scaring off predators.



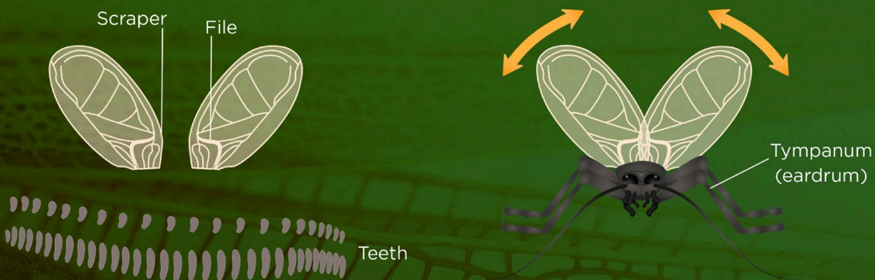
How Crickets Produce Sound

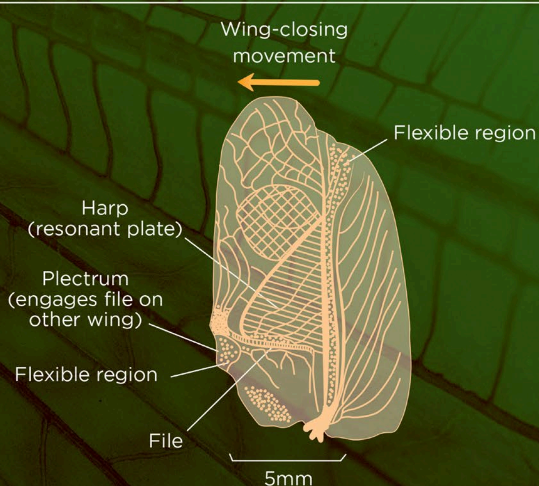
- Male crickets produce their songs by rubbing together specialized structures on their wings. Each of the two forewings has a vein at its base that is modified into a series of up to 300 tiny ridges, like a washboard. When the cricket raises and lowers its wings, the sharp edge of one forewing is scraped along the ridges on the other forewing, producing audible vibrations. Most crickets are right-winged, meaning that they always sing by rubbing the scraper on their right forewing against the file on their left forewing.

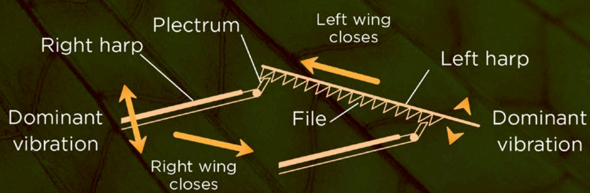
- This method of producing sound, in which two body parts are rubbed together to produce vibrations, is called stridulation. It's similar to the way a musician draws a bow across the strings of a violin to produce sound. A violin or an acoustic guitar amplifies the sound produced by the vibrating strings by allowing the vibrations to resonate on a thin wooden bridge between the strings and the hollow chamber beneath it.

- Crickets amplify the volume of their songs in various ways. For field crickets, a particular part of the wing, called the harp, allows the vibrations produced by the file and scraper to resonate. The harp is triangular in shape and located in the center of the wing. The acoustic properties of the harp determine the frequency, or pitch, of the cricket's song.

In China, keeping crickets as pets dates back to the Tang dynasty, from 618 to 907 CE. Texts from this era describe how the emperor's concubines kept crickets near their beds to hear the crickets' calls at night.


Scraper
File
Teeth
Tympanum
(eardrum)


Wing-closing
movement
Flexible region
Harp
(resonant plate)
Plectrum
(engages file on
other wing)
Flexible region
File
5mm


Plectrum
Left wing
closes
Right harp
Left harp
Dominant
vibration
File
Dominant
vibration
Right wing
closes

- In mole crickets, the male's song is amplified by calling from inside an underground burrow. The shape of the burrow is similar to that of a trumpet. The mole cricket calls from a narrow, dead end with its abdomen facing toward the burrow's entrance. The tunnel gets larger toward the entrance, much like the end of a trumpet. The sound produced at the other end resonates across the length of the opening and gets louder as the opening becomes wider.

- Like crickets, katydids sing by rubbing together a file and scraper at the base of their wings. Crickets and katydids both belong to the insect order Orthoptera, along with grasshoppers and locusts. Some grasshoppers produce sound by rubbing one of their legs against the sharp edge of their forewing. In these species, the upper section of the leg, called the femur, has bumps that function as the file.

Pitch and Rhythm

- Male crickets sing to attract mates or to announce their presence to rival males. Each insect species that sings has its own characteristic sound because females use the song to locate a male mate of the same species. The songs can differ in pitch—meaning how high or low the note sounds—and in structure, meaning the timing of the pattern in which sounds are produced.

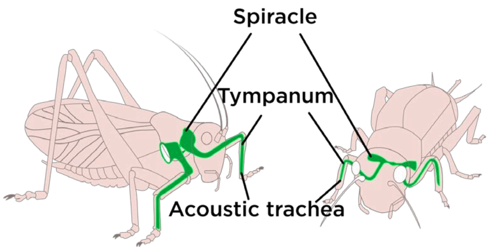
- The pitch of a song is measured in hertz (Hz). One hertz is one cycle per second, so a 1,000 Hz song has 1,000 cycles per second. Most insect songs are between 2,000 and 15,000 Hz, although some are even higher. Most people can hear sounds between 20 and 20,000 Hz, but our ability to hear high-pitched sound declines as we age. Crickets produce simple songs of a single pitch that is usually below 10,000 Hz. Katydids and grasshoppers tend to have calls that reach above 10,000 Hz.

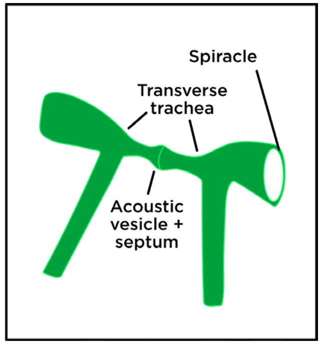
- While the pitch and rhythm of an insect's song differs by species, it also varies with temperature. Insects are ectotherms, which means they get their heat from their environment, not from their own metabolism. As the temperature falls, insects slow down. Their muscles become less capable of movement, and the neurons that send signals to the muscles slow down as well. The more slowly they stridulate, the lower the pitch of the call. Likewise, colder temperatures also cause insects that make a series of short chirps to produce chirps at a slower rate.

- The relationship between the sound of an insect's call and the temperature can be quite precise. In fact, you can get a pretty accurate reading of the temperature by listening to the call of the snowy tree cricket. If you count the number of chirps in its song in 13 seconds and add 40 to that number, you'll get the approximate temperature in degrees Fahrenheit.

How Insects Hear

- Different types of insects have a variety of sensory organs for hearing. Crickets and katydids have a tympanum, or eardrum, located on the tibia of each of their forelegs. The tympanum is a thin portion of the exoskeleton. It works much like our eardrums, vibrating in response to changes in pressure caused by sound waves.





- Behind the tympanum is the acoustic trachea, an air-filled cavity that is an extension of the tracheal system. Specialized cells along the acoustic trachea respond to pressure changes caused by the vibrating of the tympanum. These cells send signals to the insect's brain that are processed and interpreted as sound. In katydids, the acoustic trachea extends from the tympanum on the tibia and up the length of the leg to a larger cavity in the thorax. This enlargement amplifies the sound in much the way that a horn does.

- It may seem odd that insects have ears on their legs, but this reveals a clue about how these sensory organs evolved. Many insects can sense vibrations in the soil using sensory cells in their legs. In crickets and katydids, the sensory cells in their legs evolved to be more specialized in the two forelegs. Along with changes to the tracheal system and exoskeleton, this made it possible for them to hear sound transmitted through the air, even across long distances.

- Females have to not only hear and recognize the songs produced by males of their species but also locate them. Female crickets and katydids can tell which direction a call is coming from based on differences in how the sound is perceived by the tympanum in one leg versus the other. But the calls produced by male insects don't just attract females of the same species—they can also attract enemies. Some populations of Pacific field crickets in Hawaii have stopped singing in order to avoid parasitoid flies.

Cicadas

- Crickets, katydids, and grasshoppers all use stridulation, or the rubbing together of different body parts, to make sound. But there's another group of insects that's well known for the incredibly loud sound they can make, and they do so in a very different way. These are the cicadas.

- Cicadas spend the majority of their lives underground. Eggs are laid in tree bark, and when they hatch, the nymphs dig into the soil and feed on roots. When they are ready to emerge as adults, they climb out of the soil and up tree trunks or other structures. Many species of cicadas complete their entire developmental sequence in a single year. But some species of North American cicadas have a much longer nymphal stage, spending several years underground before emerging as adults. A few species in the genus *Magicicada*, known as periodical cicadas, emerge like clockwork every 13 or 17 years.

- Like all insects, the adult stage in the cicada's life cycle is focused primarily on reproduction. The males call to attract females. Male cicadas have a specialized structure called a tymbal that produces sound. The tymbal is located on the side of the abdomen, close to the thorax and just behind the base of the wing. The tymbal has a series of hard, slightly curved ridges separated by a thin, flexible membrane. A large muscle is connected to the center of each tymbal.

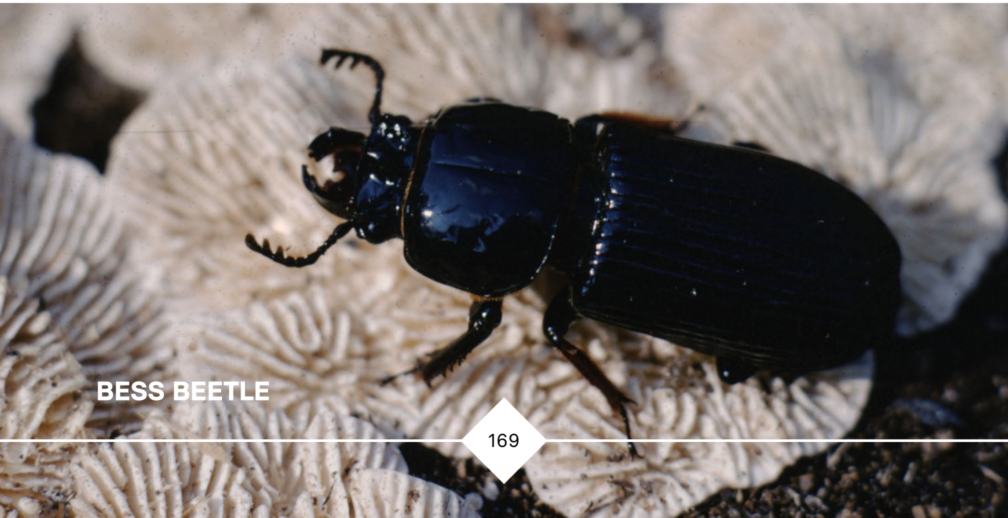
- When the muscle contracts, it pulls on the middle of each ridge, causing it to buckle in a direction opposite to the shape of its curve. This sudden buckling makes a clicking sound. When the cicada's muscle relaxes, the tension in the tymbal's ridges causes the ridges to return to their original shape, producing another click as they pop back into place. Tracheal tubes in the abdomen are enlarged to form air sacs that fill almost the entire abdomen, amplifying the sound produced by the ridges in the tymbal.

Hearing damage can be caused by sounds louder than 85 decibels, which is about as loud as a lawnmower. Cicadas' calls can be 100 decibels or higher—or as loud as a train passing right by you. One species of African cicada, *Brevisana brevis*, was measured at 106.7 decibels—louder than a jet plane flying just 100 feet above your head.

- As with other insects, each species of cicada has its own unique mating call. Cicada calls often begin softly and build to a crescendo. It's also common for cicadas to coordinate their calls among thousands or even millions of individuals. In places where enormous swarms of cicadas are chorusing, the sound can be so loud that people have to cancel outdoor events.

Beetles

- While cicadas are the loudest insects, the insects with the most complex sound repertoire are the bess beetles. One species that lives in North America, *Odontotaenius disjunctus*, uses 14 distinct sounds to communicate among family members. Adults and larvae produce sounds through stridulation. The adult beetles rub their folded hind wings, which have rows of tiny spines, against a particular spot on the top of their abdomens.



BESS BEETLE

- Interestingly, in larval bess beetles, the third pair of legs is modified into a stridulatory organ. They rub the tip of their third leg against a set of ridges near the base of the middle pair of legs. The sounds made by larval bess beetles aren't very loud, but they can be detected as vibrations by family members traveling through the wood. The sounds made by adult and larval bess beetles can also help protect them from predators. Predators often hesitate when the beetles stridulate, which can give the beetles a better chance of escaping.

- Another beetle that makes sounds is known as the deathwatch beetle. These beetles live in wood and are known to infest older houses, especially those made with a frame built of oak, as was common in England prior to the 20th century. The adult beetles tap their heads against the wood on the sides of their tunnels, making a clicking sound to attract mates. Males tap first, and then females tap to respond. These tapping sounds that resemble the ticking of a clock can be heard coming from the walls at night and were considered to be a bad omen.

Reading

Cicada Mania, https://www.cicadamania.com/.
Elliott and Hershberger, *The Songs of Insects*.
Songs of Insects, https://songsofinsects.com/.

Questions

1. Most insects produce sound to attract ______.

2. True or false: Cicadas can produce sounds in excess of 100 decibels, comparable to the volume of a passing train.

ANSWERS CAN BE FOUND ON PAGE 225.

<<< TABLE OF CONTENTS

LECTURE 19

Insects as Farmers

One of the most significant milestones in human history was the development of agriculture. But agriculture isn’t unique to humans. Three different groups of insects—ants, termites, and beetles—each developed agriculture independently of one another long before the first human farmers. Rather than cultivating plants, all three groups of agricultural insects farm fungi.

Fungus-Growing Ants

- The most familiar insect farmers are the leafcutter ants in the genera *Atta*, *Acromyrmex*, and *Amoimyrmex*. Leafcutter ants can't digest leaves themselves, so they feed the leaves to fungus and then eat the fungus. The ants effectively use the fungus as an external digestive system. A large leafcutter nest might have hundreds of fungus gardens, each within a chamber about the size of a soccer ball.

- The first ants to grow fungi some 55 to 65 million years ago did not use fresh leaves to cultivate their fungi. Fungi are decomposers, so one benefit of raising fungi for food is that they can be grown on a wide range of organic materials. The first fungus-growing ants are thought to have lived in the Amazon Rainforest, and they most likely raised their fungal gardens using organic material such as dead leaves, parts of flowers, insect feces, or the remains of dead insects.

- Many species of fungus-growing ants today still raise their fungal gardens this way. Out of about 250 species of fungus-growing ants, or attines, about a third practice a method of growing fungi known as lower attine agriculture. These lower attine ants make relatively small nests where they grow their fungus gardens on organic materials they find nearby. Most of these ants grow fungi that belongs to Leucocoprineae, a group that includes the yellow pot-plant mushroom. The ants are totally dependent on these fungi for food.

- While the fungi benefit from being protected and cared for by the ants, the fungi grown by lower attine ants are capable of living on their own. Mushrooms that are genetically identical to the fungi cultivated by lower attine ants have occasionally been found growing in the wild. However, that's not true of the fungi cultivated by most leafcutter ants and their close relatives. While there are a few exceptions, most leafcutter ants and the other species known as higher attine ants cultivate a particular strain of fungi that is no longer capable of living anywhere except inside the nests of these ants.

YELLOW POT-PLANT MUSHROOM

- Along with being dependent on ants, the higher attine fungi have also evolved specialized adaptations that make them well suited as crops. One key adaptation is the formation of swollen knobs at the end of each fungal strand. These structures, called gongylidia, are filled with nutrients. The gongylidia resemble bunches of grapes and are harvested by the ants as food. Their dependence on ants to survive, along with the fact that they evolved to be better crops, means that these higher attine fungi have been domesticated.

- The process of domestication was a key aspect of human agriculture as well. The wild ancestors of crops like wheat, corn, and rice did not have the enlarged edible seeds we eat today. Each time farmers planted crops, they selected seeds from the previous generation of plants that had the largest or best-tasting seeds. Over many generations, this process of selective breeding gave rise to strains with large, tasty, and nutritious seeds. But as these plants became better suited as crops, they no longer needed to be able to reproduce on their own.

Pests and Parasites

- Another similarity between ant and human agriculture is the threat posed by pests and parasites. In human agriculture, crop plants face a constant threat of attack by herbivores—including many insects—as well as by microorganisms like fungi, bacteria, and viruses. Billions of dollars are spent each year on preventing and treating diseases of crop plants.

- These threats are exacerbated by our industrial approach to agriculture. Planting large fields with the same crop is an efficient way to grow and harvest a lot of food, but it makes the crops more vulnerable to pests and disease by acting like a giant bull's-eye. If a disease makes its way into any individual plant in the field, it can quickly spread to others because they are all similar to one another and are grown close together.

- Fungus-growing ants face a similar threat. A specialized type of parasitic fungus can attack the fungi the ants grow for food. This parasite in the genus *Escovopsis* can quickly devastate a fungus garden. And without their main source of food, the ants in the colony will all die. Despite this threat, fungus-growing ants have managed to keep their agricultural system working for some 50 million years.

- One thing the fungus-growing ants do to keep their gardens pest-free is to constantly monitor their crops. If a worker ant finds any evidence of disease, individual garden chambers can be isolated and sealed off, preventing the disease from spreading. Another way that some fungus-growing ants fight parasites like *Escovopsis* is with antibiotics. Bacteria in the genus *Pseudonocardia* grow on the ant's exoskeleton and produce antibiotics that help keep *Escovopsis* at bay.

- Like the fungus-growing ants, our industrial agriculture also relies on chemical pesticides to fight pests. But the pests that attack our crops are constantly evolving new ways to get around our chemicals. One key aspect of how ants use antibiotics is that their antibiotics are produced by bacteria that are kept alive. That means the bacteria can evolve along with the pests, making better and better antibiotics with each generation.

Fungus-Growing Termites

- Some termites also cultivate fungi. They consist of about 330 species that belong to the family Termitidae and the subfamily Macrotermitinae. Much like the fungus-growing ants, fungus-growing termites use fungi to break down plant matter that they cannot digest themselves. Rather than fresh vegetation, the termites use decaying leaves, grass, wood, and other dead plant matter.

- Fungus-growing termites build their nests in the soil, constructing mounds that can be up to 30 feet tall. Termites build their mounds in such a way that air diffuses into and out of the nest through thin walls and an elaborate system of tunnels. Not only do the termites need to breathe, but the fungus must also take in oxygen and get rid of carbon dioxide. Unlike fungus-growing ants, whose tunnels remain open to the outside, termites and their fungi can live inside a closed nest without suffocating.

- The fungi cultivated by termites belong to the genus *Termitomyces*. In most fungus-growing termites, the fungi aren't brought directly from an existing nest to a new nest, which is how fungus-growing ant queens handle matters. Once a king and queen termite establish a new nest, the queen will lay eggs that develop into the first workers. These workers must leave the nest and retrieve fungi for the colony to cultivate.

- *Termitomyces* fungi form enormous mushrooms that sprout from the nests of mature termite mounds, and these mushrooms spread spores. When the worker termites collect dead vegetation in the environment near their nest, the vegetation often contains *Termitomyces* spores. The workers use the decaying vegetation along with the spores to establish a structure inside the nest where the fungi will be cultivated, called the fungal comb. Some worker termites feed on decaying vegetation, which also contains *Termitomyces* spores, and then defecate onto the fungal comb. This helps establish the fungus as a crop that will be harvested and eaten by worker termites for the remainder of the colony's life cycle.

Ambrosia Beetles

- Ambrosia beetles are a type of weevil, classified in the family Curculionidae. They live in the sapwood of dead or dying trees, and they grow fungi along the walls of the tunnels and galleries they dig in the wood.

- Like the fungi grown by ants and termites, the fungi grown by ambrosia beetles have been domesticated. The ambrosia beetle fungi have nutrient-rich swellings, and they also have sticky spores that make it easier for the

AMBROSIA BEETLE

beetles to spread them as they dig their tunnels. Likewise, adaptations in the beetles to make them better farmers include specialized structures in the exoskeleton called mycangia that are used to transport fungal spores.

- A variety of fungi are grown as crops by ambrosia beetles. Most of the fungi are classified in the order Ophiostomatales. The first domestication of ophiostomatoid fungi by ambrosia beetles took place about 86 million years ago, during the Cretaceous period. This makes ambrosia beetles the oldest known farmers across the entire tree of life. Other groups of ambrosia beetles domesticated different lineages of ophiostomatoid fungi between 48 and 60 million years ago, around the same time that the fungus-growing ants began cultivating fungi.

Raising Livestock

- In addition to raising plants for food, human agriculture includes raising animals as livestock. This form of agriculture, called ranching, also exists in the insect world. Many ants keep other insects as livestock. The other insects are, in most cases, hemipterans that feed on plant juices. Aphids are often tended by ants because the ants like to eat the sugary liquid that aphids produce as waste. This substance is known as honeydew, and it contains sugars and nutrients like proteins, vitamins, and minerals.

- Ants treat their aphids and other hemipterans, such as mealybugs and scale insects, in much the same way that ranchers treat their cattle. The ants protect their charges from enemies, make sure they have plenty of food to eat, and move them to new locations when food supplies run low. Ants even “milk” their livestock in a way that is reminiscent of how people milk cows. When an ant wants to drink some honeydew, it taps an aphid or mealybug with its antennae, and the bug obligingly offers up a droplet from its anus.

- Some ant species go to great lengths to tend their herds. The ant *Lasius niger* keeps aphid eggs inside its nest in the winter. Then, in the spring, it carries the young aphid nymphs to plants where the aphids can feed and be milked for their honeydew. In some species of *Acropyga* ants, the queens carry the scale insects they tend as livestock in their mandibles when they leave for their mating flights. This resembles the way fungus-growing ant queens carry a piece of fungus garden with them on their nuptial flight. In both cases, the ant queen will establish a new nest after mating and use the fungus or bug to start their own farm.

- Just as the fungi domesticated by insects have evolved to be more suitable crops, the insects kept by ants have developed ways to be better livestock. Unlike other types of aphids, which quickly expel their honeydew, the aphids tended by ants tend to expel their honeydew slowly and gently, which makes it easier for the ants to eat.

- Some species of aphids have even evolved hairs around their anus to trap the honeydew, allowing the droplet to sit there until the ants consume it. Aphids tended by ants have also lost many of their defenses, including nasty chemicals that other aphids use to protect themselves from predators. Aphids kept as livestock don't have to worry so much about protecting themselves since they are generally kept safe by the insect ranchers.

Reading

Fedoroff, "Ancestors of Science—Prehistoric GM Corn." https://www.sciencemag.org/careers/2004/10/ancestors-science-prehistoric-gm-corn.

Hölldobler and Wilson, *The Leafcutter Ants.*

Schultz, "Fungus-Farming Ants."

Questions

1 Some ants have been cultivating fungi as food for approximately how long?

- **a** 50,000 years
- **b** 5 million years
- **c** 50 million years
- **d** 500 million years

2 In addition to some ants and termites, which other group of insects practices fungal agriculture?

- **a** ambrosia beetles
- **b** mason bees
- **c** earwigs
- **d** phorid flies

ANSWERS CAN BE FOUND ON PAGE 225.

‹‹‹ TABLE OF CONTENTS

LECTURE 20

Fruit Flies and Other Research Insects

In 1865, Gregor Mendel reported the results of his experiments on pea plants, which revealed the fundamental rules by which heredity works. He discovered that traits are passed on as discrete entities, known today as genes, and that every pea plant has two alleles for each gene—one from each parent. But even once Mendel's discovery was recognized, it still wasn't clear how genes and alleles work. Where are these alleles located, and what are they made from? The answers would come from studies of insects.

Sex Chromosomes

- Walter Sutton grew up on a farm in Kansas. He knew from personal experience how common grasshoppers are, and he chose to use them for his studies of the biology of cells. This was a lucky choice. His focal species, the plains lubber grasshopper (*Brachystola magna*), has eggs and sperm with very large chromosomes. Sutton watched the grasshopper cells divide through a microscope, and he noted that the way chromosomes behave when cells divide is consistent with the rules of heredity discovered by Mendel.


PLAINS LUBBER GRASSHOPPER

- The next major breakthrough involved darkling beetles, which are better known by the common name of their larvae: mealworms. In 1903, a graduate student named Nettie Stevens used a new technique to stain the chromosomes inside the cells of living mealworms so that she could see them more easily.

- She observed that the cells of female mealworms always had 10 pairs of chromosomes. The pairs differed in size, but each pair consisted of two chromosomes of the same length. Males, on the other hand, had nine pairs of identically sized chromosomes, but the last two chromosomes didn't match one another in length. One was fairly long, but the other was tiny.

- Stevens called the small, unmatched chromosome the sex chromosome and reasoned that it was responsible for determining whether or not an individual mealworm is male. And she was correct: The small chromosome she discovered would later be called the Y chromosome, and its longer pair would be called the X chromosome.

- The fact that mealworms have X and Y chromosomes and that sex is determined the same way in mealworms as it is in humans—individuals with two X chromosomes become female and those with an X and a Y become male—was a fortunate coincidence. In some insects, like butterflies and moths, females result from the combination of two unmatched chromosomes. And in the insect order Hymenoptera, sex is determined by whether or not an egg is fertilized. In these species, there are no sex chromosomes at all.

- Stevens's work supported the idea that chromosomes somehow contain information about at least one trait—whether an individual organism develops as a male or a female. It wasn't yet clear whether information about other traits is also located on chromosomes, but this certainly seemed possible.

Variable Traits

- One biologist who doubted that traits other than sex are located on chromosomes was Thomas Hunt Morgan. Working from his lab at Columbia University, he began to breed *Drosophila melanogaster* fruit flies. Morgan chose fruit flies because they're small and easy to keep alive. They also breed very quickly, meaning he could get a new generation of fruit flies every 10 days.

- Morgan soon discovered that one of his male fruit flies had white eyes instead of the usual red. He bred it with females with the more typical red eyes. All of the offspring had red eyes, a result reminiscent of the experiments Mendel had performed with pea plants half a century earlier.

- But when Morgan followed Mendel's approach and bred the red-eyed offspring with one another, the result was an unexpected surprise. The next generation of fruit flies included both red-eyed and white-eyed individuals, which was similar to Mendel's result. Morgan's work suggested that the red-eye allele was dominant over the white-eye allele. But in the second generation of Morgan's fruit flies, all the white-eyed flies were male.

- Morgan knew from Nettie Stevens's work on mealworms that males have an X and a Y chromosome, while females have two X chromosomes. This suggested that the instructions for making white eyes may be located on the X chromosome. The rationale for this conclusion was simple: Because males only have one X chromosome, they can never have two copies of any instructions located on the X chromosome. There can't be a situation where the instructions from a recessive allele on the X chromosome are masked by a dominant allele for the same gene located on another chromosome because the other chromosome is a Y.

- Females, on the other hand, have two X chromosomes, so they can have either one or two copies of any allele located on the X chromosome. This creates specific predictions about what combinations of traits are possible between males and females and in what proportions they should occur. Morgan tested these predictions and found that the results supported the idea that the gene for eye color in fruit flies must indeed be located on the X chromosome.

Fruit flies have only four pairs of chromosomes. By comparison, humans have 23 pairs, mice have 20, and rats have 21. Working with fruit flies made studying how genes are structured on chromosomes a lot simpler.

- Little by little, other variable traits were identified in fruit flies, like body color and the length of wings. In 1911, one of Morgan's students, Alfred Sturtevant, published a map showing the relative locations of genes for a variety of traits on the chromosomes of fruit flies. It was the first map of a genome of any species and laid the foundation for the more complete genome maps of fruit flies—and humans—published at the beginning of the 21st century.

Mutations

- Finding the location of genes on chromosomes still depended on there being traits that varied from one individual to another. It was lucky for Morgan and his students that the fruit fly species they were working with, *Drosophila melanogaster*, happened to have a lot of variable traits. In fact, new traits would suddenly appear from time to time in new generations reared in the Fly Room. The appearance of these new traits—what we now call mutations—gave the researchers the opportunity to add another gene to the map of the fruit fly genome.

- One bizarre mutation gave the fruit flies an extra set of wings. Like all flies, *Drosophila* normally have just one pair of wings on the middle segment of the thorax. These mutant flies had a duplicated thorax: The normal thorax with a pair of wings on the middle segment was followed by another middle thoracic segment with a second pair of wings. The mutation was given the name bithorax, meaning "two thoraxes." An even stranger mutation, dubbed antennapedia, caused some flies to develop legs on their heads where their antennae should be.

- Both the bithorax and antennapedia mutations were traced to a cluster of genes that control the development of structures on particular regions of the body. This cluster came to be known as the *Hox* genes. Through additional studies on *Drosophila*, it became clear that the *Hox* genes control the order of segments on a fly's body as well as what body parts grow on each segment.

- The *Hox* genes are master regulators that turn other genes on or off. For example, the bithorax gene ensures that the genes for making a leg are turned on in the thoracic segments, where legs should grow. A mutation to this gene prevents the instructions for making a leg to be turned on, resulting instead in the duplication of a wing.

- Working out the function of *Hox* genes turned out to have much broader implications than just understanding the development of fruit flies. We now know that all animals have *Hox* genes. As each group of animals evolved, they inherited *Hox* genes from their ancestors. But there were many mutations along the way. *Hox* genes were duplicated twice in early vertebrates, resulting in birds and mammals having four clusters of *Hox* genes.

- The same genes that ensure a fruit fly's segments are in the proper order are also involved in developing our spinal column and ensuring that our body parts form in the right locations. They're also responsible for ensuring we have the correct number of digits on our hands and feet. Although they're rare, mutations in our *Hox* genes can lead to conditions that affect the development of our hands and feet and our urinary and reproductive systems. Other mutations in *Hox* genes are linked to various forms of cancer.

Insects and Human Bodies

- We know that humans and insects share much of the same basic genetic architecture due to the fact that we shared a common ancestor with insects from the origin of life some 3.5 billion years ago until about 600 million years ago. A lot has changed since then, but this common ancestry is what makes studying insects relevant for our understanding of how our own bodies work.

- It was known for centuries that many species, from humans to plants, have an innate sense of the time of day. These circadian rhythms control the timing of sleep. A gene called *period* was identified in the fruit fly *Drosophila melanogaster* that proved to be involved in the function of the biological clock. The *period* gene makes a protein, which is also called period, that turns other genes on and off. The *period* gene itself is more active during certain times of day and less active at others. The *period* gene in fruit flies thus provided the first example of the molecular basis for the circadian clock.

- Important discoveries about how the immune system works have also been made using *Drosophila* fruit flies. When one particular gene, called *Toll*, was deliberately inactivated in fruit flies, researchers discovered that these flies became more susceptible to certain types of infections. The *Toll* gene was known to play a role in development, but it was revealed to code for a receptor in the cell membrane that's also used to recognize pathogens.

- Once the role of the *Toll* gene and the receptor protein it codes for were understood in the immune system of fruit flies, similar genes and proteins were identified in other species, including humans. These were named *Toll*-like receptors, or TLRs. In humans and other mammals, the *Toll*-like receptors play an important role in protecting us from infectious diseases by recognizing pathogens and sending signals to activate other parts of the immune system.

- Studies on fruit flies have even been conducted in space. Thanks to the intrepid flies that have spent time in low Earth orbit, researchers are now investigating whether the immune system functions the same way in space as it does on Earth. The results of these studies will help pave the way for human exploration into deep space, including missions to Mars and beyond.

Reading

Arizona State University, "Natural Selection." https://askabiologist.asu.edu/peppered-moths-game/natural-selection.html.

Mukherjee, *The Gene*.

Questions

1 What properties make fruit flies well suited as laboratory research subjects?

- **a** their short generation time and lots of offspring
- **b** their small number of chromosomes, which in some cells are very large
- **c** individuals differ in noticeable traits
- **d** all of the above

2 True or false: Pollution from the Industrial Revolution led to natural selection favoring the lighter form of British peppered moths, while the darker form became more common after pollution levels declined.

ANSWERS CAN BE FOUND ON PAGE 226.

TABLE OF CONTENTS

LECTURE 21

Insects in Art, Literature, and Film

Insects play prominent roles in many aspects of human culture, including art, literature, and film. We have complex feelings about insects. On the one hand, we sometimes see insects as horrible monsters, mysterious aliens, or symbols of evil or death. On the other hand, we admire their beauty and fantasize about having their abilities. We also see reflections of ourselves in insects, in both positive and negative ways. In short, insects represent a diverse and complex set of human ideas and emotions.

Literature

- References to insects appear in some of the oldest texts. The Old Testament of the Bible mentions insects in several places. Of the 10 plagues that befell Egypt in Exodus, three included insects. The third plague was lice that attacked people and animals. The fourth was a swarm of flies that also attacked people and their livestock. And the eighth plague was an enormous swarm of locusts that destroyed the Egyptians' crops. A similar account of these plagues is also mentioned in the Qur'an.

- Insects are looked on more favorably in the Old Testament book of Proverbs. King Solomon advises:

> Look to the ant, thou sluggard, consider her ways and be wise. Which, having no guide, overseer, or ruler, provideth her meat in the summer, and gathereth her food in the harvest.

- The observation that ants are hardworking and industrious has long been a popular theme. Aesop's fable "The Ant and the Grasshopper" tells the story of a grasshopper that spends the summer singing while its friend the ant is busy collecting and storing food. When winter comes, the grasshopper gets hungry and asks the ant for food. The ant refuses, admonishing the grasshopper for idling away its time singing instead of planning ahead.

- Insect metamorphosis is a popular theme among authors. In Franz Kafka's 1915 novella *The Metamorphosis*, Gregor Samsa wakes up one morning to discover that he has been transformed into an enormous insect. The story explores the many types of changes that people undergo. The 1957 short story "The Fly" by George Langelaan also features a person transforming into an insect.

Associating insects with pestilence and disease was common in the ancient world. Beelzebub was an ancient Philistine god, referred to as the Lord of the Flies, who the Philistines believed was able to predict the advent of disease. Beelzebub was considered a demon by Jews and Christians, who came to associate flies with the devil.

- Comparisons between human and insect societies are another common literary trope. In *The Fable of the Bees*, published in 1714, Bernard Mandeville includes a poem about a hive of bees whose community collapses when the bees begin to behave honestly and virtuously. Mandeville was arguing that when individual people engage in behaviors considered to be vices, like gambling or buying luxury items, it can have beneficial effects on society at large.

- A darker view of social insects is seen in H. G. Wells's 1905 short story "The Empire of the Ants." The story describes a voyage by a Brazilian sea captain who is sent up the Amazon River to help defend a town that's being attacked by ants. The captain and his crew discover they're too late—the large, intelligent, and well-organized ants have already taken over the town and killed or scared away all of its inhabitants. The story concludes with the ominous suggestion that the Amazonian ants could spread and take over the world.

Art

- Insects have a long history of appearing in art. In medieval paintings, flies can represent death, the devil, or evil more generally. Bees are often used in Christian art to symbolize hard work and self-sacrifice. Moreover, because worker bees are unmated, they have also been used in the Catholic tradition to represent virginity and the Virgin Mary. The preference for candles made from beeswax in Catholic churches is connected to this association.

- As art became more secular in the 14th and 15th centuries, artists began depicting landscapes and still lifes, which often included insects. In the 17th century, the still life artist Maria Sibylla Merian created many finely detailed illustrations of insects. Having raised silkworms as a child, Merian was especially interested in butterflies and moths. She reared caterpillars and made observations of their biology and life cycles, including illustrations of the various stages in their developmental process. As such, Merian contributed not only to insect art but also to the disciplines of entomology and scientific illustration.

- Vincent van Gogh featured insects in many of his paintings, including his 1889 *Death's Head Moth*. Salvador Dalí's work often included depictions of insects as well. Ants appear in many of his paintings, including one of his most famous works, *The Persistence of Memory*, where a group of ants are crawling over one of the many clocks.

- Among East Asian artists, depictions of insects reflect philosophical and religious traditions that emphasize harmony with nature. Grasshoppers, cicadas, dragonflies, and butterflies frequently appear in Chinese and Japanese paintings.

- Insects have also been popular subjects in Asian sculpture. This is particularly true for the Japanese art of netsuke—miniature sculptures that began as functional accessories but developed into an art form unto themselves. Because Japanese kimonos did not traditionally have pockets, small containers were made for carrying one's most important belongings. These containers were attached to the belt by a string and held shut by the netsuke. Because of their small size, netsuke carved into the shape of insects were very popular.

- For other artists, the insects themselves are the medium. Christopher Marley's *Biophilia* exhibits feature taxidermied animals, including different types of insects. Some are individual specimens, chosen to highlight their spectacular colors and patterns. Others are mosaics of brightly colored beetles or butterflies, showcasing the incredible diversity and aesthetic appeal of these insects.

Animated Films

- Insects have been especially popular in animated films, owing partly to the fact that they are easier to draw than humans. In fact, one of the first animated films was the 1912 silent film *How a Mosquito Operates* by Winsor McCay. Using simple line drawings, it shows a large, personified mosquito trying to bite a sleeping man. The man repeatedly swats at the mosquito, but eventually it's able to feed. As the mosquito feeds on the man's blood, it grows larger and larger and eventually explodes. In addition to being comical, McCay's animation gives the mosquito personality. It wears a top hat and carries a briefcase, and at one point it waves to the viewers.

- Endearing insects would become a staple of animated films. Walt Disney's 1940 animated film *Pinocchio* starred Jiminy Cricket as Pinocchio's sidekick. Like real crickets, Jiminy Cricket has some musical talent. But he also exemplifies the ways in which animators often ignore aspects of insects' real anatomy. Jiminy Cricket has two arms and two legs, like a human, rather than a cricket's six legs. He doesn't have wings or antennae. His eyes have a single pupil rather than the thousands of ommatidia that make up the compound eyes of insects. And he has a humanlike mouth with teeth and a tongue rather than the mandibles that real crickets use for chewing.

- As animation technology improved, insects continued to be popular subjects. The second film released by Pixar Animation Studios was *A Bug's Life*. The story is a twist on Aesop's fable about the ant and the grasshopper, in which the grasshoppers have come to expect the ants to provide them with food. One worker ant protests the demands of the grasshoppers and organizes a ragtag group of other insects to stand up to them. There are some funny insect jokes, too: In one scene, the worker ants panic when a leaf falls onto their path, covering their pheromone trail, and they become immediately lost.

- Like many portrayals of insects in popular stories and films, *A Bug's Life* gets some entomological details wrong. For example, the main character, Flik, is a male worker ant. But in reality, worker ants are always female. This basic aspect of ant biology is often overlooked in popular depictions of ants, including the 1998 animated film *Antz*. Woody Allen voiced the role of the main character, Z, a male worker ant who is sad because he wants to express his individuality. This film's worker ants are shown as being either workers or soldiers, both led by higher-ranking ants who direct them. But in real ant colonies, there is no leadership hierarchy.

- Ants aren't the only social insects whose biology is often ignored by Hollywood. The 2007 animated film *Bee Movie* is about a male worker bee named Barry, voiced by Jerry Seinfeld. Like ants, worker bees are always female. While that aspect of bee biology is clearly wrong, the film does highlight the fact that humans take honey from the hardworking bees. Barry thinks this theft, as well as the use of smoke by beekeepers when harvesting honey, is inhumane.

Live-Action Films

- Shrinking humans down to insect size is a popular theme in stories and films. In the 1989 family comedy *Honey, I Shrunk the Kids*, the children of an eccentric inventor are accidentally shrunken by a machine he invented. As they try to make their way through their backyard to get back to their house, the kids encounter several insects, including an ant who helps save them from a menacing scorpion.

- Whereas films in which people become tiny often generate empathy toward insects, the opposite trope—in which insects become big—often casts insects as terrifying monsters. The 1954 film *Them!* featured giant, killer ants that were the accidental result of testing the first atomic bomb in New Mexico. This film's success launched an entire genre known as big bug films that was popular in the 1950s. A common plot theme was that radiation from nuclear weapons caused insects to reach enormous sizes, triggering them to terrorize people.

- On a lighter note, some superheroes, like Ant-Man, are based on insects. Ant-Man can shrink down to the size of an ant and communicate with ants to help him fight bad guys. But there are a few things the filmmakers got wrong. They refer to fire ants as *Solenopsis mandibularis*, which is an outdated species name. The current name for that species is *Solenopsis geminata*.

- Beyond the name, the fire ants in the movie do some things that real fire ants aren't capable of. For example, in one scene, the fire ants link their bodies together to form a ladder that allows Ant-Man to climb up and get into a building. This is actually something that weaver ants in the genus *Oecophylla* do.

- The fire ants also form a living raft that Ant-Man uses to travel through a pipe with flowing water. Some fire ants can actually do this: A related species, the red imported fire ant (*Solenopsis invicta*), forms living rafts when their colonies flood. Their bodies are hydrophobic, meaning they repel water, so when they link their bodies together, they create a floating mass of ants. The larvae, pupae, and queen stay on top of the raft until it floats to dry land.

> Public interest in big bug films seemed to stem from anxieties about the use of nuclear weapons in the aftermath of World War II. But it also coincided with the widespread use of chemical pesticides like DDT. These pesticides were being advertised as a high-tech solution to the challenges that insect pests posed to industrial agriculture. Vilifying insects may have played into the willingness of people to accept pesticide use in their food and in their homes.

- The biggest biological blunder in *Ant-Man* is the fact that the ants are repeatedly referred to as male. One of the ants is a flying queen who carries Ant-Man from place to place. But Ant-Man names it Antony and says "good boy" when it does its job well. Not only is the queen he rides on clearly a female, but the worker ants that help Ant-Man must be female as well. And given that ant colonies are run almost entirely by females, any superhero based on ants should probably be female, too.

Reading

Hollingsworth, *Poetics of the Hive*.
Tsutsui, "Looking Straight at *Them!*"

Questions

1 Insects are often used as symbols. For example, in many cultures, _______ represent the human soul.

2 Which are examples of incorrect portrayals of insect biology in stories and films? Select all that apply.

a insects having humanlike eyes instead of compound eyes
b worker ants and bees being portrayed as males instead of females
c insects having two-segmented bodies instead of three-segmented bodies
d leadership hierarchies in social insect colonies

ANSWERS CAN BE FOUND ON PAGE 226.

LECTURE 22

Collecting Insects

The best way to admire and learn about insects is to observe them up close. While having specialized entomological equipment is helpful, it's also possible to start your own insect collection using materials you probably already have at home.

If you're in a protected area, like a state or national park, you'll need to get approval from the authorities before collecting any insects. And be aware that some insects are protected by law. The US Fish and Wildlife Service keeps a list of federally protected insect species on their website. Each state also has its own list of protected species.

Insect Nets

- What gear you need will depend on what insects you're hoping to collect, but there is some general equipment that can be used for a lot of different purposes.

- There are two basic types of insect nets. An aerial net has fabric with tiny holes in it, like a fine mesh. These are great for catching flying insects like butterflies or dragonflies. The advantage of this kind of net is that you can swing it around quickly because the air passes through the holes in the fabric. That's important for catching fast insects. The pole can be a simple wooden rod, like a broomstick, or a collapsible metal rod that's easier for traveling.

- Another advantage of an aerial net is that it's easy to see what you've caught because of the small holes in the fabric. But a disadvantage of aerial nets is that they are somewhat delicate. You'll want to avoid getting your aerial net caught in any vegetation, which can rip the fabric. A more durable type of insect net is a sweep net, made of thick fabric. This type of net is good for collecting insects on or near vegetation.

- You can buy aerial nets and sweep nets from entomological suppliers like BioQuip. Or you can make one using some fabric, a broomstick, and a wire coat hanger. A pillowcase works well, and it doesn't need to be cut or sewn.

Making a Kill Jar

- Once you've captured one or more insects in your net, it's time to get them out for observation or for preparation. If you're collecting specimens you want to preserve, you'll need to euthanize them. There are several effective, humane, and safe ways to prepare insects for a collection. One way is making a kill jar, which is easy to do, and the jar can be reused each time you go out collecting.

- You'll need a glass jar with a tight-fitting lid, like a mason jar. It's helpful if the lid is one piece. You can use an old jar of pasta sauce or something similar—just make sure it's thoroughly cleaned first. You'll also need plaster of paris and a chemical for euthanizing the insects.

If you're not comfortable killing insects, you can still put together a nice collection of preserved specimens by looking for insects that recently died. You'd be surprised how many good specimens you can find just by walking around and keeping an eye out for dead insects. Just be sure they aren't already decomposing or too brittle.

- Ethyl acetate is commonly used by entomologists and can be found in many drugstores or purchased online. Some nail polish remover contains mostly ethyl acetate—look for some that's acetone-free. It's mildly toxic to people, so you'll want to avoid inhaling it directly, and it's best not to use it in an enclosed space or with young children. Isopropanol, also known as rubbing alcohol, doesn't work as quickly as ethyl acetate, but it's safer to use and easy to find.

- To make a kill jar, first mix the plaster of paris with water and pour it into the jar. You only want about one inch of plaster at the bottom, or else the jar will be very heavy. Once the plaster is completely dry, pour your chemical—ethyl acetate or isopropanol—onto the plaster. With ethyl acetate, you only need a few drops for it to be effective. If you're using isopropanol, you'll need more. You want to be sure the chemical gets fully absorbed by the plaster. Close the lid to keep the chemical from evaporating.

- It takes some practice to get an insect from a net into a jar. First, grab the net below where the insect is located. Open the jar and place the net over it. Your hand should be holding the net closed directly above the opening of the jar. Little by little, pull the fabric of the net through your clenched fist with the net's fabric covering the open jar. When the insect falls into the jar, quickly put the lid back on.

Aspirators

- Nets are great for collecting relatively large insects, but for small insects, they're too big and clumsy. A great way to collect small insects is by using an aspirator. An aspirator works like a vacuum cleaner to suck up bugs, except you create the vacuum using your mouth. While the idea of sucking up bugs may sound unappealing, rest assured there's no way to suck the insect into your mouth.

- The collection vial is usually a small, cylindrical plastic container with a plastic lid that snaps onto the top. You replace the lid with a rubber stopper with two holes drilled into the top. In one hole is a hollow metal tube with a small piece of mesh at its base. A long piece of surgical tubing connects to this metal tube, and the other end goes in your mouth. The other hole in the rubber stopper also has a metal tube that's longer and is used for sucking up insects. When you suck on the tube, it creates a vacuum that draws the insect into the tube. The mesh prevents the insect from being drawn up into the tube that goes to your mouth.

- One thing you do need to be careful about is inhaling tiny particles of dirt, sand, or fungal spores. Instead of aspirating insects directly from soil or the surfaces of plants, one technique is to scoop up a bunch of insects using a small shovel or a spoon and then transfer them to a notecard or a piece of concrete first. It's also helpful if you add a small piece of wet sponge to catch any small particles or spores that do get sucked in. Just clean it between uses so the sponge doesn't grow its own fungal spores.

Traps

- There are other types of traps that are useful for collecting insects. One of the simplest is a pitfall trap. This consists of a container that is buried in the ground with an open top that's flush with the surface of the ground. Insects walking along the surface will fall into the trap.

- You can make a basic pitfall trap with a plastic cup. Some insects, especially larger ones or ones that can fly, might be able to get out, so it's helpful to put some type of liquid in the bottom. Since some insects can walk across the surface of water, it's also a good idea to add one or two drops of detergent to make some bubbles to break the surface tension.

- Another way to collect insects from soil and leaf litter is to use a Berlese funnel. You can buy one from an entomological supplier or make a simple one at home. Take a plastic two-liter soda bottle and cut the top off about four inches down. Turn the lid upside down, take off the cap, and place the lid inside the base of the bottle. It's best to place a piece of wire mesh with holes about a quarter or half inch wide in the bottom of the upside down lid. This will allow little insects to crawl through while preventing leaves and sticks from falling through as well.

- Collect some soil or leaf litter in a plastic bag and place it in the inverted lid. In the bottom of the bottle, pour some water with a few drops of detergent or, better yet, some rubbing alcohol. The insects that live in soil and leaf litter instinctively crawl down to escape, so they will fall through the opening and into the base, where they will be trapped in the liquid at the bottom.

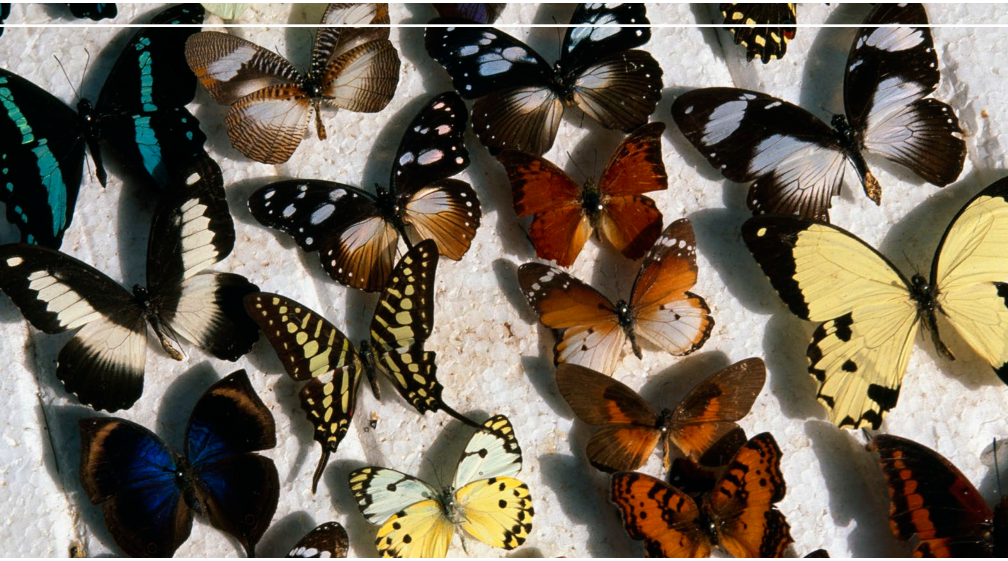
- Another way to collect flying insects is with a malaise trap. Unlike soil-dwelling insects that instinctively crawl down, most flying insects will instinctively crawl up. Malaise traps are designed to funnel the insects as they crawl up into a narrow tunnel that ends in a bottle with fluid at the bottom. Because malaise traps are often set up for weeks at a time, the fluid is usually some kind of preservative, like rubbing alcohol. You can purchase malaise traps from entomological suppliers. But beware—they often catch a lot of insects.

Preserving Specimens

- There are two main ways that insects are preserved in entomological collections. A few types of insects—mostly those that are especially small or very soft-bodied—are kept in vials filled with alcohol. These include aphids and termites as well as most larvae and nymphs. The alcohol of choice for most entomological collections is 70% ethanol, although sometimes the percentage is higher when DNA preservation is part of the goal. Rubbing alcohol diluted to between 70% and 90% is perfectly fine for most amateur collectors.

- For almost all other insects, the best way to preserve and protect them is to pin them. Insect pins are inexpensive, and you can order them from entomological suppliers. It's helpful to have a range of sizes for different specimens. In addition to the pins themselves, you'll want to have something to stick the pin into, like a piece of Styrofoam. For most insects, the pin should be placed in the thorax, just to the right of the midline.

- When an insect has been freshly killed, it's usually flexible, and you can move the legs to reposition them. But as the insect dries, it will stiffen, and it will become harder to move any body parts without breaking them. If your specimen has already stiffened, you can relax it by placing it in a small airtight container along with a piece of damp paper towel. The humidity will cause the insect to soften after about a day or two. But be sure not to leave it any longer, or it will get moldy.



- Insects like ants and small wasps and flies are too small to pin directly without damaging them. Instead, you point them. The insect is glued to a small triangle of stiff paper or cardstock, and the pin is stuck through the paper rather than the insect. You can use regular paper glue and either cut the triangles yourself or buy a specialized device called a point punch from an entomological supplier.

Observing Specimens

- Once you've pinned and labeled your specimens, you're ready to observe them up close. One of the advantages of having an insect on a pin is that you can move the pin around to look at the insect from all angles. The best way to observe your specimens up close is with a dissecting microscope, but you can see quite a lot with just a magnifying glass. There are also some smartphone apps that allow you to use your phone like a magnifying glass, and these can be used to take some great photos of your specimens as well.

- The best way to ensure your insect collection lasts a long time is to keep it in a cool, dry place. A simple shoebox can work for short-term storage, but to preserve specimens properly, you should buy an insect display box with a tight-fitting glass lid. This will keep your insects safe and allow you to admire them as well. The other important consideration is to protect your collection from pests. If it looks like there is a pest infestation, the entire collection can be put in a freezer overnight to kill the pests.

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Texas Parks and Wildlife, "Make Your Own Sampling Equipment." https://tpwd.texas.gov/education/resources/texas-junior-naturalists/bugs-bugs-bugs/make-your-own-sampling-equipment.

Questions

1. True or false: The proper technique for preparing all insect specimens involves placing a pin through the center of the thorax.

2. Insect collections can be kept free of damaging pests by placing them in a ______ overnight.

ANSWERS CAN BE FOUND ON PAGE 226.

‹‹‹ TABLE OF CONTENTS

LECTURE 23

The Disappearing Insects

Analyzing data from different types of insect collections, researchers have noticed an alarming trend: Many insect populations are declining, both in number and diversity. These threats should be cause for concern. Insects occupy a critical role in food webs. They break down waste and dead plants and animals, and they help control the populations of pests and weeds. Insects serve as pollinators, providing an essential service for 80% of the crop plants we depend on for food. In short, life as we know it would simply not be possible without insects.

Studies on Insect Populations

- One of the first studies to document a large-scale decline in insects examined butterflies in Great Britain. The researchers recruited volunteers to conduct extensive surveys of butterflies across the region between 1970 and 1982 and again between 1995 and 1999. They also included data from museum specimens that were collected within the same time spans. Over this span of 29 years, two of the 58 species of butterflies native to Britain became extinct.

- The researchers also tracked the locations in which particular butterfly species were found throughout the surveys, dividing the region into squares measuring 10 kilometers on each side. They found that the number of places where particular species of butterflies were found declined for 71% of the species. The median decline in distribution across all butterfly species was 13%, with some species declining by as much as 80%.

- In 2017, a study reported a 75% decline in the total biomass—the combined weight of all individuals—of flying insects collected over a span of 27 years in Germany. This study used data collected by a dedicated group of amateur insect enthusiasts known as the Krefeld Entomological Society. The group set up malaise traps in 63 different nature preserves around the town of Krefeld in northwest Germany.

> Despite the many studies that document reductions in insect populations, not all insects have experienced declines. Some aquatic insects have increased in abundance and diversity. Overall, though, the trend seems to be that insects as a group are experiencing many threats around the world.

- The first large-scale study to combine data on changes in insect populations from surveys conducted around the world was published in 2014. The researchers analyzed data on 452 different invertebrate species, most of which were insects. They found that for one-third of the species, the number of individuals had declined since 1970. The most data available was for butterflies and moths, which are the insects most often noted by amateurs. On average, the number of individual butterflies and moths declined by 35%. The declines were more severe for other groups of insects, like beetles, grasshoppers, ants, bees, and wasps. Across all groups of insects, the number of individuals declined by 45%.

- Declining numbers of honeybees were also reported by beekeepers. In 1947, there were 5.9 million honeybee colonies managed by US beekeepers. But by 2005, the number of colonies had fallen to just 2.4 million. In addition to this long-term downward trend, in 2006, beekeepers began noticing a more acute problem. Large numbers of worker bees that flew off in search of nectar and pollen weren't returning to the hive. The phenomenon, known as colony collapse disorder, poses a real threat to farmers who depend on honeybees to pollinate their crops. Declines in the number of wild pollinators, including many native bees, have been noted as well.

Reasons for Insect Decline

- Declines in insect populations are mirrored by declines in other groups of animals, including amphibians, birds, and mammals. Some of the same causes, like habitat loss, affect all of these groups. As the human population has grown, more forests and grasslands have been cleared and converted into pasture or cropland for agriculture. Cities have grown, too, and the expansion of urban and suburban areas has meant there's less space available for wildlife, including many insects.

- Climate change is likewise affecting insects. More frequent and severe floods, droughts, fires, and storms threaten many species. They can also make it more likely that invasive species, which typically thrive in disturbed areas, can become established. Climate change has also caused species to move in response to warming temperatures. An analysis of changes to the geographic ranges of 35 species of European butterflies during the 20th century found that 63% shifted their ranges to the north. By comparison, only 3% shifted their ranges to the south. Likewise, some tropical insect species are moving into more temperate regions.

- Insects are also directly affected by many human activities in ways that don't necessarily affect other types of wildlife. The widespread use of pesticides is a clear example. Chemical pesticides have been used to minimize damage from pest insects, and genetically engineered crops are now being developed with genes that allow the crop plants to make their own pesticides. While these technologies have largely been successful at controlling the impact of the relatively small number of pest insect species, they can cause significant collateral damage by killing other types of insects as well.

- Urbanization leads to more artificial lights at night, which can impact insects. Moths are especially vulnerable to light pollution because they are often nocturnal and attracted to artificial lights. This can disrupt their normal behaviors, including feeding and reproduction. The presence of artificial lights can also affect the development of moths by reducing the feeding activities of caterpillars, which are also sensitive to light. Studies comparing moths in areas with different amounts of light pollution have found that in areas with lots of artificial light, the caterpillars don't grow as large and are less likely to enter the pupal stage.

Documenting Insect Diversity

- One especially troubling aspect of the apparent decline in many insects is that they are disappearing before scientists can fully document and understand them. But new species are actually discovered quite often. While scientists have formally described around a million species of insects, at least 4.5 to 7 million additional species of insects are thought to be awaiting discovery.

- Some groups of insects are better known, while others remain obscure even to entomologists. The six major insect orders—Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, and Lepidoptera—contain about 973,000 described species of insects, or 93% of the roughly 1,047,700 known insect species. The remaining 7% of described species are scattered across the other 22 orders of insects.

- Biologists are in a race against time to collect, document, and describe insects before they disappear. But luckily, you can play a role in helping to document insect diversity and to help prevent further losses. One of the best ways to contribute toward our understanding of insect species and their distribution in space and time is to make your own observations. You might consider donating your own insect collection to a local museum or university, where your specimens could be used by generations of future scientists.

- Another way to contribute to the world's understanding of insects doesn't require you to kill—or even touch—a single bug. Websites like BugGuide and iNaturalist provide a way for anyone to share pictures of insects they've observed. You don't need any specialized photography equipment—the camera on your smartphone will work just fine for many insects. And because your phone automatically records the time and location where you took a photograph, that information can easily be incorporated into photos you post.

- These websites can also help you identify what you see. For example, iNaturalist uses a machine learning algorithm to match your photo with similar photos from the same area that have been previously identified. A community of professionals and knowledgeable amateurs regularly monitor the site for pictures of species that they can help identify.

- You can also join community science projects in which observations or collections made by the general public contribute toward research conducted by professional scientists. Community science projects range from tracking the migration of monarch butterflies to monitoring the timing of when flowers and their insect pollinators appear. You can find examples of community science projects at www.scistarter.org.

Preventing Insect Loss

- In addition to helping document the insect species around you, you can also help prevent the loss of insects through simple changes to your home and habits. One of the biggest things you can do is limit pesticide use in your home and garden. Most pesticides act broadly to affect all insects, not just the handful of pests you're usually targeting. And pesticides often linger long after the target insects have been killed.

- Consider letting nature take its course by allowing natural predators—like birds, bats, and dragonflies—control the pests in your garden. But if you feel you must control the insects in your garden, try chemical-free alternatives. You can spray tomatoes with a solution of diluted soap to get rid of aphids. You can also treat fire ant mounds in your yard with boiling water rather than poison baits. Not only is this more immediately effective, but it also avoids accidentally poisoning the harmless native ants living nearby.

Many butterflies and other insects feed on rotting fruit. Before throwing away your banana peels and apple cores, consider offering these to your neighborhood insects.

- Another great thing you can do for insects is plant native plants. Most of the insects in your area evolved with particular types of plants, and those are typically the species that provide them with the best sources of food and shelter. Many species of insects, like some butterflies, can feed on only one particular species of plant. When these insects can't find their host plants, they either die or fail to reproduce.

- Planting a pollinator garden is a great way to help the insects in your region while also attracting lots of beautiful bees, butterflies, and other insects for you to enjoy. It's helpful to include a combination of different types of plants, including species that flower at different times of year, to provide nectar and pollen over a wider time range. Find out which species work best in your area.

- Lastly, light pollution is a problem for many insects, especially moths. Consider reducing the number of lights you have on outside your home at night. Lights that point down at the ground are less distracting to flying insects than those that point up at the sky. If you're concerned about security, consider getting lights with a motion detector that turn on only when someone walks in front of them.

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Vogel, "Where Have All the Insects Gone?" https://www.science.org/content/article/where-have-all-insects-gone.

Questions

1 Which of the following factors is contributing to declining numbers of insects?

a widespread use of pesticides
b habitat loss
c light pollution
d all of the above

2 True or false: Researchers have observed changes in where some insects live that are attributed to climate change.

ANSWERS CAN BE FOUND ON PAGE 226.

TABLE OF CONTENTS

LECTURE 24

Sharing Planet Earth with Insects

Insects don’t exactly have the best reputation. But the more you learn about them, the less mysterious and alien they seem, and the more likely you are to come away with a sense of awe and respect for them. Through education and experience, you can come to see insects for what they are—mostly harmless, endlessly fascinating, and incredibly important.

Insect Phobias

- According to one survey that combined insects with other arthropods, like spiders, 38% of people say they don't like arthropods in their yards and 84% don't like them in their homes. In the United States, 19 million people report having entomophobia, a fear of insects. The most commonly feared insects include ants, beetles, butterflies, caterpillars, grasshoppers, and moths, although some people are afraid of anything with more than four legs.

- For some people, a fear of insects is more serious. An estimated 90,000 Americans suffer from delusory parasitosis, also known as Ekbom syndrome, in which a person is mistakenly convinced their body is infested by insects, mites, or parasites. The artist Salvador Dalí was afflicted by this condition. According to one account, he was once so convinced that a flea or a bed bug was biting him on his back that the artist cut himself with a razor blade in an attempt to remove it. It turned out to be a pimple.

- Evolutionary psychologists suggest that deeply rooted fears and phobias originated in our early ancestors. According to this view, a fear of certain insects and other arthropods would have been advantageous among early humans living a hunter-gatherer lifestyle. Those individuals who were a bit more wary of spiders, scorpions, ants, and wasps may have been more likely to survive into adulthood and pass on their fears. A similar argument is used to explain a fear of snakes.

- A key assumption of the evolutionary psychological view of the origin of such fears and phobias is that they have a genetic basis. Consistent with this assumption, some studies have found that a fear of insects is instinctive rather than learned. Likewise, studies of identical twins indicate they are likely to share a fear of insects even if raised by different parents, suggesting a strong genetic component for such fears.

- But the notion that a fear of insects has been deeply rooted in our psyche—indeed, in our DNA—doesn't seem to explain why some people are bothered by insects that pose no threat to people, like moths or grasshoppers. Indeed, some insects are an important source of food for many people, and having a fear of insects would seem to make it more difficult to collect them for food. That makes it harder to use an evolutionary explanation for insect phobias.

- For some people, a fear of insects can be traced to a childhood experience, like being startled by a cockroach or stung by a wasp. In other cases, the traumatic experience can happen later in life. About half of people with insect phobias can trace them to events at some point in their lives. Children also learn to fear insects from adults. The way we act when we encounter an insect can have a big influence on how children perceive insects. About 20% of children who fear insects say they learned their fear from a family member or friend.

Why People Fear Insects

- What is it about insects that makes them scary or repulsive to so many people? Why are insects more commonly feared than, say, earthworms or snails? Studies of entomophobia suggest there are several properties of insects that make them more likely than other creatures to evoke fear.

- Some insects invade our personal space by coming into our homes or touching our bodies. They can startle us by making sudden, unexpected movements or intimidate us by forming large swarms. Some can hurt us by biting, stinging, or transmitting diseases. And they can damage our property, including our homes, clothes, or food.

- Some insects mystify us with behaviors that appear to involve mindlessness or a lack of free will. They can appear so different from us that they seem alien. We have a tendency to fear things we aren't familiar with or that we don't understand.

- In addition to these factors, there are also the associations we sometimes make between certain insects and filth, death, and decay. Cockroaches in a home or restaurant are often thought to indicate a general lack of cleanliness, which may suggest a health risk. Flies and their maggots can be associated with human or animal waste as well as with the carcasses of dead animals or human cadavers. These associations can cause people to develop a sense of disgust toward insects. Disgust, in turn, can sometimes develop into fear.

- Of course, there are some ways in which certain insects truly can be dangerous or harmful. Insect pests like corn rootworms and boll weevils cause tremendous damage to agricultural crops. Insects like termites can cause structural damage to homes and other buildings. The spread of invasive insect species like fire ants can threaten native species and cause damage to ecosystems. And insects like mosquitoes can transmit infectious diseases.

- But the vast majority of insects are harmless—and essential. They play an important role in food webs by serving as prey for other animals. They break down waste as well as dead plants and animals. Many plants depend on insects to defend them from herbivores and to spread their seeds, and many insects are important as pollinators for wild plants and crops.

- Insects have played important roles in many cultures, serving as symbols in mythology and religion as well as inspiration for artists and storytellers. They are also eaten as food in many cultures, and insects may become even more important as food in the future.

- Insects are used in scientific research, and some inspire the development of new technologies. And scientists and engineers may be able to learn from insects how to manage industrial-scale agriculture without succumbing to attacks by pests. While acknowledging the harmful roles that some insects play, one can objectively conclude that, as a group, insects are indispensable.

How to View Insects Positively

- Anyone with a true phobia of insects—and especially anyone suffering from delusory parasitosis—should seek help from a mental health professional. Fortunately, people with such conditions typically respond well to treatment. But for those who have a more mild aversion to insects, the best advice is to gradually expose yourself to insects and to learn as much as you can about them.

- Start by taking a closer look at the insects around you. You can find many harmless insects in and around your home. Get a magnifying glass, or take some photos, and learn to identify them. Putting a name on an insect gives it an identity and helps demystify it. Challenge yourself to learn at least one interesting fact about that species. Resist the urge to kill it and instead watch what it's doing.

- Consider going even further and keeping an insect as a pet. Once you've cared for a creature, it's harder to fear it and more likely that you'll even develop an affection for it. Rearing butterflies is a great way to start. You can order chrysalids online. Or, if you find a caterpillar in your yard, try collecting it along with some of the leaves you've seen it eating. Keep it in a small container with some air holes. After a few weeks, you'll get to watch it undergo metamorphosis and emerge as an adult butterfly.

- It's common for children to be interested in insects. Unfortunately, those interests often wane as they age. Yet there is encouraging evidence that interest in insects—even among adults—is on the rise. Insect zoos, butterfly gardens, and insect-themed festivals have become popular attractions worldwide. There are many entomology clubs and societies, some of which are open to amateurs. And online communities like BugGuide are supportive of anyone who wants to learn more about insects.

Connecting with Insects

- Given that so many people feel antipathy and fear toward insects, how can it be that insects are simultaneously celebrated and revered by so many others? Some insects, like many butterflies and beetles, are strikingly beautiful. People are often drawn to these insects simply to admire their beauty from an aesthetic perspective. Others, like artists and photographers, are motivated by a desire to try to capture the beauty of insects.

- Insects allow us to make meaningful connections with the natural world. Because insects are so ubiquitous, they can serve as a tangible representation of nature itself. Like plants, insect motifs are often used as decorations in homes and businesses, as many people enjoy seeing elements of the natural world in their everyday lives.

- Our connections with insects may have to do with what biologist Edward O. Wilson calls biophilia, the innate affinity that humans have toward all living things. Whether it's petting a dog, smelling a flower, or watching a ladybug crawl along a leaf, interacting with living things makes us feel good. Indeed, spending time in nature has been shown to lower blood pressure and improve mental health.

- There is still a lot we can learn from insects to help improve our own lives. For example, consider organizational structure. Most human organizations—like companies, governments, and the military—are organized hierarchically. Each person in the organization reports to their superior, all the way up the chain of command. Colonies of social insects aren't structured this way. Because there are no leaders, insect societies can't become corrupt.

- While having a centralized hierarchy is an effective way of maintaining control, organizations with centralized control are often less nimble in the face of change. They can't respond as quickly to threats or opportunities because decisions must be vetted by individuals at each level of the hierarchy. And the individuals at the top of the hierarchy have limited time, so they must prioritize how they spend it.

- Some human organizations have had success with adopting a more decentralized structure like that of ants and other social insects. Examples include crowd-sourced websites like Wikipedia, the online encyclopedia where content is created and edited by hundreds of thousands of individual users with minimal oversight or control. Wikipedia contains more than 6 million articles in English alone and has more than 20 billion unique visits each year.

- We still have a lot to learn about how social insects achieve some of their efficiencies. The lives of insects are incredibly complex, and the more we learn about their biology, the more questions arise, encouraging us to probe even deeper.

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Questions

1. True or false: A fear of insects can be explained by the fact that most insects are harmful or dangerous.

2. True or false: Some companies have a decentralized organizational structure that resembles the structures of colonies of social insects like ants and bees.

ANSWERS CAN BE FOUND ON PAGE 226.

Answers

Lecture 1

1 False. While a few species—like bed bugs, fleas, and termites—can be harmful to people, pets, or buildings, the majority of the insects commonly found in homes are harmless or even helpful.

2 Using baits treated with chemical pesticides like chlordane and DDT to kill cockroaches caused the few cockroaches that happened to avoid the baits to be more likely to survive and pass on their genes. Later generations of cockroaches inherited the genes for avoiding baits, making them harder to kill.

Lecture 2

1 b

2 ultraviolet

Lecture 3

1 d

2 Mayflies are the only insects that have wings prior to the adult stage. As mayflies develop, they undergo a stage called the subimago, in which they have wings but are not yet capable of flying or reproducing.

Lecture 4

1. b

2. pheromones

Lecture 5

1. d

2. elytra

Lecture 6

1. True. Bees generate static electricity as they move, causing them to become positively charged. Pollen tends to have a negative charge. So, a bee that is close to a flower can get pollen stuck to it without actually coming into contact with the flower.

2. d. The titan arum is pollinated by carrion beetles and blowflies that are attracted to the heat and smell of rotting meat produced by the inflorescence.

Lecture 7

1. cochineal

2. true

Lecture 8

1. d

2. Integrated Pest Management

Lecture 9

1. The swamps around Rome were home to mosquitoes that transmitted malaria, making it difficult for invading armies to lay siege to the city without succumbing to the deadly disease. However, the Romans themselves were also weakened by malaria, and bubonic plague transmitted by fleas killed a large number of Romans, contributing to the empire's decline.

2. true

Lecture 10

1. d

2. False. The silk used to bind leaves together is produced by weaver ant larvae.

Lecture 11

1. d

2. true

Lecture 12

1. true

2. shellac

Lecture 13

1. true

2. glowworms

Lecture 14

1 galls

2 true

Lecture 15

1 true

2 c

Lecture 16

1 Odonata

2 false

Lecture 17

1 false

2 true

Lecture 18

1 mates

2 true

Lecture 19

1 c

2 a

Lecture 20

1 d

2 False. The darker form of the peppered moth was favored when pollution levels were high, while the lighter form became more common following restrictions on air pollution.

Lecture 21

1 butterflies

2 a, b, d

Lecture 22

1 False. Butterflies and moths should be pinned through the center of the thorax, but for most other insects, the pin should be inserted just to the right of the midline. Other insects, such as aphids and most larvae, should be preserved in alcohol.

2 freezer

Lecture 23

1 d

2 true

Lecture 24

1 false

2 true

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