ak Woodland Invertebrates

The Little Things Count

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The Little Things Count

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"When we try to pick out anything by itself, we find it hitched to everything else in the universe."

This well-known quote from the pioneering conservationist John Muir serves as both a starting point and a framework for our exploration of a largely unnoticed universe. This universe exists within one of California's most important and environmentally impacted ecosystems: the oak woodlands. The universe we explore here is the realm of the *invertebrates,* minute animals whose lives are "hitched" to almost every part of the oak woodland ecosystem.

Filbert Weevils and Filbert Worms

Whether you are collecting acorns for eating, as California's Native American population did, or for planting, wormy acorns can be a problem. Insect larvae can destroy much of an acorn's insides and may introduce fungi and bacteria that will decay what is not eaten. A large percentage of the acorn crop from a given tree may be destroyed by these insects, but damage levels can vary widely from tree to tree and year to year. Although acorn feeders do not harm mature oak trees, they can reduce oak regeneration.

The two different types of insect larvae that are responsible for most wormy acorns are the filbert worm *(Cydia latiferreana)* and filbert weevil (*Curculio* spp.) larvae. Although both types of larvae are whitish, they can be distinguished in several ways. The filbert worm is the larva, or caterpillar, of a brownish, nondescript moth. Filbert worm larvae are relatively active and have true legs. When disturbed, a filbert worm larva may drop down on a silk strand as a spider does.

Larvae of the filbert weevil do not make silk. They are legless, relatively inactive, and tend to curl up in a C shape. Filbert weevil adults are brown beetles with extremely long, thin snouts. Typically, only a single filbert worm larva is found in an acorn, but up to eight filbert weevil larvae can be found in one acorn.

Zooming in on a Hidden World

California oaks (*Quercus* spp.) are the dominant tree species in the coastal ranges and the foothills surrounding the Central Valley. Oak trees cover about 10 million acres, roughly 10 percent of California's land area. Many woodlands in California include several different types of oaks. More than 25 oak species, natural hybrids and varieties, are native to California, and nine of these occur only in California. Some oak woodlands contain other native trees, including gray pine *(Pinus sabiniana)* and California buckeye *(Aesculus californica)*, and a variety of shrub species. The ground below the oaks is typically carpeted with non-native grasses introduced from the Mediterranean region. However, native bunch grasses and a variety of forbs occur in many woodlands, and springtime displays of native wildflowers often brighten the understory.

Oak woodlands teem with a wide variety of animal life. Over 300 species of vertebrates (animals with backbones) use California's oak woodlands, including 170 bird species, 80 mammal species, and 60 species of amphibians and reptiles. Although oak trees provide valuable habitat elements (nesting sites, cover, thermal protection, food) for many different vertebrates, relatively few species make direct use of oaks as a food source. For example, less than 20 percent of the bird and mammal species in oak woodlands eat acorns, and the percentage of mammals that browse directly on oak leaves, twigs, and roots is even smaller. But the myriad of invertebrates in oak woodlands converts the sunlight, carbon dioxide, and mineral nutrients absorbed by oak trees into food for many birds, reptiles, amphibians, and mammals.

When we look closely at individual oak trees, we begin to glimpse the universe of the invertebrates. They

buzz and drift through the air; climb along and tunnel through oak leaves, stems, and roots; dig through the soil; and swim in watercourses and seasonal ponds. Inver-tebrate organisms vastly outnumber their vertebrate counterparts in the oak woodlands: 10 to 100 million individual inverte-brates may be present within a single acre of oak woodland.

Invertebrates lack not only backbones, as their name implies, they have no internal skeleton at all. This lack of internal support limits the size that these animals can attain. In our oak woodlands, most invertebrates are less than 1 inch (2.5 cm) long; some are microscopically small. Nearly all of the invertebrates in the oak woodlands fall within a large tax-onomic group or phylum called the Arthropoda: literally, "joint-footed" invertebrates. The arthropods are further divid-ed into classes that include the Insecta (insects), Arachnida (spiders, ticks, mites, and scorpions), Crustacea (pill bugs and crabs), Chilopoda (centipedes), and Diplopoda (milli-pedes). All of these classes are represented in the oak wood-lands, but insects and arachnids are by far the most numer-ous. More than 5,000 species of insects and arachnids may be found in California's oak woodlands.

Oaks for Dinner

Virtually every part of an oak tree—roots, trunk, bark, branches, leaves, and acorns—serves as food for a number of invertebrates (see Filbert Weevils and Filbert Worms on page 2). Invertebrates, especially insects, may be categorized as oak pests if they feed on living plant tis-sues. However, only a handful of the more than 800 species of insects that feed directly on the tissues of living oaks can cause enough damage to be considered significant pests.

Insect-infested acorns typi-cally fall earlier than intact acorns. This observation may have led to the Native American practice of burning the oak understory to control these pests. Properly-timed burning would destroy wormy acorns from the current season and reduce pest populations in the following year.

Present-day acorn planters generally use water rather than fire to help separate good acorns from bad. Feeding by filbert worms and filbert weevils creates air-filled pockets in the acorn, which cause acorns to float in water. Pitching out the "floaters" leaves only the viable acorns for planting. Alternatively, discard-ing acorns with one or more exit holes—small holes produced by mature larvae as they leave the acorn to pupate—also eliminates many nonviable acorns from a seed lot.

Most of the insects that feed on oaks are specialists that can tolerate the high levels of tannins in oak tissues. Tannins are bitter-tasting chemicals produced by plants and can discourage feeding by both vertebrates and invertebrates. As California's oak-feeding arthropods have evolved along with their host plants over the past 15 million years, the oaks have waged chemical warfare by varying their tannin content and composition to discourage would-be oak feeders. This strategy has been only partly successful. As they coevolved with the oaks, oak-feeding insects accumulated adaptations that allow them to tolerate or even utilize the tannins in oak tissues. In the most extreme example of coevolution, cynipid wasps and other arthropods that produce oak galls (see Oak Galls on page 8) actually put oaks to work for them by manipulating oak biochemistry. Many oak-feeding arthropods subsist exclusively on oaks.

Who Is Eating Whom? Oak Enemies' Natural Enemies

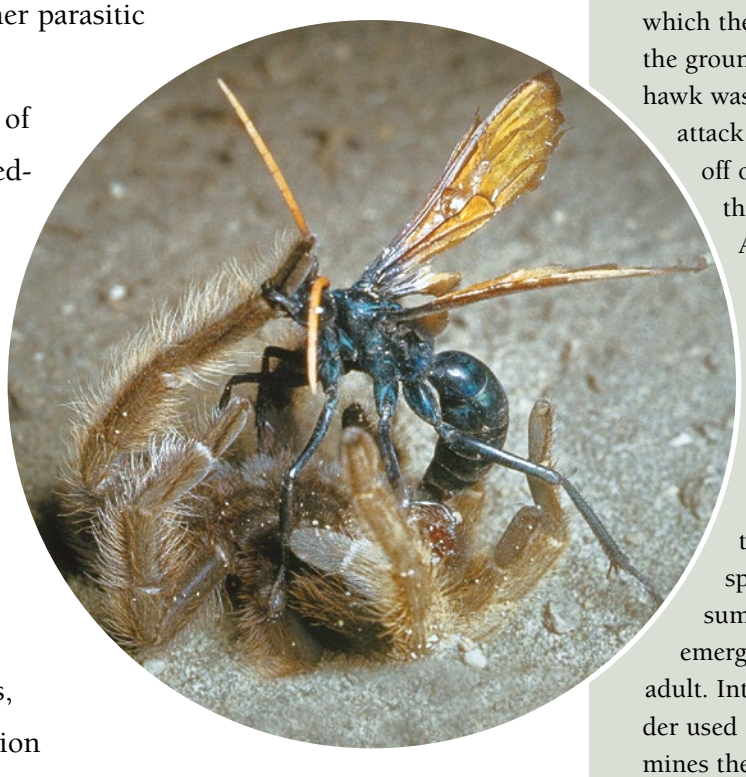
In the ongoing battle against hungry invertebrates, oaks have many allies, including other hungry invertebrates. That is, many of the native oak-feeding arthropods that exploit oaks for food are themselves food for other arthropods. Many general predators, such as spiders, dragonflies, mantids, and lacewing larvae, feed on almost any arthropod they can subdue, including other predators. Some other predatory arthropods are

Cocoons of a braconid parasitoid wasp (*Apanteles* sp.) are attached to a caterpillar feeding on a valley oak leaf. Braconid wasps are internal parasites (parasitoids) of various insect groups, and many form silken cocoons on the outside of the host insect's body. Parasitic insects like braconid wasps help reduce populations of leaf-eating insects under natural conditions, thereby minimizing the amount of insect-related leaf damage on oaks.

more specialized. For example, lady beetles generally feed on only aphids, scale insects, and mealybugs.

Parasitic insects (technically, parasitoids) also eat other insects, but do so while living either inside or on the host insect's body. Most parasitic insects eventually kill their hosts. Many families of wasps and several families of flies parasitize arthropod eggs, larvae, nymphs, pupae, or adults (see Tarantula Hawk Wasps at right). Even wood-boring insects tunneling within oak branches are not safe from parasites. Some parasitic ichneumonid wasps use their slender "stingers," or ovipositors, to penetrate overlying wood. This allows them to lay their eggs on or inside wood-boring insects tunneling beneath the bark. Indeed, even parasites are not safe from hyperparasitic species, that is, insects that parasitize other parasitic insects.

The intricate system of interactions between oak feeders and their arthropod predators and parasites helps to limit populations of destructive insects, restricting the amount of damage that they cause. Populations of oak feeders sometimes surge when conditions are unfavorable for their predators and parasites, leading to extensive defoliation



A tarantula hawk wasp (*Pepsis* sp.) paralyzes a tarantula by stinging it, sometimes following an intense struggle. The tarantula hawk drags the paralyzed spider off to its nest in the ground where it lays a single egg on the outside of the tarantula. The emerged larva of the tarantula hawk wasp then consumes the tarantula.

Tarantula Hawk Wasps

When walking through the oak woodlands during spring and summer, you may hear, then see, the tarantula hawk wasp (*Pepsis* sp.). The buzzing produced by this wasp as it flies can be loud enough that people sometimes think it is a black hummingbird with orange wings. The tarantula hawk is the largest wasp in California. Specimens with wingspans as large as 3½ inches (9 cm) and bodies exceeding 1½ inches (4 cm) have been found. The body is an iridescent, steel blue, sometimes with a greenish tint.

As its name implies, females of this wasp species prey on tarantulas, which they hunt by flying low over the ground. The female tarantula hawk wasp is usually successful in her attack on the spider, often biting off one of the spider's legs and then feeding on its body fluids. After stinging and paralyzing the spider, the wasp drags the spider up to 100 yards (91 m) to an already-prepared hole. The wasp places the tarantula in the hole and lays an egg on its abdomen. A larva emerges from the egg and eats the paralyzed spider. Once the spider is consumed, the larva pupates and emerges the following spring as an adult. Interestingly, the size of the spider used to provision the larva determines the size of the adult wasp that emerges.

Tarantula hawk wasp adults sip nectar from milkweed blossoms and mate on or near milkweeds. As with all wasps, only the female can sting. Only a few humans have been stung by tarantula hawks. While not considered dangerous, the sting is said to be indescribably painful.

California Oak Worm

Because of the severe defoliation it can cause during major outbreaks, the California oak worm or oak moth *(Phryganidia californica)* is one of the best known and most important native insect pests of oaks. Young oak worm larvae skeletonize the lower leaf surface, whereas larger larvae chew through the entire leaf blade. Two generations of the oak worm are typically produced in Northern California, but a third generation can occur in the south, or in the north following warm, dry winters. The oak worm occurs along most coastal areas in California and can be found on both live oaks and deciduous oaks. Deciduous oaks are less likely to be affected early in the growing season because most overwintering larvae and eggs are destroyed when deciduous oaks drop their leaves.

Oak worm populations are usually kept under control by natural enemies and diseases, but periodic population explosions can occur in 3- to 7-year cycles. During such outbreak years, affected trees may become almost completely defoliated. The constant rain of caterpillars and their excrement from heavily infested oaks can render the area under the canopy uninviting at best. Healthy oaks are not significantly harmed by the infrequent episodes of defoliation, but weakened or unhealthy trees may be further debilitated and may decline and die if severe defoliation occurs repeatedly.

(see California Oak Worm at left). However, damage is typically limited either by the insect's own life cycle or by a resurgence in populations of natural enemies. A mature oak tree has considerable energy reserves and is therefore not threatened by an occasional bout of defoliation. For a healthy oak, a new flush of leaves normally replaces the damaged set—and, life goes on. However, if an oak is weakened by disease, construction damage, or chronic stress, a serious defoliation episode can push a tree into a decline that may result in its death.

Human Impacts: Usually More Harm Than Good

Humans often disrupt the stability of the interactions between oaks, their arthropod residents, and natural enemies of oak pests, generally to the detriment of the oak. Although various methods can be used to reduce populations of injurious insects, in most cases human actions result in unnaturally high levels of insect damage.

Negative human impacts are especially common among oaks that are incorporated into urban landscapes. Fertilization can increase plant tissue succulence that favors insect damage. Summer irrigation of oaks can lead to unseasonal growth flushes that are highly susceptible to insect attack. Summer irrigation also increases the risk of various debilitating root diseases. These diseases can stress trees, making them more attractive to insects that specialize in attacking weakened trees.

To counter pest problems brought on by improper cultural conditions, some oak owners resort to applications of broad-spectrum insecticides. Unfortunately, such products usually do more harm to populations of predatory and

parasitic insects than to the oak feeders; therefore, they often thwart the pest control provided by natural enemies. As a result, sprays of nonselective insecticides may increase populations of pest species, including species that were not causing problems before the spray was applied.

Humans have also created problems for California's oaks by unintentionally introducing exotic invertebrates that feed on oaks. Non-native oak feeders pose a distinct threat, not only to urban oaks, but to all of California's oaks. The complex interactions between native, oak-feeding arthropods and their natural enemies has developed over many millennia into a system that maintains a fluctuating but stable equilibrium. In contrast, when oak-feeding insects are unwittingly introduced from other regions, they are generally free of the attendant predators and parasites that would normally limit their populations in their native habitats. Free of such constraints, these pest populations can explode and cause serious damage. Poten-tially dangerous pests such as the gypsy moth are excluded from California by quarantines and inspections, but eternal vigilance is required to stem the flow of exotic arthropods in our highly mobile society.

A number of invertebrate pests have become established in California. Examples include two species of oak pit scale from Europe that have become serious pests of California oaks, especially in urban areas. These greenish-yellow to golden insects suck sap from twigs and branches. Their feeding causes tissues to swell around the scale and forms a pit-shaped depression in the bark. Heavy infestation of pit scales can cause branches to die, distort growth of twig tips, and severely weaken mature trees that are stressed by other factors.

Top left: Spherical galls produced by the *Andricus brunneus* wasp are attached to the midrib and petioles of these valley oak leaves.
Top right: A slender stalk attaches this minute, spindle-shaped gall, produced by the *Dros pedicillatum* wasp, to the edge of a blue oak leaf.
Bottom left: The *Disholcaspis plumbella* wasp forms this beaked twig gall on scrub oak.
Bottom right: These oak apple galls on valley oak stems are caused by the California gallfly *(Andricus californicus)*.
Opposite page: This wasp is known as the live oak gallfly *(Callirhytis pomiformis)*.

Oak Galls

More than 130 species of cynipid wasps form galls on the leaves, twigs, catkins, and acorns of California oaks. These galls are an overgrowth of plant tissue produced in response to chemicals secreted by gall wasp larvae. Because each wasp species produces a unique chemical, a unique type of gall is formed. Most wasp galls cause little or no lasting damage to oaks. However, a few galls distort the stem to the point that nutrient flow inside the branch is obstructed, and the portion of the branch beyond the gall may die.

Many gall wasp species have two alternating generations: a bisexual generation (females and males) followed by a unisexual generation (only females). Each of these generations produces a unique gall, often on different parts of an oak. Galls produced by the bisexual generation are usually found during winter on permanent parts of the tree, such as twigs. The unisexual generation is typically produced during spring and summer, and galls are often on leaves and catkins.

The gall made by the urchin gall wasp *(Antron echinus)* is found during spring and summer and looks like a small sea urchin. The gall is about ¼ inch (7 mm) in diameter, reddish to pink, and occurs on blue and scrub oak leaves. Galls produced by the crystalline gall wasp *(Andricus crystallinus)* often occur in groups of 3 to 12 on the leaves of blue, scrub, leather, and Oregon oaks. Galls are pink to reddish and densely covered with white to reddish or brownish hairs. Masses of these galls look like a gathering of fuzzy caterpillars huddling together on the underside of an oak leaf. If the larva in a gall fails to develop normally, possibly due to parasite attack, the fuzzy hairs are not produced and the gall remains bare.

One of the most conspicuous and common oak galls is the oak apple (see photo at left), which occurs most commonly on valley oak trees. These galls, caused by the California gallfly *(Andricus californicus),* can grow up to 4 inches (10 cm) in diameter. Early in the summer, galls look similar to apples: they are glossy and rounded, have a firm texture, and are initially green but later become tinged with a reddish blush. Despite the superficial resemblance to apples, the very bitter flavor of the gall would quickly convince anyone that the inedible apple gall is not a real apple. Old oak apples may remain attached to branches for up to 4 years. They become hard and tan colored before eventually blackening as they slowly decay.

The gall wasps (Cynipidae) are the most diverse group of invertebrates that utilize oaks in California. Adult gall wasps are minute (1/16 to ⅛ in [2 to 3mm]), but galls range in size from about that of a grain of sand to that of a baseball.

What's in the Soil? Invertebrates Down Below

Many invertebrates subsist on oak tissues without ever nipping at a living tree. Each year oaks produce great quantities of castoffs: leaves, acorns and acorn caps, dead twigs, rotted branches, and expired rootlets. Many invertebrates feed on these discards and, in the process, help recycle the mineral nutrients in these materials for use by oaks and other plants. Large pieces of oak litter are broken down by the feeding of insects such as earwigs, beetles, and fly larvae and other arthropods such as millipedes and sow bugs. Minute fragments of oak litter are food for smaller invertebrates such as springtails and mites.

Many invertebrates rely on microorganisms to assist them in decomposing oak parts. Termites and larvae of wood-boring beetles that feed on wood are only able to do so because they have specialized microorganisms in their digestive tracts that break down wood fiber into simpler compounds that the insects can then digest. Some invertebrates, including many beetles, wait until woody branches and twigs are decayed by fungi and then graze on the more digestible fungal tissues.

Soil invertebrates are also important in creating and maintaining soil conditions that allow oaks to survive and grow. In a healthy oak woodland, any shovel full of soil taken from beneath an oak tree can contain thousands of invertebrates. Earthworms, milli-

Invertebrates like millipedes (Diplopoda) are important for recycling nutrients because they break down fallen debris, such as decaying bark and leaves. They also serve as food for other animals higher in the food chain.

pedes, and insects burrow through the soil, creating minute channels. These tiny channels allow necessary oxygen to reach oak roots. When soils are compacted by vehicles or livestock, these channels are destroyed, and the flow of oxygen to the roots is blocked. As oxygen-deprived roots die, the overall health of the oak tree may suffer to the point that the tree ultimately declines and dies.

The Big Picture

The complex interactions between the oak, the soil, and the invertebrates that inhabit both the aboveground and belowground niches are just a small portion of the big picture. The largely unseen world of the invertebrates is the base that supports much of the visible wildlife community in oak woodlands. Invertebrates form an important part of the diet of many wildlife species, including salamanders, lizards, frogs, toads, moles, bats, and a wide variety of birds. For example, during the breeding season, insects comprise 90 to 100 percent of the diet of the adults and young of many species of oak woodland birds. Birds hunt for insects because of their availability and the rich source of protein they provide. It has been demonstrated that with some bird species a greater availability of insect foods during the nesting season is linked to larger clutch size, more clutches per breeding season, better survival of young, and even greater reproductive success of offspring the following year.

Invertebrates form an important part of the diet of nearly all oak woodland songbirds. While adults of some species, such as these acorn woodpeckers *(Melanerpes formicivorus),* rely on oak woodland berries, fruits, and fungi for food, their nestlings are fed insects and other invertebrates exclusively.

California's ancient oak woodland ecosystems have been drastically altered since settlement, and human activ-

ities continue to imperil their long-term sustainability. Loss of oak woodlands not only degrades our soil, air, and water resources, but deprives future Californians of these unique, diverse, and beautiful natural communities. While we can plant oaks to restock depleted woodlands, we cannot simply transplant into a new planting all of the plant and animal diversity associated with mature woodlands. Reserves of undisturbed woodlands are important for providing a reservoir of other plant species, vertebrate and invertebrate animals, and microorganisms that are all integral parts of a functioning oak woodland ecosystem. All the denizens of the woodlands, from the largest oaks to the smallest invertebrates, are "hitched" together in a system that we have only just begun to understand. While we keep our eye on the big picture, it is important to remember that the little things—the myriad of oak woodland invertebrates—count.

Invertebrates form a large part of the diet of many vertebrate animals in the oak woodlands, such as this western skink (*Eumeces skiltonianus*). Abundant invertebrate populations are critical to the maintenance of the biological diversity of oak woodlands.

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