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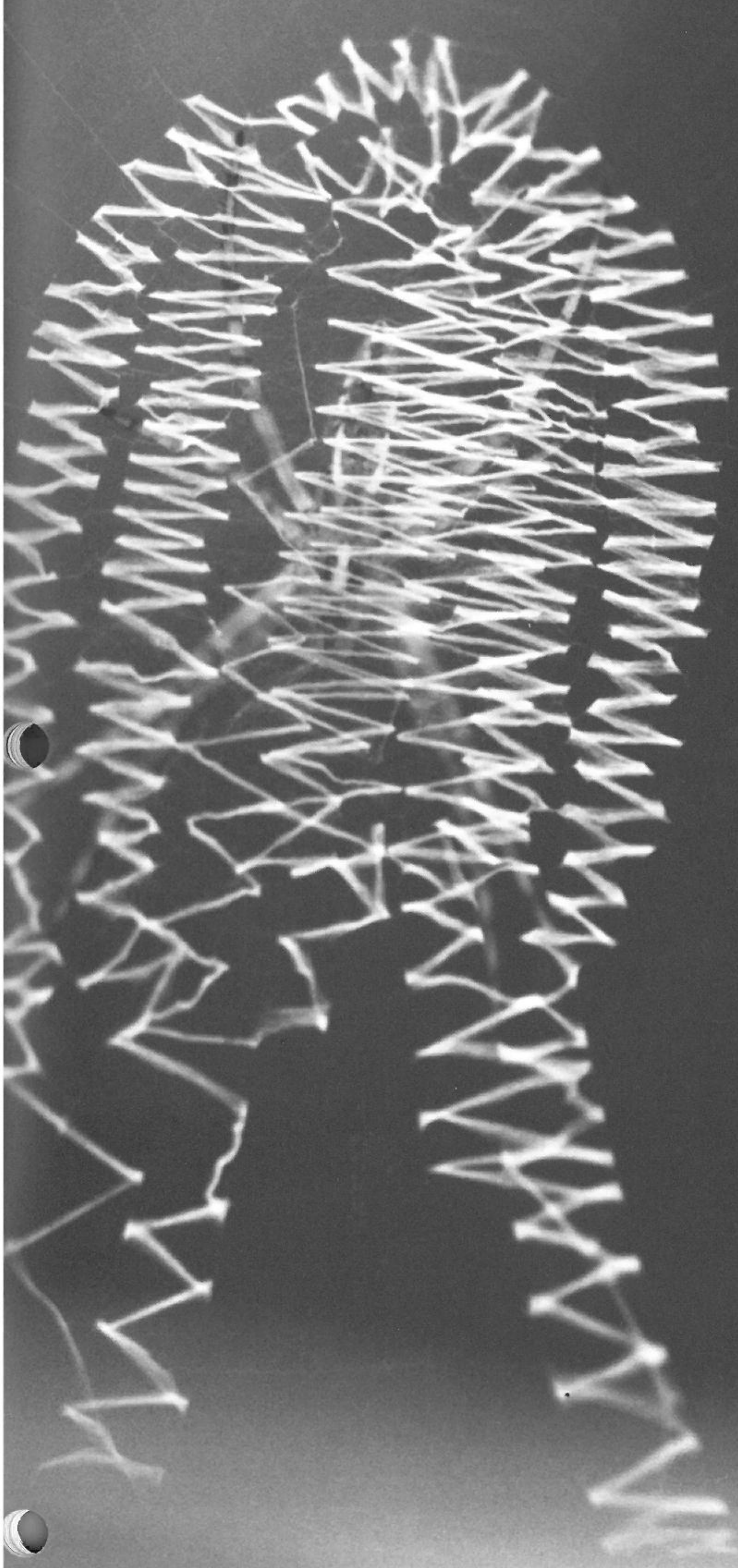
WHAT'S BUGGING COASTAL SAGE SCRUB?

by G.R. Ballmer



AS IS TRUE OF other natural communities, coastal sage scrub is dependent on invertebrates to play essential housekeeping roles. Insect pollinators mediate plant reproduction. Invertebrate herbivores convert plants into animal biomass, while predators (chiefly predatory insects and spiders), together with microbial pathogens and insectivorous vertebrates, then disperse the biomass throughout the food web. To complete the nutrient cycle, invertebrate scavengers (chiefly arthropods, earth worms, and nematodes), together with fungi and microbes, consume and break down dead and decaying organic matter. Edward O. Wilson has aptly referred to invertebrates as "the little things that run the world," for their great abundance and varied activities are responsible for maintaining ecological processes that support most life on earth.

A rich but largely unquantified diversity of invertebrates inhabits coastal sage scrub. Charles Hogue estimated that 3,000 to 4,000 species of insects and their arthropod relatives inhabit the Los Angeles Basin, much of which was originally covered by coastal sage scrub. Perhaps three to four times that many invertebrate species inhabit coastal sage scrub in all of Southern California. Such high diversity can be attributed to a broad spectrum of local conditions and the proclivity of small organisms to become specialized to live efficiently within narrow environmental parameters. A combination of a broad climatic gradient (from cool, moist maritime to hot, dry desert fringe), topographic variables (slope, drainage, and elevation), distinctive soil types, and a rich flora have created a mosaic of communities within the broader context of coastal sage scrub. In addition to major geographic subdivisions, there are numerous local community assemblages or subassociations, each of which has a unique mix of invertebrate housekeepers.

Although the identities and life histories of many (but far from all) invertebrates are known, this information is often fragmentary and widely scattered in the literature.

Web-spinning spiders are important predators of flying insects. Photographs by the author.

Centipedes such as this *Scolopendra* are voracious predators.

Even for insects, the most intensively studied invertebrate group, there is no comprehensive reference for coastal sage scrub or any other major plant community in California. The less well known mites and nematode worms may be equally diverse. The dearth of collated information on invertebrates in coastal sage scrub is due in part to the relatively recent recognition of coastal sage scrub as a distinctive and threatened community in need of study. It is also partly due to the daunting and largely unrewarded task of assembling such information.

Biodiversity

An insight into the nature of invertebrate diversity in coastal sage scrub may be gained by analysis of two intensive surveys of limited geographic scope within Southern California. One survey was conducted in the coastal El Segundo Dunes near Los Angeles International Airport. Faunal and floral collections during 1938-39, prior to large-scale urban development, provide an incomplete baseline by which the results of a recent survey of the remaining 302 acres can be compared. A second, and ongoing, survey of the Deep Canyon Transect surrounding the University of California's Philip L. Boyd Deep Canyon Desert Research Center in Palm Desert covers 161,280 acres. Because much of the transect is nearly pristine, extensive faunal and floral species lists compiled over the past thirty years provide a good estimate of natural biodiversity.

Both surveys include many groups of invertebrates other than nematodes; and, while neither survey represents typical coastal sage scrub, each contains some elements of it under opposite extremes of cool maritime and hot desert conditions.

The dunes community is a unique, but degraded amalgam of widespread coastal sage scrub components and local sand obligate species. Prior to intensive human disturbance, the dunes contained ninety-one native plants, 825 invertebrates (eighty-five percent insects), and 120 vertebrate species, including transients. Thus, there were about ten invertebrates for each native plant species. By the late 1980s, the dunes community was in a state of ecological collapse; thirty-six native plants had been extirpated, while eighty-three invasive and ninety-eight non-invasive exotic ornamental or weedy species had become established. Additionally, sixty-six invertebrate and seventy-nine vertebrate species had been extirpated, while twenty exotic invertebrate and eleven exotic vertebrate species had become established on the dunes. Non-native plants and animals have contributed greatly to the decline of natives.

The much larger Deep Canyon transect covers a series of communities ranging from desert scrub to coniferous forest over an elevational gradient from thirty to 8,716 feet above sea level. The invertebrate fauna of the transect is perhaps more comparable to that of coastal sage scrub *per se* in diversity of participants in various ecological housekeeping functions because it encompasses a much larger area and broader range of habitats than the dunes. Although the transect lacks coastal sage scrub, it shares at least twenty-four native plant and 116 native invertebrate species with the dunes.

Inventories of the flora and vertebrate fauna of the transect are considered complete, while only a fraction of the invertebrates have been cataloged. According to records maintained at the Entomology Research Museum of the University of California's Riverside campus, the transect contains 619 plants, 319 vertebrates, and more than 2,844 identified invertebrate species (ninety-five percent insects). Some large groups (e.g., mites, spiders, and nematodes) have been poorly surveyed; additionally, many specimens, including still-unnamed forms, await inspection by taxonomic specialists, who are in woefully short supply. The number of insect species in the transect may represent ten to twenty percent of the insect fauna of California, as conservatively estimated by J. A. Powell and C. H. Hogue.

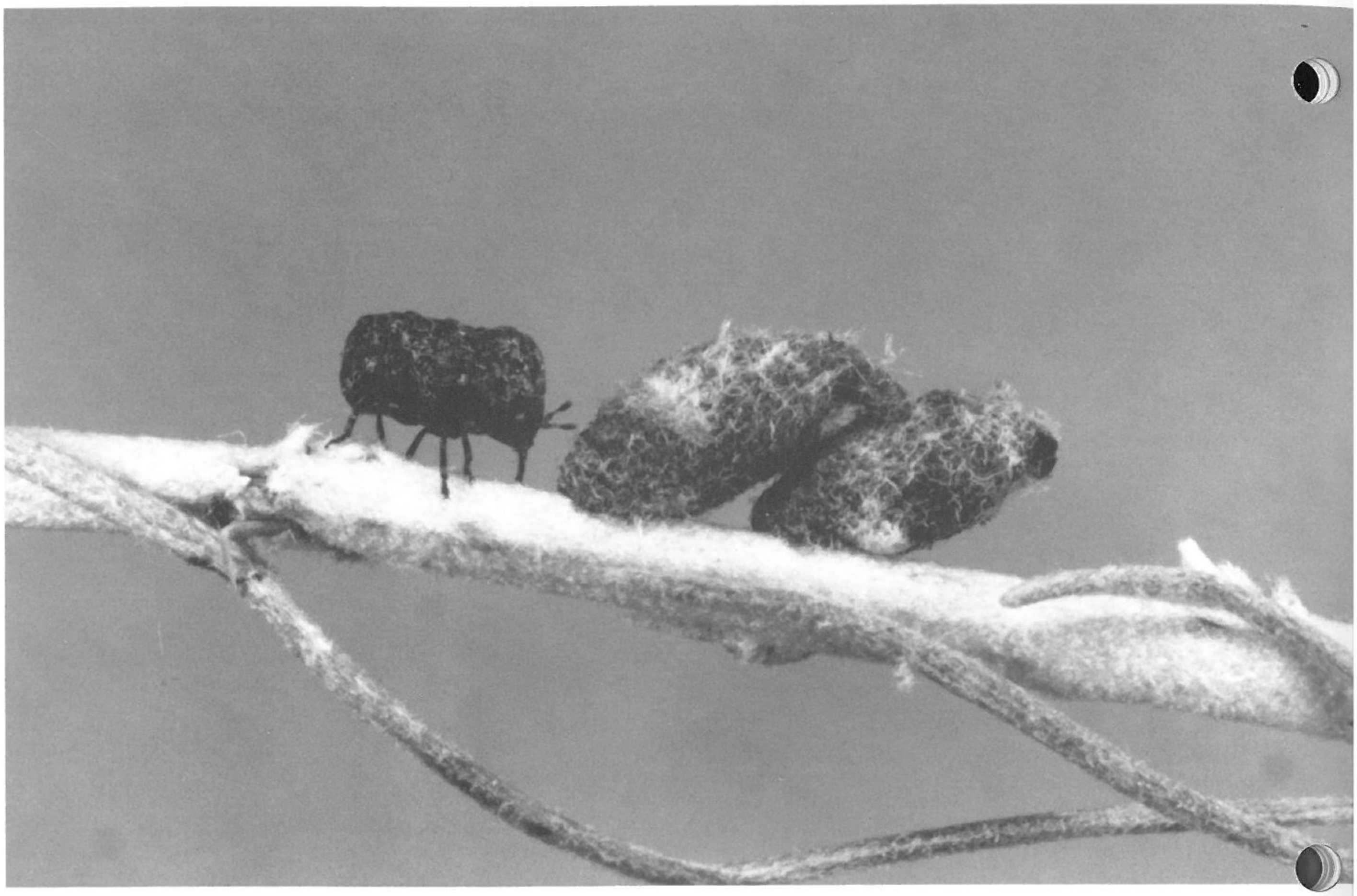
The extensive and virtually complete invertebrate survey of the dunes allows a breakdown of the number of species contributing to four primary ecological housekeeping functions. Although changes in nutritional behavior accompany development in many insects, the invertebrates may be roughly categorized as fifty-two percent herbivorous, thirty-five percent predaceous, four percent pollen-gathering, and eight percent scavenging species. Herbivores derive their nutrition primarily from plant tissues (leaves, roots, seeds, stems, etc.). Predators eat other animals and include both generalists (spiders, mantids, etc.) and host-specific forms (chiefly parasitoid flies and wasps). Pollen-gathering bees, along with many other flower-visiting insects, are important in pollination. Scavengers include darkling beetles, carrion- and dung-feeding flies and beetles, cockroaches, ants, termites, pill bugs, and many other soil-dwelling invertebrates.

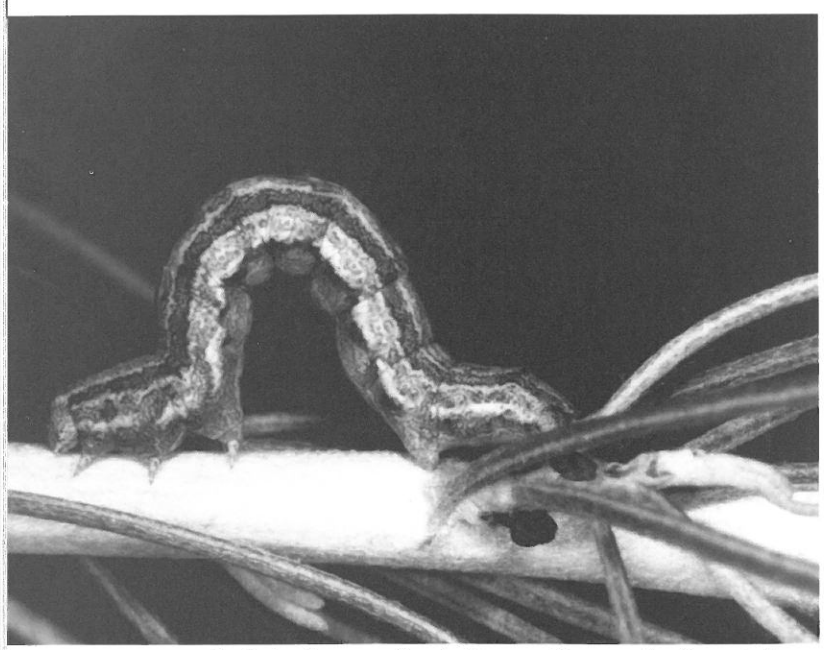
The transect's provisionally known invertebrate fauna is comprised of thirty-nine percent herbivorous, forty-five percent predaceous, six percent pollen-gathering, and ten percent scavenging species. In spite of similarities to the dunes in proportions of invertebrates in the four major ecological categories, major differences exist with respect to the proportions of some constituent taxonomic groups. For example, wood-boring beetles in the well surveyed families Buprestidae and Cerambycidae together constitute 0.35 percent and 5.56 percent of the invertebrate fauna of the dunes and transect, respectively, reflecting the much greater diversity of woody perennials capable of serving as hosts in the transect. A similar diversity of woody perennials also occurs among the various coastal sage scrub series, indicating the need to avoid generalizations based on surveys of limited scope.

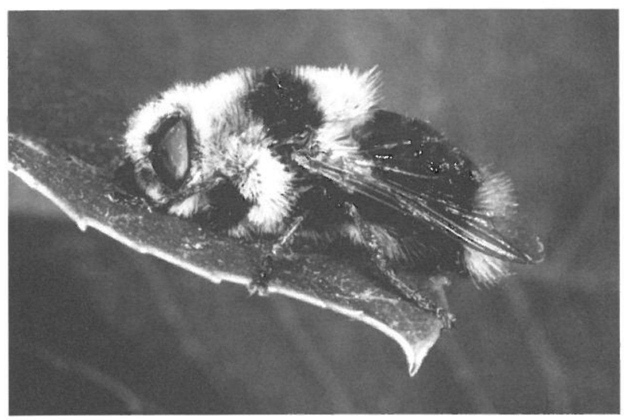
The Jerusalem cricket (also known as potato bug and child of the earth) spends most of its life underground feeding on roots.

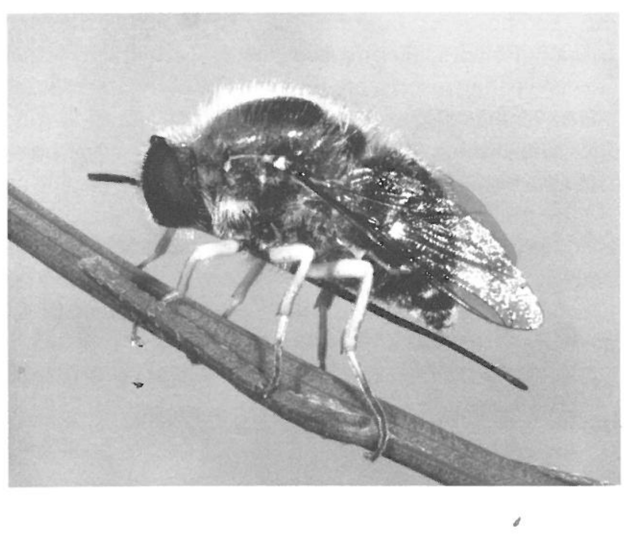
Approximations of invertebrate species diversity in coastal sage scrub can also be gleaned from a few regional surveys of large taxonomic groups. Perhaps most illuminating is the diversity of native bees, which are intimately associated with the ecology and evolution of flowering plants. Of the approximately 3,500 species of bees in North America north of Mexico, only about 800 occur east of the Mississippi River, while more than 1,600 species occur in California. Cismontane Southern California, much of which is covered by coastal sage scrub, has the largest complement of bees (555 species) of all biotic regions of the state.

Butterfly diversity is also high in coastal sage scrub. Southern California's 154 resident species and fourteen occasional or temporary migrant species represent about sixty percent of butterfly species in California and twenty-five percent of the total for North America north of Mexico. Plants commonly found in coastal sage scrub serve as larval hosts for forty-eight butterfly species, while another twenty-eight species utilize plants typical of communities found adjacent to or intermixed with coastal sage scrub (e.g., chaparral, grassland, oak woodland, and riparian). Because many butterflies are closely associated with larval host plants that are not restricted to a single plant community, their distributions often cross community boundaries. Aside from the Avalon hairstreak (*Strymon avalona*), which is confined to Santa Catalina Island, and unlike









Clockwise from top: disguised to resemble caterpillar frass, the larvae and adults of *Exema conspersa*, a chrysomelid beetle, feed on leaves of California sage brush; the deer botfly, *Cephenemyia*, resembles a bumble bee; its larvae are parasitic in the nasal sinuses of deer; this acrocerid fly (*Eulonchus*) uses its elongate proboscis, here tucked under the body, to feed on nectar; its larva is parasitic on spiders; caterpillars, such as this inchworm on California sage brush, are major converters of plants into animal biomass.

many less mobile invertebrates, no butterfly species is strictly confined to coastal sage scrub. Nevertheless, two species, the Hermes copper (*Hermelycaena hermes*) and Gabb's checkerspot (*Charidryas gabbii*) are nearly confined to coastal sage scrub. Butterfly subspecies endemic to coastal sage scrub and related communities include the El Segundo blue (*Euphilotes battoides allyni*), Quino checkerspot (*Euphydryas editha quino*), and the Palos Verdes blue (*Glaucopsyche lygdamus palosverdesensis*), all of which are near extinction.

Herbivores

Herbivorous invertebrates comprise the major initial step in converting plant biomass into animal biomass in most, if not all, terrestrial communities. The largest cohorts of herbivores in coastal sage scrub are Coleoptera (beetles), Hemiptera (plant bugs, aphids, leaf hoppers, etc.), Hymenoptera (ants, bees, and wasps), and Lepidoptera (moths and butterflies). Thrips (Thysanoptera) and mites (Acarina) can also be exceptionally abundant, but, due to small size, are frequently overlooked by casual observers and may represent a minor portion of total invertebrate biomass. Native terrestrial snails are seldom encountered due to their restricted distributions and secretive habits, but the pestiferous European brown garden snail (*Helix aspersa*) often invades scrub lands adjacent to irrigated gardens, especially within the coastal fog belt. Ten species of native terrestrial snails in mainland coastal sage scrub and fifteen others on the offshore islands are considered rare or endangered due to restricted distribution and/or habitat loss.

All parts of a plant are potential resources for specialized invertebrate herbivores. For most insects, the immature nymphs or larvae do most of the feeding, while adult activity is oriented primarily toward reproduction and dispersal. In addition to external leaf-eaters, many species feed inside plant tissues. Aphids, plant bugs, leaf hoppers, and scale insects suck plant sap. Larvae of many small flies and moths mine the inside of leaves. Gall-forming arthropods include beetles, flies, mites, moths, and wasps. Larvae of several beetles, moths, and sawflies bore inside stems, trunks, crowns, and roots. Some beetles, flies, moths, and wasps also develop inside flowers, fruits, and seeds. Many adult insects imbibe nectar, while bees, thrips, mites, and some beetles also feed on pollen.

Many coastal sage scrub insects have life histories much like annual plants, undergoing a burst of growth and reproductive activity (triggered by photoperiod, temperature, and moisture cues) for a few weeks followed by a period of dormancy (diapause) for the remainder of the year. This is particularly pronounced in insects having complete metamorphosis (egg, larva, pupa, and adult), such as Coleoptera, Diptera (true flies), Hymenoptera, and Lepidoptera, whose adult activity period is usually of short duration and coincides with maximum abundance of reproductive resources. Diapause in insects is achieved by arrested development in one of the immature stages (egg, larva, or pupa), or more rarely in the adult stage.

Invertebrates are collectively most abundant in coastal sage scrub during winter and spring, coinciding with maximum plant growth. A lesser number of "annual" species appear later in the year, coinciding with the flowering periods of summer- or fall-blooming plants. As with summer-dormant plants, many insects are tolerant of drought conditions while in diapause but are susceptible to pathogens if exposed to unseasonal moisture. This may explain why some desert-adapted species that occur in the relatively dry Riversidian sage scrub have not colonized moister portions of the coastal plain. Likewise, many coastal species lack the heat and drought tolerance to survive further inland.

The few attempts to inventory insect fauna associated with individual plant components of coastal sage scrub indicate that the majority are polyphagous (feeding on many hosts). Insect faunal studies of fifteen Southern California plants summarized by Goeden and Teerink include three coastal sage scrub plants, ragweed (*Ambrosia acanthicarpa*), sweetbush (*Bebbia juncea*), and thistle (*Cirsium californicum*), which are frequent in the relatively arid inland valleys. On average, sixty-five herbivorous species were found on each of these plants. Monophagous and oligophagous species (feeding on a single host or a few hosts, respectively) comprised no more than thirty percent of the total.

Larger and longer-lived plants (especially woody perennials) provide a more stable resource for herbivores than do short-lived annuals and can be expected to harbor both more monophagous and oligophagous species and a broader array of all invertebrate associates. Thus, the desert shrub, jojoba (*Simmondsia chinensis*), which barely infiltrates coastal sage scrub, was found by J. D. Pinto *et al.* to have 204 associated insect species, including 100 herbivores, nine of which are apparently monophagous. Nevertheless, species composition on jojoba varied from site to site, reflecting differences in local environmental variables and plant community structure. Additionally, although general predators were not systematically recorded, thirty-nine species of spiders and three species of predatory mites were reported from one site (Radec) transitional between Riversidian sage scrub and desert scrub.

The number of individual invertebrate herbivore species in coastal sage scrub is perhaps less important than their collective abundance and biomass. The latter can be estimated from the number and weight of organisms associated with individual plants and can be expressed as a fraction of total plant weight. The invertebrate biomass per unit area can vary according to local plant community composition, growth condition, and season. Climatic fluctuations can also cause invertebrate abundance to vary greatly from one year to the next.

While the larvae of *Tegrodera erosa*, a blister beetle, are parasitic in subterranean bee nests, the adults are partial to *Eriastrum* flowers, a common plant in the coastal sage community.

In an ongoing survey of arthropods on California sagebrush (*Artemisia californica*) at five locations in western Riverside and San Bernardino counties, I have found approximately forty phytophagous species and a similar number of predators. The sampling method (beating branches) provides an indication of the diversity and abundance of invertebrates occurring externally on sagebrush foliage; detection of organisms occurring elsewhere on or in the plant requires other sampling techniques. The most abundant organisms found have been sap-feeding plant bugs and leaf hoppers (Hemiptera) and leaf-eating caterpillars (Lepidoptera). The predominant predators include spiders, lacewings and snakeflies (Neuroptera), and parasitoid wasps (Hymenoptera).

The arthropod biomass on California sagebrush declined forty-three percent from late February to mid-March and another twenty-seven percent by mid-April. This is largely attributable to fluctuations in species composition and overall abundance of tiny moth larvae (Lyonetiidae) and plant bugs (mean adult masses 0.24-0.35 mg, dry weight). The largest organisms were moth larvae (Geometridae and Noctuidae), usually found as second and third instars weighing 3-8 mg (dry weight). At maturity (fifth instar), these larvae are about an inch long, weigh 20-70 mg (dry weight) and are likely candidates for the diet of hunting wasps and scrub-dwelling birds.

Pollinators

Many insect groups incidentally contribute to pollination in the course of visiting flowers to feed on nectar or pollen. Insects that habitually utilize floral resources often have anatomical specializations for imbibing nectar (e.g., tubular mouthparts in bees, butterflies, some flies, and some beetles) or for harvesting pollen (e.g., body hairs and comb structures in bees and some beetles). Bees are certainly the most important insect pollinators and are most highly specialized to collect and transport pollen, on which they rear their young.

Local bee diversity is related to availability of suitable pollen sources and nesting substrates along with climatic variables. Many bees require a full year to complete their life cycles and are active as adults for just a few weeks. Because bee activity is synchronized with host plant bloom, the greatest diversity and overall abundance of native bees in coastal sage scrub coincides with spring, when the greatest number of native plants bloom. Some bees appear later and utilize summer and fall blooming plants.

In a recent month-long survey of vernal bees in Riversidean sage scrub, I have inventoried 2,170 bees, provisionally estimated to represent 239 species. The 1,323 bees for which plant visitation was observed represent approximately 180 species. Three plant species that accounted for the majority of host records, brittlebush (*Encelia farinosa*), deerweed (*Lotus scoparius*), and flat-top buckwheat (*Eriogonum fasciculatum*), were also the dominant floral resources during the survey period. Brittlebush was by far the most frequently recorded host for all bee families except Apidae (bumble bees) and Megachilidae (leafcutters). The latter family displayed a co-equal preference for deer weed, which was much less frequently utilized by other bee families.

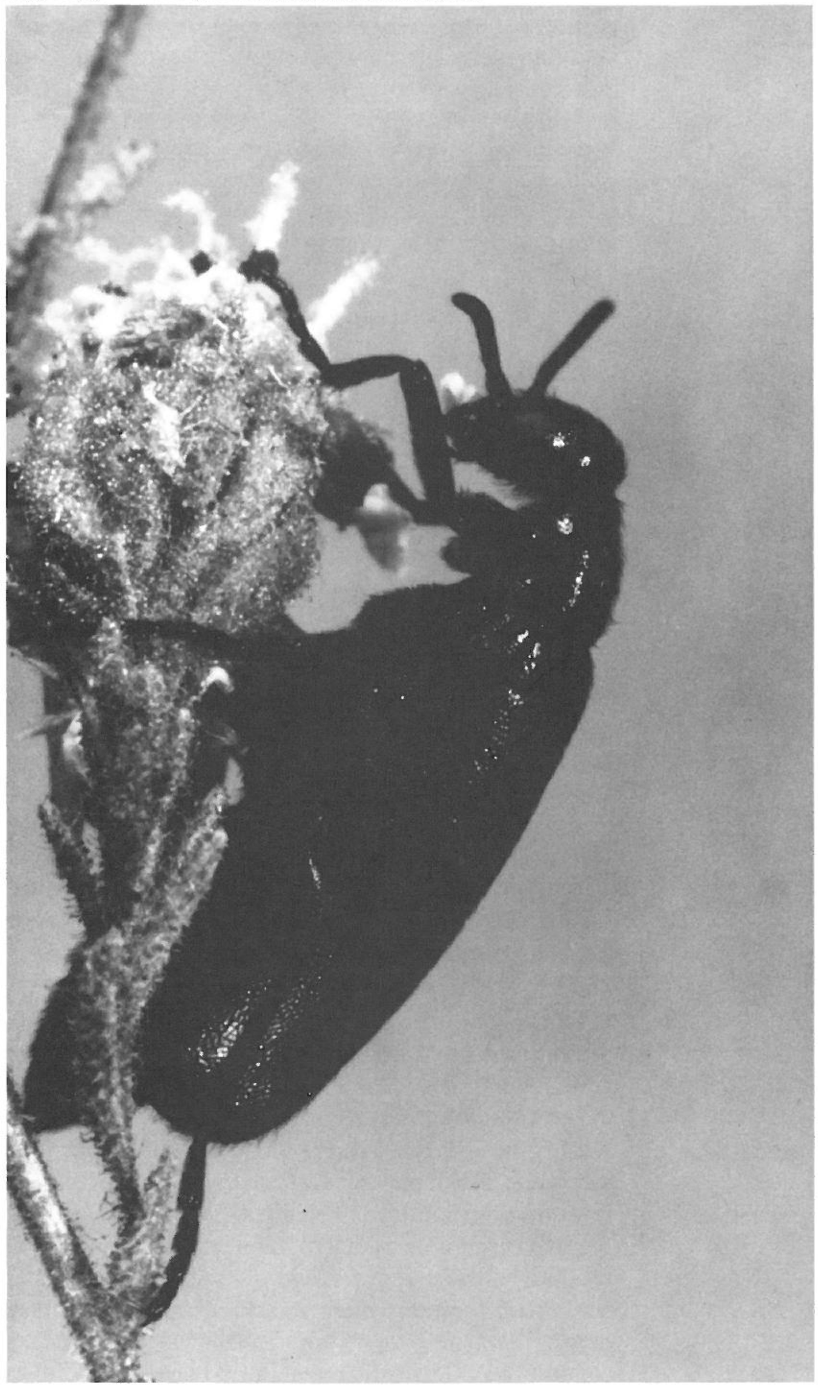
Local bee diversity is largely related to climate and plant diversity. Many species are mono- or oligolectic (depending on pollen from only one or a few related plant species, respectively). The bees of cismontane Southern California are nearly equally divided between oligolectic and polylectic (using many different plant hosts) species. In some cases males visit one host and females visit another. Additionally, some species gather pollen from one host, but obtain nectar from one or more others. The resource breadth of the imported European honey bee (*Apis mellifera*), which visits virtually all lowland nectar and pollen sources throughout the year, exceeds that of any native species.

Host plant preference often correlates with anatomical structure. Bees that specialize in tubular flowers generally have long tongues. Complex floral structures in some plants (e.g., *Astragalus, Lotus, Trichostema*) require bee pollinators that are predominantly robust, as well as long-tongued (e.g., bumble bees and leaf-cutter bees). Conversely, small bees and bees with short tongues tend to frequent plants with small blossoms (e.g., *Ceanothus, Eriogonum, Euphorbia*) or large open blossoms (e.g., *Camissonia, Malvastrum, Ranunculus*).

Another factor contributing to bee diversity is the presence of suitable nesting substrates. Most species excavate solitary burrows in soil, but some burrow into dead wood or twigs. Still other bees utilize existing cavities in rock crevices, under loose bark, in old bee burrows, and some construct external shelters of mud, cemented sand, or plant materials fastened to rocks or twigs.

In general, solitary female soil-nesting bees excavate a tunnel with individual brood cells. Each day, a new cell is excavated and provisioned with pollen; after an egg is deposited, the cell is sealed. Some solitary bees nest in close proximity and thus may appear to be colonial. Hundreds or even thousands of nests may be crowded into a small area, such as a dirt embankment or patch of soil with desirable nesting properties. Nesting sites often differ among species according to preferences for different soil textures, moisture contents, and exposures. About twenty

The larvae of *Epicauta punticollis*, a blister beetle, are predators of grasshopper eggs in the soil, while the adults feed on flowers.



percent of North American bees are cleptoparasites of other bees. Instead of building and provisioning nests, these cuckoo bees place their eggs in the nests of other bees, where their larvae kill the egg or larva of the host and consume the nest provisions. Cuckoo bees tend to parasitize the nests of one or a few related species of bees. Although they do not collect pollen, cuckoo bees visit flowers to obtain nectar. Some other insects, chiefly beeflies (Bombyliidae) and blister beetles (Meloidae), also parasitize bee nests.

Bumble bees are the most social native bees and are also most closely related to the honey bee. Spring-emergent female bumble bees (queens) establish a colony in a soil cavity (often an abandoned rodent burrow). The queen's initial progeny remain as workers to maintain the hive, which persists for a single season. The fall-winter brood emerges the following spring and disperses to found new colonies and repeat the process. The highly social European honey bee, which forms very large and long-lived colonies, is well adapted to life in coastal sage scrub. Because of its year-round activity and extreme polylecty, the honey bee is used to pollinate forty-seven of California's agricultural crops annually worth $1.5 billion. Unfortunately, honey bees also visit a wide range of native plants and usurp resources that would otherwise support native species.

Because the majority of native bees nest in soil, edaphic conditions may affect their presence in a particular area. Excess soil moisture promotes growth of fungi and other pathogens that can kill immature bees in their cells. A moist climate favors vegetation cover, which may reduce access to the soil surface and promote cooler and moister soil conditions, which in turn inhibit nesting behavior and retard development. Thus, dry and/or well drained conditions generally are more favorable for bee reproduction. Variables of soil type, slope, elevation, and exposure, which often result in differential plant community composition within coastal sage scrub, also provide a broad range of soil conditions suitable for the specific nesting requirements of many different bees.

Carnivores: Predators and Parasites

The number of predatory invertebrates in coastal sage scrub probably approximates or exceeds that of herbivores, as indicated in the dunes and transect surveys and in the surveys of arthropods on jojoba and California sagebrush discussed above. Along with general predators, there are a great many host-specific forms, which attack one or a few related species. Additionally, the different life stages (egg, larva, pupa, and adult) of insects may be specifically attacked by different predators.

General predators often wait in ambush where their prey are likely to gather. Thus, crab spiders (Thomisidae), ambush bugs (Phymatidae), assassin bugs (Reduviidae), and mantids (Mantidae) frequently occur on flowers and feed on whatever insects come their way. These relatively slow-moving predators rely on cryptic coloration to remain invisible to prey and other predators while waiting in ambush.

Some predators attack many types of prey within relatively narrow habitat parameters. Centipedes, scorpions, tarantulas, and trap-door spiders primarily prey on nocturnal soil-dwelling arthropods. Flying insects are ensnared by web-spinning spiders or captured on the wing by dragonflies (Odonata) and robber flies (Asilidae). Mobile surface predators, including jumping spiders, wolf spiders, carabid beetles, and tiger beetles, actively hunt prey.

There are many species of hunting wasps, most of which attack a narrow range of hosts (e.g. aphids, caterpillars, crickets, or spiders) to provide food for their young. Yellow jackets and paper wasps carry prey back to the nest piecemeal to feed growing larvae. Most other hunting wasps paralyze their prey with a sting and carry it intact to a nest or bury it in the soil to create a solitary brood chamber. These wasps seal the brood chamber after depositing an egg on the body of the prey; the larvae develop without any further parental care. Velvet ants (Mutillidae) and cuckoo wasps (Chrysididae) parasitize the nests of bees or other wasps.

Among the most host-specific predator-parasitoids are flies and wasps that fasten their eggs onto or inject them into their larval hosts. Unlike true parasites, which seldom kill the host, these parasitoids feed internally on the host and usually kill it. Minute wasps in the families Trichogrammatidae and Mymaridae develop inside the eggs of other insects. Somewhat larger parasitoid wasps and tachinid flies attack larvae of many insects. Sluggish and sedentary organisms, such as caterpillars and scale insects, are especially susceptible to attack and parasitism may exceed ninety percent.

Some invertebrates feed on vertebrates. The largest component of these organisms in coastal sage scrub are Diptera, particularly blood-sucking mosquitoes (Culicidae), no-see-ums (Ceratopogonidae), deer flies and horse flies (Tabanidae), and snipe flies (Rhagionidae), which generally occur near their breeding sites in water, mud, or moist soil. Bot flies (Cuterebridae, Gasterophilidae, and Oestridae) do not feed at all as adults, but their larvae live under the skin, in the digestive tract, or in the sinuses of specific mammalian hosts (primarily rabbits, wood rats, deer, cattle, and horses). Another blood-sucking insect is the kissing bug (*Triatoma protracta*), named for its South American relatives' habit of sucking blood from the lips of sleeping hosts. This insect is largely associated with wood rats (*Neotoma*) but occasionally bites people sleeping outdoors and can cause a severe allergic reaction. Ticks (specialized parasitic mites) frequently occur on the tips of low vegetation along game trails, waiting for a host to pass by. All blood-sucking arthropods are potential vectors of disease organisms.

Recyclers

The natural recyclers in coastal sage scrub include ants, termites, various beetles, many kinds of flies, millipedes, and isopods (pill bugs). Together, these organisms scavenge, devour, and recycle nutrients in dead wood, fallen leaves, fecal wastes, and animal carcasses.

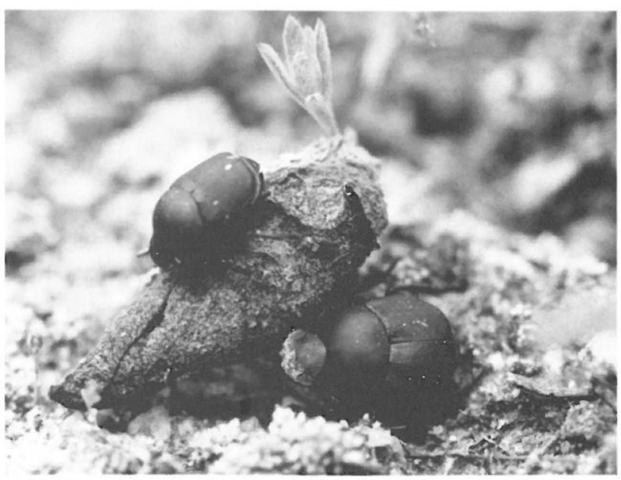
Termites (Isoptera) are especially important in breaking down cellulose, which they do with the aid of intestinal microbes. Approximately ten species of termites inhabit cismontane Southern California. The nests of subterranean species are ubiquitous, and buried wood (including dead roots) is quickly attacked. Both subterranean and dry-wood termites also attack dead wood above ground. The activities of termites and other soil- and leaf litter-dwelling invertebrates are important in building soil and maintaining its fertility by increasing the content of fine organic material and making chemical nutrients available for uptake by plants. Although fire more quickly reduces wood to its basic components, it does not affect underground plant parts and causes much of the accumulated nutrients to go up in smoke or downslope with subsequent runoff.

Many species of wood-boring beetles (chiefly in the families Anobiidae, Bostrichidae, Buprestidae, and Cerambycidae) comprise another cohort of organisms that effectively speed the breakdown of cellulose by reducing it to powder. While larvae of many wood-borers feed only on dead wood, others attack living plants, especially those weakened by disease or drought. One peculiarly specialized buprestid beetle (*Melanophila acuminata*) specifically attacks fire-killed shrubs and trees, often arriving before the partially burned vegetation has cooled.

Many scavengers dwell in leaf litter and topsoil or wander about on the soil surface. Springtails (Collembola), mostly less than one millimeter in length, feed on decaying plant matter and can be extremely abundant in winter and early spring when soil is moist. Approximately two dozen species of millipedes occurring in cismontane Southern California remain underground most of the time, but after winter rains may be found on the soil surface or under debris. These organisms also feed on decaying vegetation, can live for several years, and may achieve the largest size (five to six inches) of all local invertebrates. Perhaps the largest cohort of scavenger-recyclers in coastal sage scrub consists of true flies, many species of which feed, as larvae, on decaying animal and vegetable matter.

The larvae of June beetles, dung beetles, and their relatives (Scarabaeidae) primarily consume decaying vegetable matter (some feed on roots). The organic matter they consume is initially fermented by microbes, much like the digestive process that occurs in cattle. The C-shaped grubs of these insects live in soil, rotten logs, old leaf litter, buried feces, and back-yard compost piles.

Several beetle species in the genus *Eleodes* and their relatives (Tenebrionidae), often incorrectly referred to as stink bugs, are common and conspicuous scavengers in coastal sage scrub. These slow-moving black beetles are related to the meal worms sold in pet stores as food for lizards and fish. When disturbed, some tenebrionid beetles raise the tip of the abdomen, while lowering the head, and can exude a noxious brown fluid to deter predators. Because tenebrionid beetles are resistant to desiccation, they are well adapted to coastal sage scrub.



Tenebrionid beetles, such as these rare *Stethasida muricata* (top) and *Microshatia inaequalis* (middle), are soil surface scavengers. Dung beetles, such as this pair of *Canthon simplex* (bottom), bury animal waste and deposit their eggs in it.

Ants (Formicidae) are ubiquitous and through their diverse habits are intimately associated with the biology of many organisms in coastal sage scrub. Their tunneling and nest maintenance activities contribute to soil aeration and transport of organic nutrients to the root zones of plants. Ant foraging behavior ranges from almost entirely carnivorous in army ants (*Neivamyrmex*) to almost entirely herbivorous in harvester ants (*Pogonomyrmex* and *Messor*). Most ants are at least opportunistic predators and scavengers, feeding on dead or moribund insects and even the larger carcasses of vertebrates.

Harvester ants are often conspicuous in coastal sage scrub along trails and in patches of bare soil. Their broad conical nest entrances are often accompanied by piles of discarded seeds and chaff. The harvesting, transport, and storage of seeds by these ants aid in plant dispersal and in creation of a sequestered seed bank. Harvester ants also are an important item in the diet of horned lizards (*Phrynosoma*).

Many ant genera (e.g., *Camponotus, Crematogaster*, and *Formica*) collect nectar from flowers and honeydew secretions from aphids, scale insects, and lycaenid butterfly caterpillars. The honeydew secretions are a rich nutritional source of carbohydrates and amino acids. The presence of ants serves to protect the honeydew producers from attack by wasps and other predators.

The imported Argentine ant (*Linepithema humilis*, formerly *Iridomyrmex humilis*) is omnivorous and competitively displaces virtually all native ant species near human habitations. This species is probably the most common ant pest in homes and gardens. Because *L. humilis* needs a dependable source of moisture, it is less competitive under non-irrigated conditions and successfully invades coastal sage scrub primarily near the coast and/or adjacent to irrigated gardens.

Two groups of more-or-less omnivorous exotic invertebrates in coastal sage scrub are terrestrial isopods (sowbugs and pillbugs) and earwigs (Dermaptera). Native sowbugs and pillbugs are uncommon in coastal sage scrub, but European sowbugs (*Porcellio laevis*) and pillbugs (*Armadillidium vulgare*) are sometimes abundant, especially near human habitations. Likewise, the European earwig (*Forficula auricularia*) has been established in Southern California since the 1930s and is sometimes considered a garden pest. Because these three species require damp soil, they are frequently abundant near the coast and in association with moisture-retaining clay soils.

Coastal Sage Biodiversity Vulnerable

The invertebrate inhabitants of coastal sage scrub comprise a major portion of California's native biodiversity. The activities and interactions of these organisms support and sustain coastal sage scrub while also linking it to the larger ecosystem. The high species diversity is indicative of a specialized and resource-efficient community resulting from a long coevolutionary history. Although coastal sage scrub is well adapted to, and in some respects dependent on, the usual environmental perturbations (fire, flood, and drought), it is poorly equipped to survive invasion by foreign species. Most of the coastal sage scrub community not already denatured by human disturbance remains vulnerable to invasion by exotic pests. Without thoughtful and enlightened conservation and management practices, coastal sage scrub will become further endangered along with an increasing number of California's native species.

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