



FREMONTIA

A JOURNAL OF THE CALIFORNIA NATIVE PLANT SOCIETY



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CALIFORNIA NATIVE PLANT SOCIETY

Dedicated to the Preservation of the California Native Flora

The California Native Plant Society (CNPS) is an organization of laypersons and professionals united by an interest in the native plants of California, open to all. Its principal aims are to preserve the native flora and to add to the knowledge of members and the public at large by monitoring rare and endangered plants throughout the state; by acting to save endangered areas through publicity, persuasion, and on occasion, legal action; by providing expert testimony to government bodies; and by supporting financially and otherwise the establishment of native plant preserves. Much of this work is done by volunteers through CNPS Chapters throughout the state. The Society's educational work includes: publication of a quarterly journal, *Fremontia*, and a quarterly *Bulletin* which gives news and announcements of Society events and conservation issues. Chapters hold meetings, field trips, and plant and poster sales. Non-members are welcome to attend.

Money is provided through member dues and funds raised by chapter plant and poster sales. Additional donations, bequests, and memorial gifts from friends of the Society can assist greatly in carrying forward the work of the Society. Dues and donations are tax-deductible.

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THE COVER: Showy milkweed (*Asclepias speciosa*) with a male bumble bee (probably *Bombus vosnesenskii*) gathering nectar, common checkered beetle (probably *Tri-cbodes ornatus*) resting on flower petal, and monarch butterfly larvae (*Danaus plexippus*) foraging on leaves. Photograph by S. Sharnoff.

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INTRODUCTION

by Gordon Frankie

It is well known that insects and plants display a wide variety of highly predictable relationships, such as lepidopteran caterpillars and other larval types that feed on different parts of plants, or the many kinds of insects that gather nectar from flowers and pollinate them. Researchers have invested considerable time in field and laboratory study to elucidate the fundamental biological and ecological bases of these relationships. Presented in this special *Fremontia* issue are nine articles that reflect diverse California native insect-plant interactions and some of the interesting history behind them.

The volume can be divided into three sections. The first contains three articles concerned with common herbivorous insects and their plant hosts. The second presents four articles on bees, which are known to be the most important insect pollinator group in California and in many other regions of the world. The final section, which contains a strong sociobiological message, includes two articles which demonstrate the complexity of insect-plant relationships.

The order Lepidoptera, containing moths and butterflies, is one of the largest orders of insects. In California there are about 4,500 moth species and 260 butterfly species. In the first article, Powell characterizes the general life cycle of lepidopterans and the many patterns of use that their larvae have with native host plants. Common uses include leaf feeding, boring in fruits and seeds, and flower feeding. Most of these relationships are beneficial when viewed in the context of an ecosystem, such as the close relationship between pierid butterfly species and their mustard and legume host plants, which gave rise

to the development of the coevolution concept in the 1960s.

Insects of several orders are capable of inducing gall formation in many California native plants. In the second article, Schick examines one group of gall inducers, the cynipid wasps, which commonly form galls on California oaks. Depending on the wasp species, females carefully lay their eggs in specific plant tissue such as leaf buds, stems, flower buds, or even roots. Upon

hatching, larvae feed on plant tissue and simultaneously secrete chemicals that interact with plant compounds to produce galls that are characteristic of the wasp and plant. These complex relationships have a long evolutionary history dating back millions of years.

Some California native insects have the reputation of killing large numbers of native plants, such as bark beetles, which cause occasional die-offs of some forest tree popula-

Pale swallowtail (*Papilio eurymedon*) drinking nectar from flowers of western thistle (*Cirsium occidentale*). Photograph by L. Vorobik.



tions. Wood and Storer provide an information-packed article based on years of research that has greatly helped to characterize bark beetles and their relationships with host plants in California. Although there are 170 species of these small beetles in California, only a few of them, restricted to a few genera, are tree killers. All species provide ecosystem services through feeding activities that lead to nutrient cycling in forest succession. Results from the handful of economic species that have been intensively studied reveal many complex relationships with their hosts, each other, and other insects such as predators and parasites, fungi, and humans.

Bees are known to be the most important pollinators in many, if not most, temperate and tropical regions of the world. In recent years, the increasing evidence of global pollinator decline has motivated researchers to learn more about bees and how to conserve and protect these valuable pollinators. Articles four through seven are concerned with bees and the California plants they visit in a variety of wildland and human-altered systems.

The article by Thorp et al. begins the series on bees by providing a biological and ecological overview of the 26 species of native California bumble bees. They occur in many different habitats, but reach their greatest diversity in the northwestern part of the state. Bumble bees are considered generalists because of the wide variety of plant species they visit and also because of several behavioral and morphological adaptations that allow them to pollinate diverse flower types. Thorp et al. call attention to monitoring studies on two California bumble bees that are on the decline in the western United States. One is a candidate for federal listing. International trafficking of foreign bumble bees for pollination of hot-house tomatoes may exacerbate the decline trend in native species.

Tropical regions, in contrast to temperate areas, are well-known for their rich flora and fauna. It is becoming increasingly clear, however, that some temperate zones have diverse biota that are comparable to the tropics. Mediterranean climates, for example, often contain bee-rich areas. Messinger and Griswold provide a case history study of native bees and their host plants in a chaparral community at Pinnacles National Monument, near Hollister, where more than 500 flowering host plants provide floral resources for about 400 bee species. The authors focus on the diverse flora and various adaptations (including climatic, seasonal, annual, and responses to fire) that this group of bees displays.

Recent declines in honeybee populations in the US, which are largely attributable to mortality from parasitic mites, pathogenic diseases, and pesticides, have raised concerns about shortages of hive bees to pollinate crop plants. This is of special concern to agriculturally diverse states such as California. Kremen et al. have been working in three northern California counties since 1999 to evaluate the potential of unmanaged native bees in crop pollination. They have also recorded 192 native bee species on 41 native plant species in wild habitats that are in close proximity to agricultural crops. These researchers offer abundant evidence of important ecological relationships that exist between native bees, honeybees, California native plants, and crop pollination.

Wild areas are not the only habitats where bee pollinators are found. Frankie et al. report on a recent study of native bee diversity and ecology in residential neighborhoods of Albany and Berkeley in the San Francisco Bay Area. In addition to the relatively high diversity of native species discovered (72 plus two exotic bee species), they report that native California orna-

mental species are preferred over exotic ornamentals by a factor of four. They also offer reasons why urbanites might want to encourage bees and their host flowers in their yards.

Many California environments have been invaded by exotic plants, which have become well-established and have led to new ecological relationships with native insects and native plants. A few of these may be viewed as beneficial, but many have created new problems. In article eight, Ehler et al. describe the ecological relationships between a native pestiferous stink bug on tomatoes, the exotic weed species on which the bugs develop, and native perennial grasses in the Sacramento Valley. Their ongoing work indicates that by replacing exotic weeds with native grasses along roadsides, stink bugs can be reduced to levels that will lead to reductions in insecticides aimed at the bugs infesting tomato crops.

In the final article, Rubinoff uses three case history examples to illustrate that there are numerous unique relationships between California endemic insects, endemic plants, and the communities in which they are found. He urges more study of these relationships, and at the same time suggests that habitat conservation planning in ecosystems may be the only way to conserve many of California's unique plants and endemic insects.

REFERENCES

- Buchmann, S.L. and G.P. Nabhan. 1996. *The forgotten pollinators*. Island Press, Covelo, CA.
- Shapiro, A.M. 2002. The California urban butterfly fauna is dependent on alien plants. *Diversity and Distribution* 8:31-40.
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Aposematic butterfly caterpillars rendered distasteful to vertebrate predators by the chemistry of their host plants. Pipevine swallowtail larva (*Battus philenor*, Papilionidae), on *Aristolochia* (pipevine). See discussion on pages 13 and 14. All photographs except Figure 9 by J.A. Powell.

LEPIDOPTERAN CATERPILLARS FEEDING ON CALIFORNIA NATIVE PLANTS

by Jerry A. Powell

Moths and butterflies and their caterpillars (Order Lepidoptera) are among the most familiar insects in both urban and rural habitats. In terms of species richness, this is the second or third largest order of insects, with more than 150,000 described species, about one-tenth of which live in North America.

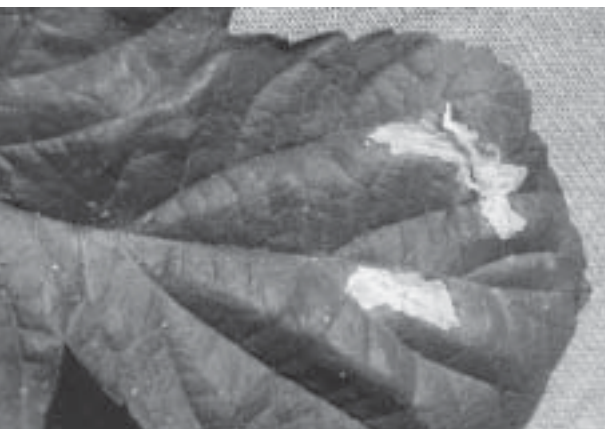
The caterpillars (larvae) of the vast majority of species feed on living plants and are the most diverse group of animals that depend on

plants. Only a few are serious pests, as defoliators of forest trees, causing damage to agricultural fruit and vegetable crops, and invading stored products. Contrary to common belief, most Lepidoptera are beneficial and fulfill a wide range of services in ecosystems. These include acting as pollinators, providing important food sources for birds, bats, rodents, and lizards, and assisting in nutrient recycling by feeding on dead leaves, rotting wood, and fungi.

We do not have an accurate es-

timate of the number of species of Lepidoptera in California, but there are more than 3,500 named and described, and many smaller species have yet to be classified. Butterflies are among the most beautiful and admired insects, but in diversity they are vastly outnumbered by moths. There are about 260 species of butterflies and probably at least 4,500 species of moths in California.

Our knowledge of larvae and life histories is very incomplete. There is some information on host plants



for perhaps 60–70% of the described species, but often it is limited to one larval collection or a single population. As is true of all insects with complete metamorphosis (those going through egg, larva, pupa, and adult stages), all growth occurs during larval feeding, with successive stages (instars) molting to shed the outgrown skin (exoskeleton) and head capsule, usually four or five times. Adults of most species feed on nutritive sources such as nectar from flowers, rotting fruit, and bird droppings, but they do not grow. Thus caterpillars are the culprits responsible for damaging plants.

LIFE CYCLE

In a typical life cycle of moth or butterfly, adults mate soon after emergence of the female from the pupa (which is termed the chrysalis in butterflies). She selects plants on which larvae will feed and deposits eggs, singly or in masses, depending upon the species. First instar larvae hatch after seven to ten days incubation and begin to eat the plant or other food material. Sometimes larvae begin feeding after migration to appropriate sites, such as the new leaves at the growing terminals. Larval feeding and growth requires 35–50 days in most species.

At maturity the caterpillar prepares a pupation site in the host plant material or in leaf litter or soil. Skipper butterfly caterpillars and those of most moths construct a cocoon made of silk that they produce from glands under the head. Most other butterfly and some moth larvae pupate without a cocoon, either exposed directly to the air or in cells in the ground. Transformation into an adult occurs in as little as 10–14 days, and the moth or butterfly then breaks the pupal shell to hatch. Emergence often occurs via a special track or aperture prepared by the larva, which enables the adult to escape from the substrate.

At any of these stages—egg, larva (often first or last instar), pupa, or adult—there may be a period of lengthy delay, called diapause, in

Figures 1-5: Leaf mines of microlepidopteran larvae. 1, *Stigmella variella* (Nepticulidae) (top left) on *Quercus agrifolia* (coast live oak). • 2, *Tischeria splendida* (Tischeriidae) (second from top left) on *Rubus ursinus* (blackberry). • 3, *Coprodiscia arbutiella* (Heliozelidae) (second from bottom left) on *Arctostaphylos* (manzanita). • *Gracillariidae*: 4, *Cameraria nemoris* (bottom left) on *Vaccinium ovatum* (California huckleberry). • 5, *Marmara opuntella* on *Opuntia* (cactus) (bottom). • 6, *Caloptilia reticulata* (F) adult (below), a leaf miner on *Q. agrifolia* in early instars.



which metabolic development is postponed. This allows the insect to avoid seasons when necessary resources are not available. Diapause has been the key to the enormous evolutionary success of Lepidoptera and other plant-feeding insects in temperate zones characterized by harsh winters, and in arid regions and tropical areas of seasonal drought.

The challenge to California insects of surviving both the dry season and winter is met by a variety of life cycle strategies. Larval feeding by most species takes place during spring foliation. Development in many proceeds to the emergence of adults in late spring. Some then produce eggs that enter diapause. Instead, larvae may also diapause as first instars, or adults may enter a reproductive diapause and hibernate. Doing so delays mating and egg-laying until late winter or early spring just before foliation begins.

Some species continue to develop and produce a second generation, with adults flying again in the fall. Alternatively, many spring-feeding species enter diapause as last instar larvae or pupae. They wait until late winter to resume development, timing their emergence with the budding of the host plants. Other species pass the summer as prepupal larvae or pupae, metamorphose, and fly in the fall. Then they produce eggs that diapause, or the adults hibernate.

Initiation of diapause and onset of development when diapause ends usually is controlled by day-length and temperature changes with the seasons. Remarkably, many species can hold over for one or more years as an adaptation to inconsistent larval food sources. Examples are seed feeders associated with conifers that produce cone crops erratically or in alternate years, and desert species whose host plants appear sporadically in response to rainfall. Diapause may last 5 or 6 years in such species, and successful development

has been recorded after 20, 25, and even 30 years in one species of yucca moth in experimental conditions. This suggests the potential of some species to survive many years of drought, analogous to seed banks of annual plants.

PATTERNS OF HOST PLANT USE

Almost all native plant species are fed upon by caterpillars, at least occasionally, and host selection is not random. There are guilds of species that specialize on grasses, sedges, and other monocots, or on conifers. However, perennial angiosperms serve as hosts for the overwhelming majority of moths and butterflies. Few species specialize on annual plants. In general, trees host the greatest diversity of caterpillars, followed by woody shrubs of high architecture, then low shrubs, perennial herbaceous plants, monocots, and annual dicots.

Patterns of host acceptance and specificity vary widely among Lepidoptera, and inherited instincts dictate host plant recognition by egg-laying females and acceptance of foods by caterpillars. Commonly a given species is restricted to a few hosts within one plant family or genus, and chemical similarities among plants presumably underlie such specialization. Thus, specialist larvae reject any but the “right” host, sometimes even closely-related plant species, and in the lab will not accept a synthetic diet that is nutritionally sufficient for development of many other species.

“Microlepidoptera” is not a formal taxon; it is a nickname applied to the more ancestral lineages and superfamilies in which most of the species are tiny moths, 2–10 millimeters in length. Microlepidoptera larvae are mostly concealed feeders. They may be leaf miners, borers in stems, roots, and seed, or they may feed externally but con-



Figures 7-9: Case-bearing larvae. 7, *Adela septentrionella* (Adelidae) (top), which feeds on fallen leaves under *Holodiscus* (oceanspray). • 8, *Thyridopteryx meadii* (Psychidae) (middle) on *Larrea* (creosote bush). • 9, *Coleophora* species (Coleophoridae) (bottom) on *Baccharis pilularis* (coyote brush). Photograph by R. Coville.

struct shelters with silk in the foliage.

Although a few are generalists, the great majority are relatively host-specific—confined to a single plant species in some instances (such as leaf miners), or several within one genus. By contrast, larger moths,

the so-called “macrolepidoptera” or “macro moths,” are nearly all external feeders, and many—perhaps half the species in North America—feed on several or many unrelated plants. Butterfly species in general tend to be host plant specialists, in contrast to macro moths.

Superimposed on the mosaic of differing host plant preferences, the resources of any given plant community are partitioned through the use of specialized niches within each plant species. This is accomplished by behavioral and often morphological adaptations. Some caterpillars feed as miners in leaves. Others bore into roots, stems, or seeds,

Figures 10-14: Root and stem borers, including plant gall feeders (below and opposite page). 10, Wasp moth, *Carmenta* species (Sesiidae) adult and its pupal shell (below) protruding from root of *Solanum* (nightshade) from Puebla, Mexico. • 11, Pitch nodule produced around stem-boring larva of *Petrova metallica* (Tortricidae) (bottom) on *Pinus contorta* (lodgepole pine).



sometimes causing the plant to create galls of a particular form in which the larva resides. Still others make portable cases from which they feed, using silk and plant fragments or other debris.

External feeders also usually restrict their feeding to particular parts of the plant: new terminals, old leaves, inflorescences, fruit, and so on. As result, a local flora consisting of 350 plant species will have more than twice that number of Lepidoptera species dependent on it.

LEAF AND STEM MINERS

Several families of Lepidoptera are characterized by leaf mining habits, in which larvae spend early instars or their entire life feeding within a leaf. Usually the species of each genus form mines of a particular depth, often in either the upper or lower half of the leaf, or just under the epidermis. Mines are excavated in linear and serpentine forms, or blotch-like and full-depth in the new and not yet hardened leaves.

Experienced lepidopterists can identify the mine to the genus level, and most are host specific, so the presence of leaf mining species can be ascertained throughout the season, long after the insect is gone. Some species are subcuticular sap feeders as stem miners or can move from one leaf to another via a stem mine.

With few exceptions, mines in woody plants in California are lepidopterous, whereas those in herbs are caused by members of the order Diptera (two-winged flies). Other regions, such as the southeastern US and the tropics, have rich faunas of leaf-mining beetles (Coleoptera) and sawflies (Hymenoptera), but those specialized groups are poorly represented in California.

Typical leaf miners include *Stigmella* (Nepticulidae) (Figure 1, page 6), our tiniest moths, with a forewing length of 2–3 millimeters. Their larvae create serpentine mines in the upper part of the leaf of many shrubs, such as *Rhamnus* (coffeeberry), *Heteromeles* (toyon), and *Toxicodendron* (poison oak), and trees including *Quercus* (oak), *Salix* (willow), and *Alnus* (alder). At maturity the larva cuts a slit at the enlarged end of the mine and drops to the ground for cocoon formation. Most *Stigmella* species are unnamed, and some are known only from the abandoned mines.

Tischeria (Tischeriidae) make short, trumpet-shaped mines (Figure 2, page 6) that are densely lined with silk, causing a whitish appearance even when still occupied. Although fewer than nepticulids, they occur in many shrubs and trees, as diverse as *Malvella leprosa* (alkali mallow), *Rubus* (blackberry), *Ceanothus*, and *Quercus*.

Members of the superfamily Incurvarioidea insert their eggs by piercing plant tissues with a saw-like ovipositor. Most oviposit into young seed, but species of the family Heliozelidae are leaf miners. Larvae of *Coptodisca* leave characteristic oval holes by cutting out disks from the upper and lower epidermis after completion of the mine (Figure 3, page 6) and use them to construct a portable case in which they pupate. Sometimes they are conspicuous by their numbers, with many mines per leaf on *Salix* (willow), *Arbutus* (madrone), *Arctostaphylos* (manzanita), and *Quercus* (oak).

The family Gracillariidae contains the greatest diversity of lepidopterous leaf miners. There are about 150 species known in California, with some remarkable differences in larval biologies. All are miners, and larvae of most species change to a different form in one or more late instars. For instance, *Cameraria* begin as flattened larvae that form blotch mines beneath the upper side epidermis. In the last instar they become cylindrical caterpillars, and use silk to buckle the mine roof, creating a tent-like space in which they pupate (Figure 4, page 6). Species of a sister genus, *Phyllornorycter*, often using the same host plant, make similar mines—usually inside the lower epidermis—and do not change their body form. Species of both genera occur on a wide variety of shrubs and trees, including oaks, willow, Caprifoliaceae (honeysuckle and snowberry), madrone, *Gaultheria shallon* (salal) and other Ericaceae, and various Rosaceae. Members of the similar genus *Cremastobombycia* make bloated blotches in the leaves of *Baccharis pilularis* (coyote brush), *Artemisia douglasiana* (mugwort), *Isocoma* and *Hazardia* (goldenbush), and related plants.

Marmara larvae are extremely modified, with flattened head and mandibles and are sap-feeders just under the cuticle, creating very long, convoluted mine tracks that gradually enlarge (Figure 5, page 6). They occur on broad-leaved plants such as *Arbutus*, in stems of *Opuntia* cactus, *Rubus* (blackberry), *Ceanothus*, and other plants.

Species of *Caloptilia* (Figure 6, page 6) mine in early instars, then change form, emerge, and form an external shelter by folding a leaf tip in a characteristic manner, within which they graze. After completing growth, the larva leaves to pupate in a silken hammock constructed nearby. *Caloptilia* are host specific and occur on many kinds of trees and shrubs, including *Acer* (maple), *Quercus*, *Salix*, *Toxicodendron*, and

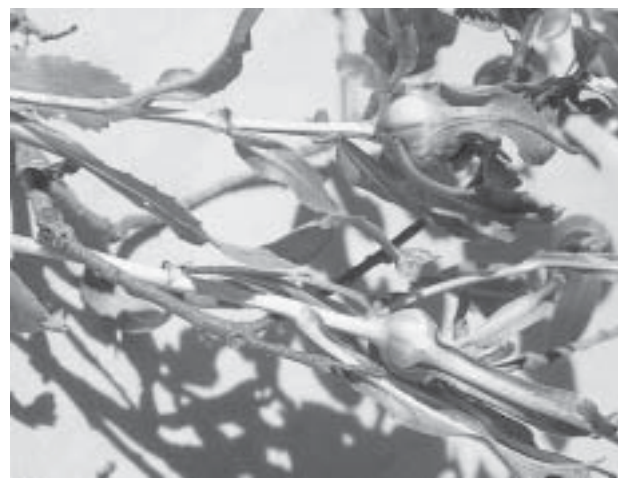
Umbellularia (California bay). An introduced European species lives on garden azaleas.

Elachistid moths specialize as monocot miners. Nearly all *Elachista* form linear mines in grass blades, while a few species in other genera make blotch mines in plants of the Caprifoliaceae (*Lonicera* and *Symphoricarpos*), or Hydrophyllaceae (*Eriodictyon* and *Phacelia*). About 40 species are recorded in California, of which 26 have been named in the past several years, so it is likely that many more remain to be discovered. They are poorly known because the mines are inconspicuous, and because the adults fly at sundown and dawn (they are not often attracted to lights), thus avoiding most collectors.

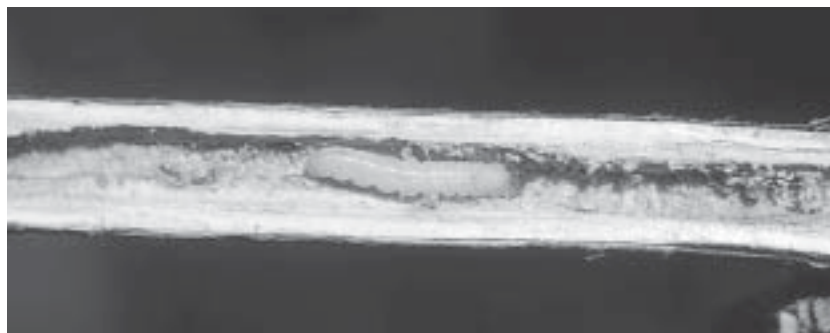
CASE-BEARERS

Some caterpillars make portable cases from which they feed. This behavior evidently has originated several times, since it occurs both in primitive moths (superfamily Incurvarioidea) and in evolutionarily more recent groups (Tineoidea and Gelechioidea). Early instar larvae of Adelidae (long-horned fairy moths) leave the developing seed where the eggs were inserted, form portable cases of silk covered with debris (Figure 7, page 7), and feed on fallen leaves. California species include specialists on *Linanthus*, *Castilleja* or *Orthocarpus* (owl's clover), *Platystemon* (cream cups), *Gilia capitata*, and *Holodiscus* (oceanspray).

Psychidae are called “bag-worms” because most species construct sack-like cases covered with



12, Woody stem gall induced by *Gnorimoschema baccharisella* (Gelechiidae) on *Baccharis pilularis* (coyote brush) (top). • 13, Soft-stem galls caused by *G. grindehiae* on *Grindelia birsutula* (gumplant) (middle). • 14, Adult of *Epiblema rudei* (Tortricidae) and its pupal shell protruding from stem gall on *Gutierrezia* (matchweed) (bottom).



Figures 15 and 16: Inflorescence-feeders. 15, Stem-boring caterpillar of *Grapholita edwardsiana* (Tortricidae) (above) on *Lupinus arboreus* (bush lupine). • 16, *Tegeticula maculata* (Prodoxidae) pollen-carrying female (left) depositing an egg in flower of *Yucca whipplei* (our lords candle).

fragments of the host plant, such as grass, sticks, or leaves. The family is diverse in the southeastern US, but only a few species are known in California. *Hyaloscotes fumosa* in the Sierra Nevada has been recorded feeding on *Purshia* (antelope brush) and *Arctostaphylos*. Most psychids are general feeders, but *Thyridopteryx meadii* in the Mojave Desert is host-specific on *Larrea* (creosote bush) (Figure 8, page 7). An introduced European species, *Apterona helix*, which appeared in El Dorado County in 1950, has spread widely through the Sierra Nevada and eastward, feeding on numerous low-growing plants such as *Wyethia* (mules ears), in cases that resemble miniature snail shells covered with mud. Its spread is remarkable because the population is entirely parthenogenic (reproduces without males) and flightless; the larviform females oviposit in their larval cases, and dispersal occurs by wind-blown first instar larvae on silken strands.

Coleophoridae make up the largest group of case-bearers; 1,000 species are estimated for North America, 85% of them unnamed, and there are probably 200–300 in California. The cases are highly variable in form, cigar-shaped (Figure 9, page 7), slender and curved,

bundled stacks of leaf or flower bits, and so on. The larva mines from the attached case as far as it can reach, then moves to a new site, leaving a series of characteristic circular mines with a round hole off-center.

They are host-specific on a variety of angiosperms, including *Alnus*, *Aster*, *Baccharis*, and other Asteraceae, and in the inflorescences of *Lotus*, *Grindelia*, sedges, and other plants. Typically the case is enlarged basally as the larva grows, in the manner of mollusk shells. However, *Coleophora glaucella* mines leaves of *Arctostaphylos* and makes its cases by cutting out linear pieces of upper and lower epidermis, replacing them with successively larger ones during growth.

ROOT AND STEM BORERS

Many moth larvae live entirely inside roots or stems. The primitive ghost moths (Hepialidae) are large but broadcast tiny spherical eggs in appropriate habitats. Larvae enter the ground and feed on roots externally, or burrow into them and continue up into the larger basal branches of coastal bush lupines and other plants. Goat moths (Cossidae) are similarly robust, and their larvae bore into root crowns of woody shrubs such as *Suaeda* (alkali blite) in the Central Valley, or feed in larger limbs in trees weak-

ened by bacterial cankers or other damage.

Sesiid moths (Figure 10, page 8) are day-flying and colorful, resembling wasps and bees with mostly transparent wings. There are about 30 species in California, all of them specific feeders on particular plants. The larvae bore in root crowns of Asteraceae, *Eriogonum* (buckwheats), bark of conifers, stems of blackberries, and many other hosts.

Many Tortricidae, especially *Eucosma* and *Phaneta* with more than 120 species in California, are root and root crown borers, mostly in woody Asteraceae (*Chrysobamnus*, *Gutierrezia*, *Isocoma*, etc.). Some *Phaneta* bore into buds or terminal twigs of herbaceous perennials (*Artemisia*, *Eriophyllum*, *Gnaphalium*), as do *Rhyacionia* in pines. Larvae of *Petrova* feed in terminal branches of pines and other conifers, creating a nodule of pitch and frass (insect excrement) around themselves (Figure 11, page 8).

PLANT GALL FEEDERS

Galls are a specialized kind of reaction by plants to wounding caused by the presence of insect larvae, which results in a species-specific form of enlargement of a leaf or stem. Larvae of gall-inducing species live in the galls, feeding

on the continually growing tissue. Most galls are caused by “gall midges” (Diptera, Cecidomyiidae), on herbaceous and woody plants, such as the amorphous tip galls of *Baccharis pilularis*. Next most numerous are galls caused by cynipid wasps (Hymenoptera), primarily on *Quercus* and Rosaceae. Gall induction by lepidopterans is less common but has evolved several times in unrelated superfamilies.

In California gall induction by Lepidoptera is most prevalent in Gelechioidea, in the families Cosmopterigidae, Momphidae, and Gelechiidae. Species of *Mompha* cause several different forms of tip and stem galls on *Epilobium canum* (California fuchsia), while other *Mompha* bore into growing tips or stems without gall induction in *Epilobium* (fireweed), *Oenothera* (evening primrose), and other

Onagraceae. *Stagmatophora* (Cosmopterigidae) induce gall-like swellings in stems or roots of *Trichostema* (bluecurls and turpentine weed).

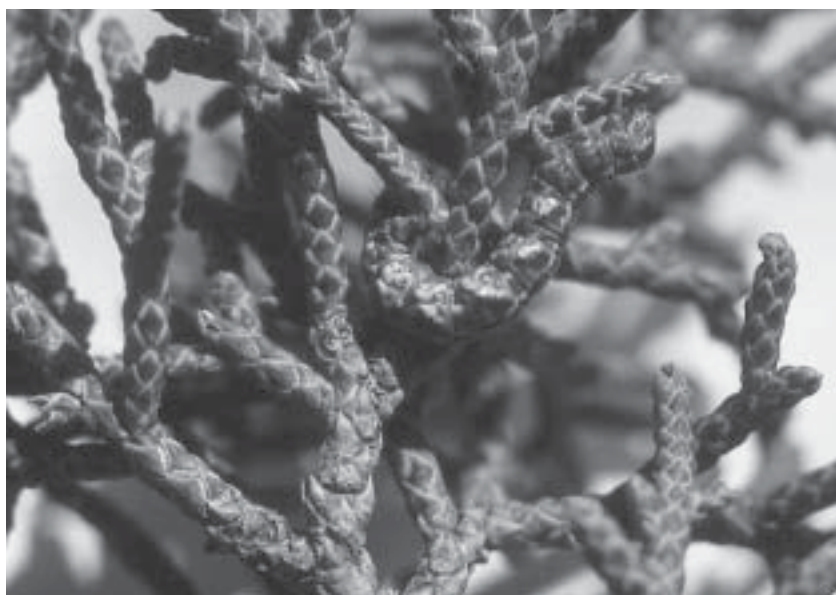
Some members of *Gnorimoschema* (Gelechiidae) cause tip or stem galls in Asteraceae (*Aster*, *Baccharis*, *Ericameria*, *Grindelia*, *Isocoma*) (Figures 12, 13, page 9), whereas other *Gnorimoschema* feed as leaf miners or externally on buried leaves of *Ambrosia* and other plants in active sand dunes. Several tortricid moths in the genus *Epiblema* also cause stem galls in Asteraceae (e.g., in rhizomatous stems of *Ambrosia*, or woody stems of *Gutierrezia*) (Figure 14, page 9).

A few species are regular intruders (called inquilines) in galls caused by other insects. Thus *Cydia latiferreana* (Tortricidae) feeds in “oak apple” galls, such as on *Quercus lobata* (valley oak), which are caused by cynipid wasps, while larvae of *Batrachedra* (Coleophoridae) eat the contents of the red willow leaf galls induced by a sawfly (Hymenoptera, Tenthredinidae), moving from gall to gall as they are depleted.

INFLORESCENCE-FEEDERS

Many lepidopteran caterpillars eat flowers preferentially when available, such as generalist “woolly bears,” which are the caterpillars of tiger moths (Arctiidae) that feed on low-growing annuals. Others are specialist feeders in inflorescences. Examples include a suite of *Ethmia* species (Ethmiidae) that fly in early spring and depend upon flowers and young seed of annual borages (*Am-sinckia*, *Cryptantha*) and a scroph, *Collinsia heterophylla* (Chinese houses). This food source is more reliable than foliage during poor rainfall years. Related ethmiid species feed on leaves of hydrophylls (*Eriodictyon*, *Phacelia*) later in spring or summer.

Figures 17 and 18: External feeding caterpillars of macro moths. Camouflage coloration in *Juniperus*-feeding caterpillars. 17, an unidentified inchworm (Geometridae) (below). 18, *Abagrotis mirabilis* (Noctuidae) (bottom); there are similarly patterned caterpillars of several other families, characteristic of Cupressaceae-feeders.





Figures 19-22: External feeding caterpillars of macro moths (this page and facing). 19, Trash-carrying inchworm, *Synchlora* species (Geometridae) (top), adorned with fragments of its host flower, *Helenium* (sneezeweed) from Virginia. • 21, Larva with urticating spines, *Hemileuca eglanterina* (Saturniidae) (bottom), a generalist feeder.

Larvae of one species of *Grapholita* (Tortricidae) specialize in flowers of perennial *Lupinus*, while other *Grapholita* feed on the seed of *Lupinus* and other legumes, or burrow in the inflorescence scape (Figure 15, page 10). Larvae of the related genus *Cydia* mostly are seed feeders, including the notorious codling moth, the “worm” in apples, and the Mexican “jumping bean,” which is a carpel of a *Croton* (Euphorbiaceae) that hops about when warmed, caused by quick movements of the larva inside it. Several species of *Cydia* infest pine cones in California. Seed capsules

of legumes are a rich resource for insect larvae, and *Astragalus* (locoweed) is particularly favored, with at least three common species of pyralid moths (*Etiella*, *Pima*), a butterfly (Lycaenidae, *Everes*), and *Grapholita vitrana* all boarding there.

The most celebrated instances of obligate seed-feeding and plant-insect mutualism are species of *Tegeticula* (Prodoxidae), females of which have specialized mouthparts used to gather pollen of *Yucca*, which they purposefully transfer to the stamens after they oviposit into the flower’s ovary.

Tegeticula females (Figure 16, page 10) deposit only a few eggs per flower, probably regulated by a pheromone signal to sisters, and the resulting larvae eat only a portion of the seeds. Caterpillars of the related genera *Prodoxus*, *Agavenema*, and *Mesepiola* burrow in sterile tissues of capsules and stalks of *Yucca*, *Agave*, and *Nolina* respectively, with three *Prodoxus* species partitioning the niche in *Y. whipplei* in California.

EXTERNAL FEEDING CATERPILLARS

Leaf miners, case-bearers, root and stem borers, including gall inducers, are estimated to comprise about 15% of described North American Lepidoptera, a proportion that will rise appreciably when microlepidoptera are better classified and cataloged. Larvae of the remainder feed externally. About 40% of these are microlepidoptera that live concealed, usually in shelters constructed by tying leaves or other plant parts together with silk.

Typically, concealed feeding caterpillars are small, green or brownish, with little or no integumental pattern other than a dark head. They feed within or forage outward from the shelter, often at night, and are most easily detected

by the misshapen foliage. Large numbers of species in several families (e.g., Oecophoridae *sensu lato*, Gelechiidae, Plutellidae, Tortricidae) feed in this manner, usually as host plant specialists, on an enormous array of conifers, dicots, and monocots, including virtually every perennial plant.

Larger moths and butterfly caterpillars, by contrast, mostly feed exposed. They depend on an amazing array of cryptic forms, colors, and behavior to elude predators. Often the highly cryptic caterpillars remain exposed when at rest, exactly matching foliage colors (Figures 17 and 18, page 11). Some are covered with brown patches that resemble necrotic spots of leaves. The “trash-carrying” species are covered with flower fragments attached by hooked setae on their backs (Figure 19, left). Others stand erect mimicking a twig (Figure 20, page 13).

Many less cryptic caterpillars feed only at night, thus avoiding heat, desiccation, and daytime predators. Still others are protected by modified hairs or spines that discharge urticating chemicals that can cause respiratory inflammation or skin rash in humans, for example, caterpillars of Californian buck moths (Saturniidae, *Hemileuca*) (Figure 21, left). Species in several moth families protect themselves by constructing communal shelters of dense silk, e.g., tent moth caterpillars, Lasiocampidae (Figure 22, page 13), from which they forage and derive protection from climatic variables. Finally, caterpillars of some species do not hide but are protected by toxic chemicals they sequester from the plants they eat.

GENERALISTS OR SPECIALISTS?

Leaf miners and root or stem borers, especially those that cause galls, usually are highly specific, of-

ten restricted to one or a few closely-related species. Concealed feeders often feed on several plant species or genera, and there is no precise definition of host plant specialist versus generalist. Students of plant-insect relations sometimes refer to all species that feed on unrelated plants as polyphagous (eating many), but in reality the situation is more complex.

Some species feed on an array of angiosperms, or conifers, some even on both, but rarely does their diet include monocots, which mainly serve specialists with modified mandibles. The *Argyrotaenia franciscana* complex (Tortricidae) in coastal California is a good example; larvae have been found on a vast array of angiosperms, both woody and herbaceous, native and exotic, and occasionally on conifers. Even within populations, *A. franciscana* is polyphagous, recorded on 24 species of plants in 15 families at the UC Big Creek Reserve in Monterey County. These include *Sequoia* (coast redwood), *Cupressus macrocarpa* (Monterey cypress), and the succulents, *Sedum* (stonecrop) and *Dudleya*, feeding in the inflorescences. On San Miguel Island, *A. franciscana insulana* larvae have been found on 22 species, which is 10% of the flora, but not on monocots.

A common pattern for tree- and shrub-feeding macro moth caterpillars (Geometridae, Noctuidae, etc.) is use by individual species of unrelated families, including Betulaceae, Fagaceae, Rosaceae, and Salicaceae, but not non-toxic herbaceous plants. Alternatively, polyphagy may vary spatially or temporally. Some species, such as certain silk moths (Saturniidae) and sphinx moths (Sphingidae), are generalists over their broad ranges but specialists at any one locality or in a particular season. For example, the giant silk moth *Hyalophora euryalus*, in California, sometimes called the “ceanothus silk moth,” shows strong preference for Rhamnaceae in many

populations, but in others it selects willow or even Douglas-fir.

Many different plant families have evolved natural plant chemicals that typically are repellent to vertebrates and to non-adapted insects. As a result, even the broadest spectrum generalists do not feed on all kinds of plants. For example, Brassicaceae (mustards) harbor specialist guilds of Lepidoptera (plutellid moths and pierid butterflies), but rarely are used by polyphagous species. Fabaceae (legumes) serve as hosts for many Lepidoptera, especially the seeds, but general feeders are deterred.

Many macro moth and butterfly specialists feed on plants characterized by toxic chemicals that render them distasteful or eremetic to vertebrate predators, which learn to recognize the bright (aposematic) colors of these insects. This has led

to the evolution of complex “model-mimic” associations among insects, especially in tropical regions. The pipevine family, Aristolochiaceae, provides a classic example. Swallowtail butterflies of several genera have adapted to its chemicals, represented in California by the beautiful blue and orange-spotted pipevine swallowtail, *Battus philenor*. Caterpillars and adults of this



22, Tent moth larvae of *Malacosoma californicum* (Lasiocampidae) (top) on *Quercus agrifolia* (coast live oak). • 20, Stick-like larva of *Synaxis truxaliata* (Geometridae) (bottom) on *Baccharis pilularis* (coyote brush).

species are distasteful to birds and advertise their presence by their distinctive aposematic color pattern (photograph, page 5). Several non-toxic nymphalid butterfly species have evolved resemblance to the color pattern of *Battus*, including species of *Limenitis* that feed on willows, females of *Speyeria diana* (Diana fritillary), a *Viola* feeder, as well as some females of yellow swallowtail butterflies.

Numerous chemically dissimilar plants have evolved secretory canals containing latex or resin, and discharge viscous, often toxic, "milky" fluids when cut by herbivores. Caterpillars in several families overcome this by severing the canal basally on the leaf, thus lowering the fluid pres-

sure before feeding. One example in California is *Apocynum* (dogbane), eaten by a pyraloid moth (*Saucrobotys futilalis*). Another is *Asclepias* (milkweed) eaten by specialized arctiid moths (*Euchaetes*) and danaid butterflies (monarchs and queens) (Figure 23, below), which have willow-feeding mimics (*Limenitis*, Nymphalidae). Some members of the plant families Convolvulaceae, Euphorbiaceae, and Asteraceae similarly produce repellent milky toxins that serve as the basis for specialization and speciation in Lepidoptera, while remaining free of generalist caterpillars.

Indeed, the close association between pierid butterfly species and their mustard and legume host

plants helped lead Paul Erhlich and Peter Raven in the 1960s to propose the concept of coevolution. The butterfly acting as parasite induces changes in plant chemistry, leading to reciprocal adaptations in a step-wise fashion. The term, however, over time has been applied to a much broader array of relationships, diminishing its usefulness.

In any event, the study of interrelations between plants and their caterpillars is a fascinating and fertile field for investigation. We are still a long way from answering most of the questions raised by our current store of knowledge.

ACKNOWLEDGMENTS

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REFERENCES

- Ehrlich, P.R. and P. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- Jermey, T. and A. Szenti, eds. 1991. *Insects and plants*. S.P. Bakker Academic Publications, The Hague, The Netherlands.
- Powell, J.A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7:10–15.
- Powell, J.A., C. Mitter, and B. Farrell. 1999. Evolution of larval feeding preferences in Lepidoptera. In *Lepidoptera, Moths and Butterflies*, ed. N.P. Kristensen, 403–422. Vol. 1 of *Evolution, Systematics, and Biogeography. Handbook of Zoology*, Vol. 4 of *Arthropoda: Insecta*, Part 35. W. de Gruyter, Berlin and New York.
- Stamp, N.E. and T. Casey, eds. 1993. *Ecological and evolutionary constraints on caterpillars*. Chapman and Hall, New York.

Figure 23. Aposematic butterfly caterpillars rendered distasteful to vertebrate predators by the chemistry of their host plants. *Danaus plexippus* (monarch butterfly) is shown here on *Asclepias fascicularis* (narrow-leaf milkweed).



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Oak apple gall (*Andricus quercuscalifornicus*) on valley oak (*Quercus lobata*). Photograph by K. Schick.

CYNIPID-INDUCED GALLS AND CALIFORNIA OAKS

by Katherine N. Schick

Watching a tiny female *Andricus fullawayi* wasp through a magnifying glass, I am amazed at the amount of time she spends carefully grooming her wings and antennae with the special combs on her front legs. As I wait anxiously to see where she will fly to lay her eggs, she crawls awkwardly, brushing her antennae against the twig to test its odors. She takes her time. More than 20 minutes elapse after I release her from the rearing container before she finally becomes airborne.

Suddenly, a gust of wind sweeps the tiny wasp into the branches of a nearby valley oak (*Quercus lobata*) and she is lost to sight. I wonder where this tiny creature is going, and whether her offspring will develop within a gall on the stem, leaf, flower, or root of an oak tree.

Like many other cynipid wasps, this tiny, ungainly female is smaller than this typeset number "1," yet she and other gall wasps have managed to colonize every native oak tree species in California. They trick their host trees into forming strik-

ing plant growths called galls, filled with nutritive tissues. The galls provide food and shelter for the developing larvae of the wasps.

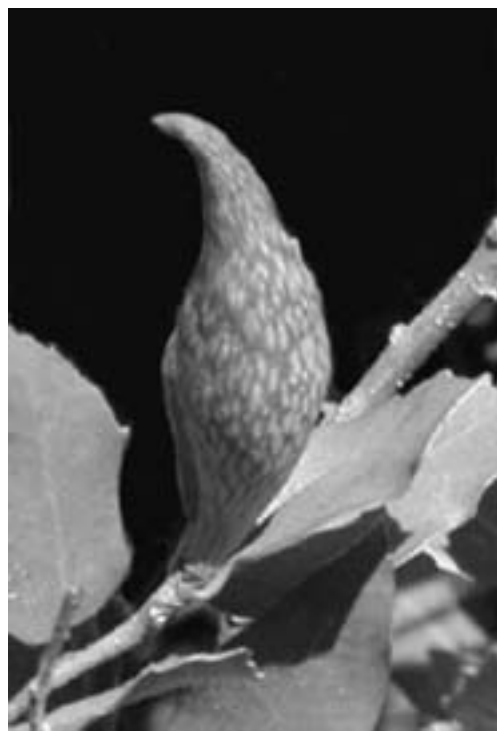
Oak gall wasps are members of the insect order Hymenoptera, family Cynipidae, and tribe Cynipini. Unlike bees, ants, and stinging wasps, in which the ovipositor has evolved into a stinger, cynipid wasps have retained ovipositors with which they can carefully position their eggs inside plant tissues without harming any plant cells.

The most primitive living

relatives of modern cynipid wasps use their long ovipositors to lay eggs into the larvae of wood-boring wasps and beetles, much as their earliest ancestors probably did. From such primitive ancestors two modern families of wasps evolved: Figitidae, which parasitize the larvae of flies, lacewings, and other wasps; and Cynipidae.

Apparently early in their evolu-

Wasp of *Andricus quercuscalifornicus* (top) on gall. • Spindle gall (bottom), unisexual generation of *Heteroecus paci-ficus*, on *Quercus vaccinifolia* (huckleberry oak). Photographs by K. Schick.



tionary history, ancestors of cynipid wasps began to skip the insect host and consume plant tissue directly through gall induction. The oldest known fossil cynipid galls, approximately 115 million years old, are found in Cretaceous deposits.

Regular readers of *Fremontia* will be familiar with some of the exotic and bizarre shapes of modern cynipid galls on blue oak (*Quercus douglasii*) from the excellent photographs in an article over a decade ago by Russo (1990). Each species of cynipid wasp induces its oak host to form a unique shape of gall. While many other gall-inducing insects, such as tenthrinid wasps, inject chemicals into plant tissue along with their eggs so that gall formation begins before larvae emerge, gall induction in Cynipidae begins in response to chemicals secreted by growing wasp larvae.

Cynipid galls are more complex than galls of many other insects. They contain several tissue layers and a separate central chamber for the developing larva. Cynipid larvae complete their development by becoming pupae and then adults before they emerge from their galls to lay eggs for the next generation.

Galls may contain a single larva, as do those of the jumping gall *Neuroteras saltatorius*, a tiny spherical structure about the size of this “o” which forms on the underside of oak leaves. These tan-colored galls hop up and down under *Quercus lobata* oaks from June through August in the Central Valley of California. The dropping galls jump around for a while after they fall from the leaves, eventually maneuvering themselves into crevices in the ground where they will endure the winter, and from which the adult females will emerge in early spring.

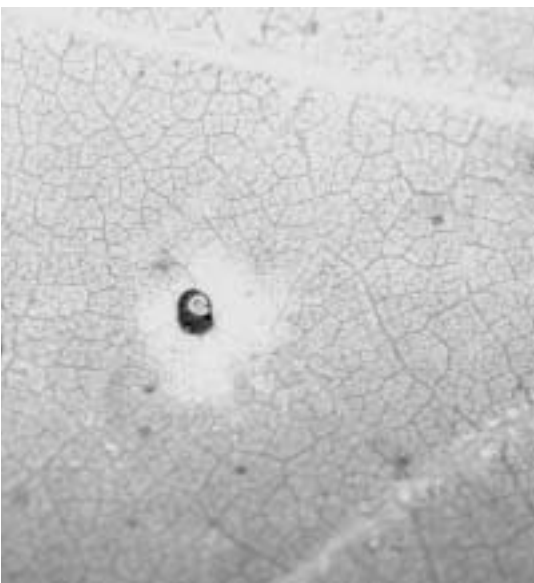
Other cynipid galls may contain more than one larva such as the large “oak apple” gall induced on *Quercus lobata* by the wasp *Andricus quercuscalifornicus* (see photograph, page 15). This stem gall

gets as big as a baseball and may contain as many as 16 developing larvae. The galls generally start forming in early spring and grow into round green spheres that resemble juicy green apples, even to the point of developing a reddish blush when they mature. The color quickly fades and the drying galls turn beige during the summer. The wasps within finish pupation and emerge as adults in autumn, leaving the gall behind on the tree. After the first year, old galls turn black, covered in sooty mold.

ALTERNATION OF GENERATIONS

Distinctly different galls—often on different parts of the host tree—are produced not only by different wasp species, but also by different generations of the same cynipid species. Most cynipid species in the oak-galling tribe Cynipini have two alternate generations each year: a bisexual generation with both males and females developing in spring galls, and a unisexual generation of only females in autumn galls. This phenomenon of alternating generations is called *heterogony* and results in females so different from those of their alternate generations that many were originally described as separate species, sometimes even in separate genera.

The unisexual generation of the wasp *Antron douglasii* produces striking pink star-like spiny turbans in summer on the leaves of *Quercus lobata*, *Q. dumosa* (Nutall’s scrub oak), and *Q. douglasii*. The bisexual generation of this wasp produces twig galls that look like large white semi-translucent mistletoe berries in early spring, later fading and hardening to woody knobs. Wasps emerging from these spring galls were first placed in the genus *Dryophanta* because they looked so strikingly different from their alternate generation.



Jumping gall, the unisexual generation of *Neuroterus saltatorius*, under *Quercus lobata* leaf. Photograph by K. Schick.

Surprisingly, even though their homes are so distinctive and thus the insects should be easy to locate, scientific knowledge of the gall wasp fauna in California is far from complete. Many oak galling species have yet to be described, and alternate generations are currently known for fewer than a fourth of the 122 described California species.

In the British cynipid fauna, which is well known, some cynipids species are known to have alternate generations on separate oak tree species, as well as strikingly different morphologies and colors with size ranges differing more than five-fold.

After many years of caging *Andricus quercuscalifornicus* wasps on young oak trees, which then produced new oak apple galls within these cages during the second year, I suspect this species has lost its alternate generation. If an alternate generation does exist, the adults must be significantly smaller than the unisexual generation and must induce inconspicuous galls on stems or leaves. Only after several more years of study will we truly understand heterogony for this single species. Finding alternate generations

for the remaining cynipid species in California will require a lifetime of study.

A COMMUNITY OF WASPS IN AN OAK GALL

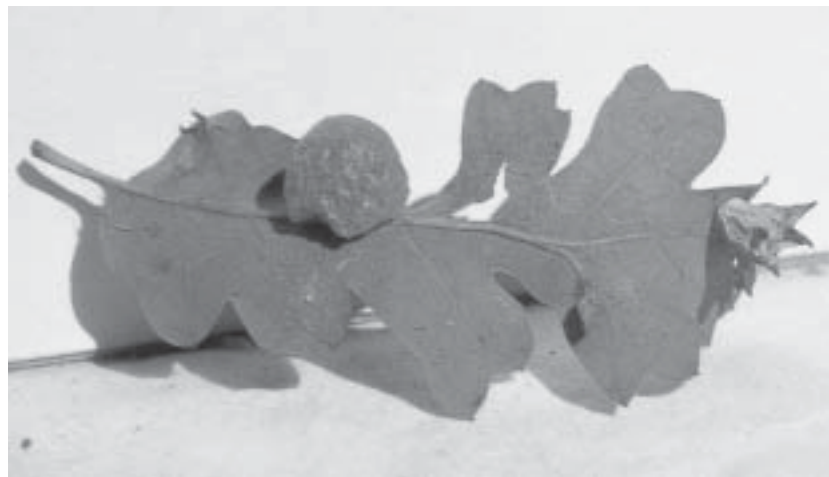
At first glance, an oak gall might seem an ideal refuge from predators and other dangers to young larval insects. Oak galls are especially rich in tannins, much more so than normal plant organs, so the gall tissue should not be especially attractive to plant-eaters. However, these galls cannot move so they are predictable food resources, attracting herbivores as well as insect-eaters. Also abundant in oak galls are two other groups of wasps: herbivorous inquiline ("guest") cynipid wasps and very specialized parasitoids in the superfamily Chalcidoidea.

The inquiline wasps all belong to the tribe Synergini within the family Cynipidae and appear to have lost the ability to secrete gall-inducing chemicals. Instead, they locate developing galls into which they

lay their eggs. When inquiline larvae emerge they may consume all the nutritive cells, starving the gall-inducer. Some species may even deliberately kill the gall-inducing larva in order to consume its food resource.

A very few cynipid inquilines actually induce changes in the shape of the gall, indicating that they have not entirely lost the ability to secrete appropriate chemicals. One such inquiline species in the genus *Synergus* causes unisexual galls of *Heteroecus pacificus* forming on either *Quercus chrysolepis* (canyon oak) or *Q. vaccinifolia* (huckleberry oak) to change from a narrow spindle shape to a rounded globular shape. I have dissected these galls and found as many as five larval chambers for the smaller inquiline wasps around a single central chamber for the larger gall-inducer, all of which

Oak apple gall (*Andricus quercuscalifornicus*) (right), on valley oak (*Quercus lobata*). • Three galls on leaf of *Quercus lobata* (below): clockwise from tip, *Antron douglasii*, *Xanthboteras clavuloides*, and *Besbicus conspicuus*. Photographs by G. Frankie.



apparently matured and emerged as adults.

Parasitoids are similar to predators in that they kill their host animal, and they are also similar to parasites in having a single host animal for their entire lifetime. The majority of chalcid parasitoids found in oak galls lay their eggs in cynipid larvae. The growing larvae of the parasitoids slowly consume developing cynipid larvae or pupae. These wasps come in an amazing array of forms and colors, and I am constantly amazed at the number of different parasitoid species found on each cynipid species.

One of my favorite oak gall parasitoids, *Torymus californicus*, belongs to the chalcid wasp family Torymidae and can be reared from *Andricus quercuscalifornicus* oak apple galls. The female of this species is a metallic coppery red with a long, pin-like ovipositor extending twice the length of her body. The long ovipositor allows the female parasitoid to lay her egg directly into the cynipid larva deep in the gall. The male of this species is metallic green and much smaller than the female. These parasitoids emerge from old oak galls in late spring after the season's galls are nearly half their mature size.

EFFECTS ON THE OAKS

A quick glance at any California woodland will reveal some oak trees with numerous galls while neighboring oak trees remain virtually gall-free. Scientists are only beginning to understand the mechanisms gall wasps use to turn on certain plant genes with auxin-like chemicals, and the corresponding immune response of the trees. While there is an energy cost to the oak tree that grows galls, most healthy oak trees have more than enough energy left over from photosynthesis to spare tissue and sugar to shelter a com-

munity of wasps. However, problems can arise when individual trees are diseased or stressed.

Callirhytes quercusuttoni, a common gall wasp on *Quercus agrifolia* (coast live oak) and *Q. wislizeni* (interior live oak) forms a large spherical stem gall slightly smaller than a tennis ball in the center of a twig. This gall appears to block vascular tissues, and frequently all of the branch extending past the gall dies. At any given time many *Quercus agrifolia* trees along the coast in Monterey County will be growing several of these galls and appear rather ragged. But the majority of cynipid galls are not nearly so stressful to the host tree as is this species.

A very unusual situation has recently developed in Canada. Since 1986, people on Vancouver Island have observed a tragic interaction between their Garry oaks (*Quercus garryana*) and the jumping gall wasp, *Neuroterus saltatorius*. The jumping gall wasp had moved north into this area only a few years earlier and for reasons still not clearly understood, it induces many galls to form close together on Garry oak leaves.

The brown spots of necrosis around each growing gall are not a problem in California, where these same wasps induce only a few galls on each leaf, but they cause entire leaves to die when galls grow too densely in Canada. Some of the Vancouver Island Garry oaks actually lose all their leaves mid-summer as a result of this abundance of galls, and even a formerly healthy tree will die after two or three years of mid-summer leaf loss. Many heritage trees have died as a result.

There seems little danger that the Canadian problem with *Neuroterus saltatorius* will ever occur in California. One major difference between Californian and Canadian populations of this wasp is the percentage of galls that are parasitized. When I have collected and reared these galls in California, 80 to 90 percent of the galls yield parasitoids

instead of gall-inducers. When my Canadian colleagues have made similar collections on Vancouver Island, they find far lower rates of parasitism in galls, which they believe is a result of their cooler, wetter weather. Death of these Canadian trees may also be related to the recent introduction of two species of oak phylloxera to western Canada.

The Vancouver Island oak-cynipid interaction is an extreme exception to the norm of gall wasp and host tree interactions. California cynipid galls provide colorful and spectacular decoration to our oak woodlands, costing trees only a tiny fraction of the energy they gain through photosynthesis and providing homes for a diverse and interesting wasp community.

REFERENCES

- Csóka, G. et al. 1998. *The biology of gall-inducing arthropods*. Forest Service, US Department of Agriculture, St. Paul, MN.
- Duncan, R.W. 1997. *Forest pest leaflet No. 80: Jumping gall wasp*. Pacific Forestry Centre, Victoria, BC.
- Meyer, J. 1987. *Plant galls and gall inducers*. Gebrüder, Borntraeger, Stuttgart, Germany.
- Redfern, M., and R.R. Askew. 1992. *Naturalists' handbooks 17: Plant galls*. Richmond Publishing Company, Slough, England.
- Russo, R. 1990. Blue oak: A gall wasp nursery. *Fremontia* 18:68-71.
- . 1979. *Plant galls of the California region*. Boxwood Press, Pacific Grove, CA.
- Shorthouse, J.D., and O. Rohfritsch. 1992. *Biology of insect-induced galls*. Oxford University Press, New York, NY.
- Weld, L.H. 1957. *Cynipid galls of the Pacific Slope*. Privately printed, Ann Arbor, MI.
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BARK BEETLES INFESTING CALIFORNIA'S CONIFERS

by David L. Wood and Andrew J. Storer

Bark beetles (Order Coleoptera; Family Scolytidae) colonize most trees and other woody plants throughout the world. There are in excess of 6,000 named species with about 477 species occurring in the United States (S.L. Wood 1982). More than 170 species in 44 genera are found in California's forests and woodlands (Bright and Stark 1973).

Bark beetles play an important role in forest succession (natural changes that occur in the forest plant community over time) and in the decomposition of woody plant material. While some bark beetle species may reach epidemic levels and cause tree mortality over thousands of hectares, most species escape notice because of their cryptic habits. They are one of only a few insect families that, as adults, penetrate their hosts in order to feed, mate, and reproduce. In so doing they introduce fungi (either directly or indirectly) that are capable of degrading plant cell walls and thus help recycle nutrients from trees.

Only a few species in the genera *Conophthorus*, *Dendroctonus*, *Ips*, *Scolytus*, and *Trypodendron* are considered pests (see photograph at right). Most research over the past three-quarters of a century has been directed at these destructive pests. There is very little information on the biology of the remaining species other than taxonomy, geographic and host range, and gallery patterns (Bright and Stark 1973).

Some conifer-feeding bark beetles confine their feeding activities to xylem (sapwood), phloem (nutrient-transporting tissue in inner bark), or outer bark, and produce distinctive gallery patterns (see photographs, page 21). Bark beetles may

be found colonizing cones, branches, limbs, trunks, and roots (Furniss and Carolin 1977).

For example, on ponderosa pine (*Pinus ponderosa*), the ponderosa pine cone beetle (*Conophthorus ponderosae*) colonizes the cones (see photograph, page 22); the twig beetle (*Pityophthorus confertus*) colonizes small branches; the western pine beetle (*Dendroctonus brevicornis*), and the California five-spined ips (*Ips paraconfusus*) feed on the phloem of the larger branches and trunk; the ambrosia beetle (*Gnathotrichus sulcatus*) tunnels into the xylem and feeds on fungi growing in the maternal gallery; and another bark beetle (*Hylastes macer*) infests the roots.

Bark beetles vary greatly in the number of tree species infested. For example, the Jeffrey pine beetle,

Dendroctonus jeffreyi, only colonizes Jeffrey pine (*Pinus jeffreyi*) while the red turpentine beetle (*D. valens*) colonizes most pine species in California. Some species typically colonize trees in certain size classes. Thus, the California five-spined ips infests young, pole-sized trees, while the western pine beetle infests large mature and overmature trees.

HISTORY

In the spring and early summer of 1899, Dr. A.D. Hopkins, then vice-director and entomologist of the West Virginia Agricultural Experiment Station, conducted a reconnaissance trip to investigate insects injurious to forests of California, Oregon, Washington, and

Extensive white fir (*Abies concolor*) mortality caused by the fir engraver beetle, Lake Tahoe Basin, 1991. Photograph by D.C. Perkins.



Idaho. On the day after his arrival in San Francisco (April 17, 1899), he visited the University of California at Berkeley.

Hopkins notes: "I called on Professor Woodworth, entomologist, and Prof. J.B. Davy, botanist of the Agricultural Experiment Station, who offered every facility and gave valuable assistance in my study of the native forest trees represented in the university arboretum. Here I collected numerous species of Scolytids from the pines and other conifers."

In his first reference to the western pine beetle, he writes: "One species which I have provisionally identified as *Dendroctonus brevicomis* Lec. was found to be a most destructive enemy of the yellow pine (*Pinus ponderosa*) in northern California, southern and eastern Oregon, northeastern Washington, and western Idaho. A large amount of the finest timber in all of these localities had died within the past seven or eight years, evidently as a direct result of attacks by this bark beetle."

Although first described by LeConte in 1876, this species was not considered distinct from the southern pine beetle, *D. frontalis*, until Hopkins observed it on this trip: "Just as *D. frontalis* has proven to be the most destructive enemy of Eastern conifers, the Western representative of this species will doubtlessly prove to be, under similarly favorable conditions, equally as destructive to the Western forests in which the conifers permeate."

Thus, Hopkins was the first to record the habits and hosts of the western pine beetle. He observed further, "... It [western yellow pine] has in *Dendroctonus brevicomis* a most pernicious enemy, which penetrates, and excavates winding galleries through the living bark of the finest trees, thus speedily causing their death."

Hopkins's words were prophetic. In 1928, F.P. Keen, ento-

mologist for the US Bureau of Entomology, estimated losses of the "... longest and finest western yellow pines ..." due to *D. brevicomis* at 300 million board feet per year in California. He stated that "... in some localities particularly favorable to the beetles ... loss for the year may represent as much as ten percent of the pine stand" (Keen 1928).

CHEMICAL ECOLOGY

Bark beetles usually infest trees that are dead, or that are under some form of stress. However, apparently healthy trees may be killed by some species. Bark beetles use a complex chemical communication system to locate a new host, upon which they can feed, mate, and reproduce (D.L. Wood 1982).

They have evolved a pheromone that elicits behavior resulting in aggregation of the population on the new host. This population aggregation must be both timely and, with tree-killing species, of a sufficient magnitude to exploit the new resource. As a result of their capacity to kill living trees, often over very large areas, bark beetles influence age, size, and species distributions, and thus are a significant factor in forest succession.

The process of host colonization has been divided into four phases: dispersal, selection, concentration, and establishment (D.L. Wood 1982). These phases are defined as follows:

Dispersal begins with emergence from the brood tree and ends with a response to host stimuli and/or attractive pheromones.

Selection begins with the response to host stimuli prior to (or after) landing on the tree, and ends with sustained feeding in the phloem. Host selection is either a random process in which beetles land indiscriminately on host and nonhost

trees, or a directed process in which they land preferentially on host versus nonhost trees and on weakened versus healthy host trees.

Concentration begins with the response to attractive pheromones (chemicals secreted by individuals of one species that stimulate behavior or development of individuals of the same species) that are produced by beetles feeding or tunneling in the host. Depending on species, individuals of either sex or both sexes may produce pheromones, tunneling may occur in the phloem or xylem, and host compounds released during attack may enhance or reduce the effect of the pheromones. This concentration phase continues beyond the beginning of the establishment phase because of continued pheromone production and release. Termination of this phase occurs when antiattractants are released or no more aggregation pheromones are produced.

Establishment (for tree-killing species) begins when sufficient fungal inoculum has been introduced into the xylem to assure death of the tree, so that beetle mating, gallery excavation, and oviposition can occur. The number of beetle attacks and when and where they occur determine the effectiveness of the fungal inoculum in overcoming tree resistance. With species that do not kill trees, this phase begins with the first pairing of sexes in the new host or when inseminated females begin tunneling into the host. This phase ends when elongation of egg galleries and oviposition cease.

INTERACTIONS WITH THEIR HOSTS

Healthy trees have mechanisms to defend themselves from attack by bark beetles. Resin pressure, flow, composition, and crystallization rates may each be involved in

the determination of whether an attack is successful or not. Other mechanisms, including those that are a result of the introduction of fungi by the bark beetles, are all important in the host-bark beetle interaction.

Various patterns of forest succession are related to the activities

of tree-killing bark beetles. For example, at the Blodgett Forest Research Station (University of California at Berkeley) on the western slope of the central Sierra Nevada, logging activities and a fire in the early 1900s resulted in a pure stand of ponderosa pine. In the 1960s, blackstain root disease became prevalent in this forest and the western pine beetle population increased, causing extensive tree mortality.

The bark beetle, *Hylastes macer*, is a vector of the blackstain root disease pathogen, *Leptographium wageneri*. This beetle apparently selects healthy trees which become weakened as disease develops. This pathogen also infects adjacent trees through their fine roots. Western pine beetle aggregates on healthy and diseased trees, resulting in many inoculation sites for bluestain fungi (*Ophiostoma minus*), and eventually leads to the death of the pines. At the Blodgett Forest Research Station site, white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*), both shade-tolerant species that were growing as small trees in the understory, showed increased productivity after beetle infestation, due to reduced competition from the pines. This resulted in an over-

story of these species, as well as a few scattered ponderosa pines, sugar pines (*Pinus lambertiana*), and Douglas-firs (*Pseudotsuga menziesii*).

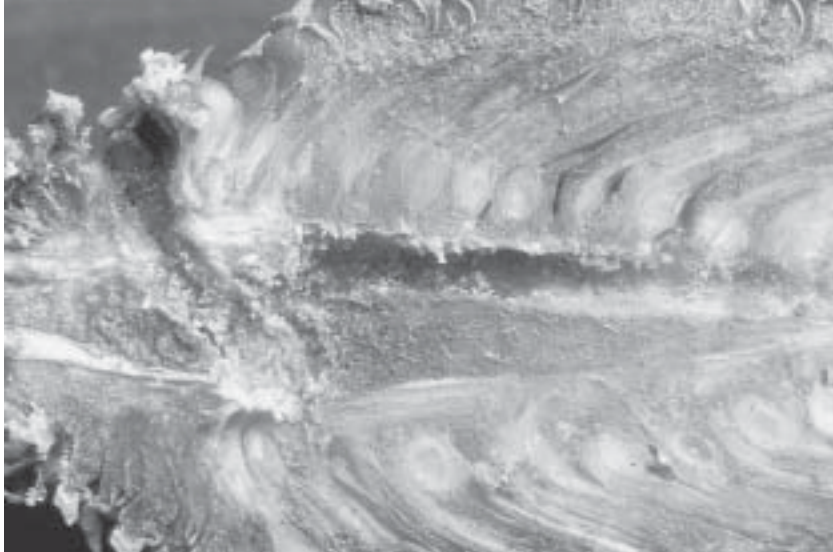
INTERACTIONS WITH OTHER INSECTS

The complex interactions among bark beetles and other insects include those with other bark beetles, with other insects feeding on trees, and with predatory and parasitic insects. Bark beetles often



Examples of gallery patterns produced by bark beetles. • Western pine beetle (*Dendroctonus brevicomis*) (above). Each winding egg gallery is excavated by one female. The male joins the female soon after she enters the phloem. Eggs are laid in niches in the phloem of the gallery wall. Larvae feed on phloem for the first larval stage, packing frass in their galleries, and then turn out to feed in the outer bark. Photograph by R.W. Stark. • Twig beetle (*Pityophthorus* spp.) (top right). Maternal galleries radiate from a central nuptial chamber. Larval tunnels radiate from these maternal galleries and are packed with frass. Photograph by P.L. Dallara. • California 5-spined ips (*Ips paraconfusus*) (middle row, left). Three egg galleries are each excavated by one female. Eggs are laid in niches in the phloem of the gallery wall. The nuptial chamber at the intersection of the three egg galleries is excavated by the male. Larvae feed on phloem until pupation, excavating galleries that are packed with frass. Photograph by T.W. Koerber. • Pine engraver (*Ips pini*) (middle row, right). Four egg galleries are each excavated by one female. Eggs are laid in niches in the phloem of the gallery wall. The nuptial chamber at the intersection of the four egg galleries is excavated by the male. Larvae feed on phloem until pupation, excavating galleries that are packed with frass. Photograph by A.J. Storer. • Monterey pine ips (*Ips mexicanus*) (bottom row, left). After leaving the nuptial chamber, the female beetle excavates a "C"-shaped maternal gallery in the phloem laying eggs in groups of 3-4 on the outside of the "C." Larvae tunnel individually in the phloem, excavating galleries that are packed with frass. Photograph by A.J. Storer. • Fir engraver (*Scolytus ventralis*). One female excavates two egg galleries which radiate horizontally from a central nuptial chamber (bottom row, right). The male joins the female soon after she excavates the entrance tunnel. Larval tunnels run vertically from the maternal gallery and are packed with frass. Photograph by T.W. Koerber.





Ponderosa pine cone beetle (*Conophthorus ponderosae*) (top). The female beetle tunnels in at the base of the cone, and then excavates an egg gallery along the axis of the cone. Larvae feed in the seeds and scales inside the cone. Photograph by T.W. Koerber. • **Adult twig beetle** (*Pityophthorus* sp.) (bottom) on pine foliage. Photograph by A.J. Storer.

exploit trees weakened by other insects, especially defoliators (Furniss and Carolin 1977). In northeastern California, for example, white firs defoliated by the Douglas-fir tussock moth (*Orygia pseudotsugata*) are infested by the fir engraver beetle (*Scolytus ventralis*). Outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) have been recorded in lodgepole pines defoliated by the lodgepole needleminer (*Coleotechnites milleri*) in Yosemite National Park. In these examples, white firs and lodgepole pines utilize the space and light following mortality of the overstory trees to develop into the next overstory generation.

Competition for space and resources may be reduced by interrupting the response of other bark beetles to their pheromones (D.L.

Wood 1982; Raffa et al. 1993). The compound verbenone is produced by both male and female western pine beetles and interrupts response of the California five-spined ips to its pheromone. Such chemical interactions confer an advantage to the first-arriving species because its pheromone will interrupt the attractant pheromone of the late-arriving species. Thus competition for food and space is reduced. This compound benefits the sender and is termed an "allomone."

Bark beetles have a wide range of insect enemies that cause mortality beneath the bark of infested trees, in addition to other natural enemies such as woodpeckers (Stark and Dahlsten 1970). Several species of bark beetle predators and parasites are attracted to bark beetle pheromones (D.L. Wood 1982; Raffa et al. 1993). Where the chemical signal benefits the receiver, such as a predator or parasite, and is detrimental to the sender (the bark beetle in this case) in a multi-species interaction, the compound is referred to as a "kairomone."

The red-bellied clerid, *Enoclerus lecontei* (Coleoptera: Cleridae) is a general predator of bark beetles. It is attracted to ipsenol and ipsdienol, pheromone components produced by the California five-spined ips. The compound *exo*-brevicomin which is produced by the female western pine beetle, is highly attractive to another predatory beetle, the blue-green trogositid, *Tem-*

nochila chlorodia (Coleoptera: Trogositidae). These predators arrive on the tree with the tree-infesting bark beetles. They consume arriving bark beetles, then mate, lay eggs, and their larvae enter the bark beetle galleries to feed on immature bark beetles and other insects and invertebrates that occur beneath the bark.

Both sexes of the parasitic wasp *Tomicobia tibialis* (Hymenoptera: Pteromalidae) are attracted by compounds that are produced by male California five-spined ips while attacking ponderosa pines. This wasp inserts eggs into the attacking beetles and the wasp larva develops entirely inside the bark beetle. Again the compound is detrimental to the sender of the compound, and is another example of a "kairomone." Other wasps that are parasitic on bark beetles, such as *Roptrocercus xylophagorum* (Hymenoptera: Torymidae) and *Dinotiscus burkei* (Hymenoptera: Pteromalidae), arrive during the establishment phase, some four to six weeks after initial attacks have occurred. Parasitoids attack their bark beetle hosts, usually during the late larval stage. The chemicals to which these parasites are attracted may result from fungal colonization of the host during the establishment phase.

INTERACTIONS WITH FUNGI

Bark beetles interact with pathogenic fungi in a number of important ways, including when they act as vectors of pathogenic fungi to healthy trees, and when they preferentially colonize diseased trees (Schowalter and Filip 1993). Tree-killing species in the genera *Dendroctonus*, *Ips*, and *Scolytus* have a close association with pathogenic fungi. Fungal propagules in the genera *Leptographium*, *Ophiostoma*, and *Trichosporium* are carried by adults and occur in their galleries in re-

cently killed trees (summarized in Harrington 1993).

Many of these fungi are co-evolved mutualistic fungi that are only found in association with certain bark beetle species. Their role in the colonization of the host by the bark beetle is not fully understood, but may include helping to overwhelm the defenses of the tree by causing a vascular wilt disease, as well as providing nutritional benefits to the larvae. These coevolved fungi are often carried inside specialized structures on the bark beetle called "mycangia."

Owen et al. (1987) wound-inoculated two-year-old ponderosa pine seedlings with fungi isolated from three species of *Dendroctonus* that colonize ponderosa pine: *Leptographium terebrantis* from the red turpentine beetle, *Ophiostoma* (= *Ceratocystis*) *minus* from the western pine beetle, and *O. clavigerum* from the mountain pine beetle. Each killed a high proportion of the seedlings. Seedling mortality caused by *L. terebrantis* was greater than that caused by the other two fungi.

This was a surprising result in light of the well-known tree-killing habit of the mountain pine beetle and western pine beetle, and the non-tree-killing behavior of the red turpentine beetle. *Ophiostoma ips* from the red turpentine beetle and mountain pine beetle reduced seedling mortality caused by *L. terebrantis* and *O. clavigerum*, respectively. *Ophiostoma nigrocarpum* from the western pine beetle produced the same result when inoculated together with the pathogenic *O. minus*.

Thus, each of these three bark beetle species carries one pathogenic fungus and one fungus that inhibits the effects of the pathogenic fungus in seedling inoculation studies. The same phenomena were observed when these fungi were inoculated into pole-sized trees (Parmeter et al. 1989).

Trees weakened by diseases can be detected by bark beetles (summarized in Goheen and Hansen 1993). In the central Sierra Nevada, ponderosa pines infected by the fungus that causes blackstain root disease are predisposed to infestation by the western pine beetle. Ponderosa pines growing in pure stands are killed by the western pine beetle. Then these stands are replaced by shade-tolerant incense cedar and white fir, both of which are apparently immune to this root pathogen.

The blackstain fungus causes a similar root disease in Douglas-fir, which predisposes trees to attack by the stem-infesting bark beetles, *Pseudohylesinus nebulosus* and *Scolytus unispinosus*, as well as several other species. Root-infesting bark beetles, *Hylastes nigrinus*, and *H. macer*, as well as the weevils, *Pissodes fasciatus* and *Steremnius carinatus* (Coleoptera: Curculionidae), are vectors of this root pathogen to Douglas-fir. While the origins of blackstain root disease are unclear, it is likely that the vector and predisposition relationships described above have evolved together over time.

Some bark beetles carry fungi with which they have not coevolved. Perhaps the best-known example comes from hardwood forests where the exotic Dutch elm disease fungus is carried from host to host by both native (*Hylurgopinus rufipes*) and exotic (*Scolytus multistriatus*) bark beetles.

In California, the exotic fungus that causes pitch canker, *Fusarium circinatum*, has developed associations with a number of native bark beetle species that infest Monterey and other pines in central coast of California. In many cases, these bark beetles have been shown to vector the pathogen to healthy trees (summarized in Storer et al. 1999).

The California five-spined ips, a twig beetle (*Pityophthorus setosus*), and the Monterey pine cone beetle (*Conophthorus radiatae*), have been

shown to be associated with diseased trees, and are known to visit and infest non-diseased trees. Individuals of these species carry *Fusarium circinatum* propagules, and transmission of the pathogen has been demonstrated in controlled studies. Hence, all of these species are regarded as vectors of the pitch canker fungus in California.

Other species in the same genera feeding on Monterey pine are also considered to be likely vectors as they associate with healthy and diseased trees, and carry propagules of the pathogen. Analysis of the native host ranges of the proven vectors and their congeners (species of the same genus), and the geographic distribution of their hosts, indicate many possible avenues of spread for pitch canker to the North Coast and Sierra Nevada (Gordon et al. 2001).

INTERACTIONS WITH ENVIRONMENTAL AGENTS

Environmental factors such as air pollution, drought, windthrow (uprooting of trees by the wind), flooding, and snow breakage can cause an increase in bark beetle population levels, resulting in increased tree mortality. In particular, the effects of drought have dramatic impacts on forest dynamics. The extended drought between 1986 and 1992 resulted in greatly increased levels of tree mortality caused by bark beetles throughout California. Thousands of bleached white fir stems are visible today throughout the Lake Tahoe Basin, a result of an epidemic of the fir engraver beetle during the extended drought (see photograph, page 19).

Damage caused by the air pollutant, ozone, may also predispose trees to attack by bark beetles. Ozone damage was initially referred to as "X-disease" because the causes

of chlorotic mottling on pine needles and reduced needle size and retention were unknown. These symptoms had been observed since the early 1950s in the San Bernardino Mountains of southern California. A relationship between needle symptoms and photochemical air pollutants was subsequently made, and it was found that, as the severity of oxidant injury increased, the incidence of bark beetle infestation by the western pine beetle and the mountain pine beetle increased. Specifically, ozone damage resulted in reduced resin flow, which thus facilitated bark beetle gallery excavation in the phloem. This favored the successful establishment of western pine beetle and mountain pine beetle in ponderosa pines that had been damaged by photochemical atmospheric pollution (Lorio 1993).

INTERACTIONS WITH HUMAN ACTIVITIES

Logging activity has undoubtedly increased the breeding material available for root-infesting bark beetles. This activity may have created a larger vector population for *Leptographium wageneri*, with a concomitant increase in the incidence of black-stain root disease. Logging also has probably increased the incidence of annosum root disease caused by the root pathogen, *Heterobasidion annosum*. Freshly-cut stumps are colonized by spores of this root pathogen.

Similarly, human activity is probably responsible for the recent introduction and spread of the pitch canker fungus in California. The increasing incidence of this disease is likely a result of increased abundance of many potential bark beetle vectors (i.e., *Conophthorus* spp., *Ips* spp., *Pityophthorus* spp.) which can be moved around by humans, as well as carry the pathogen from tree to tree in nature. The new associa-

tion between native bark beetles and this pathogenic fungus results in the death of cones, twigs, branches, tree tops and ultimately the death of the entire tree.

TREATMENT TACTICS AND STRATEGIES

Once bark beetles reach epidemic levels and cause extensive tree mortality, treatments aimed at reducing densities of the beetles are futile (D.L. Wood et al. 1985). Felling and burning infested trees or treating them with insecticides have been attempted, but with little effect on the course of the epidemic.

The symptoms of tree death appear quite suddenly as the foliage turns yellow. Valuable lumber can be recovered from infested trees if they are cut in the same year or the year after they were killed. However, in spite of early removal of infested trees, lumber will likely be devalued by bluestain fungi introduced into the tree by the bark beetles and by tunnels of wood boring beetles (*Cerambycidae*, *Buprestidae*, *Scolytidae*) and woodwasps (*Siricidae*) that colonize trees killed by bark beetles. Dense, single-species stands of conifers are especially susceptible to bark beetle infestation because growth of these trees is reduced by competition for water, nutrients, light, and space.

Plantations of a single species, such as ponderosa pine or Douglas-fir, are especially susceptible to bark beetle infestation. Manipulation of density and species composition is one of the most valuable strategies available to forest managers to reduce the impact of bark beetles. For example, by thinning a pure stand of ponderosa pine in the mixed conifer forest of the west side of the Sierra Nevada, the growth rate of the remaining pines is increased, and susceptibility to bark beetle at-

tacked is decreased. At the same time, smaller incense cedar and white fir growing in the understory grow to occupy the space left from the thinning operation. This increases the diversity of the stand which further reduces the impact of bark beetles.

Treatments aimed at reducing bark beetle densities so as to prevent infestations on living trees have utilized techniques including the use of insecticides; the use of behavioral chemicals, such as anti-aggregation pheromones; destroying infested material by cutting and burning; or debarking and removal from the forest. These "direct control" or "remedial" methods have not been proven effective in forest-wide applications because treatment effects could not be separated from other naturally-occurring mortality agents. Therefore, these techniques are rarely used in managing bark beetles in forests and large plantations.

However, insecticides are available for treating high-value trees in the urban forest and in campgrounds in forested areas. These compounds are applied to the trunk of the tree to prevent tunneling by beetles.

A promising and more environmentally acceptable method utilizes "behavioral" chemicals. For example, the Douglas-fir beetle anti-aggregation pheromone has been registered by the Environmental Protection Agency to prevent attacks by the Douglas-fir beetle on individual trees (Ross 2001). It can also be used in forest-wide applications to prevent the infestation of trees that have blown down. Populations of this beetle build up in fallen trees and then emerge and infest nearby living trees.

Other antiaggregation pheromones such as ipsdienol produced by male western pine beetles and male California five-spined ips, and verbenone produced by male and female western pine beetles, are promising candidates to protect

ponderosa pine from infestation by these species. The natural role of these chemicals is to prevent too many beetles from attacking the tree, which would result in a low survival of offspring due to competition among them. Further research is needed to develop a treatment to prevent attacks on individual trees, especially Monterey pines, which are widely planted in urban environments in California.

Forest management practices may also help to reduce the impacts of bark beetle populations. Strategies available to foresters include the removal of susceptible trees, thinning of stands to increase tree vigor, prescribed burning to eliminate susceptible host material, and enhancement of natural enemy populations. For instance, thinning lodgepole pine stands reduces tree mortality caused by the mountain pine beetle. Also, setting prescribed fires following harvesting operations in ponderosa pine forests reduces populations of the California five-spined ips that breed in logging debris. This practice lowers the probability of these populations emerging and killing living trees in the area.

SUMMARY

Bark beetles are a natural component of coniferous forest ecosystems in California. They provide an essential role in the cycling of nutrients and in the process of forest succession. They are involved in a myriad of interactions with other entities in their environment, including their hosts, each other, other insects, fungi, and humans. Research has focused on the few species that cause economic damage and has uncovered many of the mechanisms by which these interactions occur. In turn, this information has provided insights into ways of managing bark beetles to reduce economic losses in situations

where they have or can become damaging pests.

REFERENCES

- Bright, D.E. and R.W. Stark. 1973. *The bark and ambrosia beetles of California, Coleoptera: Scolytidae and Platypodidae*. Bulletin No. 16 of the California Insect Survey.
- Furniss, R.L. and V.M. Carolin. 1977. *Western forest insects*. USDA Forest Service, Miscellaneous Publication No. 1339, Washington, D.C.
- Goheen, D.J. and E.M. Hansen. 1993. Effects of pathogens and bark beetles on forests. In *Beetle-pathogen interactions in conifer forests*, ed. T.D. Schowalter and G.M. Filip, 175–196. Academic Press, NY.
- Gordon, T.R., A.J. Storer, and D.L. Wood. 2001. The pitch canker epidemic in California. *Plant Disease* 85:1128–1139.
- Hopkins, A.D. 1899. *Preliminary report on the insect enemies of forests in the Northwest*. USDA, Division of Entomology, Bulletin No. 21, Washington, D.C.
- Harrington, T.C. 1993. Biology and taxonomy of fungi associated with bark beetles. In *Beetle-pathogen interactions in conifer forests*, ed. T.D. Schowalter and G.M. Filip, 37–58. Academic Press, NY.
- Keen, F.P. 1928. *Insect enemies of California pines and their control*. State of California, Department of Natural Resources, Division of Forestry, Bulletin No. 7.
- Lorio, P.L. 1993. Host response to bark beetle and pathogen colonization. *Beetle-pathogen interactions in conifer forests*, ed. T.D. Schowalter and G.M. Filip, pp. 81–101. Academic Press, NY.
- Owen, D.R., K.Q. Lindahl Jr., D.L. Wood, and J.R. Parmeter. Jr. 1987. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* 77:631–636.
- Parmeter, J.R. Jr., G.W. Slaughter, Mo-Mei Chen, D.L. Wood, and H.A. Stubbs. 1989. Single and mixed inoculations of ponderosa pine with fungal associates of *Dendroctonus* spp. *Phytopathology* 79:768–772.
- Raffa, K.F., T.W. Phillips, and S.M. Salom. 1993. Strategies and mechanisms of host colonization by bark beetles. In *Beetle-pathogen interactions in conifer forests*, ed. T.D. Schowalter and G.M. Filip, 103–128. Academic Press, NY.
- Ross, D.W., K.E. Gibson, and G.E. Daterman. 2001. Using MCH to protect trees and stands from Douglas-fir beetle infestation. USDA Forest Service, Forest Health Technology Enterprise Team, FHTET-2001–09.
- Schowalter, T.D. and G.M. Filip, eds. 1993. *Beetle-pathogen interactions in conifer forests*. Academic Press, NY.
- Stark, R.W. and D.L. Dahlsten, eds. 1970. *Studies in the population dynamics of the western pine beetle, Dendroctonus brevicomis LeConte (Coleoptera: Scolytidae)*. Division of Agricultural Science, University of California, Berkeley.
- Storer, A.J., D.L. Wood, and T.R. Gordon. 1999. Insect vectors of *Fusarium circinatum* in California, and their potential for the spread of pitch canker disease. In *Current and potential impacts of pitch canker in radiata pine*, eds. Devey, M.E., A.C. Matheson, and T.R. Gordon, 45–48. Proceedings of the IMPACT Monterey Workshop, 30 November to 3 December, 1998, Monterey, CA. 1998. CSIRO Australia.
- Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology* 27:411–46.
- Wood, D.L., R.W. Stark, W.E. Waters, W.D. Bedard, and F.W. Cobb Jr. 1985. Treatment tactics and strategies. In *Integrated pest management in pine-bark beetle ecosystems*, eds. W.E. Waters, R.W. Stark, and D.L. Wood, 121–139. John Wiley & Sons, New York, NY.
- Wood S.L. 1982. *The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph*. Great Basin Naturalist Memoirs, No. 6.

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Worker of *Bombus fraternus* buzz pollinating senna (*Cassia fasciculata*). The wings are blurred due to thoracic muscle vibration. All photographs by R. Thorp.

BUMBLE BEES: BOISTEROUS POLLINATORS OF NATIVE CALIFORNIA FLOWERS

by Robbin W. Thorp, Peter C. Schroeder, and Carol S. Ferguson

Bumble bees (*Bombus* spp.) are large, fuzzy insects with eye-catching colors and noisy flight. Their boisterous behavior around flowers easily captures the attention of nearly everyone. These salient traits overshadow the bumble bee's less apparent features, such as specialized structures for collecting and transporting pollen, unusually long tongues for gathering nectar, and a unique ability to shiver for warmth. Each of these characteristics help join the food-gathering needs of bumble bees with the reproductive needs of flowering plants.

Bumble bees depend on pollen and nectar for satisfying their energy needs and for rearing their young. In turn, by altering the availability of nectar or pollen, flowering plants shape the life history, community structure, and foraging habits of bumble bees. This binding partnership between bees and flowers makes bumble bees a vital component of natural communities. Habitat fragmentation from urbanization and agriculture and the introduction of non-native bees threaten the livelihood of bumble bees and other native pollinators.

We hope the following information will lead you to appreciate bumble bees and inspire you to help protect and conserve these native pollinators in your community.

BUMBLE BEE LIFE HISTORY

Worldwide there are about 240 species of *Bombus* (including the cuckoo bumble bees, *Psithyrus*, which is now considered a subgenus of *Bombus*). Most bumble bees are confined to the Holarctic re-

gions of the earth, although some extend into the Oriental and Neotropical regions as well. None are native to Africa south of the Sahara or within the Australasian region.

There are 26 species of bumble bees native to California, where they inhabit plant communities from the Pacific Coast to above timberline. Bumble bee populations in California are most diverse in the northwestern part of the state and within the Sierran-Cascade ranges. In general, bumble bees prefer moist, cool habitats and show life cycles well-adapted to habitats ranging from cool temperate to arctic climates. Few are found in semi-arid to arid or dense coniferous forest habitats.

Bumble bees are social and form annual colonies more similar to social wasps (yellowjackets and paper wasps) than to honey bees, whose societies are perennial. Only fertile females (queens) overwinter, emerging the following spring from their shallow underground chambers (hibernaculae). Robust newly-emerged queens search for suitable nesting sites by flying low and erratically over the ground in relatively open areas. Abandoned small rodent shelters or burrows often serve as nesting sites. Other sheltered areas that contain fibrous materials such as abandoned bird nests, upholstery, or insulation can provide a suitable nesting site as well.

Once she finds a nesting site, the founding queen constructs a wax cell or "honey pot" for nectar storage. She then visits flowers for nectar to give her energy, and pollen to serve as food for her prospective young. While foraging, the queen holds gathered nectar in her crop (a specialized region of her digestive tract) and grooms pollen from her body. She then mixes the groomed pollen with a small amount of nectar and forms it into moist lumps, which she carries in special pollen baskets (called corbiculae) on the outside surface of her hind legs.

When she returns to the nesting site, the queen regurgitates nectar into the honey pot, forms the pollen into a single loaf, lays eggs on the mass, and sometimes covers it with wax. She then extends her abdomen on top of the mass and incubates her developing brood with heat generated by rapidly shivering her wing muscles. To gain energy while incubating her brood, she drinks from the nearby honey pot. The queen feeds her young mixtures of honey and pollen.

When mature, larvae spin cocoons and transform into sterile adult females (workers). The first workers to emerge in the colony are much smaller than the founding queen and cooperate in constructing cells, regulating nest temperature and humidity, and rearing their sisters. As workers in the colony become more numerous, they assume the foraging duties of the queen who eventually confines her activity solely to egg-laying. Worker

larvae are better fed by the larger worker force and, when they emerge as adults, are larger than their sisters who emerged before them. Eventually, as workers continue to increase in size, the colony produces new queens.

At about the same time the new queens emerge, males develop from unfertilized eggs laid either by the original queen or by her unmated daughters. Adult males selfishly forage during the day and rarely return to the nest, usually resting on vegetation at night. Young queens mate with males away from the nest, then actively forage to store energy necessary for hibernation. All other members of the colony (the old queen, workers, and males) die as the season ends. Newly mated queens overwinter in shallow burrows and emerge the following spring to start the cycle again. Overwintering queens emerge the following spring to start the cycle again. All other remaining mem-

Worker of *Bombus occidentalis* stealing nectar from larkspur (*Delphinium*).



bers of the colony, the old queen, workers, and males, die as the season ends.

THE STRUCTURE OF BUMBLE BEE COMMUNITIES

Bumble bee communities in the Klamath Ranges (including the Siskiyou Mountains) of northern California and southern Oregon commonly contain six to a dozen species that often coexist in areas as small as 100 square meters. Structure (diversity of members) of a bumble bee community is largely determined by the tongue lengths

of the bumble bee species comprising the community. In most localities, bumble bee communities contain a variety of species possessing different tongue lengths.

Bumble bee tongue length is related to the depth of nectaries of available host flowers and, within a species, is correlated with body size (larger bees have longer tongues) and head shape (bees with triangular heads have longer tongues than bees with rounded heads). Tongue lengths are usually uniform among queens of the same species. However, tongue lengths among worker bumble bees (who show a wide variety of body sizes) vary greatly among individuals and between

colonies of a given species. Consequently, the relationship between tongue lengths and community structure is closest (and possibly only applicable) early in the season when queens are most predominant in the community.

This relationship is further confounded by phenological differences in emergence patterns, and subsequently tongue lengths among bumble bee queens. For example, queens that emerge early in the season (typically *B. bifarius*, *B. melanopygus*, and *B. vosnesenskii*) have moderate tongue lengths, whereas queens that emerge later (typically *B. appositus*, *B. flavifrons*, and *B. nevadensis*) have longer tongues. A mixture of long-tongued (*B. californicus*) and short-tongued (*B. franklini* and *B. occidentalis*) bumble bees emerge even later in the season.

Worker of *Bombus vosnesenskii* foraging for pollen on lupine (*Lupinus*).



FORAGING HABITS OF BUMBLE BEES

Bumble bees visit flowers to gather nectar or pollen. They are typically considered “generalists” and visit a broad array of flowering plant species. Many species of plants restrict the types of visitors that seek their flowers by limiting the accessibility of pollen or nectar. For example, snapdragon (*Antirrhinum*) and scotch broom (*Cytisus*) conceal their pollen or nectar within flower parts that must be pushed aside by large-bodied, strong visitors like bumble bees.

The flowers of nightshade (*Solanum*), tomato (*Lycopersicon*), and senna (*Cassia*) contain apically-pored (salt shaker-like) anthers that release pollen in response to vibration (see photograph, page 26). While visiting these flowers, bumble bees and a few other bees are capable of vibrating their bodies by rapidly oscillating their wing muscles without engaging the wings (honey bees lack this ability). Con-

sequently, bumble bees are among the most efficient pollinators of these flowers. The ability to “buzz pollinate” is one reason that bumble bees are used commercially to pollinate hothouse tomatoes.

When foraging for nectar, bumble bees preferentially seek flowers with high nectar rewards accessible to their tongues. Some plants store their nectar within deeply recessed parts of the flower, such as the floral spurs of larkspur (*Delphinium*) or the long corolla tubes of beardtongue (*Penstemon*). Long-tongued bumble bees like *B. appositus*, *B. flavifrons*, and *B. nevadensis* can successfully and legitimately acquire nectar from these flowers.

To obtain the same nectar, shorter-tongued bumble bees like *B. franklini* and *B. occidentalis* must resort to “nectar-robbing” by biting the tip of the spur or base of the tube that conceals the nectar and imbibing the nectar through the resulting hole (see photograph, page 27). Bees that rob nectar this way avoid contact with the anthers or stigma of the flower and consequently do not pollinate the flower. Nectar robbing may also reduce seed set by reducing the amount of nectar available to legitimate pollinators.

Nectar-rich flowers of horse mint (*Agastache*), coyote-mint (*Monardella*), and black sage (*Salvia*) ensure pollination by depositing their pollen on the foraging bee’s back (a process called nototriby). Thus deposited, the pollen cannot be groomed and packed into loads destined as brood food back at the nest. The pollen is eventually transferred to the stigma of another flower as the bee continues to forage for nectar.

Some flowers offer no nectar and rely solely on pollen to attract potential pollinators. Examples of plants with nectarless flowers attractive to bumble bees include lupine (*Lupinus*), California poppy (*Eschscholzia*), and wild rose (*Rosa*) (see photograph, page 28). Because



Queen of Franklin's bumblebee, *Bombus franklini*, foraging on California poppy (*Eschscholzia californica*).

they receive no immediate energy from pollen, bumble bees must intermittently visit nectar-bearing plants while foraging for pollen.

We have often observed these “flower-switching” bees carrying reddish orange pollen while visiting nectar-rich flowers of mints or thistles that produce light-colored pollen. When plants with nectar-producing flowers are rare or widely spaced among plants with pollen-only flowers, bumble bees may imbibe nectar stored in the nest before they leave to forage for pollen—an advantage enjoyed by bumble bees over non-social bees.

At cool temperatures, bumble bees are capable of warming their bodies by shivering their wing muscles (muscular thermogenesis) prior to foraging. The ability of bumble bees to alter their body temperature through muscular thermogenesis allows bumble bees to forage at temperatures otherwise too cold for most other foraging insects and therefore gain first access to early spring or high elevation flowers such as fireweed (*Epilobium*). However, bumble bees use a relatively large amount of energy to generate heat by muscular thermogenesis. And, as Bernd Heinrich revealed in his work on bumble bee energetics (Heinrich 1979), they must carefully balance their energy needs or expenditures with the nectar rewards of flowers.

FLORAL ASSOCIATIONS OF BUMBLE BEES

The Klamath Ranges of the Northwest Region of the California Floristic Province contains a diverse natural geography and hosts a wide assemblage of flora frequently visited by bumble bees (over 7,400 flower records in California revealed 61 families and 226 genera of plants visited by bumble bees). In California, the most frequently visited native plant genera by bumble bees are listed in Table 1 (page 30).

Recent studies in the United Kingdom as well as the California Floristic Province suggest that bumble bees prefer long-lived biennial and perennial flowering plants rather than annuals. Early spring queens visit manzanita (*Arctostaphylos*), gooseberry (*Ribes*), and willow (*Salix*) while fall queens commonly visit thistles (*Cirsium*). Males, who typically appear near the end of the nesting season, primarily visit thistles and rabbit brush (*Chrysothamnus*).

However, because bumble bee colonies persist beyond the individual blooming period of most plant species, bumble bees depend on a succession of nectar and pollen sources during the course of a season. Besides those from native plants, bumble bees also benefit from pollen and nectar resources provided by many introduced plants, including agricultural crops such as alfalfa (*Medicago sativa*), horticultural introductions such as rhododendron (*Rhododendron* spp.), and even invasive weeds such as yellow star-thistle (*Centaurea solstitialis*).

CONSERVATION OF BUMBLE BEES AND OTHER POLLINATORS

Most flowering plants are pollinated by insects (including butterflies, moths, flies, and beetles),

TABLE 1. NATIVE CALIFORNIA PLANTS MOST FREQUENTLY VISITED BY BUMBLEBEES

Plants are listed by relative rank of visitation frequency (1 = most frequent), genus, common name, life cycle (annual or perennial, listed in order of importance), and resource (nectar or pollen) offered to bumble bees. From Thorp et al. 1983.

RANK	GENUS	COMMON NAME	LIFE CYCLE	RESOURCE
1	<i>Cirsium</i>	Thistle	Ann. Per.	Both
2	<i>Chrysothamnus</i>	Rabbit brush	Per.	Both
3	<i>Helianthus</i>	Sunflower	Ann. Per.	Both
4	<i>Lupinus</i>	Lupine	Per. Ann.	Pollen
5	<i>Trifolium</i>	Clover	Ann. Per.	Both
6	<i>Melilotus</i>	Sweetclover	Ann. Bien.	Both
7	<i>Eriogonum</i>	Wild buckwheat	Per. Ann.	Both
8	<i>Isocoma</i>	Goldenbush	Per.	Both
9	<i>Ceanothus</i>	California lilac	Per.	Both
10	<i>Aster</i>	Aster	Ann. Per.	Both
11	<i>Solidago</i>	Goldenrod	Per.	Both
12	<i>Solanum</i>	Nightshade	Per. Ann.	Pollen
13	<i>Phacelia</i>	Phacelia	Ann. Per.	Both
14	<i>Penstemon</i>	Beardtongue	Per.	Both
15	<i>Monardella</i>	Monardella	Per. Ann.	Nectar
16	<i>Rhododendron</i>	Rhododendron	Per.	Nectar/Both
17	<i>Ribes</i>	Gooseberry	Per.	Both
18	<i>Arctostaphylos</i>	Manzanita	Per.	Nectar/Both
19	<i>Vicia</i>	Vetch	Ann. Per.	Both
20	<i>Astragalus</i>	Locoweed	Per. Ann.	Both
21	<i>Salvia</i>	Sage	Per. Ann.	Nectar
22	<i>Rubus</i>	Blackberry	Per.	Both
23	<i>Senecio</i>	Groundsel	Ann. Per.	Both
24	<i>Lotus</i>	Trefoil	Per. Ann.	Both
25	<i>Asclepias</i>	Milkweed	Per. Ann.	Nectar

though some are pollinated by birds and bats. Bees are most important among these pollinators because they collect both pollen and nectar as food. Buchmann and Nabhan (1996) recognized that many groups of pollinators are declining, including the European honey

bee, on which we rely heavily as the principal pollinator of our crops.

Recent declines in bumble bee populations have been documented in the European community, and we have been tracking similar declines in the western United States,

especially in the once common and widespread western bumble bee (*B. occidentalis*) and the narrowly endemic Franklin's bumble bee (*B. franklini*). Franklin's bumble bee (see photograph, page 29) has the smallest range of any North American bumble bee. Its entire distribution

extends only 144 miles north to south and 75 miles east to west in south-central Oregon and north-central California.

Because of its narrow endemism, *B. franklinii* is listed as a candidate species for protection by the US Fish and Wildlife Service. Data regarding the habitat requirements of Franklin's bumble bee are currently being gathered by Robbin Thorp to try and determine its suitability for listing, an effort we feel is particularly important considering recently observed declines in the populations of this species.

We are collecting similar data on the western bumble bee, which is closely related to and whose range encompasses that of Franklin's bumble bee. The western bumble bee is a widespread polymorphic species that occurs from Monterey and Tuolumne counties of California north to Alaska and south through the Rocky Mountains to northern Arizona and New Mexico. Colonies of the western bumble bee have been commercially reared for pollinating greenhouse tomatoes since 1992.

From 1998 to date, natural populations of this species have steadily and precipitously declined in the area between California and southern British Columbia. These declines may be caused by a protozoan (*Nosema*) disease which appeared in commercial rearing stocks of the western bumble bee in 1998. Current studies hope to determine if the protozoan disease is responsible for declines in natural populations of the western bumble bee, and possibly Franklin's bumble bee as well.

Urban development and agriculture alters habitats otherwise suitable for bumble bee nesting and reduces the variety of flora used by bumble bees as forage resources. Commercial trafficking of bumble bees for pollination of hothouse tomatoes further threatens native bumble bees by introducing alien

bumble bees into the areas where they can compete or possibly interbreed with native bumble bee species. Such has been the case with the European *Bombus terrestris* which has been introduced to many areas of the world including Japan, where native bumble bees suitable for commercial rearing could have been used instead.

The potential introduction of foreign pathogens to bumble bees raises further concerns about the ecological risks of trafficking bumble bees for commercial use. Recently an internal parasitic mite of a genetic strain different from local Japanese mites has been found in bumble bees imported to Japan from Europe.

Preservation of plant-pollinator systems will require a better understanding of bumble bee ecology, particularly the floral associations of bumble bees. Current studies typically rely on observations made in the field, often in cooperation with naturalists, botanists, and other field personnel. However, accurate identification of bumble bees in the field is often difficult.

Populations of native bumble bees may benefit most by the preservation of appropriate habitat. Landowners and gardeners can help preserve bumble bee populations by establishing landscapes that provide suitable habitat for bumble bee nesting and by planting flower gardens that offer a season-long supply of nectar and pollen. Details on methods for preparing and maintaining bumble bee gardens can be found in various gardening publications.

With over two dozen species, bumble bees represent a diverse and important group of insects in California and southern Oregon. Their foraging habits and life history secure them as important pollinators of a wide variety of flowering plants. Their close and binding relationship to flowering plants is revealed by their specially adapted bodies and unique behaviors that ensure effi-

cient nectar and pollen gathering. Bumble bees are undoubtedly worthy of any effort to conserve them. To protect them, however, we need to know more about their habitat requirements so that we can effectively manage and protect their natural foraging and nesting areas. To encourage others to assist in this effort, field guides that assist in the identification of bumble bee species are needed.

REFERENCES

- Buchmann, S.L., and G.P. Nabhan. 1996. *The forgotten pollinators*. Island Press, Covelo, CA.
- Heinrich, B. 1979. *Bumblebee economics*. Harvard University Press, Cambridge, MA.
- Kearns, C.A. and J.D. Thomson. 2001. *The natural history of bumblebees. A sourcebook for investigations*. University Press of Colorado, Boulder, CO.
- O'Toole, C., and A. Raw. 1999. *Bees of the world*. Sterling Publishing Company, New York, NY.
- Schmidt, M.G. 1980. *Growing California native plants*. California Natural History Guides: 45. University of California Press, Berkeley, CA.
- Sladen, F.W.L. 1912. *The bumble-bee. Its life-history and how to domesticate it*. Macmillan & Company, Ltd. London, U.K. Reprinted in 1989 by Logaston Press, Wootton, U.K.
- Thorp, R.W. 2003. Bumble bees (Hymenoptera: Apidae): Commercial use and environmental concerns. In *For non-native crops, whence pollinators of the future?*, ed. K. Strickler and J. Cane, Thomas Say Publications in Entomology: Symposium Proceedings of the Entomological Society of America. In press.
- Thorp, R.W., D.S. Horning, Jr., and L.L. Dunning. 1983. Bumble bees and cuckoo bumble bees of California. *Bulletin of the California Insect Survey* 23:1-79.

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View of Pinnacles National Monument showing the nearly continuous blanket of chaparral over much of the uplands. All photographs by O. Messinger.

A PINNACLE OF BEES

by *Olivia Messinger and Terry Griswold*

*To make a prairie it takes a clover
and one bee,
One clover, and a bee.
And revery.
The revery alone will do,
If bees are few.*

—Emily Dickinson

While floral displays are attractive to the eye, the bright and luminescent petals comprising these often fragrant bouquets play a role far more important than just aesthetics. Ecologically, fields of flowers are competing ad campaigns; yellow spangles of asters and orange washes

of poppies are vying for prospective pollinators.

Bees are notable pollinators in California (Moldenke 1976a), effectively bussing pollen grains from one effulgent floret to consecutive mates. But from the bee's perspective, pollination is a secondary role; each trip to a floret is a purposeful attempt to harvest loads of pollen with which to provision nests. Such interdependence between bees and their flowers raises several community-level questions. Central among these is to what extent these two groups of organisms are dependent upon each other. But we also pon-

der some related issues: Do abundant flowers relate to bee diversity? What is the role of bees in plant success? And what happens when one of these two actors (flower or bee) fails to appear? What does happen, as Ms. Dickinson mused, if bees are few?

Such questions are easier to pose than to answer. Bees are highly mobile and generally short-lived creatures. A complete understanding of bee community dynamics requires not only extensive surveying time, but also unaltered landscapes with little unnatural influence. Pinnacles National Monument is one

such natural laboratory. Comprised of several distinctive habitats and a myriad of flowering plants, this refuge has been virtually untouched by agricultural practices.

It was with high expectations that we accepted an offer from Amy Fesnock, wildlife biologist in Pinnacles National Monument, to embark on a multiyear, systematic study of such a critical faunal component on this 25-square-mile preserve. Here was a rare opportunity to go beyond basic inventory—to study bee spatial and temporal patterns across years and to investigate their complex relationship with plants. By systematically collecting bees from portions of the monument across an entire flowering season, the intricacies of a bee community could be explored. In the face of changing environments, such knowledge is essential to monitoring pollinator health.

Pinnacles National Monument is part of the rugged landscape that lies along the San Andreas Fault in the inner South Coast Range. The diversity of plants in Pinnacles is notably high. While nearly 600 species of flowering plants occur here, chaparral dominates this landscape (see photograph, page 32). Stands of buck brush (*Ceanothus cuneatus*) intermingle with manzanita (*Arctostaphylos* spp.). Holly-leaved cherry (*Prunus ilicifolia*), woolly bluecurls (*Trichostema lanatum*), and black sage (*Salvia mellifera*) prevail amidst the rocky crags of the High Peaks.

Chamise (*Adenostoma fasciculatum*) fills in any remaining gaps, coating rolling hillsides, clothing the highest point (Chalone Peak at 3,304 feet), and often forming pure, impenetrable stands. At the lowest points (minimum elevation, 824 feet) river bottoms support more open communities of blue oak (*Quercus douglasii*) and valley oak (*Q. lobata*).

The park receives an average of only 16 inches of rain each year, primarily in winter precipitation (January to March). The resulting

bloom commences in February with the flowering of manzanita (*Arctostaphylos* spp.). While flowering continues to some extent at least through the middle of October, most of the species at Pinnacles bloom in the spring (March to mid-June).

Pinnacles National Monument was ideal for a bee study not only for its pristine nature, but for other reasons as well. We had high expectations for a rich bee fauna, a presumption that arose from several sources. While most genera achieve their highest diversity in tropical climates, bees flourish in more temperate zones. Drier soils have been hypothesized as the likely explanation for this trend, as they decrease the chance of nest failure due to fungal infection (Linsley 1958).

Previous studies in Mediterranean (Michener 1979) and chaparral regions have produced impressive laundry lists for bees in both North and South America (Moldenke 1976b), leading us to believe the same could be expected in Pinnacles. As anticipated, an exploratory visit to Pinnacles in 1996 yielded 87 species in just four days.

Further incentives for studying bees in Pinnacles included the presence of several recently burned habitats. The largest of these is a burn from August 1993 that charred many acres of chaparral, clearing the way for rare, fire-following plants, as well as providing ample open ground for plants otherwise constrained to rather small sunlit patches. Two additional burns occurred during our study: one was a prescribed burn in the fall of 1997, while the other was a large burn that occurred in August 1998.

Fire is thought to play a vital role in chaparral ecology, as evidenced by the many chaparral shrubs adapted to intense heat. Many fire-following plants appear only in areas that have recently burned. What one might perceive as relatively catastrophic when looking at the remaining crowns of once

robust chamise plants sparked just the opposite response from our bee researchers. Such burns provided us with the opportunity to seek answers to some additional questions: How does the presence of transients like fire-following plants influence bee composition? Since fire and the subsequent bloom are unpredictable, can concrete relationships exist between fire-following plants and bee species?

Minor catastrophes seemed to be a recurring theme during the course of our research, and enabled us to investigate rarely studied processes in bee communities. One such opportunity came in the second year of our study during the torrential rains and cold spring temperatures of the 1998 El Niño event. In the wake of the storms, we were able to observe just how resilient bees are to a climatic change of this magnitude.

METHODS

In order to characterize the bee fauna and its floral relationships, we attempted to collect foraging bees on all flowering plants that occur within Pinnacles across representative areas of the monument. Systematic sampling by net was conducted along trail segments and in other open areas within the typically dense habitats of the monument. Collected bees were first pinned and then labeled with plant association, date of capture, and habitat descriptors (i.e., chaparral or riparian habitat). Finally, our specimens were identified.

Our first concerted collecting effort began in late March 1997. A strict regimen of weekly collections was maintained along a set of selected trails. We returned for two days in late June and once in September to capture what we expected to be a limited summer and fall fauna.

Observations from our first year

of fieldwork indicated the need for an earlier start in the flowering season, so plans were made to begin the 1998 field season in late February (nearly a month earlier). Analysis of 1997 data also indicated that seasonality in bees could still be assessed if sites were collected on a 10-day cycle instead of weekly. This would allow us to expand into more areas of the monument within each round of collecting.

Our carefully laid out plans for 1998 did not anticipate dramatic weather. The spring field season in 1997 was marked by only one rainy day. In contrast, spring 1998, influenced by El Niño, was defined by cold rain and frequent clouds. Creeks that typically were ankle deep became, at times, torrents forceful enough to destroy bridges, closing the monument for nearly a month. In the wake of the downpours, quicksand replaced gravelly beaches, fallen trees and limbs littered last year's groves, and fields of flowers inundated the grasslands of past years.

Restless bee collectors spent many days watching for sunny skies (good "beeing" weather). Indeed, one unbearably long period of sunless skies lasted for 11 days! While the subsequent bloom was incredible, bees that survived the deluge had to cope with a new environment characterized by unseasonably chilly days, repeated rains, and markedly delayed blooming even among the most hardy of chaparral plants. The wet, cool spring delayed and then extended the flowering season beyond our planned end to the field season. To supplement our thorough spring collections and to catch latecomers detained by the weather, we made sporadic collections in June, July, August, and October.

Our final field season was an attempt to assess the effects of the El Niño event. We sampled only during the last three weeks of May 1999—the height of bee activity.

TABLE 1. THE BEE FAUNA OF PINNACLES NATIONAL MONUMENT

Two asterisks indicates *all* members of the genus in Pinnacles are specialists, one asterisk indicates *some* members of the genus in Pinnacles are specialists.

Family	Genus	Number of Species	Clepto-parasites	Oligolectic
Colletidae	<i>Colletes</i>	5		*
	<i>Hylaeus</i>	18		
Andrenidae	<i>Ancylandrena</i>	1		**
	<i>Andrena</i>	60		*
	<i>Calliopsis</i>	7		**
	<i>Panurginus</i>	5		*
	<i>Perdita</i>	13		**
	<i>Conanthalictus</i>	1		**
Halictidae	<i>Dufourea</i>	6		**
	<i>Micralictoides</i>	2		**
	<i>Augochlorella</i>	1		
	<i>Agapostemon</i>	1		
	<i>Dialictus</i>	12		
	<i>Erylaeus</i>	15		
	<i>Halictus</i>	3		
	<i>Lasioglossum</i>	3		*
	<i>Sphecodes</i>	10	•	
	<i>Hesperapis</i>	2		**
	<i>Ashmeadiella</i>	14		*
Megachilidae	<i>Atoposmia</i>	3		**
	<i>Chelostoma</i>	7		**
	<i>Heriades</i>	1		
	<i>Hoplitis</i>	17		**
	<i>Osmia</i>	37		*

Our focus was on the most thoroughly collected areas of previous years. We also sampled the burn that occurred during the late summer of 1998.

RESULTS

Despite rainy days, unexpectedly delayed blooming, and plenty of "strikes" when swinging nets and missing bees, our efforts were richly rewarded. They demonstrated that the diverse flora of Pinnacles is

matched by an amazing array of bees. Nearly 400 bee species are now known to reside in the monument, representing 52 genera and all six North American bee families (see Table 1, pages 34 and 35). The bees at Pinnacles range in size from miniscule (mosquito-sized) to gargantuan (the size of one's thumb), and come in colors as varied as the plants they visit—from coppery greens, to steely blues, or glossy black.

At least two of these bees appear to be endemic to the monu-

TABLE 1 (CONT.)

Family	Genus	Number of Species	Clepto-parasites	Oligolectic
Apidae	<i>Protosmia</i>	1		
	<i>Anthidiellum</i>	1		
	<i>Anthidium</i>	6		*
	<i>Dianthidium</i>	4		*
	<i>Protostelis</i>	2	•	
	<i>Stelis</i>	11	•	
	<i>Trachusa</i>	2		
	<i>Dioxys</i>	4	•	
	<i>Coelioxys</i>	5	•	
	<i>Megachile</i>	17		*
	<i>Xylocopa</i>	1		
	<i>Ceratina</i>	11		*
	<i>Nomada</i>	21	•	
	<i>Epeolus</i>	3	•	
	<i>Triepeolus</i>	3	•	
	<i>Oreopasites</i>	2	•	
	<i>Townsendiella</i>	1	•	
	<i>Exomalopsis</i>	2		
	<i>Diadasia</i>	5		**
	<i>Melissodes</i>	10		*
	<i>Synhalonia</i>	10		*
	<i>Anthophora</i>	11		
	<i>Habropoda</i>	3		
Apidae	<i>Centris</i>	1		
	<i>Melecta</i>	3	•	
	<i>Xeromelecta</i>	2	•	
	<i>Bombus</i>	6		
	<i>Apis</i>	1		
Total		393		

ment and surrounding areas. *Andrena annectans* has been collected only in Pinnacles and the nearby town of Bitterwater; *Ceratina burdi* is known only from Pinnacles and a single site to the west at the north end of the Santa Lucia Mountains. Additional endemics are probable among the 15 new species found in Pinnacles.

Pinnacles also supports a number of species not previously known to occur in the South Coast Range. Several of these are inhabitants of xeric areas to the south, which ap-

pear to reach their northern limit in Pinnacles. Included are the most northerly records for the genera *Ancylandrena* and *Centris*. Four non-native bees are present in the monument. Honey bees (*Apis mellifera*), originally brought over from Europe nearly 300 years ago, are the most prevalent of these. Feral (meaning they have escaped from domestication and become wild) honey bee populations can be found in many hollow stumps throughout the monument. *Megachile apicalis*, a more recent accidental introduction

to the Western Hemisphere, was found almost exclusively on flowers of the non-native, meadow-invading star thistle (*Centaurea solstitialis*).

The vast majority of bees at Pinnacles are solitary. Each female is responsible for her own nests, the cells of which she carefully provisions with collected masses of pollen and nectar. In addition to being solitary, most female bees in Pinnacles nest independently, choosing nesting sites at fair distances from any neighbors. However, some gregarious nesters build aggregations more akin to apartment complexes.

A few sites in Pinnacles seemed particularly popular with certain species, and looking down on such sites is reminiscent of a gopher town with holes by the hundreds peppering the ground. Bees at Pinnacles also include some social species, identified by the fact that all members live together in one nest. These include the well-known honey bee, bumble bees (*Bombus*), and sweat bees (Halictini).

Even within the relatively small area of Pinnacles, bees appear to prefer certain habitats. Burned areas harbored a diverse bee fauna. Well over half of the species in the monument were caught within these areas, yet only a handful of species appear to be restricted to this short-lived habitat. *Centris californica* and *Megachile davidsoni*, previously unrecorded from the Coast Ranges, were present only in the burned areas. In addition, we found that unburned upland areas were home to over half of the total bee fauna. The greatest diversity in Pinnacles, however, exists in and near riparian areas. For example, over 260 species were encountered along the 2.3-mile Old Pinnacles Trail.

The rich bee fauna in Pinnacles National Monument is certainly related to the diverse flora harbored within its boundaries. Bees were found on half of the roughly 600 flowering plants in Pinnacles, visit-

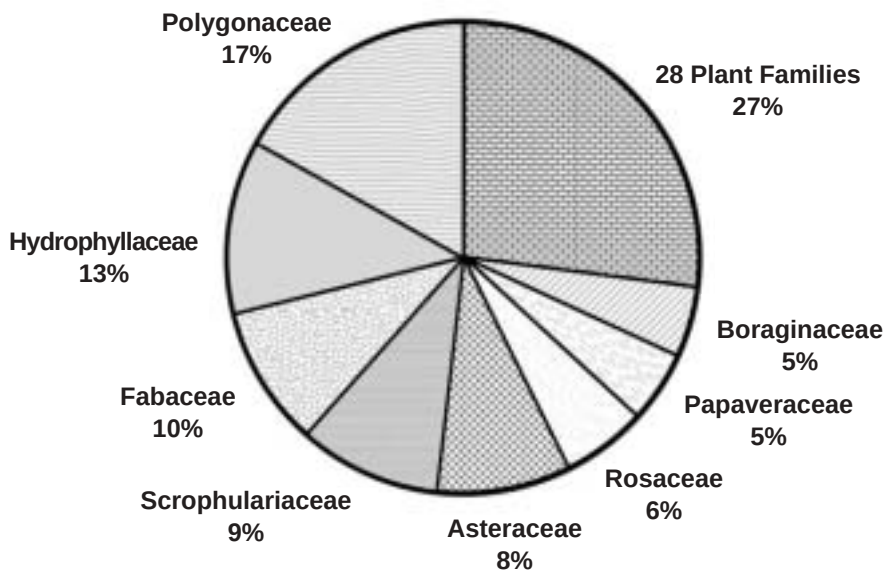


Figure 1. Floral utilization by bees in Pinnacles National Monument. Proportion of females from all years visiting plant families (28 families with less than 4% of bees were combined).

ing nearly two-thirds of the 70 or so plant families in the monument (see Figure 1 above).

While bees visit a large proportion of the flora in the monument, a few plants together support the greatest diversity of bees (see Table 2 on page 37), attracting 53% of all bee species collected in the monument (but representing only 13% of all bee specimens). Buckwheat (*Eriogonum fasciculatum*) alone was found to support over 100 species of bees. The sight of a buckwheat bush obscured by a blurry cloud of miniscule bees is truly amazing, and presents a vivid reminder of the importance of floral resources to bees.

There are several early season plants that were not sampled equally across years. For example, some flowering species that were highly attractive in 1998 were not sampled in 1997, or were sampled only at the very end of their flowering; they might well belong in this table. These plants include: buck brush (*Ceanothus cuneatus*: 18 species), California goldfields (*Lasthenia californica*: 39 species), popcorn plant (*Plagiobothrys nothofulvus*: 50 species), and willow (*Salix* spp.: 28 species).

We noticed that plants which are heavily visited by bees do not necessarily support the highest species diversity; some plants are dominated by only a few species. Nor is plant abundance necessarily indicative of the quality of food resources (pollen and nectar) available to bees. Willow, while sparsely present in the 5% of the monument that is riparian, supports as diverse a bee fauna as does chamise, which dominates in over 90% of the monument.

While bees visit flowers for both nectar and pollen, it is pollen for nest provisions that drives floral visitation patterns for most bees. Some bees (generalists or “polylectic”) collect from a wide array of plants, providing their offspring with a smorgasbord of pollens. Other mothers are more discriminating. These bees (specialists or “oligolectic”) consistently gather pollen from a single genus of plants or a closely-related group of plants.

The evolutionary advantage of such specialization is unclear. Possibilities include more efficient use of time when collecting pollen, less competition with other bees for pollen and nectar, and differences

in larval dietary restrictions. In contrast, the flexibility of generalists may make them less susceptible to the vagaries of flowering times and abundance. Since the flight season of social bees is relatively long compared to the short flowering period of many plants, only solitary species are specialists.

Within Pinnacles, approximately 25% of all pollen-collecting bees are specialists. For example, *Chelostoma cockerelli* and *C. phaceliae* females visit almost exclusively woolly yerba santa (*Eriodictyon tomentosum*) and species of *Phacelia*, respectively. *Megachile davidsoni* consistently visits golden eardrops (*Dicentra chrysantha*), though it is interesting to note that despite consistent bloom and reasonable sampling across all three years of the study, we detected *M. davidsoni* only in 1997. This relationship is made even more interesting by the fact that *Dicentra chrysantha* is a fire-following plant, typically found only in areas that have recently burned, and its populations dwindle as post-fire changes in vegetation occurs. One wonders how this specialist bee manages to detect plant populations as patchy and unpredictable as those of golden eardrops.

A variety of structural and behavioral traits are associated with pollen specialization (Thorp 1979, 2000). Most solitary bees have an area of stiff hairs, called a pollen brush or scopa, into which pollen grains are pushed. In Pinnacles, the bee *Hoplitis* (*Proteridides*) has mouthparts with hooked hairs for pollen extraction from the narrow throats of *Cryptantha* flowers. The specialist bee *Diadasia* accommodates the large pollen grains of *Clarkia* and morning glory (*Calystegia*) with widely-spaced hairs in its scopa. Mouthpart lengths in the bumble bees *Atoposmia* and *Hoplitis* are differentially proportional to corolla depth in flowers, and may allow these bees to collect nectar while harvesting pollen.

Behavioral traits include seasonal emergence from nest cells synchronous with the first bloom of their preferred flowers, foraging coincident with when pollen is available (e.g., early morning foraging by *Synhalonia venusta*, when *Clarkia* pollen is present), and manipulation of flowers with hidden pollen. For example, *Megachile davidsoni* was observed to stand on its head to access the nectar and pollen in flowers of golden eardrops.

Though they are not as common, plant species visited by specialist insects enjoy advantages as well. A generalist flying from a California goldfield (*Lasthenia californica*) to an owl's clover (*Castilleja exserta*) is not likely to leave behind the right kind of pollen. Indeed, such bees are likely to clog the

stigma with useless foreign pollen. In contrast, a specialist bee that only forages on *Lasthenia* flowers can be expected to deposit only conspecific pollen. In this way, the potential for successful fertilization of this plant species is greatly increased.

The form and structure of many plants in Pinnacles demonstrates how plants encourage specialization, thereby narrowing the pool of possible contaminating vectors. The tubes of *Penstemon* flowers are narrow enough that only "skinny" bees can crawl inside where the anthers are located. Many pea flowers require very specific bees. Not only must the bee be able to open the lower keel petal by spreading it with her hind legs; she must also have pollen-collecting hairs on the underside of her abdomen in order to

reap the rewards of the anthers thus exposed. (The majority of bees have pollen-collecting hairs on their legs.)

Most plants in Pinnacles play host to diverse suites of both generalist and specialist bees. This is most easily demonstrated for *Clarkia* because of the comprehensive study by MacSwain et al. (1973) on bee relationships with this plant genus throughout cismontane (in this case, west of the Sierra crest) California. (Such studies are rare for the California flora.)

In Pinnacles, 85 pollen-collecting species visited *Clarkia* at one or more of the 12 sampling sites where it was present. Though the majority of these species were generalists (76), the handful of specialists represented over half of the visits to *Clarkia*. This high dependence

TABLE 2. DIVERSITY OF BEES ON MAGNET PLANTS IN PINNACLES

Diversity is based on females only. As sole collectors of pollen, their visitation patterns are more indicative of the importance of floral components.

COMMON NAME	LATIN NAME	1997		1998	
		NUMBER OF SPECIMENS	SPECIES	NUMBER OF SPECIMENS	SPECIES
California buckwheat	<i>Eriogonum fasciculatum</i>	1196	104	1139	78
California broom	<i>Lotus scoparius</i>	490	67	210	49
Yerba santa	<i>Eriodictyon tomentosum</i>	337	53	31	19
California poppy	<i>Eschscholzia californica</i>	248	44	68	20
Clarkia	<i>Clarkia unguiculata</i>	243	48	99	26
Chinese houses	<i>Collinsia heterophylla</i>	181	39	107	34
Summer mustard	<i>Hirschfeldia incana</i>	133	53	27	15
Chamise	<i>Adenostoma fasciculatum</i>	90	19	225	30

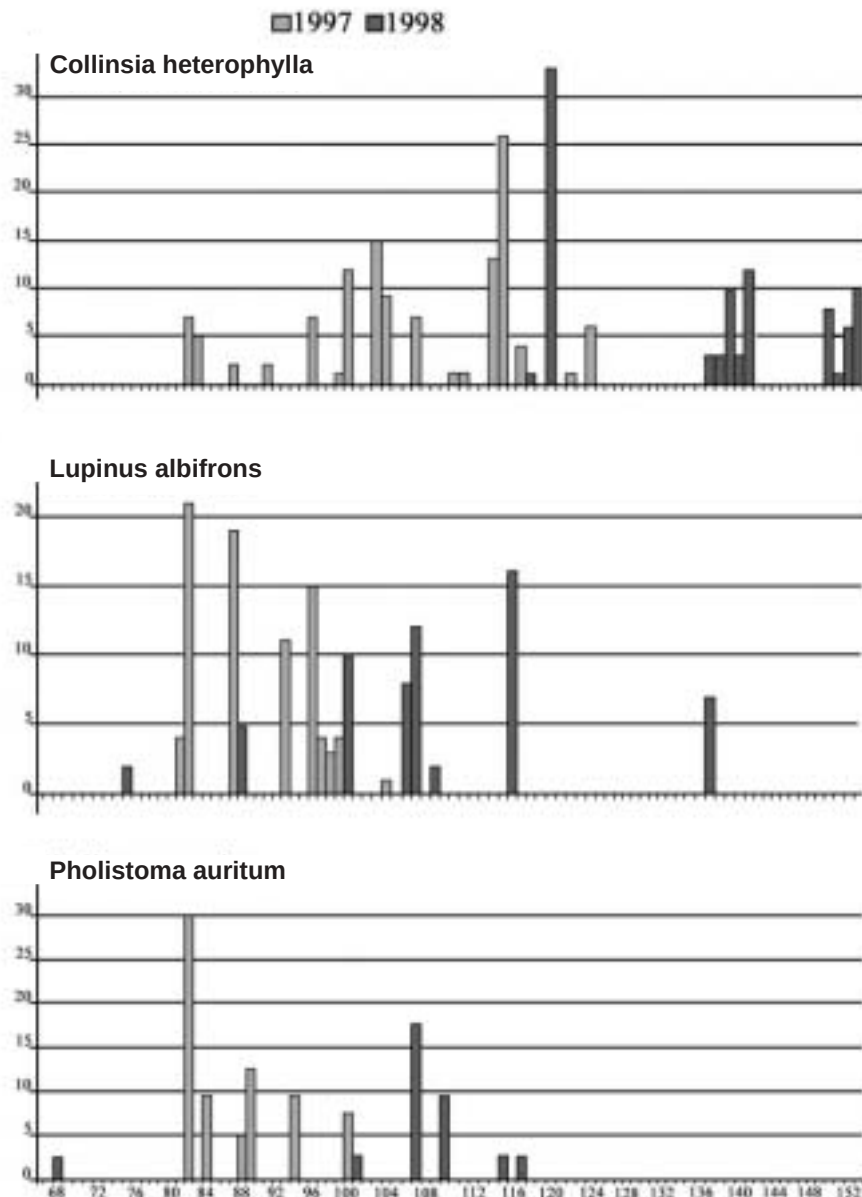


Figure 2. Phenological shift of bee activity in Pinnacles between successive years for three flowering plants. X-axis = day of year; Y-axis = relative number of flower visits.

makes *Clarkia* specialists more predictable. All nine *Clarkia* specialists known to occur in the South Coast Range (MacSwain et al. 1973) are present in Pinnacles. Indeed, specialist bees could be accurately predicted in the 12 *Clarkia* sites 44% of the time, versus 22% of the time for generalists. One such bee, *Hesperapis illicifoliae*, was present wherever *Clarkia* was found.

On the other hand, and despite the fairly broad distribution of *Clarkia* in Pinnacles, *Diadasia angusticeps* (another specialist) was consistently present in only one lowland *Clarkia* patch across all three spring seasons. The reason for this restriction is un-

known, though *Diadasia* may be limited to fine-grained, hard-packed level ground for nesting. *Diadasia*, with its particular food and nesting habits, is a nice example of the variety of factors that play a strong role in bee patterns of abundance.

The restrictions on bee ranges are additive. A species can only exist where all the environmental components necessary for survival occur; for example, where appropriate nesting conditions and adequate flowers overlap. While nesting preferences were not the focus of this study, we did observe a diversity of nest site preferences for bees in Pinnacles. The majority of nonpara-

sitic bee species in Pinnacles (62%) nest in the soil. Most excavate their own nests, and some show preference for specific sediments.

A significant number of bees nest in stems or wood (28%), including all of the exotic bees. Most of these are "renters," bees that occupy already existing holes, but a few drill into pithy stems or soft wood. Many of the renters also require specific nest-building materials for construction of nest cells, such as mud, gravel, resin, or leaf material. Certain *Osmia*, for example, were found in large numbers along the moist banks of waterways in Pinnacles, likely because this was an excellent place to mine mud for their nests.

By comparison, *Trachusa* populations were found in two dry locations with friable soils higher up in the monument. These soils were in proximity to manzanita, whose leaves *Trachusa* cut into narrow strips to line their nests. This shrub, then, may be a determinant in defining this bee's distribution. Other bees (for example, *Dianthidium*) take advantage of the prevalent rocky surfaces throughout the monument, building their nests like miniature masons on the craggy cliffs.

Not all the bees of Pinnacles are pollen collectors. Some surreptitiously deposit their eggs in the nests of other bees (cleptoparasites). Fully 17% of the bees at Pinnacles display such behavior (see Table 1, pages 34 and 35). Upon hatching, the parasite larva destroys the host egg or larva and then consumes the pollen provisions. Since these bees parasitize specific pollen-collecting bee genera, their distributions are defined by that of their hosts.

Most bees in Pinnacles only live for a short time. Exceptions include many of the social species, like the honey bee. Seasonal patterns observed in Pinnacles suggest that the average duration of adult activity for a solitary species is roughly a month to six weeks, with individual life spans likely less. Since the sea-

son of bee activity spans nine months, the bee population is therefore constantly renewing itself. The bee species flying in the spring are not the same species flying in the fall. In fact, of the bees flying at any given time in the spring, 50% finish provisioning nests and die over the next two weeks. Perhaps this high rate of turnover is related to the incredible number of species present in such a relatively small area.

A comparison of the seasonal abundance of bees between 1997 and 1998 demonstrates the effect El Niño had on both bee and plant activity (see Figure 2, page 38). Like a baseball game perpetually postponed, nearly all budding flowers in 1998 waited at least a month longer than they did in 1997 to bloom—presumably as a result of the extremely cold, wet spring months of the El Niño year. A look at the bee patterns of emergence (indicated by first collections) shows a similar seasonal shift. More interestingly, such delayed emergence coincides very closely with times of plant bloom.

Though bees appear to track their floral resources, bee populations may experience rapid declines independent of the availability of floral resources, leaving blooms largely unattended. In 1997 we observed a flurry of activity as an entire hillside in the 1993 burn buzzed with a single species of bumble bee (*Bombus crotchii*) that was taking advantage of snapdragon (*Antirrhinum*) flowers. By our estimation, several thousand bumble bees were foraging on that hillside at any one time.

Snapdragon continued to bloom substantially in subsequent years, yet bumble bees were few. Perhaps, like their flowered partners, bees can be capricious too. The relationship is a complex one—bee population size is determined by resource availability in the year prior to their emergence. Conversely, the population size of annual plants de-

pends on a seed bank and is determined by resource availability immediately prior to germination.

As an example, consider two successive years. In the first one, little rain falls, and few flowers germinate. Bee mothers have a limited pollen supply with which to provision nest cells, and they lay few eggs. The following year may be relatively wet with abundant flowers. However, bees are scant because of the drought the previous year, and so open blossoms go unvisited. Perennials, while less influenced by variations in rainfall, still flower in response to the precipitation from the current year.

Relationships may be further complicated by variation in the availability of nest sites. Bumble bees, which often utilize rodent burrows for nests, may be affected by fluctuations in rodent populations. Nesting queens in the cold, wet spring of 1998 may have experienced high mortality due to the inability to forage or may have been drowned out of their nests.



The crags of Pinnacles.

Weather in 1998 severely impacted other bees. All species of small carpenter bees (*Ceratina*) experienced radical reductions in populations despite the fact that they are generalists and active throughout the blooming season. *Ceratina* nest in pithy stems, and the relative fragility of this nesting material may have made them particularly susceptible to the severe weather. *Hylaenus*, which frequently nest in stems, also appear to have suffered population crashes.

TABLE 3. GENERIC AND SPECIES DIVERSITY AMONG BEE FAUNA IN THE UNITED STATES

LOCATION	GENERA	SPECIES	APPROX. TOTAL AREA (sq. mi.)
Clark County, Nevada	67	598	7,910
Mojave Natl. Preserve, California	58	305	2,500
Pinnacles Natl. Mon., California	52	398	25
San Rafael Desert, Utah	49	333	2,000
Curlew Valley, Idaho	43	340	1,930
Albany County, Wyoming	40	194	4,273
Channel Islands, California	36	154	349
Sand Mt. & Blow Sand Mt., Nevada	28	59	4.8
New England	43	365	63,851

Modified from Griswold et al. 1998.

SUMMARY

Our study suggests that this region may be one of the hotspots of bee diversity in the world. Comparisons with other well-studied bee faunas in the United States (see Table 3 on page 39) support this contention, particularly when one considers the much greater size and habitat diversity of most of the other studies. Pinnacles, with significantly less than 1% (more like 0.001%) of the total landmass of the contiguous United States, is home to over 10% of all US bee species, and 43% of the genera. The diversity of bees in Pinnacles compares favorably not only within the US but with other regions around the world.

A five-year study of a Mediterranean site in Greece amassed only 262 bee species (Petanidou and Ellis 1993). Studies in a chaparral community in Chile yielded just 183 species (Moldenke 1976b). Even within the South Coast Range, Pinnacles may be unusually diverse. A four-year study of *Osmia* in the UC Hastings Reserve, located less than 25 miles west of Pinnacles, resulted in 30 species (Barthell et al. 1997) compared to 37 within the monument (35% of all *Osmia* in California, 24% of those in the US). Though comparisons for other genera are not available, such high numbers for *Osmia* are indicative of a rich diversity for other components of the bee fauna of Pinnacles.

Three years of fieldwork have demonstrated that the bees of Pinnacles are diverse and ubiquitous. While the sheer numbers of bees encountered leave no doubt as to the importance of this often overlooked element, field observations indicate that relationships between pollinators and host plant populations are fluid across seasons and sites. There remains little doubt that bees and flowers are mutually dependent on each other. Indeed, for Pinnacles we now have floral pref-

erence information for a wide array of bees, some of whom have ranges that extend far beyond the monument, but the consequences of their fickle natures is ponderous.

These observations warrant additional studies on many fronts: How do bees time their emergence with flowers? What, if any, safeguards might bees (particularly specialists) possess to ward off extinction when flowers fail to flourish? And alternatively, what measures might a plant incorporate for their own preservation in the face of inconsistent bees? Further, such fluctuations emphasize the importance of multi-year studies to document the full fauna of a pollinating community—the significant find of *Megachile davidsonii*, for example, a bee collected in only one of the three years.

As stewards in Pinnacles National Monument, managers must efficiently monitor long-term trends in inherently variable pollinator populations. Such an in-depth understanding of pollinator faunas is the first step to ensuring healthy pollinator services in what increasingly threatens to become an island in a sea of development. Conserving such pollinator functions and the wealth of bee diversity it requires is pivotal in maintaining the flowering fields of spring.

ACKNOWLEDGMENTS

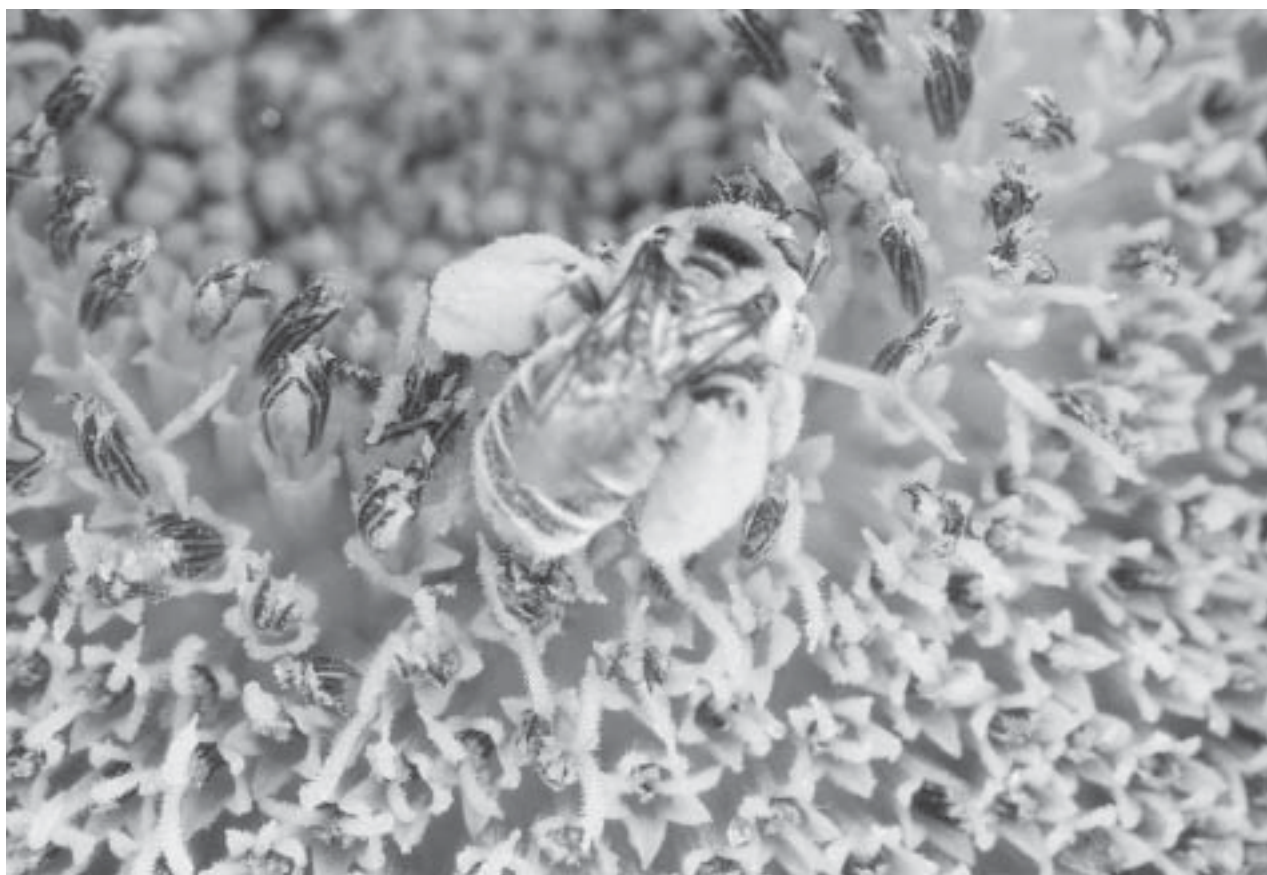
Our work in Pinnacles National Monument would not have been successful without the assistance and encouragement of the monument staff. We particularly want to thank members of the resource division, Amy Fesnock, Larry Whalon, Tom Leatherman, and Chad Moore. Thanks also to Melissa Andres and Carol Shultz, who assisted with the summer fieldwork; to Susanna Messinger, Wensdae Miller, and Gina Garvin for processing specimens; and to Linda Kervin, who

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REFERENCES

- Barthell, J.F., T.L. Griswold, G.W. Frankie, and R.W. Thorp. 1997. *Osmia* diversity at a site in central coastal California. *Pan-Pacific Entomologist* 73:141–151.
- Griswold, T., F.D. Parker, and V.J. Tepedino. 1998. The bees of the San Rafael Desert: Implications for the bee fauna of the Grand Staircase—Escalante National Monument. In *Learning from the land: Grand Staircase—Escalante National Monument Science Symposium Proceedings*, ed. L.M. Hill, pp. 23–34. Cedar City, UT.
- Linsley, E.G. 1958. The ecology of solitary bees. *Hilgardia* 27:543–599.
- MacSwain, J.W., P.H. Raven, and R.W. Thorp. 1973. Comparative behavior of bees and Onagraceae. IV. *Clarkia* bees of the western United States. *University of California Publication in Entomology* 70:1–80.
- Michener, C.D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Gardens* 66:277–347.
- Moldenke, A.R. 1976a. California pollination ecology and vegetation types. *Phytologia* 34:305–361.
- Moldenke, A.R. 1976b. Evolutionary history and diversity of the bee faunas of Chile and Pacific North America. *Wasmann Journal of Biology* 34:147–178.
- Petanidou, T. and W.N. Ellis. 1993. Pollinating fauna of a phryganean ecosystem: composition and diversity. *Biodiversity Letters* 1:9–22.
- Thorp, R.W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Annals of the Missouri Botanical Gardens* 66:788–812.
- Thorp, R.W. 2000. The collection of pollen by bees. *Plant Systematics and Evolution* 222:211–223.

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Diadasia, the sunflower bee, on *Helianthus annuus*. Photograph by D.L. Briggs.

NATIVE BEES, NATIVE PLANTS, AND CROP POLLINATION IN CALIFORNIA

by Claire Kremen, Robert L. Bugg, Nikki Nicola, Sarah A. Smith,
Robbin W. Thorp, and Neal M. Williams

California is recognized globally as an area of exceptional plant diversity containing a host of plants found nowhere else in the world. It is also the most important agricultural area in North America, producing half of the US supply of fruits, nuts, and vegetables at an annual value of \$16.45 billion, and exporting \$6.5 billion of food and agricultural commodities abroad.

Insect pollinators are critically important both for the maintenance of California's diverse natural ecosystems and for its agricultural productivity. In 1997, honey bees alone

were credited with contributing \$4.2 billion to crop productivity in California (E. Mussen, pers. comm.). Here we focus on the under-appreciated role that native bees play in California's agricultural productivity, and how California's native plants support these native bee populations.

A large number of flowering plants (Angiosperms) rely on an animal for pollination, successful seed set, and fruit growth. Even self-fertile plants (e.g., tomatoes) or plants

Osmia lignaria, the blue orchard bee, on almond. Photograph by D.L. Briggs.





The Cache Creek Valley, showing large areas of chaparral-oak woodland adjacent to farm fields. Photograph by C. Kremen.

that are typically wind-pollinated (e.g., grapes) can benefit from animal “vectors”—animals that help to transport pollen. Their help makes possible cross-pollination, which can produce larger, better-tasting fruits with more viable seeds, and enhanced genetic diversity in seedlings.

In the United States, over 100 crops are bee-pollinated, and 15–30% of the average American diet is comprised of bee-pollinated foods. Thus, bee-pollinated crops make up an important component of human dietary stability and diversity. Some of the fruits and vegetables requiring bee pollination include: alfalfa, almond, apple, avocado, cantaloupe, cucumber, kiwi, plum, squash, sunflower, watermelon, and selected cultivars of apricot, citrus, peach, and strawberry. In addition, a far larger set of fruits and vegetables require insect pollinators for seed or hybrid seed production.

Bees (superfamily Apoidea) are thought to be the most important group of pollinators for both crop and non-crop plants. Female bees are one of the few insect groups that specialize in pollen collection to feed their larvae. Over time, they have developed physical traits designed for collecting pollen. These include numerous “hairs” on their bodies to which pollens adhere, and specialized structures known as scopae or corbiculae for storing and transporting pollen on their legs or abdomens.

Bees also tend to forage consistently on one plant species before returning to the nest to deposit their pollen loads. This behavioral fidelity enhances the chance that pollen will be transported from flower to flower of the same species, ensuring reproduction. Although male bees do not collect pollen, they too are often hairy and can transfer pol-

len as they visit flowers in search of nectar or mates.

Over 4,000 species of bees occur in North America, and 1,500 are currently found in California (Thorp, observations). The vast majority of these bees are “solitary” species rather than the familiar social honey bees and bumble bees. Females of solitary species collect pollen, mold it into a pollen “loaf,” and seal it along with a single egg into a nest cavity.

Within this nest the larvae then hatch, complete development, and pupate, finally emerging as adults. All of this occurs with no further maternal care. Each bee species is specific in its choice of nesting substrate: these range from simple to elaborate tunnels dug into the ground, to cavities in twigs or dead wood.

Many farmers import colonies of the European honey bee, *Apis*

mellifera, to ensure adequate pollination of crops requiring bee visits for fruit set. Unfortunately, declines in the availability of colonies due to diseases, loss of bee-keeping subsidies, and pesticides, have led to shortages of pollination services at times. Overall, there are now less than half the number of bee colonies that existed back in the 1950s, although the demand for bees in some areas continues to increase.

California uses over a third of the available 2.6 million commercial hives each year for almond pollination alone, importing many hives from other states as distant as the Dakotas, Texas, and Florida (E. Mussen, pers. comm.).

Native bee pollinators may be taking up some of the slack caused by honey bee shortages, but the quantitative importance of most native bee species in crop pollination remains largely undocumented. In a few cases, native bees are known to be more effective pollinators than honey bees. Examples include the alkali bee (*Nomia melanderi*) on alfalfa; bumble bee species on watermelon and blueberry; and various native bees on sunflower.

Native bees may be at risk, however, from environmental change. Pesticides have taken their toll on native bee populations as they have on honey bees, and have been responsible for the failure of the blueberry crop in Canada. Habitat loss, fragmentation, and degradation are suspected agents in the decline of native bee populations and diversity. Native bees require natural habitat to provide blooming plants throughout their flight period, and nesting sites for rearing young. As natural habitats are converted to industrial or agricultural uses, available areas that can support bees are declining.

Thus while natural ecosystems may be providing pollinators—and hence pollination services—for free, non-sustainable land use is potentially eroding these benefits. We

therefore set out to understand the role of unmanaged native bees in crop pollination, and how the services they provide change as environmental conditions are altered. Since 1999 we have carried out this work in California in Yolo, Solano, and Napa counties; on farm sites situated in the Central Valley; and in the Cache and Putah Creek watersheds on the eastern edge of the Inner Coast Range.

ROLE OF NATIVE BEES IN CROP POLLINATION

To date, we have identified 65 native bee species that visit and potentially pollinate a variety of principally summer California crops, and 14 additional bee species that visit crops but probably do not contribute to pollination (see Table 1 on page 44). The latter species are either parasitic “cuckoo bees” that

do not collect pollen themselves, or are bees that carry pollen internally.

Further investigation of spring crops (mostly orchards) will undoubtedly increase the number of species involved. For crops that we have investigated in detail, we found that native bees often make up a high proportion of the total bee visits (i.e., visits that include honey bees), suggesting that native bees can be as or more important than managed honey bees for these crops (Table 1).

In watermelon, a crop that requires multiple bee visits and deposition of 500–1,000 pollen grains for production of a marketable fruit, we found that the native bee community alone could provide sufficient pollination for the crop. This ability, however, depended on the diversity and abundance of bees in the community, which in turn was dependent on the abundance of native habitat in the area.

As agricultural operations have

A typical conventional farm field in the Sacramento Valley. No floral resources, other than those provided by the crop (in this case watermelon) are available. Photograph by C. Kremen.



expanded and intensified in areas of California, native habitat declined and could no longer support a sizeable native bee community. Consequently, native bees could no longer provide the needed pollination services without the addition of honey bee colonies.

The majority of organically-managed farms located near native habitat obtained sufficient pollination solely from the native bee community. For those located far from native habitat, a much smaller percentage of organically-managed farms and no conventionally-managed farms received sufficient pollination from native bees. These latter farms relied on honey bees for pollination.

We also found that crops typically thought of as "self-pollinated" benefited substantially from native

bee visitation. Tomato flowers produce no nectar, and their pollen can only be accessed from poricidal anthers by high frequency vibration. Honey bees are unable to vibrate the flowers, and thus obtain few rewards from tomato flowers (hence the low proportion of honey bee visits, as shown in Table 1). However, bumble bees and other bees (e.g., *Anthophora urbana*) can obtain the pollen through vibration, and can often be found exploiting this honey bee-free niche.

By excluding bees from certain flowers, cross- and self-pollinating other flowers by hand, and then comparing these against flowers accessible to bees, Smith and Kremen (in prep.) found that native bees significantly increase the fruit set and size of Sungold cherry tomatoes by promoting cross-pollination.

WILD HABITAT AND CROP POLLINATION

Many native bee species require a diversity of floral resources to provide nectar and pollen throughout their flight season. In addition, they require protected areas for nesting, including twigs, dead wood, bare soil, and abandoned rodent nests. It therefore seemed that native bee crop pollinators would more likely be found on farms close to natural habitat.

In order to test this hypothesis, we conducted two types of studies. First we measured the diversity and abundance of crop visitors to watermelons and tomatoes on farms that varied in nearby natural habitat from 0-80% cover within a 1 kilometer radius. For watermelon crop visitors, nearby natural habitat strongly affected both native bee diversity and total abundance. For tomato, which has only two types of frequent visitors, bumble bees (*Bombus* spp.) and *Anthophora urbana*, we found that the amount of natural habitat positively affected visitation by bumble bees but not by *A. urbana*.

Bumble bees nest in abandoned rodent nests and have long flight seasons, extending from early spring to late summer. In addition, bumble bee colonies produce only one reproductive generation per year, and thus only one nest is established per colony per season. Solitary *A. urbana* females excavate nests in the ground; this species has a shorter flight season from late spring to late summer. It is multivoltine (multiple reproductive generations per year), and nest sites could therefore shift over time to track the available floral resources from place to place.

Perhaps bumble bee queens seek out nest sites close to abundant floral resources in the early spring, which are largely concentrated in wild habitat. Later in the summer when most California wildland species have finished blooming, bumble bee workers forage at floral resources

TABLE 1. NUMBERS OF NATIVE BEE SPECIES AND PROPORTIONS OF TOTAL NATIVE BEE VISITORS (out of all bee visits including honey bees) to selected crops in Yolo and Solano counties, California

Crop	Native bee visitors (number of species)	Additional non-pollinating visitors (number of species)	Average proportion of total bee visits from native bees	Range across farms (proportions)
Watermelon	30	9	0.27	0.0 – 0.88
Sunflower	25	2	0.37	0.01 – 0.99
Strawberry	16	2	0.96	0.87 – 1.00
Muskmelon	11	0	0.08	0.0 – 0.42
Tomato	6	0	0.98	0.89 – 1.00
Almond	5	1	–	–
Eggplant	5	0	0.74	0.33 – 1.00
Cucumber	3	0	–	–
Squash	2	0	–	–
Total	65	14		



Riparian habitat including *Cercis occidentalis* (western redbud), an important spring resource for bumble bees and other bees. Photograph by C. Kremen.

on farms, but are constrained to foraging within a certain distance of their nest sites in the wildlands.

In contrast, both farm and wild resources are abundant when *A. urbana* begins nesting, so females can choose either area for nesting. In addition, subsequent generations of *A. urbana* may shift nest sites to track resource availability and gradually move nest sites into agricultural areas.

We also surveyed bees in wild habitats in the Cache and Putah Creek watersheds in order to determine which of our crop pollinators also occur in the wild areas. These sites were characterized as either

riparian or mixed chaparral and oak woodland. In fact, we found all of them there—54% in both habitat types, 17% in riparian alone, and 29% in chaparral/oak woodland alone.

CALIFORNIA NATIVE PLANTS AND BEES

Finally, we explored the habitat relationships and resource needs of bee species by sampling bees on California native plants in six chaparral/oak woodland and riparian sites from January through October of 2001. Our main focus was on

perennials, shrubs, and trees. We now have detailed records of which native bee species utilize which plant species in this area. We are currently complementing the work presented here with a more comprehensive study that also includes native annuals, weeds, and crops monitored at biweekly intervals at 22 farms and natural area sites.

The results for the 2001 study are summarized in Table 2 (on pages 46 and 47). Table 2 shows which California perennials provide resources for the greatest number of important crop pollinator species. Importance of crop pollinator species was defined as those insects

TABLE 2. CROP AND NON-CROP VISITORS TO CALIFORNIA

NATIVE PERENNIALS. Organized by the maximum number of important crop visitors (see text) visiting a plant. Species currently used in hedgerow or tail water plantings in Yolo and Solano counties are indicated by “Y”; other species available in nurseries are indicated by a *. A + indicates that European honey bees (*Apis mellifera*) were also observed foraging on these plants.

Plant species	NUMBER OF BEE SPECIES					
	Currently used in hedgerow or tailwater plantings	Important crop visitors	Other crop visitors	Parasitic bee crop visitors	Non-crop visiting bees	All bees
<i>Heteromeles arbutifolia</i> ⁺	Y	10	8	1	20	39
<i>Eriogonum fasciculatum</i>	Y	8	8	4	11	31
<i>Baccharis salicifolia</i> ⁺	Y	5	8	0	19	32
<i>Mentzelia laevicaulis</i> ⁺	–	5	2	0	1	8
<i>Eriodictyon californicum</i> ⁺	–	4	4	1	26	35
<i>Cercis occidentalis</i> ⁺	Y	4	9	1	10	21
<i>Rosa californica</i> ⁺	Y	4	1	1	0	6
<i>Lotus scoparius</i> ⁺	–	3	3	0	15	21
<i>Adenostoma fasciculatum</i> ⁺	*	3	7	1	3	14
<i>Lupinus succulentus</i> ⁺	–	3	1	0	3	6
<i>Cornus sericea</i> ⁺	*	3	3	0	1	6
<i>Eremocarpus setigerus</i>	–	3	1	1	1	6
<i>Eriophyllum lanatum</i>	–	2	2	0	8	12
<i>Baccharis pilularis</i> ⁺	Y	2	4	0	6	12
<i>Hemizonia congesta</i>	–	2	0	0	1	3
<i>Lupinus microcarpus</i>	–	2	0	0	1	2
<i>Ceanothus cuneatus</i> ⁺	Y	1	8	0	11	20
<i>Lepechinia calycina</i> ⁺	–	1	4	1	10	16
<i>Epilobium canum</i> ⁺	*	1	4	0	4	9
<i>Stephanomeria virgata</i>	–	1	1	0	4	6
<i>Salix laevigata</i> ⁺	Y	1	4	0	2	7
<i>Mimulus aurantiacus</i> ⁺	Y	1	2	1	2	6
<i>Rhamnus californica</i>	Y	1	3	0	2	6

TABLE 2 (CONT.)

Plant species	NUMBER OF BEE SPECIES					
	Currently used in hedgerow or tailwater plantings	Important crop visitors	Other crop visitors	Parasitic bee crop visitors	Non-crop visiting bees	All bees
<i>Sambucus mexicanus</i> ⁺	Y	1	2	0	2	5
<i>Madia elegans</i>	—	1	0	0	1	2
<i>Arctostaphylos manzanita</i> ⁺	Y	1	2	0	1	3
<i>Rupertia physodes</i>	—	0	0	0	7	7
<i>Ceanothus oliganthus</i> ⁺	—	0	2	0	6	8
<i>Salix sessilifolia</i>	—	0	1	0	3	4
<i>Wyethia helenioides</i> ⁺	—	0	1	0	3	4
<i>Calystegia purpurata</i>	—	0	3	0	2	5
<i>Lupinus albifrons</i> ⁺	*	0	1	0	2	3
<i>Fraxinus dipetala</i>	—	0	0	0	2	2
<i>Clarkia</i> sp.	—	0	0	0	1	1
<i>Phacelia imbricata</i>	—	0	0	0	1	1
<i>Toxicodendron diversilobum</i> ⁺	—	0	0	0	1	1
<i>Triteleia laxa</i>	—	0	0	0	1	1
<i>Aesculus californica</i> ⁺	Y	0	1	0	0	1
<i>Clematis lasiantha</i>	*	0	1	0	0	1
<i>Eriogonum nudum</i>	—	0	1	0	0	1
<i>Eschscholzia californica</i>	Y	0	1	0	0	1
Total bee species in category		16	49	14	113	192

visiting three or more of the crops listed in Table 1. In total, we document records of 192 native bee species on 41 native plant species. Table 2 also lists the number of other crop visitors and of non-crop-visiting native bee species.

Many of the plant species important for the crop pollinators also provide resources for other bee spe-

cies. Six of the 10 plant species with the greatest number of records for important crop pollinators were also critical for other bee species (*Eriodictyon californicum*, *Heteromeles arbutifolia*, *Baccharis salicifolia*, *Lotus scoparius*, *Eriogonum fasciculatum*, and *Cercis occidentalis*). The remaining top 10 plants for crop pollinators included *Mentzelia laevicaulis*, *Rosa*

californica, *Adenostoma fasciculatum*, and *Cornus sericea*, and for non-crop visitors were *Ceanothus cuneatus*, *Lepechinia calycina*, *Eriophyllum lanatum*, and *Rupertia physodes*.

Since the honey bee, *Apis mellifera*, is also an important, although non-native, crop pollinator, Table 2 lists the native plants at which we observed *A. mellifera* foraging. This

species makes use of a wide variety of the California flora, and beekeepers clearly benefit during off-crop seasons by using wild areas for bee forage.

CONCLUSIONS

Our work during the past four years has documented that California's native bees make an important contribution to crop pollination. This contribution could become even more valuable as an "insurance policy" if honey bees become more scarce or fail altogether. We have also shown that all of these native bee species occur in

wild habitats and show some degree of dependence on the native California flora.

Finally, the destruction of native habitat in the Central Valley appears to be related to a decline in the diversity and abundance of native bees found there, along with a concomitant reduction in the crop pollination services they provide. A hopeful sign, however, is that even small fragments of wild or semi-wild habitat still sport diverse and abundant bee faunas, such as at the Cache Creek Nature Preserve, a 130-acre riparian and upland area that is currently being restored.

It is important to conserve bee habitat to maintain the valuable

crop pollination services that bees provide. In Yolo, Solano, and Napa counties, certain areas are already protected to some degree, including, for example, the Cache Creek Nature Preserve, Jepson Prairie, Yolo Basin Wildlife Area, Putah Creek UC Davis Campus Reserve, Quail Ridge Reserve, Cold Creek Canyon Reserve, Cache Creek Canyon Regional Park, Nichols County Park, and the Bureau of Land Management lands along Blue Ridge. All but the first four sites, however, are located in the hilly areas of the Inner Coast Range, and very few natural or semi-natural lands remain within the Sacramento Valley itself.

Eriodictyon californicum (yerba santa) and *Mimulus aurantiacus* (sticky monkeyflower) of chaparral. *E. californicum* is visited by a wide number of bee species, whereas *M. aurantiacus* is rarely visited, and only by a few species. Photograph by C. Kremen.



Bringing bees back to the Sacramento Valley would require an extensive restoration effort. Nonetheless, the dream of restoring healthy communities of pollinators by restoring their plant communities is not outside the realm of possibility. On-going restoration efforts along Cache Creek and Putah Creek can ultimately provide archipelagoes and corridors of bee-friendly habitat. Over the next 30 years, 1,000 acres of restoration efforts are planned along Cache Creek alone (J. Lowrey, pers. comm.).

Farmers can assist the restoration process and benefit their own crops through the planting of "insectary plants" that provide habitat and resources for beneficial insects ranging from predators to pollinators. The Community Alliance of Family Farmers and the Yolo County Resources Conservation District actively encourage the planting of hedgerows and tailwater ponds using native plants (including some of the plants listed in Table 2).

Many of the plants that farmers are already using were selected because they provide pollen or nectar to other beneficial insect species, primarily predators and parasitoids of crop pests. Our data show that many of these plants also benefit some of the most important crop pollinators, as well as other bee species.

Some potentially important plants for pollinators, however, are either difficult to include in hedgerow plantings because they cannot be brought into cultivation, such as *Eriodictyon californicum* (J. Gerland, pers. comm.) or have not yet been tested (e.g., *Lotus scoparius*). Some of these plants may prove critical—providing resources for a particularly important bee species, or filling in a "phenological window" during which no bee-attractive plants from the current hedgerow list are blooming.

Our current research will provide a rich dataset for identifying

new plants to add to existing reserve and farm restoration efforts for the benefit of the pollinator community. And "bringing back the bees" will ensure a much rosier future for California's native flora.

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REFERENCES

Bugg, R.L., J.H. Anderson, C.D. Thomsen, and J. Chandler. 1998. Farmscaping in California: Hedgerows, roadside plantings and wild plants for biointensive pest management. In *Enhancing biological control: Habitat management to promote natural enemies of agricultural pests*, ed. R.L. Bugg. University of California Press, Berkeley, CA.

California Technology, Trade and

Commerce Agency. www.commerce.ca.gov/state/ttca/ttca_homepage.jsp

Frankie, G.W., S.B. Vinson, M.A. Rizzardi, T.L. Griswold, S. O'Keefe, and R.R. Snelling. 1998. Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. *Journal of the Kansas Entomological Society* 70:281–296.

Kevan, P.G., E.A. Clark, and V.G. Thomas. 1990. Insect pollinators and sustainable agriculture. *American Journal of Alternative Agriculture* 5:12–22.

Kevan, P.G., and W.E. LaBerge. 1979. *Demise and recovery of native pollinator populations through pesticide use and some economic implications*. IVth International Symposium on Pollination, 489–508. Maryland Agriculture Experiment Station, College Park, MD.

Matheson, A., S.L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams. 1996. *The conservation of bees*. Academic Press, San Diego, CA.

McGregor, S.E. 1976. *Insect pollination of cultivated crop plants*. USDA-ARS, Washington, D.C.

Moldenke, A.R., and J.L. Neff. 1974. *The bees of California: A catalogue with special reference to pollination and ecological research*. International Biological Program, Santa Cruz, CA.

Nabhan, G.P., and S. Buchmann. 1997. Services provided by pollinators. In *Nature's services: Societal dependence on natural ecosystems*, ed. G.C. Daily, 133–150. Island Press, Washington, DC.

O'Toole, C., and A. Raw. 1992. *Bees of the world*. Facts on File, New York, NY.

Proctor, M., P. Yeo, and A. Lack. 1996. *The natural history of pollination*. Timber Press, Portland, Oregon.

Tepedino, V.J., S.D. Sipes, J.L. Barnes, and L.L. Hickerson. 1997. The need for "extended care" in conservation: Examples from studies of rare plants in the western United States. In *Proceedings of the International Symposium on Pollination*, ed. K.W. Richards, 245–48. ISHS.

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Eschscholzia californica (California poppy) and other native plants in flower beds of the Peralta Garden, Berkeley. Photograph by G.W. Frankie.

BEES IN BERKELEY?

by Gordon W. Frankie, Robbin W. Thorp, Mary H. Schindler,
Barbara Ertter, and Margaret Przybylski

The bee fauna of California has received considerable study over the years by numerous researchers who focused much of their attention on the systematics, distribution, and biology of bees in mostly wildland environments. Based on these studies, it is estimated that the highly diverse habitats of California probably house about 1,500 species (Thorp, pers. obs.); about 4,000 are thought to occur in the continental US.

The vast majority of these bees are solitary in their life history habit, in contrast with the social habit of

honey bees and bumble bees. In California wildlands, bees are regarded as the most important group of pollinators.

Much still remains to be learned about California bees, especially about their dynamic relationships in the ever-changing landscape of the state. Recent and ongoing studies are now focusing more on long-term bee population trends at specific sites, direct human impacts on bees (e.g., destruction of habitat), and interactions between exotic and native bee species on exotic and native plant species.

In our study, we have used basic information on wildland bees to ask new questions about bees in the urbanized environments of northern California. More specifically, we wanted to know if urban areas supported a low or high diversity of bee species. We also wanted to know how urban bees used floral resources of native and exotic plant species.

To answer these two questions, we initiated a survey of urban bees and their host flowers in two cities in the San Francisco Bay Area in 1999. A progress report of this on-

going study is presented here; it is scheduled to continue through 2003. It is noteworthy that with the exception of a few limited studies, little is known about bees in urban California.

METHODS

Bee surveys were conducted on ornamental plants in residential neighborhoods of Albany and north Berkeley in the San Francisco Bay Area of northern California. Casual surveys of plants in flower and their bee visitors were made at least twice each week from 1999 to 2002 by walking through different streets of both cities. Once bee-attractive plants were located, follow-up visits were made to collect bees and qualitatively assess relative attraction of plants to their bee visitors. Voucher collections of host flowers were also taken for later identification.

Bee visitation or frequency counts were experimentally initiated in 2001 and were standardized in 2002 in the following manner. Flowering vegetation plots measuring 1.5m² (or the equivalent in the case of linear plantings) were observed for three minutes in order to record the number of bees that entered this space and made contact with the reproductive parts of the flowers. The number of flower visits by a given bee was not recorded.

Replications of bee counts were made on the same plants (usually different sides) and on other plants of the same species whenever possible. Counts were made on warm, sunny days when temperatures were about 65° F or higher during a period of high atmospheric pressure. Plants with dense flowering in sun-exposed sites were selected for counts whenever possible. The basic guideline was to record bee visits under the most optimal plant and climatic conditions.

Based on average count data, the following three categories of mea-

surable attraction were established: "Common" for averages of 5 or more bees per three minutes; "Occasional" for averages of 1 to <5 bees per three minutes; and "Rare" if averages were consistently low, ranging between 0.5 to <1 bees per three minutes. Extremely rare bee visits to flowers were noted but not tabulated for the purposes of this study.

The exotic honey bees (all European) were separated from native bees in these counts. In some cases there was not enough flowering vegetation to make a standardized bee count. In these situations, we estimated relative bee attraction (see footnote 5 of Table 1 on page 52).

At times it was difficult to identify certain plants, as some urban plants have numerous subspecies, varieties, and cultivars. In most cases it was possible to identify a plant to species or subspecies by using *The Jepson Manual* (1993) or the *Sunset Western Garden Book* (2001). In other cases, we were only able to take the plant to the genus level (e.g., *Calendula*, *Lavandula*, and *Nepeta*). Finally, with the help of local nurseries and their knowledge of local plant usage, we were also able to identify some plants to cultivar.

Native and exotic ornamental plants were designated, and weedy species were also noted. In the case of natives, we regarded a plant as native if it was known to occur naturally in northern California. Plants native to southern California and elsewhere outside the state were regarded as exotics to the Berkeley and Albany areas.

SURVEY RESULTS

The residential environments of Albany and Berkeley contain extremely diverse offerings of exotic and native plant elements. For example, in a given two-hour walk through either city during spring or summer, it was common to observe about 200 plant types in



Megachilid bee (*Megachile fidelis*) drinking from disk flowers of the head of a member of the sunflower family. Photo-graph by R.E. Coville.

flower. The vast majority of these were exotic to the two East Bay cities and to northern California. During the course of our intensive research period from 2001 to 2002, we estimated that we had observed 600–700 plant species, subspecies, varieties, and cultivars in flower from March through October.

Despite the great available diversity of flowers at any given period, only a small percentage of plants showed measurable attraction to honey bees or native bees. Based on our visitation counts, only about 5–10% of the flowering plants examined in any given month had measurable bee numbers. Plants that attracted bees for pollen or nectar are listed alphabetically by genus in Table 1 (see pages 52–54). About 75% of these plants are exotics, whereas 25% are natives to northern California. In addition, there was also a mixture of families and plant life forms (ranging from herbs to trees) among both exotic and native plants that attracted bees.

In general, honey bee and native bee populations appear to be low in Albany and Berkeley, as evidenced by the relative counts of both bee groups (see "Attraction" column of Table 1). Most of the 72 "bee plants" listed in Table 1 attracted honey bees (44 plant species or 61%) and native bees (62

TABLE 1. PLANTS AND BEES IN BERKELEY

Flowering plant species and their relative attraction to honeybees and native California bees in Albany and Berkeley.

PLANT SPECIES (FAMILY)	COMMON NAME (PLANT FORM) ¹	PLANT ORIGIN ²	FLORAL REWARD ³	FLOWERING PERIOD	ATTRACTION ⁴	
					HB	NB
<i>Aesculus californica</i> (Hippocastanaceae)	California buckeye (Tr)	NC	N	Sum.	R	R
<i>Agapanthus orientalis</i> (Amaranthaceae)	Lily of the Nile (H)	Ex	N	Spr.-Sum.	R ⁵	R ⁵
<i>Alstroemeria aurea</i> (Liliaceae)	Lily (H)	Ex ²	N	Sum.	O	R ⁵
<i>Arctostaphylos californica</i> (Ericaceae)	Cape weed (Gc)	Ex	P	Spr.-Sum.	-	R
<i>Borago officinalis</i> (Boraginaceae)	Borage (H)	Ex	N	Spr.	C	R-O
<i>Calendula</i> spp. (Asteraceae)	Marigold (H)	Ex	P	Spr.	-	R-O
<i>Ceanothus cuneatus</i> (Rhamnaceae)	Lilac (Sh)	NC	N	Spr.	?	O ⁵
<i>Ceanothus</i> 'Julia Phelps' (Rhamnaceae)	Lilac (Sh)	NC	N	Spr.	O-C	O-C
<i>Ceanothus</i> 'Ray Hartman' (Rhamnaceae)	Lilac (Sh)	NC	N	Spr.	O	O-C
<i>Centaurea cineraria</i> (Asteraceae)	Dusty miller (W/H)	Ex	N, P	Sum.	O	O
<i>Cerintho major</i> 'Purpurascens' (Boraginaceae)	Honeywort (H)	Ex	N	Spr.	-	R-O ⁵
<i>Chrysanthemum frutescens</i> (Asteraceae)	Marguerite, Paris daisy (Sh)	Ex	N	Sum.	-	R-O
<i>C. maximum</i> (Asteraceae)	Shasta Daisy (W/H)	Ex	P	Spr.-Sum.	-	R-O ⁵
<i>Cistus pulchellus</i> 'Sunset' (Cistaceae)	Rock rose (Sh)	Ex	N	Spr.-Sum.	R ⁵	R-O
<i>Citrus</i> spp. (Rutaceae)	Orange, Lemon (Tr, Sh)	Ex	N	Spr.	R	R
<i>Clarkia unguiculata</i> (Onagraceae)	Elegant clarkia (H)	NC	N	Spr.	R-O	R-O
<i>Cosmos bipinnatus</i> (Asteraceae)	Cosmos (H)	Ex	P	Sum.	-	C
<i>Cotoneaster lacteus</i> (Rosaceae)	Cotoneaster (Sh)	Ex	N	Sum.	O	O
<i>C. franchetii</i> (Rosaceae)	Cotoneaster (Sh)	Ex	N	Sum.	O	R
<i>Crataegus laevigata</i> (Rosaceae)	Hawthorn (Tr)	Ex	P, N	Spr.	C	-
<i>C. phoenopyrum</i> (Rosaceae)	Washington thorn (Tr)	Ex	N	Sum.	C	O

1. Plant form: Tr = tree; Sh = shrub; W/H = woody and herbaceous; H = herbaceous; Gc = ground cover; V = vine

2. NC = native to northern California; Ex = exotic to northern California

3. P = pollen; N = nectar

4. HB = Honey bee; NB = Native bee; R = rare, Ave. <0.5-1 bee per 3 min.; O = occasional, Ave. 1-5 bees per 3 min.; C = common, Ave. ≥5 bees per 3 min.

5. Estimated visitation frequency

PLANT SPECIES (FAMILY)	COMMON NAME (PLANT FORM) ¹	PLANT ORIGIN ²	FLORAL REWARD ³	FLOWERING PERIOD	ATTRACTION ⁴	
					HB	NB
<i>Echium candicans</i> (Boraginaceae)	Echium (Sh)	Ex	P, N	Spr.	C	O
<i>Erigeron karvinskianus</i> (Asteraceae)	Mexican daisy, Daisy fleabane (H, Gc)	Ex	P	Spr.-Sum.	-	R-O
<i>Eriogonum arborescens</i> (Polygonaceae)	Buckwheat (Sh)	Ex	N	Sum.	R	R
<i>E. grande</i> var. <i>rubescens</i> (Polygonaceae)	San Miguel Island buckwheat (H)	Ex	N	Sum.	O	O
<i>Escallonia exoniensis</i> 'Fradesii' (Escallaceae)	Frades escallonia (Sh)	Ex	N	Sum.	C	R
<i>Eschscholzia californica</i> (Papaveraceae)	California poppy (H)	NC	P	Spr.	-	R-O
<i>Geranium incanum</i> (Geraniaceae)	Crane's bill (H, Gc)	Ex	N	Spr.	-	R
<i>Geranium</i> sp. (Geraniaceae)	Geranium (H)	Ex	N	Spr.-Sum.	R	O
<i>Gilia capitata</i> ssp. <i>capitata</i> (Polemoniaceae)	Globe gilia (H)	NC	N	Spr.	O	O
<i>Grindelia</i> sp. (prostr.) (Asteraceae)	Gumplant (H)	NC	P, N	Sum.	R ⁵	O
<i>Hebe</i> 'Blue Elf' (Scrophulariaceae)	Veronica (Sh)	Ex	N	Sum.	R	R-O
<i>Heteromeles arbutifolia</i> (Rosaceae)	Toyon (Tr, Sh)	NC	N	Sum.	C	O
<i>Holodiscus discolor</i> (Rosaceae)	Ocean spray (Sh)	NC	N	Sum.	?	C ⁵
<i>Horkelia marinensis</i> (Rosaceae)	Pt. Reyes horkelia (H, Gc)	NC	N	Sum.	O	C
<i>Lavandula</i> spp. (Lamiaceae)	Lavender (W/H)	Ex	N	Spr.-Sum.	O	R-O
<i>Lavatera maritima</i> 'Bicolor' (Malvaceae)	Shrub mallow (Sh)	Ex	N	Spr.-Sum.	R	?
<i>Ligustrum japonicum</i> 'Texanum' (Oleaceae)	Wax-leaf privet (Sh)	Ex	N	Sum.	C	-
<i>L. ovalifolium</i> (Oleaceae)	California privet (Sh)	Ex	N	Sum.	C	O
<i>Linaria purpurea</i> (Scrophulariaceae)	Toadflax (W/H)	Ex	N	Sum.	-	O
<i>Lobularia maritima</i> (Brassicaceae)	Sweet alyssum (H)	Ex	N	Spr.-Sum.	-	O
<i>Lupinus</i> spp. (Fabaceae)	Lupine (W/H)	NC	N	Spr.	-	R
<i>Lyonothamnus floribundus</i> ssp. <i>asplenifolius</i> (Rosaceae)	Fernleaf Catalina ironwood (Tr)	Ex	N	Sum.	C	O
<i>Malus floribunda</i> (Rosaceae)	Crab apple (Tr)	Ex	N	Spr.	O	O
<i>Marrubium vulgare</i> (Lamiaceae)	Horehound (W/H)	Ex	N	Spr	R	O
<i>Mentzelia lindleyi</i> (Loasaceae)	Blazing star (H)	NC	P	Spr.	-	O
<i>Mimulus aurantiacus</i> (Scrophulariaceae)	Sticky monkeyflower (Sh)	NC	N	Spr.-Sum.	-	R

Key to 1-5: see page 52

TABLE 1. PLANTS AND BEES IN BERKELEY (CONT.)

PLANT SPECIES (FAMILY)	COMMON NAME (PLANT FORM) ¹	PLANT ORIGIN ²	FLORAL REWARD ³	FLOWERING PERIOD	ATTRACTION ⁴	
					HB	NB
<i>Monardella villosa</i> vel. aff. (Lamiaceae)	Coyote mint (W/H)	NC	N	Sum.	O	O
<i>Nepeta</i> spp. (Lamiaceae)	Catmint, catnip (H)	Ex	N	Sum.	R-O	R-O
<i>Papaver orientale</i> (Papaveraceae)	Oriental poppy (H)	Ex	P, ?N	Spr.-Sum.	O ⁵	R ⁵
<i>Pelargonium graveolens</i> (Geraniaceae)	Scented geranium (Sh)	Ex	N	Spr.-Sum.	O	O
<i>Penstemon gloxiniioides</i> 'Midnight' (Scrophulariaceae)	Midnight penstemon (W/H)	Ex	N	Sum.	R	O
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	Tansy leaf phacelia (H)	NC	P, N	Spr.	O	C
<i>Phylla nodiflora</i> (Verbenaceae)	Lippia (H, Gc)	Ex	N	Sum.	R	-
<i>Pittosporum tobira</i> (Pittosporaceae)	Japanese mock orange (Sh)	Ex	N	Spr.	R	R
<i>Persicaria capitata</i> (Polygonaceae)	Knotweed	Ex	N	Spr.-Sum.	R	R
<i>Prunus ilicifolia</i> (Rosaceae)	Hollyleaf cherry (Tr)	NC	P	Spr.-Sum.	C	R
<i>P. lusitanica</i> (Rosaceae)	Portugal laurel (Tr, Sh)	Ex	P	Spr.-Sum.	-	O
<i>Pyracantha</i> sp. (Rosaceae)	Firethorn (Tr, Sh)	Ex	N	Spr.	R-C	-
<i>Rhamnus californica</i> 'Mound San Bruno' (Rhamnaceae)	Coffeeberry (Sh)	NC	N	Sum.	C	-
<i>Rosa</i> 'Nozomi' (Rosaceae)	Nozomi rose (Gc)	Ex	P	Sum.	-	R ⁵
<i>Rosmarinus officinalis</i> (Lamiaceae)	Rosemary (Sh)	Ex	N	Spr.	O	R
<i>Rubus discolor</i> (Rosaceae)	Himalayan blackberry (V)	Ex	P, N	Spr.	O	O
<i>Ruta graveolens</i> (Rutaceae)	(W/H)	Ex	N	Spr.-Sum.	R ⁵	R ⁵
<i>Salvia clevelandii</i> (Lamiaceae)	Cleveland sage, California blue sage (W/H)	Ex	N	Sum.	R	R
<i>Salvia</i> 'Indigo Spires' (Lamiaceae)	Indigo spires salvia	Ex	N	Sum.	R	R
<i>Salvia ?leucophylla</i> (Lamiaceae)	Purple sage (Sh)	Ex	N	Spr.	O	O
<i>Scabiosa columbaria</i> (Dipsacaceae)	Pincushion flower (H)	Ex	N	Sum.	O	O
<i>Stachys bullata</i> (Lamiaceae)	Mint (H)	NC	N	Spr.	O	O
<i>Trichostema lanatum</i> (Lamiaceae)	Woolly blue curls (Sh)	Ex	N	Sum.	O	R
<i>Trifolium repens</i> (Fabaceae)	White clover (H)	Ex	N	Spr.-Sum.	R-O	O
<i>Vicia villosa</i> (Fabaceae)	Vetch (H)	Ex	N	Spr.	R ⁵	R ⁵

Key to 1-5: see page 52

plant species or 86%) at the Rare or Occasional levels. Relatively few plants attracted either honey bees (13 plant species or 18%) or native bees (7 plant species or 10%) at the Common level. About 65% of the plants in Table 1 mutually attracted honey bees and native bees. When they occurred together on the same flowers, there was no evidence that either bee attempted to prevent the other from gathering pollen or nectar, a phenomenon known as “interference competition.”

For many plant types, bee visitation frequency varied from one flower patch to the next, which is reflected in the attraction ranges shown in the last column of Table 1. The low end of the ranges usually occurred where host flowers were relatively isolated from other attractive flowering plants in an urban landscape. The high end generally occurred when a host plant was grouped together with several other bee-attractive plants in a garden.

Increased attraction to host flowers was especially noticeable when large numbers of attractive flowering plants were planted in close proximity to each other. Two excellent examples are the Peralta Community Garden in the Berkeley flatlands and the UC Berkeley Oxford Tract in the student community garden of the College of Natural Resources.

Native bees, in particular, were more abundant on flowers in these two gardens, and this was reflected in higher visitation counts on several plants. For example, California poppies in both gardens attracted two to three bee species at the Common level, whereas poppies in all surrounding areas of Albany and Berkeley only rarely attracted native bees, and then usually bumble bees.

In the Peralta Garden, plants such as *Cerintho major* ‘purpureascens’, *Cistus pulchellus* ‘Sunset’, *Clarkia unguiculata*, *Calendula* spp., *Erigeron karvinskianus*, and *Lupinus*



Horkelia marinensis (Pt. Reyes horkelia) being visited by a bumble bee (*Bombus bifarius*). Photograph by B. Ertter.

spp. received frequent visits from diverse native bees. In surrounding urban areas, these plants usually received only rare or no measurable visits. It is noteworthy that honey bee abundance in both gardens was about the same as in surrounding areas of Albany and Berkeley.

Not only were native bees more abundant overall, but there was also a greater diversity of native bees visiting flowers. The Peralta Garden had approximately 20 native bee species visiting a wide variety of exotic and native plant species (15–20 in any given month). The Oxford Tract, which is only one-third the size of the Peralta Garden and contains one-third its plant diversity, also had approximately 20 native bee species visiting a wide variety of exotic and native plants.

Given their small size, Peralta at 0.25 hectare (one hectare is 100 m²) and Oxford at 0.1 hectare, each garden had an unusually high diversity of bee species present. This may, in part, be due to the fact that both gardens were managed without the use of pesticides. This pattern was evident, although to a lesser

extent, in several residential gardens containing eight or more attractive plant species flowering at the same time. These gardens also had a relatively diverse group of native bees (7–10 species) as well as higher visitation frequencies.

Overall bee diversity was surprisingly high in the two East Bay cities. Five families, 20 genera, and 74 species were recorded from netted bee collections on flowers over a three-year period from 1999 to 2002 (see Table 2, page 56). Three groups of bees were most conspicuously observed on any given collection day: the European honey bee (*Apis mellifera*), bumble bees (*Bombus* spp.), and leafcutter or mason bees (usually *Megachile* and *Osmia* of the Megachilidae).

Only the European honey bee and one megachilid, *Megachile rotundata* (the alfalfa leafcutting bee), are exotic to California and the New World. Although bee collection records are still considered incomplete for many plant species, preliminary data suggest that many bee species have a wide range of host plants.

TABLE 2. MAJOR BEE TAXA FOUND IN ALBANY AND BERKELEY

Bee Families	Genera	Nos. of Species
ANDRENIDAE	<i>Andrena</i>	15
APIDAE	<i>Anthophora</i>	4
	<i>Apis mellifera</i> ¹	1
	<i>Bombus</i>	3
	<i>Ceratina</i>	2
	<i>Habrapoda</i>	1
	<i>Melissodes</i>	1
	<i>Nomada</i>	4
	<i>Synhalonia</i>	1
	<i>Xylcopa</i>	1
COLLETIDAE	<i>Hylaeus</i>	5
HALICTIDAE	<i>Agapostemon</i>	1
	<i>Halictus</i>	1
	<i>Lasioglossum</i>	12
	<i>Sphecodes</i>	1
MEGACHILIDAE	<i>Anthidium</i>	1
	<i>Coelioxys</i>	2
	<i>Hoplitis</i>	1
	<i>Megachile</i> ²	8
	<i>Osmia</i>	9
Totals: 5 Families	20 Genera	74 Species

1. *Apis mellifera* is the exotic European honey bee from the Old World.

2. *Megachile rotundata* is an exotic species from the Old World.

DISCUSSION

In comparison to the relatively large-sized patches of native plants that were once part of the San Francisco East Bay natural landscape (and still are in many places), the urban landscape consists of very small patches of both native and exotic plants. Moreover, although diversity of flowers in urban areas is high—600 to 700 plant species, subspecies, varieties, and cultivars have been seen to date in Albany and Berkeley—only a small percentage have shown a measurable attraction to bees.

The vast majority of these plants are exotics to northern California. The relatively low attraction of bees, especially native bees, to exotic plants is to be expected for at least

two reasons. First, many horticultural selections have reduced rewards (pollen and nectar) for bees as a result of commercial attempts to produce larger or more showy flowers. One example is the selection of roses for multiple petals at the expense of pollen-bearing stamens. Second, native bees have no historical (evolutionary) relationship with exotic plants.

A good indicator of the historical connection between bees and floral hosts is the fact that northern California native plants were at least four times more likely to attract measurable numbers of native bees than exotic plants. This emerging pattern is based on a comparison of absolute numbers of exotic (53) and native (19) “bee plants” in Table 1 with the estimated number of ex-

otic plants (approximately 600 types) and native plants (approximately 50 types) that have been surveyed to date.

Despite small patch size, low numbers of attractive plants, and often wide spacing among plants of the same species, we recorded a much higher overall diversity of native bee species than expected. Many bees seem to be able to locate their preferred plants, as indicated by bee type(s) on given plant species being generally consistent through time.

For example, California poppies commonly attracted bumble bees and a few small bees of the family Halictidae. Himalayan blackberries consistently attracted a wide variety of leafcutter bees, bumble bees, and honey bees. Cosmos regularly attracted large anthophorid bees of the family Apidae. Dusty Miller, *Centaurea cineraria*, regularly attracted males and females of large megachilids. It should be stressed again that some native bee collections were taken from plants that received only extremely rare visits, and these records were not listed in Table 1.

Indirect evidence suggests that honey bees were much more common on ornamental plants of Albany and Berkeley several years ago. During our study, many home gardeners observed that honey bee numbers have gone down noticeably during the past 10 years or so. This downturn in numbers seems to correspond well with the introduction of parasitic tracheal and varroa mites into California honey bee populations.

Furthermore, some plant species that characteristically attracted high honey bee numbers in the past had relatively modest visitations by this bee, including *Trifolium repens* and *Phyla nodiflora*. We believe that if this study had been conducted 10 to 15 years ago, we would have recorded higher numbers on many of the plants that were attractive to honey bees.

Although estimates of bee attraction frequencies (as shown in the last column of Table 1) were developed entirely within the cities of Albany and Berkeley, these frequencies and associated bee types should generally be expected in adjacent and nearby San Francisco East Bay cities on the same plant species. For example, during the summer of 2002 we evaluated about a dozen ornamental plant species in Martinez (about 12 miles or 19 km north of Berkeley), which also occur commonly in Berkeley. Most of the same bee species were attracted to these plants and at the same frequencies. Differences were observed, however, in the cases of catmint (*Nepeta* sp.), Shasta daisy (*Chrysanthemum maximum*), fleabane (*Erigeron karvinskianus*), and marigold species (*Calendula*), all of which had more frequent bee visits in Martinez.

As our study continues, we will be introducing various California native plant species into urban gardens in Albany and Berkeley in order to evaluate the relative attraction of resident bee populations to these plants. Candidate plants scheduled for testing include *Helianthus annuus* (California sunflower), *Grindelia camporum* (gumplant), *Rosa californica* (California wild rose), *Salvia mellifera* (black sage), and *Lythrum californicum* (California loosestrife).

We will also be testing a few relatively noninvasive plants such as *Lotus corniculatus* and *Trichostema lanceolatum*, which are known to be high-quality nectar resources for native bees. All of the above plants flower for long time periods, a condition favorable for bees.

One unique urban bee pattern did emerge from our study, suggesting that grouping bee-attractive plants together in the future will increase bee visitations, especially of native bee species. When many (eight or more) attractive bee plants are planted together in one



garden (which can range widely in size), this grouping tends to attract a greater number and diversity of bee species. In these situations, it appears that flowering patches containing the bee-attractive plants need to be equivalent to at least one meter in diameter in order to draw in a diverse population of bees.

So far we have identified urban plants that are attractive to native bees, and have also suggested ways to increase the number of bees in urban yards. But why would one want to increase bee numbers? Don't bees sting, and aren't bee stings dangerous to humans? These are questions asked frequently by home gardeners.

There are several reasons why it is desirable to have bees in your yard. On a global level, scientific evidence is mounting that pollinators are declining. Not only are bees, like other wild animals, a critical part of our natural environment, but they also provide a valuable environmental service when they pollinate our fruit and vegetable crop plants.

Urban areas may provide important habitats for greater numbers of bee species than previously suspected. If so, this might help in ongoing global efforts to conserve



California natives visited by native bees in urban gardens: *Horkelia marinensis* (Pt. Reyes horkelia) (top) and *Rosa californica* (California rose) (bottom). Photographs by B. Ertter.

and protect bees as human development continues to destroy wild habitats.

On a more personal level, it is fascinating to observe bees taking pollen and nectar from flowers. In this regard, bumble bees, which are large and easy to see, can be approached relatively closely to make these observations. Other interesting behaviors include male territorial patrolling (looking for females) around several flowers by some large leafcutter bees and large apid bees (*Melissodes*). Sleeping aggregations of large male apid bees in cosmos flowers are common and



Mixed plantings of native and non-native species in Peralta Garden, Berkeley. Photograph by G.W. Frankie.

easily observed in late summer and early fall.

You need not fear being stung since bees only use their stinger defensively when inadvertently grabbed or stepped on with bare feet—something more likely to occur in a lawn that contains white clover or some other desirable low-growing flower. Care should also be taken around nests of bumble bees, as some species can be quite defensive against would-be intruders. It should be emphasized that only female bees sting; males of all bee species lack this capacity.

Bees, like birds and butterflies and many other animals in our

yards, give us a sense of pleasure knowing that wild organisms can make productive use of artificial urban environments. In the case of bees, all but two species (see Table 2) are native Californians.

For more information and updates on our study, visit the City Bugs website: www.cnr.berkeley.edu/citybugs.

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REFERENCES

- Barthell, J.F. and H.V. Daly. 1995. Male size variation and mating site fidelity in a population of *Habropoda depressa* (Hymenoptera: Anthophoridae). *Pan-Pacific Entomologist* 71:137–141.
- Barthell, J.F., D.M. Bromberger, H.V. Daly, and R.W. Thorp. 1999. Nesting biology of the solitary digger bee *Habropoda depressa* (Hymenoptera: Anthophoridae) in urban and island environments. *Journal of the Kansas Entomological Society* 71(2):116–136.
- Buchmann, S.L. and G.P. Nabhan. 1996. *The Forgotten Pollinators*. Island Press, Covelo, CA.
- Chemsak, J.A. and R.W. Thorp. 1962. Note on the sleeping habits of males of *Melissodes robustior* Cockerell (Hymenoptera: Apoidea). *Pan-Pacific Entomologist* 38(1):53–55.
- Grissell, E. 2001. *Insects and Gardens*. Timber Press, Portland, Oregon.
- Frankie, G.W., R.W. Thorp, et al. 1998. Monitoring solitary bees in modified wildland habitats: Implications for bee ecology and conservation. *Environmental Entomology* 27:1137–1148.
- Linsley, E.G. and J.W. MacSwain. 1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. *University of California Publications in Entomology* 16:1–46.
- Moldenke, A.R. 1976. California pollination ecology and vegetation types. *Phytologia* 34:305–361.
- Schmidt, M.G. 1980. *Growing California native plants*. California Natural History Guides: 45. University of California Press, Berkeley.

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FARMSCAPE ECOLOGY OF A NATIVE STINK BUG IN THE SACRAMENTO VALLEY

by Les E. Ehler, Corin G. Pease, and Rachael F. Long

Stink bugs are pests of crops throughout tropical and temperate regions of the world. Adults are generally long-lived and typically deposit clutches of eggs in



Egg mass, nymph, and adult of consperse stink bug. Photographs by J.K. Clark, UC Statewide IPM Program.

tight clusters on the undersides of leaves. There are five nymphal stages or instars; the first instar normally does not feed, whereas the remaining ones (and the adults) feed primarily on developing seed and fruit. Such feeding can reduce both yield and quality of the harvested product.

Crucifer and legume pods are major foods for both nymphs and adults. However, these foods tend to be ephemeral, so a sequence of host plants is usually necessary for development of successive generations during the growing season. In temperate climates, adults from the last generation enter a reproductive diapause (an arrest in development) and spend the winter months in protected places, such as beneath leaf litter or under the bark of trees.

In the spring, the surviving adults mate and seek out suitable host plants for feeding and reproduction. Hosts for the first generation of stink bugs are typically non-crop plants, especially weeds. Subsequent generations develop on crops such as soybean, cotton, rice, pepper, bean, or tomato.

In this article, we outline the seasonal life history of a native stink bug and describe how replacing exotic weeds with native perennial grasses can be employed in stink-bug management. We also note the importance of economic benefits linked to the restoration of native vegetation in agricultural landscapes.

CONSPERSE STINK BUG

In the Sacramento Valley, there are several species of native stink bugs. However, the major crop pest

is the consperse stink bug, *Euschistus conspersus*. Adults overwinter in leaf litter, then break diapause and emerge in mid to late March. This species produces two generations per year. The first develops on exotic, spring-time weeds such as common mustard (*Brassica kaber*), black mustard (*B. nigra*), wild radish (*Raphanus sativus*), and cheeseweed (*Malva parviflora*). By early June, the spring generation is complete. Adults from this generation seek new hosts such as tomato, because weedy hosts from the spring have dried up and are no longer suitable for the development of offspring.

The second generation develops primarily on tomato, a major crop in the Sacramento Valley. This is not necessarily because of a preference for this crop, but because tomato is about the only suitable host available for much of the summer. Feeding by adults and nymphs on developing fruit results in white, corky lesions that become apparent as the fruit ripens, reducing fruit yield and quality. By the end of summer, adults from the second generation enter a reproductive diapause and disperse to overwintering sites that are well drained and have a sufficient layer of leaf litter. One of the most common overwintering habitats is blackberry (*Rubus* spp.) leaf litter, particularly in riparian zones.

The consperse stink bug has a complex of natural enemies, including both native and exotic species. Native scelionid wasps, such as *Gryon obesum*, *Telenomus podisi*, and *Trissolcus euschisti*, parasitize the eggs, typically exploiting the entire egg mass. Eggs also are eaten by predators, especially by exotic species such as the Argentine ant



Farmscape ecology of the consperse stink bug in the Sacramento Valley: Adult stink bugs overwinter in riparian areas (top). First stink bug generation develops on cheeseweed, mustard, and wild radish (middle). Second stink bug generation develops on tomato (bottom). Photographs by Yolo County Resource Conservation District (upper) and J.K. Clark (middle, lower).

(*Linepithema humile*) and common pillbug (*Armadillidium vulgare*). These two predators can be especially important during the spring. Also, a number of native predators feed on the smaller nymphs.

However, these natural enemies can be slow to colonize tomato crops, allowing stink-bug populations to reach damaging levels. As a result, growers frequently apply chemical insecticides such as methamidophos, a highly toxic organophosphate material, for stink-bug control.

FARMSCAPE ECOLOGY

For a tomato grower in the Sacramento Valley, managing the consperse stink bug should take into account the whole farm or "farmscape," not just the tomato crop. A typical farmscape in the region consists of a mixture of habitat patches, such as bare ground, non-crop vegetation (e.g., weeds), riparian areas, and cultivated crops. The term farmscape describes this within-farm configuration of habitat patches. Farmscaping deals with the modification of agricultural settings, such as planting hedgerows of trees, shrubs, and perennial grasses on the farm. There are three essential components to the farmscape ecology of the consperse stink bug in the Sacramento Valley: habitat for overwintering, exotic weeds for development of the first generation, and tomatoes for development of the second generation.

Tomato growers who report stink-bug damage often have all three components on their farm, typically in close proximity. In such cases, the key to managing consperse stink bug is prevention—i.e., by removing overwintering sites or managing weedy vegetation in the spring. Unfortunately, the consperse stink bug often overwinters in riparian vegetation, which is an

important refuge for native plants and wildlife. In such cases, weed management is a more promising approach.

The weeds in question are typically part of roadside vegetation that is dominated by exotic species. In the spring, wild radish, black mustard, and cheeseweed are common along roadsides, often within a few feet of a developing tomato crop. The most obvious solution is to remove these weedy hosts, either chemically or mechanically. This is being practiced by a number of tomato growers in the area. Unfortunately, much of this weedy vegetation is on highway rights-of-way, and thus is not under the grower's control.

An alternative approach to weed management is restoration of native vegetation, especially native perennial grasses, along roadsides adjacent to riparian vegetation and tomato fields. This should also be of interest to governmental agencies that are responsible for managing roadside vegetation.

FARMSCAPING WITH NATIVE GRASSES

Some farmers in Yolo County are currently engaged in farmscaping with native perennial grasses as part of a roadside restoration project with the Yolo County Resource Conservation District. Several native grasses are being grown, usually a mix of the following: purple needlegrass (*Nassella pulchra*), nodding needlegrass (*Nassella cerinua*), California onion grass (*Melica californica*), one-sided bluegrass (*Poa secunda* var. *secunda*), and blue wild rye (*Elymus glaucus*).

Native grasses are seeded in the fall into prepared seed beds. Weeds are controlled during the first three years of establishment by mowing, burning, hoeing, or applying herbicides. Once established, native grasses can provide nearly 100%



Roadside restoration of native perennial grasses next to a tomato field in Yolo County. Photograph by L.E. Ehler.

cover. This is apparently sufficient to outcompete cheeseweed, mustards, and wild radish, thus precluding development of the first generation of consperse stink bug at that site.

These native perennial grasses are poor hosts for consperse stink bug. Our research has shown that these bugs generally do not occur in these roadside grasses during the spring, except in those cases where poor management has allowed weedy hosts of the bugs to invade. Also, consperse stink bug does not appear to overwinter in these grasses.

While we have not detected significant numbers of other crop pests in the roadside grasses, we do find beneficial insects such as hover flies, green lacewings, ladybird beetles, and damsel bugs on the grasses during the spring, and have observed hover flies and green lacewings feeding on grass pollen. Thus, such roadside restoration may help sustain populations of beneficial insects by providing key resources (e.g., pollen, aphid honeydew) during the spring, prior to the development of pests on adjacent crops such as tomato.

However, not all native perennial grasses are suitable for use in roadside restoration projects adjacent to tomato fields. A good example is deergrass (*Muhlenbergia rigens*), a relatively large bunchgrass that has well drained, protected spaces near the base of the plant that are suitable overwintering sites for a variety of insects, including the consperse stink bug. However, deergrass also is a suitable overwintering site for beneficial insects, such as ladybird beetles and predaceous bugs. In some cases, we have observed 100 or more convergent ladybeetles per plant. Thus deergrass could be used to conserve beneficial species in situations where the consperse stink bug or other potential pests it might harbor are of little or no concern to the farmer.

HIDDEN BENEFITS OF RESTORATION

Roadside restoration of native grasses in Yolo County was not originally designed to prevent build-

up of the consperse stink bug. Instead, the main goal was restoration and conservation of native grasses. The impetus for a grower or land owner to adopt such a practice depended on his or her environmental ethic and philosophy of land stewardship. This is perhaps why the practice has not been widely adopted in Yolo County.

What has been missing in this equation is a practical or economic benefit to roadside restoration. Now there is such a benefit in the form of pest reduction. We believe that, in highly agricultural regions, such economic benefits to growers and land owners will be essential in implementing and sustaining ecological restoration of native vegetation.

In summary, we believe that widespread adoption of roadside restoration with native perennial grasses would have a major impact on populations of the consperse stink bug in the Sacramento Valley. This would presumably reduce the need for chemical insecticides in tomato crops; because such insecticides are costly and tomato prices are relatively low, increasing profits is of great concern to farmers. We are currently working with interested tomato growers and processors to bring this vision to fruition.

REFERENCES

- Bugg, R.L., C.S. Brown, and J.H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: Establishment and evaluation. *Restoration Ecology* 5:214-228.
- Ehler, L.E. 2000. *Farmscape ecology of stink bugs in northern California*. Memoirs, Thomas Say Publications in Entomology, Entomological Society of America, Lanham, MD.

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ENDANGERED PLANTS AS GUIDES FOR SAVING ENDEMIC INSECTS IN CALIFORNIA

by Daniel Rubinoff

California has more species found only within its borders (endemics) than any other state, including over 1,000 kinds of plants by the latest estimates. Of these, 179 are endemic plants that are among the 292 species of plants and animals listed as endangered in California by the US Fish and Wildlife Service.

Current theories about the co-evolution of plants and insects suggest that many herbivorous insect groups may have achieved their tremendous richness by diversifying along with their flowering hosts. It might stand to reason then, that the abundance of endemic plant species in California would carry with it an intrinsically matched diversity of insects, with particular insect species dependent on specific species of plants.

Therefore, from a conservation perspective, logic tells us that if we just save some populations of each of these endemic plants, we will also save the unique insects dependent on them. In general this has been the pattern for conservation plans to date. Conservation has been geared toward specific species (with the Endangered Species Act functioning as a cornerstone of environmental protection policies) rather than toward endangered "ecosystems" or "habitat." Unfortunately, when we take a closer look at some of the areas where endemic plants occur and then look for the associated endemic insects in those areas, the story is not nearly so simple.

In this paper, I present comparative examples involving moths and butterflies from California coastal sage scrub, coastal sand dunes, and associated with two of

the most famous plants of California: coast redwood (*Sequoia sempervirens*) and Monterey pine (*Pinus radiata*). At first glance, plans to save the endemic plants might seem certain to save the insects dependent on them, but upon closer examination, the shortcomings of a species-based approach become evident.

SOUTHERN CALIFORNIA COASTAL SAGE SCRUB

Coastal southern California hosts nearly 100 species that are designated or are being considered for protection under the Endangered Species Act. Many reside wholly or partially in southern California coastal sage scrub, which is arguably one of the most endangered habitats in North America. It has been reduced to less than 162,000 hectares (one hectare is 100m²), mostly in parts of Riverside, Orange, and San Diego counties. Southern California coastal sage scrub is home to 13 endangered plant species that are found nowhere else, and represents a hotspot of diversity.

Conservation planning has been intense and contentious in this region of rampant development. A dominant paradigm emerging from the battles between conservation organizations and developers has been the use of "umbrella" species to guide preservation of habitat. The tacit assumption is: "Simply focus on a few areas where the umbrella species occurs, and the rest of the sage scrub community will be sheltered in those same fragments."

In coastal sage scrub, the presence or absence of an endangered bird, the California gnatcatcher (*Polioptila californica*, Muscicapidae), is being used to identify the size and configuration of habitat fragments that will be saved. Additional small plots with populations of endangered plants are also being preserved with the assumption that, in combination, these plant- and bird-based preserves will maintain a large measure of the region's incredible biodiversity. I decided to test the wisdom of this practice using a few coastal sage scrub insects (see photographs on pages 62 and 63).

Some of my recent research both in the field and using DNA in the

This electra buckmoth (*Hemileuca electra electra*) female ovipositing near *Eriogonum fasciculatum* (flat top buckwheat) and the butterflies on opposite page (top) were significantly more sensitive to southern California coastal sage scrub fragmentation than either the endemic bird or plant species around which the conservation plans were designed. Photograph by D. Rubinoff.





Virgulti metalmark (*Apodemia virgulti*) (left). • **Bernardino blue** (*Euphilotes bernardino*) (middle and right) female. All perched on *Eriogonum fasciculatum* (flat top buckwheat) host plant. Photographs by D. Rubinoff.

laboratory revealed a subspecies of the electra buckmoth (*Hemileuca electra*, Saturniidae) apparently found only in southern California coastal sage scrub. It was originally thought to be genetically related to much larger populations to the east in the deserts of San Diego and Riverside counties, but DNA analysis reveals the relationship to be far more distant.

One of the typical plants of the sage scrub community, California flat top buckwheat (*Eriogonum fasciculatum*), is the only food plant of the coastal electra buckmoth. While flat top buckwheat is not endemic to coastal sage scrub, it and three other plants—California sagebrush (*Artemisia californica*) and two sages (*Salvia mellifera* and *S. apiana*)—are usually dominant members of the southern California coastal sage scrub plant community.

One might think it would be easy to save the buckmoth—just set aside land for the gnatcatcher that also has the buckwheat host plant. However, saving sage scrub insects like the electra buckmoth is more complicated than setting aside habitat with the host plant, even if the threatened gnatcatcher occurs in the habitat in good numbers. The moth, and at least a few butterflies, require relatively larger plots of sage scrub than the bird or endangered sage scrub plants do to maintain populations. In southern California coastal sage scrub, conservation planning for plant and bird species is not going to save endemic insects

dependent on the same habitat, even when the insects' hostplants occur in the fragments. If we rely on umbrella species like the gnatcatcher, or the presence of typical coastal sage scrub plants to indicate habitat fragments to be saved, we will likely lose many of the coastal sage scrub insect species.

CENTRAL CALIFORNIA COASTAL SAND DUNES

The Santa Maria dunes of San Luis Obispo County harbor one of the most unusual moths known to science. The caterpillars are so adaptively modified to live beneath the sand dunes that the UC Berkeley entomologists who first collected them did not recognize them as caterpillars!

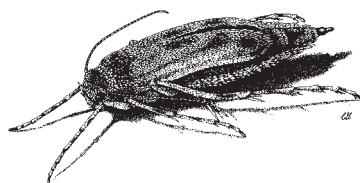
Similarly, the adults of Powell's flightless jumping sand dune moth (*Areniscythrhis brachypteris*, Scythrididae) are hardly reminiscent of your average Lepidopteran (see images below). They are the only continental moths in the world in which adults of both sexes are flightless. Although they can't fly, they do scurry and jump, catching wind

gusts to travel across loose sand during their daytime activity period. At night, or during high winds, the moths exhibit another amazing (and novel) trait—they *burrow* down into the sand and disappear, sheltered from predators and the elements.

A burrowing, flightless moth that runs around during the day on open sand?—Is it any surprise, then, that the genus and its one species remained unknown to science until 1975, despite their occurrence in a relatively accessible part of central California? Unfortunately, the moths have only been found at the Santa Maria sand dune system and the habitat has been in decline since before the moths were discovered.

Coastal sand dunes represent a very restricted and unique mosaic of habitats. There are foredunes of unstabilized sand right against the ocean, adjacent to more vegetated, stabilized dunes. Active dunes present a unique challenge to plants,

Powell's flightless jumping sand dune moth (*Areniscythrhis brachypteris*). Illustration by C. Green. • **Powell's flightless jumping sand dune moth** in its sand dune habitat. Photograph by J.A. Powell.





Habitat for Powell's flightless jumping sand dune moth. Note the presence of both active sand and dune vegetation. Photograph by J.A. Powell.

but those that have adapted to the shifting landscape are rewarded with a habitat relatively free of competition. Once a dune becomes thoroughly vegetated, these active dune specialists are quickly outcompeted and disappear.

Most of California's sand dunes originally harbored rare and specialized plants and animals. For example, San Francisco's now vanquished dune system had many endemic species including the extinct Xerxes blue butterfly (*Glaucopsyche xerxes* Lycaenidae), whose name is now used by an organization (Xerxes Society) devoted to insect conservation. The Santa Maria dune system is the largest remaining in California, and harbors 10

endemic coastal strand plants. In addition to Powell's flightless jumping sand dune moth, there are endemic species of grasshopper and robber fly, the life histories of which are virtually unknown, and a possibly extinct species of long-horned beetle which is known only from the first collected specimens.

While it is tempting to suspect that the flightless moth is restricted because of a dependence on one of the endemic sand dune plants, this turns out not to be the case. The moths exist in a narrow strip at the edge of advancing sand dunes (see the above photograph). While the adults steer clear of living vegetation, the caterpillars form silk tubes under the sand and feed on a variety

of different plants as the advancing sand dunes bury them. Plants used include *Phacelia distans* (phacelia), *Monardella crispata* (coyote mint), *Lupinus chamissonis* (bush lupine), and *Senecio blochmaniae* (groundsel). So it is these specialized conditions, not a particular plant, that allow the moth to hang on.

Sand dune habitat is threatened by sand mining, off-road vehicles, and other human activities that rip up and destroy vegetation, and by alien plants like iceplant or sea fig (*Carpobrotus edulis*) that stabilize the dunes, eliminating the active dune habitat. Efforts to save endemic dune plants may not necessarily save the dune insects, since it is the existence of moving sand in a very narrow strip next to vegetated areas that allows Powell's flightless jumping sand dune moth to exist. If the sand stops moving, or the vegetation near it disappears, so will this entire genus of moth, known only by this one charming and unusual species.

COAST REDWOOD

For a tree endemic to the California floristic province, the coast redwood (*Sequoia sempervirens*) is remarkable in how few insect species it supports. Only five insects feed solely on its foliage. The redwood is a common sight in coastal northern California. While it occurs in large swaths of contiguous forest in the northern part of its range, redwood declines to a few isolated riparian strips in steep canyons at its southern extreme in Monterey County of central California.

Although coast redwood is one of the most famous of the world's natural wonders—it is renowned as the tallest living organism in the world—it still harbors a few secrets. One such mystery is a newly discovered species of moth found near the southern extent of the natural range of redwood in Monterey and

Santa Cruz counties. The small moth is in the Tortricid genus *Syndemis* and the caterpillar feeds only on redwood (see photographs below). Part of the reason this species remained unknown is because it is very rare to find one in moth light traps set out to survey nocturnal lepidopteran faunas.

Jerry Powell at UC Berkeley and I recently stumbled upon a possible reason for this supposed rarity, almost by accident. Because the moths were found so rarely in the light traps, we put out traps baited with the scent, or pheromone, of female *syndemis* moths, which are attractive to males, and placed them in a redwood canyon at the University of California Big Creek reserve in Monterey County.

These pheromone traps, together with the typical light traps, were left out all night, but by early morning only one moth had come. Because of some daytime field work, we didn't retrieve the pheromone traps until noon, but by then more than 50 moths had arrived and by late afternoon more than 100 males had been caught (see photograph on page 66).

For a number of years we had been looking for these moths at night, but as we learned, they are active during the day—an unrecorded habit in the genus. The redwood *syndemis* had escaped notice and was thought to be rare

Redwood *syndemis* (*Syndemis* sp.) caterpillar on redwood foliage. Photographs by D. Rubinoff.



University of California Big Creek Reserve, showing strip of redwood trees along creek bottom, flanked by *Artemisia californica* (California sagebrush) dominated chaparral on south-facing slopes. Photograph by J.A. Powell.

only because scientists had been looking in the right place at the wrong time. Perhaps this denizen of the chilly central coast switched activity periods to avoid the cold and foggy summer nights.

Those interested in saving this unusual insect might think the best place to find or conserve a redwood-feeding moth would be in the large areas of forest in the northern part of the state. However, the redwood *syndemis* has only been found in the narrow, isolated, redwood-bottomed canyons of Monterey County, with one specimen recorded from the nearby Santa Cruz Mountains. Should the southern redwood groves end up being har-

vested, or if global warming eliminates the trees from the southern outposts of its range, one of the very few insects that evolved with this famous symbol of California may disappear even while its more famous host plant survives.

MONTEREY PINE

Monterey pine (*Pinus radiata*) is possibly the most important introduced timber tree in the southern hemisphere, grown extensively within Australia and especially New Zealand. Despite this abundance in the southern hemisphere and elsewhere in the world, Monterey pine



Adult male redwood syndemis (*Syndemis* sp.), perched after flying to pheromone lure at midday. Photograph by D. Rubinoff.

was originally one of the most restricted trees in North America. Prior to human intervention, it was endemic to just three groves along the central California coast: Cambria Pines, San Luis Obispo County, the southern extreme of its range; Carmel area of Monterey County in the middle of its range; and Año Nuevo, San Mateo County, in the northern portion of its range.

While the pine has now been widely planted, the original groves are in sharp decline due to an introduced pitch canker pathogen and are considered endangered. A relative of the aforementioned redwood syndemis moth is endemic to these three original Monterey pine groves and is also new to science (see photograph below). Even though the pine has been planted just over the coastal mountains in the San Francisco Bay Area, the Monterey pine syndemis has not spread from the original groves. DNA analysis suggests that the pine syndemis populations in the three original groves are isolated from each other, indicating that these moths may not be able to travel between the isolated groves.

Syndemis in California. Top row: redwood syndemis; Middle row: Monterey pine syndemis; Bottom row: "typical"-looking *Syndemis* found from Sierra Nevada and Cascade mountains through to the Eastern US. Photograph by D. Rubinoff.



Botanists are still unsure why the Monterey pine was restricted to three small groves, since it grows so easily when introduced elsewhere. It is possible that the pine syndemis moth, which remains restricted to the endemic groves, may be able to give us some insight into this question. Monterey pine as a species is now planted throughout the globe, but unless the original groves along California's central coast are saved from development and threats like the deadly pitch canker, the relationship between this endemic tree and its moth will become a part of history.

WHERE DO WE GO FROM HERE?

California's large number of endemic plants and animals present a special challenge and responsibility to those interested in preserving natural history. Although endemic plants and insects may share the same habitat, their conservation needs are not identical. Even conservation planning that assures the survival of the plants upon which rare insects feed does not guarantee that the invertebrates will persist. Reduced and fragmented habitat, specific microhabitat requirements, and an array of unknown factors may contribute to the disappearance of endemic insects, even while their host plants thrive.

The preceding examples illustrate how little is known about our endemic insect fauna. Many taxa are newly discovered or have requirements that are poorly known. Microhabitats with subtly different conditions must be identified and explored, even where plant communities are apparently identical. But this task can be prohibitively time-consuming.

Perhaps the only tenable solution to this conservation conundrum lies in regional or habitat-based conservation planning. Ecosystem

health is harder to evaluate and is certainly more nebulous than protecting a particular species of concern, but it is clear that species-based conservation plans can leave gaps large enough to cause the loss of endemic insects.

Continued research and careful planning to preserve not just the plant species, but also particular ecological features of unique floral communities, is the only way we'll preserve not only California's unique plants, but also the endemic insects in whose company they evolved.

ACKNOWLEDGMENTS

I thank G. Frankie, J. Powell, and J. Sabet-Peyman for comments on the manuscript, the staff of Point Lobos and Año Nuevo State parks for research permits, J. Smiley for access to UC Big Creek Reserve, and C. Niwa for pheromone lures. Research was supported by a National Science Foundation PEET grant and the Monterey Pine Forest Ecology Cooperative.

REFERENCES

- Hickman, J.C., ed. 1993. *The Jepson manual: Higher plants of California*. University of California Press, Berkeley, CA.
- Powell, J.A. 1976. A remarkable new genus of brachypterous moth from coastal sand dunes in California (Lepidoptera: Gelechioidea, Scythrididae). *Annals of the Entomological Society of America* 69:325-339.
- Powell, J.A. 1981. Endangered habitats for insects: California coastal sand dunes. *Atala* 6:41-55.
- Rubinoff, D. 2001. Evaluating the California gnatcatcher as an umbrella species for conservation of coastal sage scrub. *Conservation Biology* 15:1374-1383.

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NOTES AND COMMENTS

PLANT PROTECTION NOT A GIVEN

Don't take plant protection for granted: environmental protections are being assaulted by the current administration on a number of levels. Emily Roberson, CNPS Senior Policy Analyst, has compiled an excellent list entitled "Federal Environmental Proposals Affecting Native Plants, Public Lands, Waters, and Biological Diversity."

This list can be viewed on the CNPS website, www.cnps.org/NPCC, and proposed rules open for comment can be accessed by searching by agency at www.regulations.gov.

A particularly helpful website on the Bush environmental record and agenda is at www.nrdc.org—click "Bush Record."

For selected issues, see the Native Plant Conservation Campaign website, www.cnps.org/NPCC—click "Make A Difference."

If you would like to receive "NPCC News" (e-mail news on native plant science and conservation) send a request to npcc@cnps.org.

Send letters to agencies and public officials, and to President G.W. Bush (The White House, 1600 Pennsylvania Ave. NW, Washington DC, 20500).

LETTERS TO THE EDITOR

Sodaville milk-vetch

Dear Editor,

We read with interest the Letter to the Editor from James D. Morefield [Volume 30, No. 2] regarding the "inexplicable" withdrawal of the Sodaville milk-vetch (*Astragalus lentiginos* var. *sesquimetralis*) from the federal listing process. The letter raises some excellent points.

We concur that plants receive "second class" treatment under the Federal Endangered Species Act (ESA)

and other current laws and regulations. CNPS and the Native Plant Conservation Campaign (NPCC) are working to raise awareness of this inappropriate imbalance between protection afforded to imperiled plants and animals. Consult the NPCC web site for additional information (www.cnps.org/NPCC).

Though we agree that the on-the-ground benefit of each listing decision should be considered, listing determinations under the ESA should be based solely on biological data and threat information. Congress specifically mandated that the listing process be based on species status only, excluding economic impacts or other factors. If listing determinations are based on concern about "lack of awareness" of private landowners or other extraneous issues, would this not erode the intent of the ESA and integrity of the federal list?

If landowner misunderstanding of the consequences of federal listing is a problem, we suggest that an appropriate role for the US Fish and Wildlife Service (FWS) would be to educate landowners in order to dispel such unwarranted concerns, rather than to retreat from controversy and fail to list a biologically-deserving taxon. CNPS has long worked to educate the public about the ESA, and its provisions for flexibility and opportunities to minimize adverse economic impacts that may be associated with listings. We would welcome the opportunity to work with the FWS to spread this message more widely.

Importantly, it is the opinion of CNPS that federal listing *would have* afforded additional conservation benefit to this taxon. Federal listing provides an additional set of management requirements and conservation standards. Listing would also result in the development of a federal recovery plan to help coordinate conservation action among landowners and state and federal governments. Recovery plans can lead to new research which may be critical to successful conservation of highly restricted and imperiled taxa. Listing can also provide a source,

though admittedly inadequate and uncertain, of federal funding to improve management, conserve habitat, or even increase population sizes.

Moreover, though the Sodaville milk-vetch is state-listed in both California and Nevada, state listing provides questionable protection. State governments, laws, priorities, and budgets constantly change. For example, California is currently facing a budget shortfall in excess of \$30 billion. Such an enormous deficit can threaten conservation programs for California-listed plants and animals. In the current climate, it is imperative that we employ all possible avenues available to achieve long-term conservation, even if they seem redundant in the short term.

As an aside, the final listing determination (in this case, to withdraw) was made over *five years* beyond the one-year timeline for such decisions as mandated by the ESA, and only then in response to a CNPS lawsuit.

In summary, we agree with Morefield that the ESA does not always provide consistent conservation of imperiled plants, and that many landowners and other members of the public have serious misconceptions about the benefits and restrictions of the law. However, we do not believe these are sufficient reasons to decline to list species which meet the legal and biological listing criteria, particularly in this era of unprecedented habitat and species loss.

Emily B. Roberson
CNPS Senior Policy Analyst

David P. Tibor
CNPS Rare Plant Botanist

San Diego Conservation Plan

Dear Editor,

This letter is written in response to the article "Understanding the Political Realities of Regional Conservation Planning" by Allison Rolfe in the July/October 2001 *Fremontia*. That article contained a general discussion of habitat conservation planning, but it specifically focused

on one plan in the incorporated City of San Diego.

As you may recall, the Natural Communities Conservation Planning (NCCP) Act was enacted as a State program to conform to the Federal Endangered Species Act. A group of jurisdictions in San Diego County generated a local plan, referred to as the Multiple Species Conservation Program (MSCP) Plan, and this plan conforms to the NCCP process. It should be clarified that within the overall MSCP, each jurisdiction must independently approve a subarea plan to obtain a permit from the California Department of Fish and Game and US Fish and Wildlife Service (Wildlife Agencies). The MSCP serves as a framework plan. Subarea plans are limited to a particular area or jurisdiction and must conform to the framework plan. (In the case of the County of San Diego, there will ultimately be three separate subareas, the existing one covering the southwestern part of the County, a North County subarea, and an East County subarea to deal with the size and diversity of habitats and ownerships.)

The San Diego County subarea plan, adopted by the Board of Supervisors in 1997, is for the unincorporated area only and is separate and distinct from the City of San Diego subarea plan or plans for other cities within the MSCP. Ms. Rolfe is apparently most familiar with the City of San Diego subarea plan. Therefore, I would like to present the positive aspects of the County of San Diego MSCP subarea plan and the NCCP in general.

Benefits of the Plan

Of primary importance, the NCCP and MSCP programs acknowledge that large blocks of habitat are important in the San Diego region due to the diversity of species and habitats that exist here. The implementation of the MSCP, a 50-year program, has had the effect of providing a strong scientific basis for creating large, contiguous, and viable preserve areas. (Note: The Federal and State Permits are effective for 50 years. The assumption was that it might take 50 years to assemble the entire preserve system in

the plan. In fact, it is likely to occur at a faster rate. The areas being set aside as part of the preserve systems must be preserved "in perpetuity.")

This is a major accomplishment that has had a positive effect on land use planning in the region. The success of the County of San Diego MSCP has raised its visibility as a balanced approach to planning. Due to coordinated support from governmental, environmental, and building industry groups, the County has obtained consistent funding from local, state, federal, and private sources for the acquisition of open space from willing sellers for permanent preservation.

In addition, several thousand acres have been set aside as part of the MSCP for mitigation of development projects. The County of San Diego recently celebrated its Fifth Anniversary since the adoption of the MSCP.

A major positive spillover effect that has emerged from this program is that biologically diverse lands located within future MSCP subareas in northern and eastern San Diego County have received increased interest from conservationists, and are being acquired as permanent open space from a growing number of willing sellers. The County has worked with private groups including the Nature Conservancy and the Trust for Public Lands, as well as the Anza Borrego Desert Foundation, to complete these transactions. It is interesting to note that since the adoption of the MSCP, The Nature Conservancy and National Wildlife Federation have opened local offices in San Diego.

Without the MSCP, a continual process of piecemeal development with postage stamp preserves existed in the San Diego region. Though the California Environmental Quality Act required reduction and mitigation of impacts from development projects, as development occurred it usually created small areas of open space that were often disconnected from other habitat areas, and sometimes too small to support any significant populations of wildlife. While County planning staff made an effort to connect these areas, the end result was a series of isolated and potentially ineffective mitigation sites.

The increased growth rate in population, coupled with the large number of unusual and rare species in San Diego County, were leading this region toward what former Secretary of Interior Bruce Babbitt described as a "train wreck." Furthermore, as the number of individual species listed as rare and endangered by the State or Federal Government began to grow, the County, wildlife agencies, and property owners scrambled to determine the most appropriate way these species could be protected. This often resulted in decisions that were both confusing and in conflict with economic growth issues.

That is, when species are listed on a case by case basis in a non-coordinated fashion, as species were listed, it was necessary to scramble to determine the most appropriate way that the species should be protected while at the same time deal with economic growth issues. It was a situation resulting in conflicts from inefficiency, lack of coordination, and continually having to deal with additional new species and their mitigation. The overall effect of the MSCP is that it has provided for a large, connected preserve area that addresses a number of species at the habitat level, rather than species-by-species and area-by-area.

Practical Progress

Under the heading "Practical Problems," Ms. Rolfe states that there are inherent incongruities between the "reactive safety net of the CESA and FESA (California and Federal Endangered Species Acts) and the proactive mission of the NCCP program." On the other hand, a program that addresses biological issues on a regional scale by protecting large blocks of habitat for rare and endangered species should not be considered in conflict with the ESA response to species in jeopardy of extinction.

The NCCP program enhances the ESA by providing a means to deal with a number of species at the same time. San Diego County and other locations in California are considered "hot spots" for containing unique and unusual species. The only means to accommodate the protective needs of a large number of rare and endangered

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species is to address them together in a multiple-species type of habitat plan.

Measuring Success

It is obvious that the multiple species planning process is not also able to address the other regional issues of water quality, transportation, and affordable housing. It was never designed to do that, and the process of dealing with endangered species is complicated enough. However, through the MSCP—and its ability to work in a collaborative effort with local, state, and federal government agencies, landowners, conservancies, and other stakeholders—the County has been able to conserve long-term viable populations of the federal- and state-listed species and their habitats.

By building upon an established cooperative relationship with the wildlife agencies and other partners, the County has been able to embark on subarea plan development for the northern and eastern portions of the MSCP. These additional subarea plans will enlarge the County's open space preserve for the enjoyment of generations of Californians.

While the program and process may not always be implemented in a manner desired by all parties, it is the only major program that has demonstrated any success in the conservation of entire habitat areas. While Ms. Rolfe points out what she considers deficiencies in some specific plans, it is important to remember that the overall effect of this planning process is highly positive. Through partner-

ship efforts, habitat conservation plans will continue to save significant sensitive lands.

Thomas A. Oberbauer
Environmental Resource Manager,
Dept. of Planning and Land Use,
County of San Diego

ERRATA

Volume 30, No. 2, page 9. At the bottom of Table 2 in the article by Ellen Dean, the footnote, "Angiosperm Phylogeny Group," should be "Angiosperm Phylogeny Group." For more information about this group and links to synonyms for modern interpretations of plant classification, see www.systbot.uu.se/classification/APG.html.

BOOKS RECEIVED

Xeriscape Plant Guide: 100 Water-Wise Plants for Gardens and Landscapes, by Denver Water Conservation Office, with Introduction by R. Proctor. 1996. Fulcrum Publishing, Golden CO. 184 pages. Although written as a general guide for many states with arid environments, this beautifully designed volume includes many California natives. Each entry includes photograph(s), color illustration(s), and comments on landscape use, form, native range, characteristics, culture, best features, companion plants, and disadvantages. Price \$27.95, softcover.

Xeriscape Color Guide: 100

Water-Wise Plants for Gardens and Landscapes, D. Winger, Ed. 1998. Fulcrum Publishing, Golden CO. 62 pages. A companion to *Xeriscape Plant Guide* described above, with same size and format, but information summarized and re-arranged according to plant form or flower color. Price \$15.95, softcover.

Xeriscape Handbook: A How-To Guide to Natural, Resource-Wise Gardening, by G. Weinstein. 1999. Fulcrum Publishing, Golden CO. 142 pages. A companion to *Xeriscape Plant Guide* described above, with same size and format. Chapters include: climate;

the design process soil; compost, mulch, and fertilizer; planting and development, health and maintenance; and applying water. Price \$24.95, softcover.

Mediterranean Gardening: A Water-Wise Approach, by H. Gildemeister. 1995. 2002, First California Edition. UC Press, Berkeley, CA. 208 pages. This beautifully designed book with attractive photographs was originally written for the Mediterranean region, but will be useful in California because of its climate, and does include some California native species. \$24.95, softcover.

BOOK REVIEW

Flowering Plants and Ferns of Mount Diablo, California, by B. Ertter and M.L. Bowerman. 2002. CNPS Press, Sacramento, CA. 424 pages. Hardcover, \$34.95; softcover, \$19.95.

This new edition of Bowerman's original flora has been fully revised and updated by UC Jepson Herbarium botanist, Barbara Ertter. It includes over 700 species, with the addition of over 200 native and naturalized species.

Local floras provide a floristic clarity analogous to the increasing magnification of a microscope. If *The Jepson Manual* is the naked-eye view of the California flora, then the revised flora of Mt. Diablo is a 40-fold magnification. Nearly six decades elapsed (1944 to 2002) before this sorely needed revision finally appeared.

The Mt. Diablo flora interweaves text from the first edition with extensive new material. Some might quibble about this as an awkward juxtaposition

(which Ertter herself identifies, then rationalizes). However awkward this method might seem to some readers, it makes historical comparison easier. The interweaving of new material and the original occurs throughout the book in prefaces, introductory essays (soils, geology, paleobotany, vegetation, floristics), and under the discussion of each plant.

The catalog of plants is organized in the Englerian sequence, which, although it offers the advantage of plac-

ing similar families together, can be a bit of a challenge for me at times; when under the influence of a fine-scented April day, I am less likely to forget alphabetical arrangement. An index only partially solves this dilemma. Fortunately a list of page numbers for families is available as a supplemental sheet.

Nearly 900 taxa are illuminated in this small, convenient field guide (the paperback edition weighs only about 1.5 pounds). A failure of many recent county floras is the lack of voucher citations. Ertter inspected and annotated thousands of specimens, building upon the vouchers cited originally by Bowerman. Sometimes names are changed, but the reasons for changed determinations are fully discussed.

About one-quarter of the book focuses on the vegetation, while the remainder treats the flora consisting of 841 taxa, an increase of 26% over the 1944 edition. The value of the Mt. Diablo flora rests not just in its list of documented taxa—Ertter provides explicit rationale for a list of rejected records. Of most direct value are lists of potential disappearances and declines (5% of the flora), naturalized aliens (14% of the flora in 1944 increasing to 22%), waifs, and horticultural relics (aliens that have not yet become established). The change in the composition of Mt. Diablo's flora is striking, which makes the original material by Bowerman on vegetation and specific sites (springs, ponds, and unusual habitats) nearly as valuable as permanent plot analysis.

This volume should serve as the model for other local flora revisions. Several floras on the CNPS bookshelf warrant immediate attention using the Ertter model, particularly those of the Mount Hamilton Range (Kern County) and of Marin County. The 1944 first edition of the *Flora of Mt. Diablo* is now rare and valuable (I could not find a used copy for sale on the internet). Those of us fortunate enough to have a copy—likely dog-eared from repeated stuffing in and out of a knapsack—can now stow it safely away on the bookshelf, while we shift to using this fine new revision.

Dean Taylor,
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FROM THE EDITOR

We are very fortunate in this special issue of *Fremontia* to have several excellent articles portraying relationships between native plants and their insect associates. Gordon Frankie, Convening Editor, and other expert contributors have written articles that expand our attention from the plant alone to how native plants fit into their world, what they provide for other organisms, and how human-made changes affect not only plant populations but their associated insect species. The authors describe the great variety of insects occurring in various habitats and offer amazing facts about their behaviors and life cycles, from the leaf mining

larvae of “micro moths” to the specialist or generalist foraging behavior of bees.

For example, did you know that scientists can identify the pattern of a leaf mine scar to the *genus* of micro moth that makes it? Or that the sometimes apple-sized oak galls are made by wasps smaller in size than an ant? Or that there are more species of bark beetles alone in the world than there are vascular plant species in California? I have learned that sometimes up to a dozen species of bumble bees can coexist in an area as small as 100 square meters, that native bees are abundant in urban areas, and that native bees can be important crop-

pollinators. The implication of the last two facts is that more native plant habitats in cities and adjacent to croplands will support native bee populations, which would in turn be an asset to farmers. In addition, plantings of purple needle grass, *Nassella pulchra*, adjacent to tomato crops could significantly reduce the populations of stink bug pests, and thus reduce the use of insecticides. I hope that you are as inspired and edified by this selection of articles as I am, so that we can continue to educate others about the values of native plants and their natural environments.

Linda Ann Vorobik, Editor

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