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

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

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 solsititalis*).

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

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