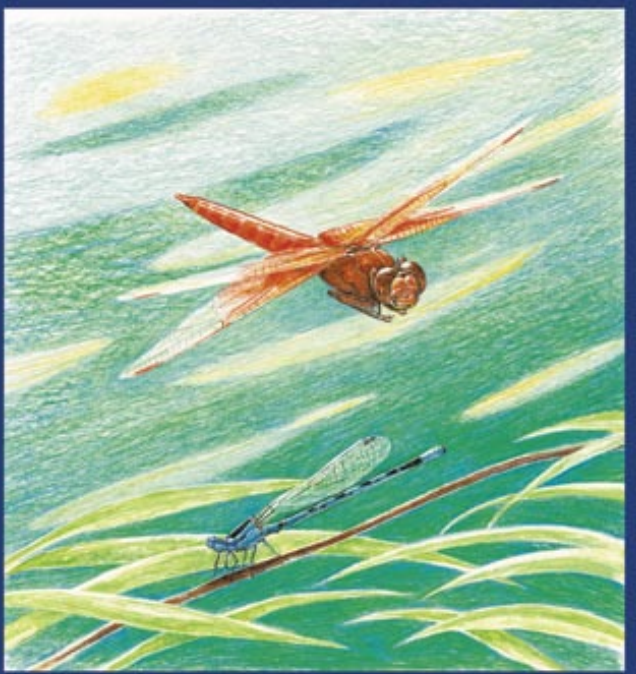
CALIFORNIA NATURAL HISTORY GUIDES

DRAGONFLIES AND DAMSELFLIES OF CALIFORNIA

TIM MANOLIS



INTRODUCTION

Dragonfly Behavior

Adult dragonflies use vision as their primary means of assessing their environment. In this way, they are like us, and their behavior, as compared to that of many other, more secretive insects, is relatively easy to understand if we simply watch what they do. Many specific behaviors are characteristic of particular species or groups of species, so in making an identification, observing behavior is often as important as noting appearance.

Dragonfly behavior has evolved in response to a few simple needs:

The need to eat
The need to avoid being eaten
The need to reproduce
The need to regulate body temperature (thermoregulation)
The need to disperse

Some of the distinctive behaviors odonates have evolved to meet these needs are discussed in the following sections.

Feeding Behavior

Dragonflies are voracious predators; they eat just about any animal they can catch and chew, including other dragonflies. Most prey of adult dragonflies are flying insects, taken on the wing. The two general types of aerial feeding used by dragonflies are hawking (the constant pursuit of flying insects) and sallying (darting out from a perch to capture prey and then return to the perch). Hawking dragonflies remind bird-watchers of swifts or swallows and often feed in swarms as do those bird species, whereas salliers are reminiscent of flycatchers. Some species are hover-gleaners,

picking prey from vegetation and other substrates while in flight. Most species use one of these foraging strategies predominantly but may occasionally use the other two as well.

Dragonflies that typically hawk for food include the darners, river cruisers *(Macromia),* baskettails *(Tetragoneuria),* emeralds *(Cordulia* and *Somatochlora),* spiketails, gliders *(Pantala),* and saddlebags *(Tramea),* among others. They are strong fliers of medium to large size. In genera such as the gliders and saddlebags, the hind wings are relatively broad based, allowing for almost effortless, gliding flight in light winds. Hawking dragonflies frequently fly back and forth along a set path or series of paths over open fields and meadows or along creeks, rivers, and even roads. They are on the wing for extended periods of time. Darners, gliders, saddlebags, and others that hawk may form feeding swarms of dozens to hundreds of individuals, most often at dusk in late summer and fall. When they eventually perch, they do so to rest, digest a meal, or avoid unfavorable weather conditions. In general, they are somewhat cryptically colored (dull earth tones predominate), tend to perch high or in the shade of dense vegetation rather than on low, exposed perches, and typically hang from a perch, their bodies oriented vertically.

Many species in the skimmer subfamily (Libellulinae) and many damselflies are salliers. From a perch on the ground, vegetation, fence post, or other surface, they alertly scan the sky for potential prey. Typically they sit in exposed situations that provide a wide field of view. When they spy a meal, they dash out to capture it and return to a perch, usually the one they just left, to finish eating. When perched and actively foraging, they tend to adopt a flight-ready position, the body oriented horizontally.

The third feeding technique used, especially by damselflies, is hover-gleaning, which involves flitting from spot to spot, picking food items off vegetation in rapid bursts, followed by a brief period of perching to chew up the prey. American bluets *(Enallagma)* are often seen feeding in this way. Other damselflies, such as the spreadwings and broad-winged damsels, sally out from a perch to fly catch or hover-glean a single prey item at a time, then perch again to finish eating.

Antipredator Behavior

Dragonflies typically avoid aerial predators—birds, bats, and insects such as robber flies, wasps, and even other dragonflies—by

agile aerial maneuvering, as anyone who tries to net them can attest. Disturbed damselflies frequently dodge into nearby vegetation. If flight is a less viable option (e.g., at cold temperatures), perched damselflies sidle around perches such as grass stems or small branches, using the perch as a screen much as woodpeckers use tree trunks.

The patterns on the bodies or wings of some species may serve as cryptic coloration against certain backgrounds, and this may in part influence perch selection. The bright colors of some species, especially the blues of darners and many damselflies, fade to gray at cooler temperatures, when mobility is reduced. Dragonflies also seem to magically disappear from conspicuous perches when the sun goes behind a cloud, perhaps to avoid detection by predators when their activity levels drop.

Reproductive Behavior

Reproduction is the major goal of an adult dragonfly's existence. After a few days or weeks of prereproductive life, during which it must feed, grow, and mature, it begins a programmed series of activities focused on reproduction.

The first step is finding a mate. In most cases, mates are sought near or at the body of water in which eggs are to be laid. In a few cases, mates are sought away from water and then escorted there. Males typically arrive at rendezvous sites before females. Peak mating hours vary among species but are often in the late morning or early afternoon. Males commonly interact aggressively with other males in order to establish territories or otherwise secure advantageous positioning for attracting or finding mates. Males of some species seek females from a perch, whereas others, such as darners, patrol in search of mates.

Courtship is rare in dragonflies, and males usually quickly pounce on females that arrive at rendezvous sites or are otherwise encountered during mate searches, even knocking them to the ground in some cases. They then quickly proceed to the next step, which is formation of tandem linkage.

Tandem linkage is the physical link of the male's abdominal appendages to the rear of the head or the thorax of the female. This linkage often provides a close fit of species-specific body parts, which may inhibit interspecific mating attempts (and coincidentally makes these body parts useful to humans attempting to identify individuals as to species).

Next is copulation, which also tends to follow quickly. Dragonflies are unique among insects in that the secondary genitalia of males are housed in the undersurface of the second abdominal segment. Usually after linking with a female, but sometimes before, a male transfers sperm from near the tip of the abdomen to a storage area in his secondary genitalia. The female subsequently bends her abdomen forward to align her reproductive structures under the eighth abdominal segment with the male's secondary genitalia. This position, which involves two points of linkage, is called the wheel (fig. 3).

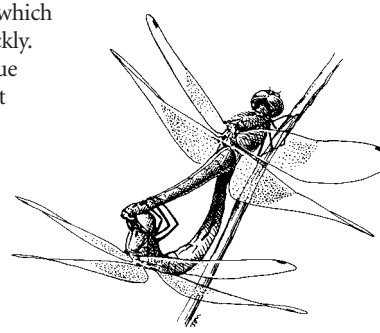


Figure 3. A pair of Western Meadowhawks copulating in the wheel position.

The elaborate complex of secondary genitalia in males not only stores and transfers sperm but is designed to remove any sperm placed by other males in prior mating attempts. Indeed, much of the time spent by a pair in the wheel (a few minutes to hours in some species) is taken up by sperm removal, followed by a relatively brief period of sperm transfer. Because the secondary genitalia also require a good fit, they, too, are useful for distinguishing a number of look-alike species.

After sperm transfer, the next step is oviposition. The female of some species (damselflies, darners, petaltails, and spiketails) uses her ovipositor, or vulvar lamina, to insert eggs into a substrate—usually some sort of vegetation. Other species use a variety of techniques, discussed in the species accounts, to drop or deposit their eggs in water, on vegetation, or on the ground.

The male may remain in tandem with the female during oviposition, apparently protecting his investment in the eggs being laid. In other species, the male hovers near the ovipositing female and chases off intruders (fig. 4), especially other males of the same species. The female of some species typically oviposits while alone. There is considerable variation within species in these modes of oviposition, however, and some species exhibit more than one type,

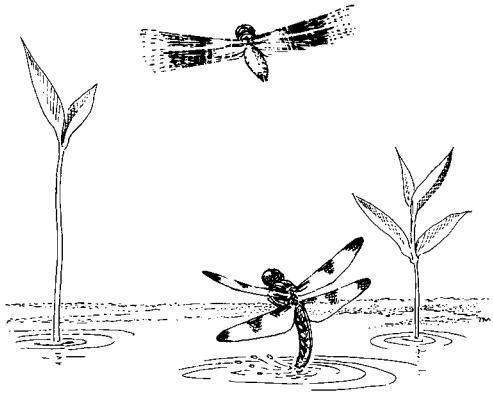


Figure 4. The male Common Whitetail hovers over an ovipositing female to guard her from other males.

depending on circumstances such as population density and habitat structure.

Thermoregulation

Dragonflies use a variety of behaviors in order to maintain an appropriate body temperature. Many of these movements and postures are designed to take advantage of solar radiation.

The most obvious of these is basking—perching on vegetation, fence wires, the ground, rocks, and other sites fully exposed to the sun, much as lizards do. The wings may be held down toward the sides to trap warm air close to the thorax. Many species that live in cooler climes, such as whitefaces *(Leucorrhinia)* and emeralds, have mostly blackish bodies, presumably to enhance absorption of solar radiation.

Some of the larger, hawking species, such as darners, can warm up by rapidly vibrating the large flight muscles in their thorax, either while perched or by flying.

Because dragonflies are most active in warm, sunny weather, they also have to worry about overheating. Simply seeking shade and reducing activity for a time can accomplish this. Some exposed perchers adopt a very distinctive position called the obelisk, in which the abdomen is pointed directly at the sun (nearly straight

up at midday) to minimize the body surface area exposed to direct rays (fig. 5). The tip of the abdomen can also be pointed down (away from the sun) to achieve a similar effect; this posture is often adopted by saddlebags in flight, the dark patches on their hind wings shading the drooped abdomen.

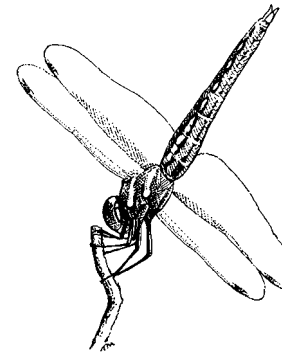


Figure 5. A Variegated Meadowhawk in the obelisk position.

As discussed in the section "Antipredator Behavior," the blue colors of many darners and damselflies and the red colors of some species such as meadowhawks *(Sympetrum)* are subject to reversible, temperature-induced changes, becoming bright at higher temperatures and dull at lower ones. The brighter color produced by higher ambient temperatures is also more reflective (absorbing less light), thus helping to reduce body temperature. Conversely, individuals at cooler temperatures increase their absorption of solar radiation via darker body color.

Dispersal

After emergence from the final larval stage, virtually all odonates disperse. For many, this involves flying a distance from a few feet to a few miles away. Such short-range dispersal probably serves a number of functions, including (1) occupation of good foraging areas, (2) avoidance of harassment by breeding adults, and (3) potential discovery of new breeding sites. Once they become sexually mature, adults return to breeding sites, from which they may commute between feeding and roosting sites.

A few species are capable of long-distance movements, although the exact nature and extent of these migrations is poorly known. Dragonflies believed to migrate in western North America are the Common Green Darner *(Anax junius),* Variegated Meadowhawk *(Sympetrum corruptum),* gliders, and saddlebags. Observations suggest that, in late winter and early spring, these species begin to emerge in large numbers in Mexico and the southern border states (including the warmer areas of Califor-

nia) and move north into the northern United States and southern Canada. They breed in summer and then die. A late summer and fall emergence resulting from this breeding activity typically produces large numbers of offspring that migrate back south to breed in fall and early winter, and their offspring in turn emerge in spring to repeat the cycle.

Life Cycles and Larvae of Dragonflies

Dragonflies are amphibians in the same general sense as frogs, toads, and many salamanders. The familiar, winged adults that are the primary focus of this guide are the final, reproductive stage in the odonate life cycle. But, like amphibians, they are preceded by an aquatic larval stage that, from hatching of the egg to emergence of the adult form, involves much of each dragonfly's total life span, growth, and development (fig. 6).

Although much less conspicuous than and markedly different in appearance from adults, odonate larvae (sometimes referred to as nymphs or naiads) are unique and fascinating in their way. Overall, larvae coloration is typically drab and designed to camouflage. Their eyes are smaller and their antennae are frequently more prominent than those of adults. Unlike adults, they use their legs for getting about, not for prey capture and handling. The abdomen is relatively short and sometimes armed with spines or knobs along the top and sides. In later larval stages, pads housing the developing wings lie on top of the front of the abdomen.

Like adults, larvae are high-level predators, feeding on a wide range of aquatic invertebrates, including other odonates. Large, active larvae are capable of capturing and subduing small fish and tadpoles. Their most distinctive feature, found only in the Odonata, is a double-hinged labium, or lower jaw. The labium consists of the postmentum, folded back under the front of the body; the prementum, hinged to the postmentum and, at rest, folded forward to cover it; and labial palps hinged to the front of the prementum and often covering the lower face. When potential prey draw within reach of this potent weapon, it is thrust forward at high speed. The movable palps at its tip, armed with hooks, teeth, and spiny hairs, capture and hold the prey. The labium is instantly retracted after capture, drawing the prey back to the chewing mouthparts. The structure of the labium varies among odonate families and is often useful for identifying larvae (fig. 7).

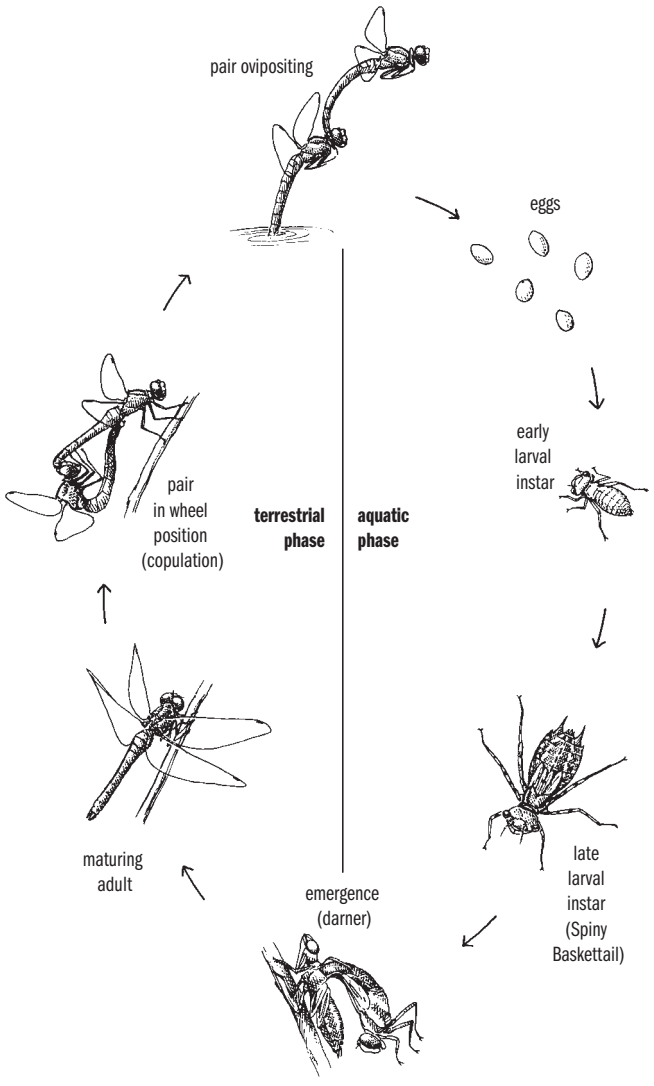


Figure 6. Life cycle of a dragonfly.

Other unique features of odonate larvae are the gills they use to extract oxygen from the water in which they live. In damselflies, this is accomplished primarily by three leaflike gills that extend from the tip of the abdomen. Typical dragonflies have internal rectal gills over which they are constantly pumping water. Both types of gill systems also aid in locomotion, although in different ways. Some zygopterans can use their external gills as a sort of tail fin, swished from side to side to help them swim along. Anisopterans can rapidly expel water out the rectum to jet forward when a quick getaway is called for.

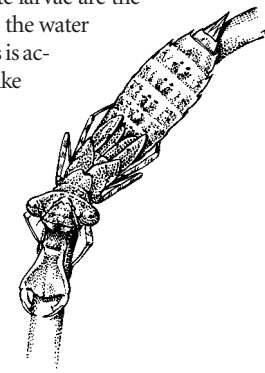


Figure 7. Variable Darner larva with labium extended for prey capture.

The basic larval body plan is modified in different species that live in different habitats and have different lifestyles. For example, dragonfly larvae that clamber about in aquatic vegetation and actively stalk prey, such as the larvae of large darners, have smooth, streamlined bodies and large eyes facing to the side. Species whose larvae sprawl in bottom sediments, such as the Pacific Spiketail *(Cordulegaster dorsalis),* have hairy bodies to which camouflaging detritus can adhere and eyes raised above the medium in which their bodies are mostly hidden. Shallow burrowers, such as the clubtails, have somewhat flattened, hairy bodies and thickened or platelike antennae that rest at the surface to detect prey. The elongate tip of the abdomen is also raised up above the surface of the mud to allow respiration through the rectal gills. Sprawlers and burrowers are ambush predators that sit and wait for prey to wander into range.

Most of California's odonates have a single generation per year. Adults emerge, mature, and lay eggs in the warmer months, primarily April through October. Eggs hatch within a few days or weeks, and the larvae grow through a series of about 10 to 15 molts. The stages between molts are called instars. Larvae usually overwinter in a relatively late stage of development. In the spreadwings and many meadowhawks, which typically breed in temporary habitats late in the season, it is the eggs that usually

overwinter, hatching in spring. Adults emerge again the following year to repeat the cycle.

There are exceptions, however. Some smaller damselflies, such as forktails *(Ischnura)* and bluets, have long flight seasons and may have two or three broods per year, the last brood of the season overwintering as larvae. On the other hand, some dragonflies, often those that live in streams or rivers, at high elevations, or in other more demanding habitats, may live as larvae for 2 to 4 years before emerging. Some darners, clubtails, spiketails, and emeralds are among these relatively long-lived species. No California odonate is known with certainty to survive winter as an adult and breed the following spring, although midwinter sightings of the Variegated Meadowhawk suggest that this species might be capable of doing so, at least in some years.

In the final stage—the metamorphosis—the last larval instar leaves the water. In some species it may move some distance from water, even climbing into vegetation. In other species it simply crawls up onto the shore. The exoskeleton along the back splits open, and the adult dragonfly emerges. It is initially somewhat stunted in form and colorless. Blood is pumped into the wings and abdomen to expand them. When the adult form is achieved, usually after a few minutes to over an hour, the young dragonfly, called a teneral, flies away from the emergence site to forage and mature fully. Teneral dragonflies typically have somewhat flimsy, glistening wings, and their bodies are still soft, so they are easily damaged if handled. This is a brief but dangerous time in a dragonfly's life, and many tenerals are preyed upon, for example, by birds and even other dragonflies.

The cast-off larval exoskeleton, called an exuvia, is paper light but often remarkably sturdy. Exuviae of species that emerge in large numbers over a short time may be found littering the shore of lakes or ponds, perched on rocks in streambeds, and hanging from emergent vegetation. The characteristic features of the larvae are preserved in fine detail on exuviae, which often can be identified to genus if not species. They also may indicate some measure of breeding distribution and habitat use by the various species in a region.

The following key will help you identify late-instar larvae (those with definite wing pads) and exuviae to family and, in some cases, to subfamily. Some larvae are especially distinctive, and a few of these are illustrated in fig. 8. However, in some

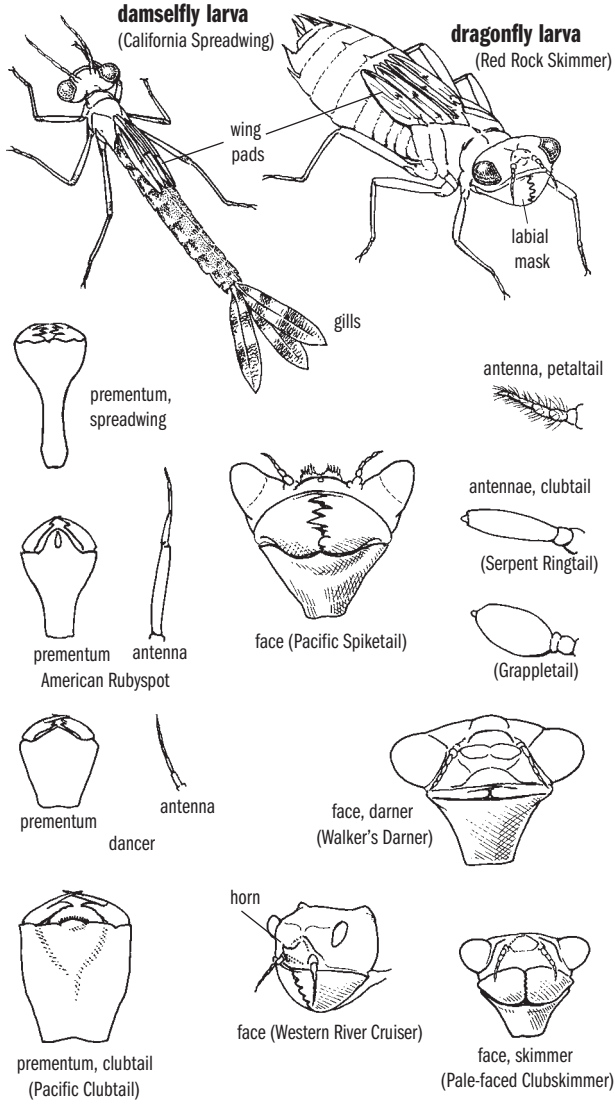


Figure 8. Key characteristics for identifying dragonfly larvae with regard to family.

groups, most notably the pond damsel family (Coenagrionidae), the differences among species and even genera are difficult to detect, requiring high-powered magnification and often reference to a large series of specimens or some of the sources cited in the "References" section.

Family and Subfamily Key to Dragonfly Larvae

1a. Small and thin bodied, with three leaflike gills at end of abdomen 2
1b. More robust, without leaflike gills. 4
  2a. First (basal) segment of antenna enlarged, longer than the other segments combined . . . . . broad-winged damsels (Calopterygidae)
  2b. All segments of antennae about equal in size 3
3a. Prementum spoon shaped, with basal stalk . . . . . spreadwings (Lestidae)
3b. Prementum not stalked . . pond damsels (Coenagrionidae)
  4a. Prementum and labial palps flat, carried under the head when retracted 5
  4b. Front of prementum and labial palps curved to form a cuplike structure (labial mask) that covers the lower half of the face when retracted 7
5a. Antennae short and thick, four segmented; segment at tip (fourth) minute or vestigial; front of prementum not cleft . . . . . clubtails (Gomphidae)
5b. Antennae slender, six or seven segmented; front of prementum with central cleft 6
  6a. Found in burrows in mossy bogs; antennae hairy . . . . . petaltails (Petaluridae)
  6b. Free swimming in ponds, lakes, or creeks; slender antennae not conspicuously hairy . . . . . darners (Aeshnidae)
7a. Labial palps with large, ragged teeth; prementum with cleft in front . . . . . spiketails (Cordulegastridae)
7b. Margins of labial palps smooth or with fine, even teeth; prementum not cleft 8

8a. Horn on top of head between antennae; legs long for body size ("spidery") . . . . . cruisers (Libellulidae: Macromiinae)

8b. No central horn atop head . . . . . emeralds (Libellulidae: Corduliinae) and skimmers (Libellulidae: Libellulinae)

Distribution

Any discussion of the distribution of California's dragonflies must be prefaced with the acknowledgment that a number of species are represented by just a few, scattered records and that large areas of the state have been little explored for odonates. That being said, the broad outlines of statewide distribution can be described for many species, and regional faunas can be defined by examining the patterns of these distributions (figs. 9, 10).

Because of its size and varied topography, California has a diverse dragonfly fauna of 108 species, ranging from subtropical to boreal forms. The group of species around a boggy Sierran lake is quite different from that of a Central Valley marsh, and both differ greatly from that of a Colorado Desert hot spring. The diverse regional landscape compensates somewhat for the fact that the arid climate of much of the state limits the extent and variety of aquatic environments that provide for rich dragonfly faunas in more humid climes. For example, Ohio, a smaller state with less geographic and climatic diversity but wetter summers than California, hosts about 162 species of odonates.

A glance at a map of California (fig. 10) quickly reveals what is well known to most Californians: the state is composed of a series of large and diverse topographic features that run from north to south. From west to east, these include a string of coastal ranges; a large, central valley; high mountains (the Sierra Nevada and Cascade Range); and desert country along the eastern border of the state (the Great Basin in the north and the Mojave and Colorado Deserts to the south).

The north-south orientation of most of the state's mountain ranges aligns them broadside to the prevailing path of winter storms headed east off of the Pacific Ocean. As a result, the mountains have a major impact on the distribution of precipita-

Figure 9. Map of California counties.

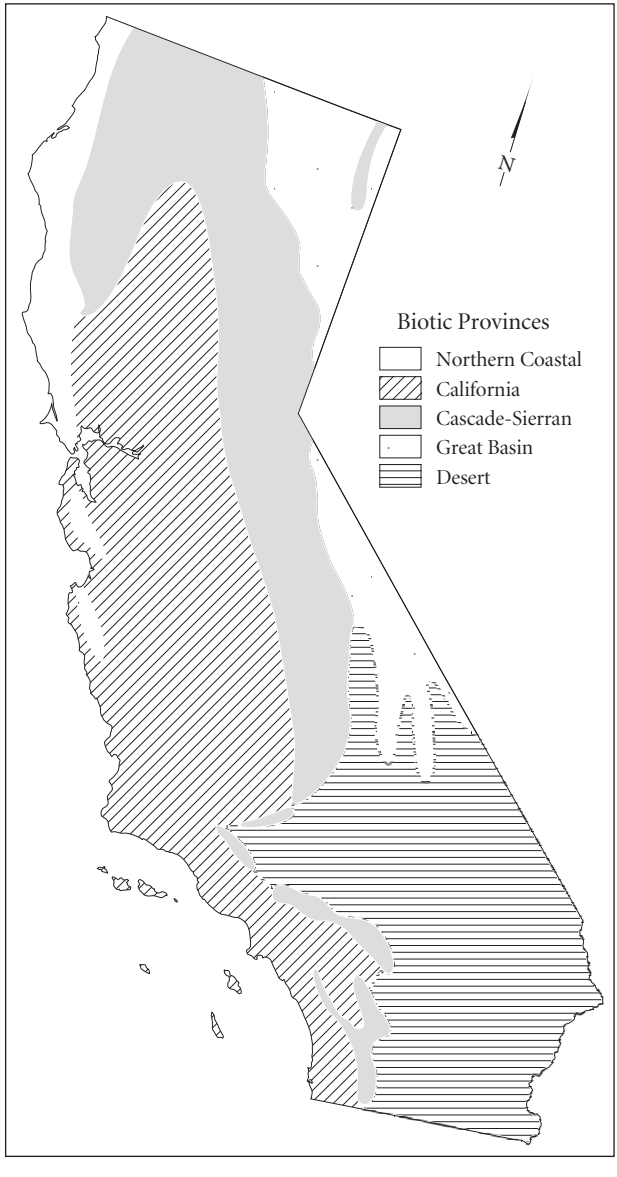


Figure 10. Map of California biotic provinces.

tion in California, most of which is delivered by those winter storms. A good deal of that precipitation is deposited in the form of rain (and some snow, primarily in the north) as moisture-laden air rises up over the western slopes of the Coast Ranges. As the cool air drops down the eastern slopes of the coastal hills, it retains some moisture, limiting precipitation in the Central Valley, especially in the south, to modest proportions. Even more rain and snow are rung out of these Pacific storms as the air rises again over the higher interior ranges; by the time the storms reach the eastern slopes they often have little moisture left to spare, resulting in desert conditions in those areas.

This dramatic disparity in the distribution of water in California has been greatly altered by human activity in the past century. Giant aqueducts carry water from rivers in the north to urban centers in the drier south. Thousands of artificial bodies of water, from immense reservoirs to small stock ponds, have been created in the mountains and foothills to harness runoff that formerly produced extensive seasonal wetlands in the Central Valley. Both the natural distribution of water in the state and its manipulation by humans are significant influences on the distribution of odonates.

Regional dragonfly faunas are perhaps best discussed in the context of biotic provinces, which are large areas primarily defined by topography, climate, and vegetation. The following provinces, and their associated odonate faunas, occur in California.

Northern Coastal Province

The Northern Coastal Province is a region of heavy winter rainfall and cool, foggy summers on the western slope of the Coast Ranges, from the Oregon border to the northern San Francisco Bay Area (where small pockets of this province are found within the next province, south to the Monterey area). This is what Californians think of as "redwood country." Most of this area was originally clothed in humid conifer forest, but much of it has been logged for timber or cleared for agriculture. Aquatic habitats are primarily fast-flowing rivers and creeks bordered by willows and alders but include some marshes bordering coastal lagoons and bays. Some mountain lakes are found, primarily in the north. Only one dragonfly species, the Swift Forktail *(Ischnura erratica),* has its range within the state almost completely re-

stricted to this province. Other species in this region are also found in the Cascade-Sierran Province (primarily at higher elevations and to the north) and the California Province (primarily at lower elevations and to the south).

California Province

The California Province is the heart of California and includes the Central Valley, the inner Coast Ranges (and valleys such as the Napa Valley) from approximately Lake and Mendocino Counties southward to the San Francisco Bay Area, and all the coastal districts from there southward to the Mexican border (except for the higher mountains of southern California). Few odonate species have been recorded from the Channel Islands, and all are species found along the nearby mainland, so those islands are best included in this province.

Although topographically varied, the various parts of this region share a Mediterranean climate (cool, wet winters and hot, dry summers). Except for the major river systems and large flood basins of the Central Valley, which receive runoff from the Sierra Nevada snowpack through spring and into summer, natural wetlands in this province historically tended to be seasonal, containing little standing water by late summer. However, a large percentage of the region's natural wetlands have been drained, developed, or altered to a great extent. The flow of water through many of the major rivers is regulated by dams, resulting in higher, colder water levels later in summer than in the past. The creation of reservoirs has provided large areas of permanent open water in areas that originally had none. Aqueducts and irrigation canals move large quantities of water over long distances from one part of the province to another. All of this activity has no doubt had a profound affect on odonate populations.

This province, which is restricted to California and part of adjacent Baja California, contains the greatest number of species of plants and animals endemic to California (i. e., not found elsewhere) of any province in the state. Not surprisingly, this includes our only endemic odonate species (the San Francisco Forktail *[Ischnura gemina]* and Exclamation Damsel *[Zoniagrion exclamationis]*). A few other species (e.g., the Lavender Dancer *[Argia hinei]* and Serpent Ringtail *[Erpetogomphus lampropeltis]*) are known only from this province within California (although they also

occur outside the state), and several others (the California Spreadwing *[Archilestes californica],* Great Spreadwing *[Archilestes grandis],* Black Spreadwing *[Lestes stultus],* Sooty Dancer *[Argia lugens],* Walker's Darner *[Aeshna walkeri],* Bison Snaketail *[Ophiogomphus bison],* Pale-faced Clubskimmer *[Brechmorhoga mendax],* and Red Rock Skimmer *[Paltothemis lineatipes]*) are characteristic of this province and relatively scarce outside of it within the state. Many other species, however, are shared with the Desert Province.

Cascade-Sierran Province

The Cascade-Sierran Province includes all the high-mountain areas, dominated by mixed-conifer forests, throughout the state—the Klamath Mountains, North Coast Ranges, Cascade Range, Warner Mountains, Sierra Nevada, and higher peaks of some of the small mountain ranges in southern California. These areas are characterized by cold winters, in which some of the precipitation falls as snow, and mild summers, with some precipitation in the form of thundershowers. Still waters at the higher elevations may be frozen during at least part of winter. The dragonfly season begins later at higher elevations, and many species in this province do not emerge in numbers until July through September, well after the peaks of emergence for most lowland populations.

This province contains a great variety of aquatic habitats, both still and flowing waters, including rivers, creeks, springs, seeps, bogs, marshes, wet meadows, and lakes of many sizes and kinds. Such habitat diversity accommodates a rich dragonfly fauna, which is dominated by spreadwings, bluets, darners, emeralds, whitefaces, and meadowhawks. Many of these species are found exclusively, or almost so, within this province in California but are distributed much more widely to the north in the mountain forests of the Pacific Northwest and the boreal forests of Canada. These include the Emerald Spreadwing *(Lestes dryas),* Taiga Bluet *(Coenagrion resolutum),* Sedge Sprite *(Nehalennia irene),* Black Petaltail *(Tanypteryx hageni),* Canada Darner *(Aeshna canadensis),* American Emerald *(Cordulia shurtleffii),* Mountain Emerald *(Somatochlora semicircularis),* Ringed Emerald *(Somatochlora albicincta),* Spiny Baskettail *(Tetragoneuria spinigera),* Four-spotted Skimmer *(Libellula quadrimaculata),*

Chalk-fronted Corporal *(Ladona julia),* Hudsonian Whiteface *(Leucorrhinia hudsonica),* Red-waisted Whiteface *(Leucorrhinia proxima),* Crimson-ringed Whiteface *(Leucorrhinia glacialis),* and Black Meadowhawk *(Sympetrum danae).*

Great Basin Province

The Great Basin Province is "sagebrush country," the area of high desert with cold winters, dominated by sagebrush-covered flats and juniper-clad hills east of the Cascade Range and Sierra Nevada. Dragonfly habitats in this region include small rivers and creeks; isolated springs, both hot and cold; freshwater marshes; and ponds and lakes, many of which are intermittent and alkaline. Species primarily restricted to this province within California include the River Bluet *(Enallagma anna),* Alkali Bluet *(Enallagma clausum),* and Pale Snaketail *(Ophiogomphus severus).* Some other species characteristic of the region, but also found in the southern Desert Province, are the Paiute Dancer *(Argia alberta),* Brimstone Clubtail *(Stylurus intricatus),* Bleached Skimmer *(Libellula composita),* and Desert Whitetail *(Plathemis subornata).* In addition, a number of species of the Great Basin—the River Jewelwing *(Calopteryx aequabilis),* Common Spreadwing *(Lestes disjunctus),* Lyre-tipped Spreadwing *(Lestes unguiculatus),* Western Red Damsel *(Amphiagrion abbreviatum),* Great Basin Snaketail *(Ophiogomphus morrisoni),* Dot-tailed Whiteface *(Leucorrhinia intacta),* and a variety of meadowhawks—are shared with the Cascade-Sierran province.

Desert Province

The Desert Province includes both the Mojave and Colorado Deserts, which have similar dragonfly faunas and also share many species with the Great Basin and California Provinces. Natural dragonfly habitats of the region are primarily spring runs and alkaline basins, but also desert rivers such as the Mojave and the Colorado. Irrigation projects, especially those involving the Colorado River, have significantly altered the distribution of water in this region and created a number of nonnative aquatic habitats, such as irrigation canals and artificial lakes and rivers. The most dramatic of these is the Salton Sea and environs, inadvertently flooded in the early part of the twentieth century.

Species characteristic of this province in California are the Powdered Dancer *(Argia moesta),* Blue-ringed Dancer *(Argia sedula),* Double-striped Bluet *(Enallagma basidens),* Desert Forktail *(Ischnura barberi),* Citrine Forktail *(Ischnura hastata),* Rambur's Forktail *(Ischnura ramburii),* Russet-tipped Clubtail *(Stylurus plagiatus),* Red-tailed Pennant *(Brachymesia furcata),* Marl Pennant *(Macrodiplax balteata),* Roseate Skimmer *(Orthemis ferruginea),* and Mexican Amberwing *(Perithemis intensa).* A number of these species were detected in the state only within the past few decades and appear to have spread into this region as a result of extensive human alterations of aquatic systems.

Watching Dragonflies

You can easily watch and enjoy many species of dragonfly with the naked eye. However, you will need a few aids to help you accurately identify most species.

A pair of binoculars is very useful. The closer they can focus, the better. Many dragonflies, if approached cautiously, will allow you to get within a few feet. The real trick is to spot them before they see you—and they can see you coming from a good ways off! By carefully approaching a perched dragonfly from behind, you increase your chances of getting close to it.

A spotting scope can also be useful for watching dragonflies. Many species that forage while constantly in flight, such as darners and gliders, are apparently resting between foraging bouts when they go to perch and will often stay perched in the same spot for some time. You should watch for the distinctive behavior of these types of foragers when seeking a roost. The dragonfly will fly in close to vegetation as if looking for a perch, and then back off a few feet. It may repeat this behavior a number of times before landing, so stand still and be patient. Once the animal lands, give it a minute or two to settle down. It may become quite unwary and allow close approach. If you have a spotting scope, get as close to the dragonfly as the focusing on your scope will allow, then study it at leisure. Even very tiny features (such as the tubercle on the undersurface of the first abdominal segment of some species of *Aeshna*) occasionally can be observed in this way.

However, in many situations, particularly those involving

small species (e.g., most damselflies) or very similar looking species (such as the baskettails *[Tetragoneuria]*), you will need a net with which to capture the animal, and some sort of hand lens with which to examine it; 10 to 12× (or higher) magnification is useful. In a pinch you can use your binoculars, turning them around and looking through them backward. A portable source of light may come in handy.

A good dragonfly net has a large mouth (at least 30 cm [1 ft] in diameter, but preferably larger) and a long handle (at least 1 m [3 ft] in length) and is constructed of a light material (e.g., wood, aluminum, bamboo). The mesh should be fine but sturdy. You may build your own net or purchase one (see the reference list at the end of the book).

When netting perched dragonflies, approach from behind. With a full, swift downward or sideways stroke, swing right through the animal, centering it in the net mouth so that it is funneled to the bottom of the net bag, then quickly flick your wrist upward to loop the bag across the rim of the net. Attempting to net dragonflies in flight is much trickier but often the only way possible to catch species that seldom perch within net range or seem to be constantly foraging on the wing. The approach, swing, and follow-through are similar and best taken from behind and below. If possible, watch a dragonfly for a while before trying to net it; if it is following a regular foraging beat, you may be able to strategically position yourself for a successful swing. Or it may perch and allow you to observe, photograph, or sketch it before you net it to make sure of your identification.

A smaller net, like those used for taking fish out of aquaria but with a long handle (about a half meter [1.5 ft]), can be dropped quickly over dragonflies on the ground or low in vegetation.

Removing a dragonfly from a net is usually not too difficult. Try keeping the animal in a small pocket of the net bag to prevent it from flying about and damaging itself or escaping. Carefully insert your hand into the net, and gently grasp the wings. Unlike butterfly wings, dragonfly wings are sturdy and can withstand gentle handling, with no harm to the animal. Hold the animal by all four wings folded together over the back. Don't worry about getting bitten. A large dragonfly may occasionally nip at you, but such a nip is usually more startling than anything else and is unlikely to draw blood or cause much pain.

Although a net will be essential for catching and identifying

all the species you encounter, it is not the only tool you can use to study dragonflies. You may prefer to use a camera—for film, digital imagery, or videotape. It is also useful to write down your observations in a notebook or make sketches of what you see.

The purpose of this guide is to help you identify dragonflies in the field without the need to collect them, although it will be necessary to examine certain species in the hand, especially when first learning to recognize them, to be sure of your identifications. For information on collecting and preserving specimens, consult the references at the back of the book.

Identifying Dragonflies

The first thing most people notice about dragonflies is their color. However, coloration by itself is usually insufficient to allow identification of most dragonflies as to species; for example, fully adult males of most of our bluets and dancers are blue and black. In addition, color can vary quite dramatically within species as a result of age, sex, geographic variation, and even temperature. Teneral dragonflies, within a few hours after emerging, often lack the adult colors and are essentially a dull tan or pale olive color. Males of many species often do not attain full adult coloration until they become reproductively active, which may take several days, and during the interim they may be colored much like females. Females may also change color with age, or they may occur in two different color phases, one different—and typically less colorful—than the male pattern (gynomorphic), and one similar to the color of males (andromorphic). In particular, females of some species (e.g., some damselflies and darners) can show a particularly complicated pattern of variation in color, occurring in two or more color phases and also changing color with age or temperature.

The wings of young adults appear bright and shiny, whereas the wings of old dragonflies typically are dull, somewhat opaque, and tattered. Breeding activity may also affect coloration: females that have oviposited in soil may have the tips of their abdomens coated with dried mud. In species in which the males become pruinose on the abdomen, the pruinescense on segments 5 through 7 is often rubbed off by the female's feet where she grasps the abdomen while in the wheel position.

Ambient temperature can affect color in species such as bluets, dancers, and darners that have blue markings (excluding blue pruinescense). The blue areas on these animals may fade when the temperature drops, becoming dark slate or dull purple, and then revert to bright blue when the temperature rises. This reversible color change can occur within minutes if the animal is rapidly chilled or warmed.

For these reasons, you can't rely on color alone to identify species of dragonflies. More important aspects to note are pattern and structure. Many species have distinctive patterns of dark (typically black or brown, perhaps with some iridescence) and light (white, yellow, blue, green, red) on the thorax and abdomen. Some species have distinctive patches of color on the wings. Differences in these patterns among species may be dramatic or subtle, but they tend to be fairly constant and usually can be viewed through binoculars at close range (if the dragonfly sits still!). Even in species that become pruinose or exhibit temperature-dependent color changes that can obscure these markings, the "ghost" of a pattern can often be seen upon close examination.

Structural features are often critical for identification, especially in large groups of similar species, such as the bluets. Often the most species-specific structures on dragonflies are those that establish the very precise linkage between the sexes during mating. In males, these include the abdominal appendages, used to grasp the female, and the secondary genitalia, under the second abdominal segment. In females, these may include the abdominal appendages and genitalia, the prothorax and plates on the front of the pterothorax of damselflies, or the back of the head in some typical dragonflies. Some of these features can be observed in the field at close range with binoculars, but more often than not individuals need to be captured and examined in the hand.

Overall appearance and behavior are often very useful indicators of the general group to which a particular dragonfly belongs. For example, a medium-sized odonate with a damselfly body type (long, thin abdomen and widely spaced eyes) that holds its wings spread to the side when perched is in all likelihood a species of spreadwing, in either the genus *Lestes* or the genus *Archilestes.* Likewise, a small, mostly black dragonfly with a bright white face is recognizable as a species of whiteface, in the genus *Leucorrhinia.*

When using this book to identify an unfamiliar dragonfly by sight, first, use the family key and fig. 11 to narrow your choices.

Once you become familiar with odonate families, you will be able to skip the key in most cases. Second, skim through the illustrations of species within the family you have selected and look for species similar to your unknown animal. Third, read the descriptions of possible candidates, as well as the section on similar species. Fourth, check the distribution of your likely candidates. At this point you should have narrowed down the possibilities sufficiently to make a confident identification in many cases, but sometimes (especially with damselflies) it will be necessary to capture the animal and examine small, structural features in order to be positive.

Species are described and illustrated as they appear in California. Some species vary in appearance in different parts of their range, so caution is warranted in using this guide well outside the state, especially in the eastern half of North America. The descriptions are useful throughout much of the northwestern part of the continent, however.

Taxonomy and Nomenclature

Both scientific and English names are provided for all species discussed in this guide. The binomial (two-name) nomenclature used by scientists to describe species includes the generic name, which is capitalized (a genus typically is a set of related species, but may be monotypic, i.e., contain only one species), and the specific epithet, which is an adjective or noun that is not capitalized (even if based on a proper name).

The scientific names are Greek, Latin, or latinized English. For example, *Libellula quadrimaculata* is a species in the genus *Libellula.* The specific epithet means *four-spotted,* in reference to the small spots at the nodus of each wing in this species. In a few instances, a third name is used to describe a recognizable subspecies (e.g., *Ophiogomphus morrisoni nevadensis,* the paler form of *Ophiogomphus morrisoni* found in the desert country of the Great Basin). The scientific nomenclature used in this guide follows that of the most recent handbooks of North American damselflies (Westfall and May 1996) and dragonflies (Needham, Westfall, and May 2000).

In this guide, I have used the English names for North Ameri-

can odonates that have recently been standardized by the Dragonfly Society of the Americas (Paulson and Dunkle 1999). To a great extent, these names have also been constructed to have both a group (i.e., generic) component and a specific component. Thus, all the species in the genus *Libellula* (often referred to as the king skimmers) are called skimmers; the English name given to *Libellula quadrimaculata* is Four-spotted Skimmer. Not all English names are this closely linked to their corresponding scientific names, and in some cases the English group name is not tied exclusively to a particular genus (e.g., the Roseate Skimmer is in the genus *Orthemis,* not *Libellula*), but they still remain useful for categorizing species into readily identifiable groups such as skimmers, darners, bluets, meadowhawks and so forth. The English names are not common names, that is, most do not have a history of widespread usage. Indeed, they are of such recent vintage that they are not that familiar even to all professional odonatologists.

Both English and scientific names are useful in certain circumstances. English names are more readily assimilated by English speakers and do not require translation, whereas scientific names are used universally by biologists. It is perhaps most useful to learn both names and use whichever seems appropriate.

The species composition and order of the various families within each suborder are also based on the handbooks referred to above and agree with those most widely accepted by North American odonatologists. However, the relationships of genera and species within families are more controversial. Indeed, a common practice of odonatologists has been to avoid adoption of any particular taxonomic arrangement and simply list genera, and species within genera, in alphabetical order. In this guide, genera and species have been ordered to facilitate field identification as much as possible. Often this means that closely related species are grouped together, but not always. As a result, you should not attempt to interpret the order of the species listed as a "family tree."

About the Maps

The best range maps are dot maps, which plot known locations as individual points. Dot maps, however, are not suited for publication at the small size required for the range maps in this guide.

The range maps provided here were created by first plotting known locations on a map of the state, encircling the appropriate cluster(s) of plotted points, and finally, shading in the enclosed area(s). In some cases, isolated locations were plotted as single points.

Determination of boundaries of each distribution was based on knowledge of topography and presence or absence of suitable habitat. It should not be assumed, however, that a species is necessarily evenly dispersed throughout the range shown. For example, the distribution of most odonates in the desert regions of the state is extremely sparse because of the limited availability of water. The maps, then, should be considered rough guides to general range and not detailed depictions of known distribution.

Family and Subfamily Key to Adult Dragonflies

1a. Delicate, slender bodied; compound eyes somewhat stalked and widely separated; fore and hind wings of similar shape and size, typically held together over the abdomen (partly spread in one family). 2

1b. Heavy bodied; large compound eyes touch each other or are relatively close together; hind wings broader based than fore wings, wings held spread out to sides 4

2a. Wings with patches of black or brown at tips or red or brown at base, not constricted near base . . . . . broad-winged damsels (Calopterygidae)

2b. Wings constricted near base (petiolate), without colored patches. 3

3a. Wings typically held partly spread out to sides; pterostigma relatively long, equal in length to width of eye . . . . . spreadwings (Lestidae)

3b. Wings typically held together over abdomen; pterostigma about as long as wide, smaller than width of eye . . . . . pond damsels (Coenagrionidae)

4a. Compound eyes well separated. 5

4b. Compound eyes touching, if only slightly 6

5a. Pterostigma long and narrow; body usually black with

spreadwing

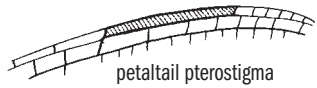
broad-winged damsel

pond damsel

spreadwing pterostigma

pond damsel pterostigma

petaltail head (top view)

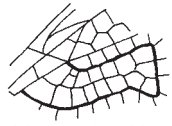


petaltail pterostigma

spiketail head (top view)

clubtail pterostigma

darner head (top view)



club-shaped anal loop
in hind wing of an emerald

skimmer head (top view)

foot-shaped anal loop
in hind wing of a skimmer

Figure 11. Key characteristics for identifying adult dragonflies with regard to family.

yellow markings; found at hillside seeps and mountain bogs . . . . . Black Petaltail (Petaluridae)

5b. Pterostigma relatively thick and oval shaped; variably patterned; usually found along rivers and streams (some at lakes) . . . . . clubtails (Gomphidae)

6a. Eyes just touching; large, black body marked with yellow . . . . . Pacific Spiketail (Cordulegastridae)

6b. Eyes broadly contiguous; variously colored 7

7a. Large (>55 mm in length); robust thorax either entirely green or brown striped with blue, green, or yellow; long, cylindrical abdomen either extensively blue or purple, or with patchwork of blue, brown, or yellow spots; females use ovipositor to insert eggs in vegetation, logs, mud, etc . . . . . darners (Aeshnidae)

7b. Variable in size, shape, and color, but not as described above; females deposit eggs in water (some on ground or vegetation) 8

8a. Large; black or dark brown with yellow saddles on top of abdominal segments 3 through 8, abdomen of male club shaped at tip; single pale yellow stripe on side of pterothorax; fast fliers patrolling streams and rivers or feeding over roads and clearings . . . . . Western River Cruiser (Libellulidae: Macromiinae)

8b. Not as above 9

9a. Anal loop club shaped; abdomen black or black with row of orange yellow patches along side of spindle-shaped abdomen; eyes glowing emerald green or turquoise; hang vertically when perched; found at wooded ponds, lakes, or boggy meadows . . . . . emeralds (Libellulidae: Corduliinae)

9b. Not as above; anal loop foot shaped; color, size, and pattern variable, many with patches of color on wings; occupy a wide range of habitats and include some of the most familiar species . . . . . skimmers (Libellulidae: Libellulinae)