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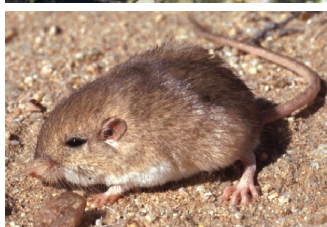
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Planning for Biodiversity: Bringing Research and Management Together

Proceedings of a Symposium for the South Coast Ecoregion

February 29 - March 2, 2000

Pomona, California



Abstract

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Southern California, recognized as a major center of biodiversity, contains some of the most diverse habitats of any landscape in North America. The ever-expanding human population of the region desires land, water, resources, and recreation, creating conflict with the habitat requirements of many rare species. Managing resources in a way that maximizes biodiversity in remaining habitats, while providing opportunities for other appropriate uses of the land, presents a formidable challenge, requiring coordination between scientists and resource managers. The papers in this proceedings volume reflect the breadth of issues facing the science and management communities in southern California, ranging from the threats of fire, air pollution, grazing, exotic species invasion, and habitat loss on native habitats and sensitive species, including birds, mammals, reptiles and amphibians, to the role of mycorrhizal fungi as indicators of biological change.

Retrieval Terms: air pollution impacts, biological diversity, California south coast ecoregion, fire management, habitat management, rare species

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Disclaimer

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Introduction

Southern California contains some of the most diverse habitats of any landscape in North America and is recognized as a major center of biodiversity. It is also home to an ever-expanding human population, with needs for land, water, resources, and recreation that conflict directly with the habitat requirements of many species. As a result, this region has more endangered and threatened species than any other area in the continental United States, and once-extensive natural communities, many of which are unique to the ecoregion, have been reduced to mere remnants.

Managing resources in a way that maximizes biodiversity in remaining habitats while providing opportunities for other appropriate uses of the land presents a formidable challenge requiring coordination between scientists and resource managers, yet few opportunities exist for regular exchange of information and ideas between these groups. In response to this need, the U.S. Geological Survey and the USDA Forest Service partnered to co-host a symposium on “Planning for Biodiversity: Bringing Research and Management Together,” held February 29–March 2, 2000 at the Kellogg West Conference Center, California State Polytechnic University in Pomona, California. The goal of the 3-day conference was to identify the current status of our knowledge and gaps in our understanding of regional biodiversity and ecosystem processes, present and future threats to species and habitats, and effective monitoring strategies for southwestern and central coastal California resources. Through a program of 52 invited presentations, 18 contributed posters, and 10 focused discussion groups, the conference created an environment for formal and informal communication among the 300 attendees about the results of scientific studies and their application to resource conservation and management, as well as the information needs of managers responsible for determining and implementing management on the ground.

Of the 45 technical papers presented at the conference, 14 are included in this volume. Authors were asked to synthesize the current state of knowledge regarding their topic and identify areas needing future research. Each paper was assigned to an editor for review and received one to three additional peer reviews. Expanded abstracts of nine posters also were reviewed by the editors and included. The topics addressed in the papers and poster abstracts reflect the breadth of the conference presentations and the issues facing the science and management communities, ranging from the threats of fire, air pollution, grazing, exotic species invasion, and habitat loss on native habitats and sensitive species of birds, mammals, reptiles and amphibians, to the role of mycorrhizal fungi as indicators of biological change.

An outgrowth of the symposium was the recognition that periodic conferences, while important for facilitating information exchange, are by themselves not enough to maintain the ongoing dialog among conservationists needed to effectively apply resources to accomplish mutual goals. As a result, the “San Diego Partners in Biodiversity” was formed, a network of scientists, field biologists, natural resource managers, and others working toward conservation of biodiversity. Building upon the relationships established at the conference, this group now meets monthly to inform and educate each other about activities, opportunities, and needs relating to resource conservation. It is our hope that this type of coordination and collaboration continues to expand and that this volume contributes to that spirit.

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Assessing Estuarine Biota in Southern California¹

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Abstract

In southern California, most estuarine wetlands are gone, and what little habitat remains is degraded. For this reason, it is often of interest to assess the condition of estuaries over time, such as when determining the success of a restoration project. To identify impacts or opportunities for restoration, we also may want to know how a particular estuary, or area within an estuary, compares with neighboring areas. Comparisons among wetlands require knowledge of different estuary types. The seven types of estuaries described in this paper can be easily grouped into two functional types, fully tidal and seasonally tidal, based on a simple biotic index: presence of horn snails. A description of the distribution, diversity, and abundance of organisms in estuaries is one way to assess resources, determine the success of a habitat restoration, and compare estuaries to evaluate the biotic consequences of degradation. In this review, I summarize techniques that may be useful for managers charged with biotic inventory and monitoring, emphasizing techniques to categorize wetlands and quantify plants, invertebrates, fishes, birds, and trematode parasites.

Key words: bird, estuary, fish, indicator, invertebrate, trematode

Introduction

Although California has a Mediterranean climate, it contains many types of wetlands. Along the coast, estuaries are the most familiar. In this paper, I first describe estuaries, provide examples of the functions that they provide, and discuss impacts, losses, and restoration. I then describe methods for characterizing and comparing the biota of southern California's estuaries.

Cowardin and others (1979) define estuaries as subtidal habitats and their adjacent tidal wetlands that are usually partially enclosed by land but have open, partly obstructed, or sporadic access to the open ocean and in which ocean water is at least occasionally diluted by freshwater runoff from the land. A combination of ample nutrients and sunlight make estuaries productive, though easily perturbed, habitats. Often, species found in estuaries are specially adapted to and, therefore, dependent on estuaries. From an ecosystem perspective, estuaries provide the following functions: (1) food chain support and nutrient cycling functions such as primary production, decomposition, nutrient export, and nutrient utilization; (2) habitat functions for native plants, invertebrates, fish, birds, mammals, and herpetofauna; (3) hydrological functions including flood conveyance, sediment control, ground water recharge and discharge, and shoreline protection; and, (4) water quality functions including water supply, waste-water treatment, detoxification

¹ An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

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of toxic substances, and modification of pollution from nutrient enrichment (Ferren and others 1995).

Why should people care about estuaries? To some, they are ugly swamps, unproductive lands, or mosquito breeding areas. Through most of history, governments around the world actively worked to eliminate estuarine habitats or convert them to more “productive” uses. A more modern view considers that estuaries, in addition to the ecosystem functions described above, provide the following socio-economic functions: (1) non-consumptive values such as recreation, research, and education; (2) consumptive values of “harvestable” physical resources such as water, gravel, and petrochemicals, and biotic resources such as fisheries, lumber, and crops; (3) cultural values by Native Americans, including activities such as basketry, gathering of food and medicinal plants, and acquisition of house building materials; and, (4) aesthetic and natural heritage values including natural landscape features, setting, and other aspects of California’s natural heritage (Ferren and others 1995).

One reason that wetlands are an area of concern is that we have lost ~90 percent of the original coastal wetland habitat in southern California as a result of filling or dredging during the last century (NOAA 1990). What is left has been degraded through fragmentation, water quality degradation, introduction of invasive plants and animals, unregulated public access, and other forms of environmental perturbation. In addition, damming, agriculture, and urbanization have greatly altered the magnitude and timing of freshwater inputs. Even in a degraded state, however, estuaries continue to provide important ecosystem functions. Of these functions, perhaps that of habitat for rare and endangered species is most important because of the many plants and animals restricted to the remaining estuary habitat (Zedler and others 1990).

Ferren and others (1995) group anthropogenic impacts to Californian estuarine ecosystems as: (1) agricultural development (for example, deforestation, draining, increased sedimentation, fragmentation, nutrient enrichment, pesticide pollution); (2) urbanization (for example, filling for development, landfill, excavation, fragmentation, diking, impoundment, runoff, effluent pollution, nutrient enrichment, and sedimentation); (3) agency activities (for example, channelization, flood control, ditching, and chemical treatment for mosquito abatement); (4) resource extraction (for example, petrochemicals, sediments, water, salts, fisheries); (5) public access (for example, compaction of soil, removal and disturbance of organisms); and (6) introduction of invasive exotic species.

The sad state of our coastal wetlands has led to increased efforts to enhance, restore, create, and recreate estuarine habitat. Such attempts are either due to conservation actions or as required mitigation for the destruction of wetland habitat elsewhere. Throughout southern California, many estuaries have been subject to habitat restoration. Unfortunately, studies of the effectiveness of estuarine restoration have been sobering (Zedler 1984, Zedler and Langis 1991). At best, most restoration has converted one type of wetland to another, often arguably resulting in an overall net loss in wetland function (Zedler and Langis 1991). Thus, mitigation as a technique to compensate for losses or impacts should presently be viewed with concern, and the ability to assess success becomes critical to wetland conservation.

Assessment

There are many reasons to assess estuarine functions. In some cases, we may wish to evaluate the success of a restoration project. We also may try to determine the extent to which a particular wetland is degraded or to obtain baseline information to be able to detect changes in function in the future. If the assessment is related to a specific function, its goals may be quite narrow. Such assessments might attempt to determine the presence of an endangered or fisheries species, the ability of a wetland to hold storm runoff, the quality of water exiting an estuary into the littoral zone, or the presence of mosquitoes. The habitat role of estuarine wetlands may be the most comprehensive function of all and the most difficult to assess. The following sections provide ideas for sampling plants and animals that use the estuary habitat.

For any assessment, it is important to consider that we can categorize southern California's estuaries along many different descriptive axes. Because the biotic community that occurs in an estuary may be influenced by the estuary's type as much as by the quality of the habitat, Ferren and others (1996) provide the following hierarchical categorization scheme for the seven distinct types of estuaries that occur in southern California:

River Mouth Estuaries: These estuaries occur at the mouths of large rivers that generally have some perennial flow, producing nearly permanently brackish conditions in the estuary. The Santa Clara River Estuary, the Ventura River Estuary and the Tijuana River Estuary are representative.

Canyon Mouth Estuaries: Emergent portions of the southern California coastline have canyons that drain watersheds. Creeks flowing through these canyons empty into the ocean through small estuaries that vary greatly in size, frequency of tidal flushing, salinity regimes and biota. Arroyo Burro and Devereux Slough in Santa Barbara County are examples of canyon mouth estuaries.

Lagoonal Estuaries: These estuaries have mouths closed by sand bars most of the year, usually have brackish fringe-marshes rather than vegetated flats, often have salinities that can approach fresh water, and support fauna typical of brackish to fresh water conditions (this is especially true where freshwater input has been enhanced by wastewater discharges and agricultural and urban runoff). Although many estuaries in southern California have lagoons at their mouths, lagoonal estuaries, such as Buena Vista Lagoon, primarily occur in San Diego County.

Coastal Dune-Creek Estuaries: These estuaries develop when wetlands near dunes occasionally connect with the ocean but have a seasonal sand bar. They are generally slightly brackish most of the year. Examples include the San Antonio Creek Estuary and Shuman Creek Estuary in Santa Barbara County. Dune encroachment into the wetlands keeps these wetlands small.

Bay Estuaries: These estuaries have large areas of subtidal habitat (bays) and low elevation salt marsh. Bolsa Chica, Anaheim Bay, Upper Newport Bay and Mission Bay are examples. There is a strong marine influence in bay estuaries because there is a consistently open and generally wide mouth. Intertidal mud flats, cord grass, and eelgrass characterize bay estuaries (Zedler 1982, Zedler and others 1992).

Structural Basin Estuaries: Tectonic activity that leads to down-faulted and down-folded geologic structures below sea-level may create estuaries of moderate

size that are most common in Santa Barbara County. Down-faulted basins include Goleta Slough, and down-folded (synclinal) basins include Carpinteria Salt Marsh.

Artificial Drain Estuaries: Agricultural and urban drains along the coast can form small, narrow estuaries when they reach the coast. They may be all that remains of a historically larger estuary or they may be new creations. Some of these exist in the form of small wetlands on sandy beaches at the mouths of culverts and storm drains, such as along Cabrillo Blvd. in downtown Santa Barbara. Others reach the coast as canals and have tidal channels with fringe marshes. Agricultural or urban runoff often pollutes these small estuaries.

An estuary is not a homogeneous habitat; each has a unique composition of landforms characterized by a specific origin, geomorphic setting, water source, and water regime (Ferren and others 1996). Associated with the large water body that defines the estuary may be channels, ditches, and ponds. Seeps and springs may provide freshwater. The water bodies may cover bottoms, beds, bars, and reefs (such as may be formed by oysters and mussels). Affiliated with the margins of water bodies may be shores, beaches, and banks. Tidal (mud) flats and deltas can be quite extensive in West Coast estuaries. They may form with the accumulation of sediments and are exposed by the retreating tide. Although natural hard substrate is uncommon in estuaries, woody and shelly debris and artificial structures such as pilings, levees, docks, and buoys can provide habitat for attached invertebrates and algae (Ferren and others 1996). The landforms an estuary possesses may affect the sorts of animals and plants that the estuary supports. In addition, because community composition may vary from landform to landform, characterizing landforms at each sampling site within an estuary will facilitate comparing communities among sites.

Another important factor associated with habitat function is how salinity varies in space and time. Two physical features influence salinity in an estuary: (1) the amount and seasonality of freshwater input and (2) the presence of a bar that can close off the mouth of the estuary from the ocean. As discussed later, invertebrates seem to be the biota most sensitive to these factors. Bay and structural-basin estuaries tend to have year-round tidal influence and relatively little freshwater input. River mouth estuaries have perennial freshwater inputs and relatively less tidal influence. Canyon mouth, lagoonal, coastal dune-creek, and artificial drain estuaries have seasonal freshwater inputs and seasonal bars that isolate them from the sea. These latter estuaries have periods of low salinity, high salinity, and tidal flushing that vary with the season. Their water levels also can fluctuate well beyond the normal tidal range.

A final physical aspect of wetlands to consider in an assessment is size. Although the technical boundaries of an estuary are based on salinity, it is more practical to use the plant community to indicate the extent of the estuary. The main reason for measuring wetland size is that it can act as a useful covariate when comparing assessments among wetlands. For example, the general ecological association between species richness and the size of a habitat sampled predicts that large estuaries should have higher species diversity by means of their size, independent of their quality of habitat. If this ecological rule holds for estuaries, large estuaries, all else being equal, generally could appear to be in better shape than small ones. For example, to determine the extent to which different estuaries are degraded, one could plot a measure of the estuary, such as species richness of a particular set of organisms, against estuary size. The prediction is that richness should increase with size, but that more degraded estuaries should fall below the line that describes the size-richness curve. Preliminary efforts show that the richness of both fishes and

birds increases with wetland size but that estuaries that have few fish species for their size do not have few bird species for their size, suggesting that these two biota respond independently to environmental factors. I have also found it useful to separately measure the flooded, unvegetated area of the marsh (the sum of pans, channels, and mudflats) because fishes and birds seem to respond more to flooded area than wetland size per se. Vegetated marsh and flooded habitats can be mapped from aerial photographs.

Sampling the Biota

An enjoyable way to understand an estuarine community is to put on waders, grab sampling gear, and count the plants and animals that live there. Plants, invertebrates, fishes, and birds all require different sampling methods. The biggest challenge when sampling wetlands is to obtain data that are comparable over time or across estuaries. This means that substantial thought must be given to standardized timing, habitat, methods, and efforts. An excellent primer on sampling estuaries is from the Pacific Estuarine Research Laboratory (PERL 1990), and interested readers should consult this reference.

Sampling strategies will vary according to the types of questions being asked. Here I briefly describe the basic rationale behind the most common types of sampling in wetlands. Central to sampling design is the selection of sampling sites. It is useful to avoid the temptation of simply sampling adjacent to access points. In most cases, it will be necessary to stratify sampling by habitat type (for example, vegetated marsh, pans, narrow channels, and mudflats adjacent to the shores of large channels) so that comparisons among sites are not confounded by differences in habitat type.

It is also important to account for gradients that may exist within habitat types. For example, when targeting a single tidal channel, we often stratify sampling so that our sites are spaced along the upstream-downstream gradient (mouth, upper extent of tidal influence, and one or more points in between). Within a channel site, we may also stratify sampling according to tidal height.

Site selection will obviously be affected by the goals of the study. If the goal is to follow some aspect of the community over time, sites can be targeted that are home to the species or community of interest. In this case, it is usually permissible to choose sites that can be conveniently revisited for monitoring. Another common goal is to assess a distinct location (for example, an impact or restoration site) and compare it to similar sites (often these comparisons are made over time). In this case, the location of the target area is often predetermined, and comparison sites are chosen in similar habitat either along a gradient of impact or free from the variable of interest. If the goal is to assess the distribution and abundance of organisms in an entire wetland, it is necessary to randomly select multiple sample sites. For this, we have used an aerial photograph of a marsh, and divided it into discrete habitat types. From each of these types, we randomly select a subset of sampling locations by using GIS or a grid system (we employ a rule so that sites are no closer than 50 m).

The remainder of this section gives a rapid introduction to some of the sampling methods that I have found most useful.

Plants

Estuaries often support thick vegetation that forms marshes and provides important habitat for animals (see Zedler 1982). Because plant assemblages are often zoned according to tolerance to inundation and soil salinity, these two characteristics can be useful estuarine indicators. Cord grass (*Spartina foliosa*) and pickleweed (*Salicornia virginica*) often dominate the lower salt marsh. The middle salt marsh is generally irregularly flooded and has varying salinities. Pickleweed usually dominates here in association with other species such as salt grass (*Distichlis spicata*), alkali heath (*Frankenia* spp.), jaumea (*Jaumea carnosa*), and sea lavender (*Limonium californicum*). Parish's glasswort (*Salicornia subterminalis*), shore grass (*Monanthochloe littoralis*), and pickleweed (*Salicornia* spp.) dominate the high marsh with its irregular flooding and euryhaline or hyperhaline salinity. Cattails (*Typha* spp.) and rushes (*Scirpus* spp., *Juncus* spp., and so forth) occur where salinity is persistently low. Zedler and others (1999) argue convincingly that the elevation-based terms (“low,” “middle,” and “high” marsh) should be replaced by a system that also considers landscape position and conspicuous species. They suggest three alternative habitat designations: (1) the high marsh—a 30- to 70-cm elevation range with *Salicornia subterminalis*; (2) the marsh plain—a 30-cm elevation range with heterogeneous topography and a mix of several species; and (3) cord grass habitat—the bayward portion of the marsh plain and lower elevations, all occupied by *Spartina foliosa*. In addition, vegetation adjacent to channel edges tends to be distinct from vegetation away from edges.

Emergent plants are food for a number of terrestrial arthropods, several of which are salt-marsh specialists. The contribution of salt-marsh plants to the diet of marine animals, however, is thought to be primarily through detritus. Fully aquatic vegetation is less apparent in estuaries but includes flowering plants such as widgeon grass (*Ruppia* spp.), eelgrass (*Zostera* spp.), and algae such as epipellic diatoms and the mat-forming filamentous alga, *Enteromorpha* spp.

Sampling estuarine plants can be relatively straightforward because plant species lists are not long, the topography is simple, and canopy heights are short enough that percent cover estimates are usually adequate. For example, in our field work, we run a series of 10-m transects in which we make point-contact assessments of the plant species composition every 10 cm and canopy height estimates every meter. Good aerial photographs are often available of southern California estuaries, and one can usually discern large patches of different plant communities. However, one almost always needs to go to the field to ground-truth these maps and determine the composition of vegetation mosaics. There are good field guides and keys to salt marsh plants (Abbott and Hollenberg 1976, Faber 1996, Jepson 1993, <http://elib.cs.berkeley.edu/photos/flora/>). Probably the single best visual indicator of an estuary in southern California is the ubiquitous and easy to identify pickleweed. It is difficult to find an estuary in southern California that lacks this plant.

Epipellic micro-algae (for example, diatoms) and mat forming macro-algae are important components of estuarine food webs. Micro-algae can be assessed microscopically or through the chlorophyll content of the sediment. Macro-algae can be quantified in transects and quadrats (like those used to quantify invertebrates; see the next section). Some macro-algal flats are extensive enough to be quantified through aerial photographs. The nutrient content of algae can be used as an indicator of nutrient enrichment in an estuary (Fong and others 1998).

Invertebrates

Estuarine invertebrates live in the water, on vegetation, on the mud, and in the mud. Most species reach peak abundance in the summer. They are relatively rare in winter after high freshwater flows. One can visually survey for crabs and snails at low tide. Some invertebrates, particularly crustaceans, will come to baited minnow traps, while some small invertebrates will seek out litter traps (see PERL 1990). Many invertebrates are out in the open or give away their presence with burrows of distinctive shapes (burrows can be difficult for novices to identify with any certainty). Estimating density requires setting a sampling unit, usually in the form of a quadrat, transect, or core. A factor that complicates density estimates is that most animals are neither uniformly nor randomly distributed across a mudflat or tidal channel. Since many species are patchy, large numbers of sampling sites are necessary to estimate density. In addition, many species are zoned according to tidal height, meaning that tidal height should be accounted for when making comparisons among sites. One method to sample invertebrates in a tidal channel is to extend band transects from the vegetated margin of the salt marsh down into the intertidal zone, noting the change in elevation and density of organisms at regular intervals of the transect.

Sediment cores are useful for sampling shallow-burrowing species but often miss the deeper-dwelling clams, shrimp, and worms. Labor increases with the length and diameter of the core taken and decreases with the size of the screen the sediment is passed through. To accommodate this difference, we take large diameter (for example, 15 cm), deep cores (for example, 40-50 mm in depth) which are passed through a coarse mesh (for example, 3-5 mm) in the field and small diameter (for example, 5 cm), shallow (5-10 cm deep) cores that are preserved and then passed through a fine mesh (1-0.5 mm) in the laboratory. Large cores can be sieved in the field. In cases where many cores are taken or the site is far from water, we find that a water pump running off a small generator greatly speeds the task. Once captured, most of the larger marine invertebrates are relatively easy to identify to species. Unfortunately, there are many small species that can be quite a challenge to identify even using the several good keys available (for example, Smith and Carlton 1975, Morris and others 1980).

Because coring is labor intensive, it is usually necessary to limit the number of cores taken. Randomly selecting coring locations provides the best estimate of densities, but, due to the patchy distribution of animals, a large number of cores is needed to obtain a representative sample of even the most numerically dominant species. Patchiness is accentuated if there is significant variation in tidal height within the sampling area. Stratifying coring effort by tidal height helps to distribute effort across zones. Nonetheless, variation in the depth profile from site to site limits comparisons among sites. More recently, we have experimented with mapping the presence of beds of benthic infauna (as indicated by clam, crab, and shrimp burrows, and so forth) within transects and then randomly subsampling these beds with cores. Such targeted sampling intensifies effort in the areas where animals are most likely to occur, thereby increasing the efficiency of coring.

In the subtidal areas of larger estuaries, coring is relatively difficult to accomplish and not frequently undertaken. Using SCUBA (self-contained underwater breathing apparatus), divers can obtain cores similar to those obtained in the intertidal zone. However, in most estuaries, diving conditions can be challenging due to low visibility and strong tidal flux. Alternatively, sediment samples can be taken by grabs

deployed off boats. Unfortunately, these usually only capture animals on the surface or in relatively shallow parts of the sediment.

One component of the estuarine invertebrate community that is often overlooked, particularly by those with training in marine biology, is the insect fauna. Aquatic insects (many of which are larval forms) can dominate the invertebrate community of some estuaries. Terrestrial insects are abundant in the warm months in and around estuaries and may play important, unappreciated roles in estuarine ecology. There are several insects, such as the pygmy blue butterfly caterpillar (*Brephidium exilis*), that feed specifically on estuarine plants.

Although assessing invertebrate communities can be very difficult (one needs to consider the resources available before embarking on an ambitious sampling program), this does not mean that one should ignore invertebrates when assessing wetlands. In particular, the invertebrate community can be a useful indicator of the type of tidal inundation that an estuary receives. As mentioned earlier, invertebrates are particularly sensitive to variations in salinity (especially compared with fishes and birds). Sandoval and Lafferty (1995) found that the invertebrate community of estuaries with regular tidal influence is dominated by relatively *marine* species such as crabs, shrimp, polychaete worms, clams, mussels, and horn snails. In estuaries with variable salinity, these species are usually absent. Instead, aquatic insects, amphipods, isopods, crayfish, small snails, and oligochaete worms can be abundant. One species, the California horn snail (*Cerithidea californica*), is abundant and is easy to see and identify because it often carpets the mudflats and channel banks where it occurs (Lafferty 1993). For example, out of the approximately three dozen estuaries in Ventura, Santa Barbara and San Luis Obispo Counties, the only four natural wetlands with horn snails (Mugu Lagoon, Carpinteria Salt Marsh, Goleta Slough and Morro Bay) are also the only four with consistent tidal flushing (nearly all the others have records of tidewater gobies, see below). The broad distribution and abundance of *C. californica* within its range make it an excellent reflection of regular tidal flushing and the associated marine invertebrate community. Horn snails may even provide a historical record of tidal influence: their shells are preserved in sediment and can be retrieved from cores. The presence of horn snails also provides the possibility for using larval trematode parasites as indicators (as discussed later). One exception to the “horn-snail rule” is Elkhorn Slough in Monterey County, a fully tidal estuary. Here, instead of horn snails, one finds an introduced ecological analogue, the mud snail, *Batillaria attramentaria*. A second exception is Campus Lagoon (in Santa Barbara County), an artificial marine pond without tidal influence (the seawater source is the outflow of the UCSB marine lab) where horns snails were planted and survived for several years.

Fishes

A few dozen fishes use southern California estuaries (a dozen are common). Particularly common or apparent species include killifish (*Fundulus parvipinnis*), topsmelt (*Atherinops affinis*), arrow gobies (*Clevelandia ios*), longjaw mudsuckers (*Gillichthys mirabilis*), tidewater gobies (*Eucyclogobius newberryi*), and mullet (*Mugil cephalus*). Diversity is relatively low, and although species are well represented in field guides for the area, it is useful to have a guide for both freshwater (for example, McGinnis 1984) and marine fishes (Miller and Lea 1972 or Eschmeyer and Herald 1983). Some, such as sharks and rays, are more typical of the open ocean but will

enter estuaries at high tide. Juveniles of reef species that are common in the near shore may enter an estuary and stay if patches of hard substrate are present. Historically, steelhead and lamprey migrated seasonally through estuaries.

There are several methods for sampling fishes in estuaries. Like invertebrates, the abundance of fishes is higher in the warmer months, and sampling in the late summer/early fall yields the greatest catch. Because estuaries are relatively calm and shallow and often have smooth bottoms, seining, when conducted properly, can give a very good indication of the diversity and relative abundance of fishes at a particular location. If one is interested primarily in obtaining a list of common fishes, the following approach works fairly well with a crew of two to five people: At slack tide, when currents are weak, we select three or more shallow locations (<1.5 m deep) within the estuary. We then take relatively short seine hauls (<30 m) that can terminate on a gently sloping, unvegetated bank or shore (avoiding areas with excessive submerged rocks or other hazards). We find that a seine 10-20 m long by 2 m high with a 1/8 – 1/4 inch (3-6 mm) mesh works well. Small mesh is better for capturing small gobies, but the extra drag associated with small mesh necessitates using a shorter seine (which is not as good for capturing large fish or schools of fish). We fish until three to five successive seine hauls do not add any additional fish species to the accumulated species list.

Minnow seines will not adequately sample larger wetlands with substantial subtidal areas. Traps can be used in areas that are too deep to seine, because most estuarine fishes will enter minnow traps (tidewater gobies are a notable exception). Traps require relatively little effort (except that they require two visits to a site) and do a better job at capturing large individuals that are able to out-swim seines. They work best when baited and left out overnight; dry dog food makes a convenient bait. However, in shallow areas fish may die if traps are left out too long because low tides may expose traps to the air; anoxia may kill fish at night in traps set in deep water; or the captives may eat one another. In general, traps seem to have a high variance in what they catch: some traps come up empty next to traps filled with fish. There is also a tendency for some fish species to enter traps more than others (Layman and Smith 2001). Although trapping is not a substitute for seining, often traps can add new species not seen in a day's seining. Gill nets are similar to traps in the sense that they are set and later retrieved. They are able to catch larger fish than minnow traps but mostly yield dead fish.

In larger wetlands, benthic trawls (and, to a lesser degree, midwater trawls) are the most tractable way to sample substantial subtidal areas. Trawling in an estuary requires a small boat, preferably one with a shallow draft. When trawling, it is important to keep track of the depth of the trawl and the area over which the trawl was pulled. Trawls can also sample subtidal epibenthic invertebrates.

Sampling fish for abundance is challenging. For traps and gill nets, the area sampled is not known and certain fishes are better able to avoid seines and trawls (by swimming or burrowing) than others. Rozas and Mellor (1997) advocate enclosure devices such as drop traps and throw samplers instead of seines. One way to obtain more accurate densities with seines is to first set up blocking nets that trap fish into a moderately sized area and then seine repeatedly (for example, at least five times) inside the area until no more fish are captured on three successive passes. Then, pull in the blocking nets carefully, one behind the other, to capture fishes that have sought refuge in the nets. Blocking nets 20 m long are sufficient to block off most narrow channels. A smaller seine (5-10 m long) can be used for the successive passes. In

areas where small gobies are abundant, 20 or more passes may be necessary to adequately sample the area due to the habit of gobies to rapidly burrow. Narrow channels are easy to sample this way because blocking nets can be run from bank to bank. Areas adjacent to open shores can be blocked by forming a triangle, with the shore acting as one side and the blocking nets meeting at the apex offshore.

A very useful indicator that an estuary is closed off to tidal flushing for at least part of the year is the presence of the tidewater goby, *Eucyclogobius newberryi*. Tidewater gobies are often the most common fish in wetlands where they occur, particularly in the summer and fall. Unfortunately, tidewater gobies are an endangered species and have been extirpated from large parts of their range, particularly in Los Angeles and Orange Counties (Lafferty and others 1996). Therefore, the absence of tidewater gobies does not indicate year-round tidal flushing; it may simply represent a local extirpation (Lafferty and others 1999).

Birds

Birds use estuaries in large numbers for food and rest during migration periods. Some species breed in southern California wetlands. Due to declines in the abundance of several species (for example, California least tern [*Sterna antillarum browni*], light-footed clapper rail [*Rallus longirostris levipes*], Belding's savannah sparrow [*Passerculus sandwichensis beldingi*], western snowy plover [*Charadrius alexandrinus nivosus*], and brown pelican [*Pelecanus occidentalis*] are federally protected, and several shorebirds are considered to be in decline), there is a growing need for understanding their status and trends. In addition, because they are charismatic and easy to view, bird communities appeal to the general public. The low topographical relief in most estuaries makes it possible to observe most bird species in a particular field of view. Some wetlands in southern California are sufficiently small that all birds can be counted from just a few fixed points. With a few exceptions (such as female ducks, dowitchers (*Limnodromus* spp.), some terns, immature gulls, and some sandpipers), most species of birds that use estuaries can be identified given a good look, basic birding experience, and a field guide (for example, Sibley 2000). Often data on birds exist in the form of notes from experienced birders, who often visit estuaries for their rich bird communities. Such notes can be useful but usually cannot replace a systematic sampling effort. However, amateur birders represent a potential pool of expert volunteers and, when using an appropriate sampling protocol, can provide excellent data.

Because migration and breeding alter the sorts of birds that visit our estuaries from month to month, it is necessary to limit comparisons among estuaries to samples taken in the same season. In addition, the bird community can be affected over short periods of time by weather, tide, and time of day. For example, as the tide retreats, birds may move from roosting sites in the upper marsh or beach to forage on exposed mudflats. Tide and other variables should be controlled for in sampling or accounted for in comparisons.

Sampling in the spring provides a chance to detect breeders such as least terns, while sampling in the fall yields a community augmented by migrants. Limiting sampling effort to aquatic birds (for example, gulls and terns, shorebirds, waterfowl, divers, rails, kingfishers, herons, and egrets) and birds of prey, while ignoring terrestrial passerines, is one means to reduce effort and simplify analyses. However, in many cases, terrestrial passerines may be of particular importance if they are of

conservation concern or use the margins of the estuary. Due to their smaller size and more cryptic habits, terrestrial birds may not be effectively sampled by the techniques described below.

One may be able to survey a small (<50 acre) estuary in a few hours, but large estuaries may require subsampling or substantial sampling effort. In a small estuary, a simple and repeatable approach is to count and identify all birds visible within defined perimeters from fixed locations and fixed periods of time (for example, 30 minutes). Choosing locations that provide good vantage of the mouth, middle and back sections of an estuary provides a good estimate of abundance by species. Then, to determine a more complete total species list, one can roam throughout the estuary for 30-minute viewing periods until a period passes without detecting any new bird species. This facilitates the inclusion of the presence/absence of uncommon birds.

To quantitatively subsample birds in an estuary, we have employed the following sampling method: Sites are selected from a map of the estuary (in our case, these sites are the randomly chosen locations for sampling other taxa). A 100-m radius is then drawn around the sampling point. Using a GPS unit and a map of the site, observers approach the perimeter of this circle, mapping the location of birds once they have a vantage of the interior of the plot. Then, over a 20-minute time interval, observers walk to and along a transect located along the circumference of a 50 m radius around the central point. Birds are counted and mapped when observed. This approach has the advantage of standardizing sampling time and transect length. It also tends to flush cryptic species that would otherwise not be observed from a fixed point.

Recently, (with R. Hechinger) we have used remote video surveillance to determine bird visitation rates of small areas (on the scale of 10 by 10 meters). We have had success by taking five seconds of video every minute over a two week period. Although this is the only way that we know how to effectively sample birds in small areas, it has various limitations such as the expense and effort required to sample several remote sites simultaneously. Improvements in remote surveillance technology may soon increase the practicality of this approach for larger scale studies.

New Approaches

The Environmental Protection Agency is presently funding over 30 investigators in the exploration and development of new ecosystem indicators through the Pacific Estuarine Ecosystem Indicator Research (PEEIR) Consortium. The objective of this project is to develop indicators of wetland ecosystem health through evaluations of stressor-response patterns in wetland biota. The goal is to create an integrated suite of indicators to evaluate impacts of toxic contaminants, nutrient enrichment, microbial contamination, and exotic species invasions. The ecosystem-indicators component of PEEIR (led by S. Morgan) is investigating new ways of sampling the biota that may some day be added to the more traditional methods discussed previously. Some examples are described below.

Measures of microbial community composition and diversity (led by T. Holden) using DNA from the T-RFLP (terminal restriction length polymorphism) method are highly transferable among sites and ecosystems, making them potentially valuable indicators of pollution and enrichment. Assessment of nitrogen isotope ratios in

selected biota at southern California sites (led by M. Page) has promise for assessing ecosystem responses to nutrients. Refinement of methods to describe ammonification, decomposition, and nitrification rates (led by S. Williams) may generate information on trophic support and biogeochemical performance indicators. One method to investigate impacts to ecosystems is to evaluate changes in growth and reproduction of individual organisms by linking contaminant effects in dynamic mass-energy budget models. For example, analysis of fish otoliths to indicate growth and rates (led by W. Bennett and A. Brooks) may provide a means to indirectly assess habitat suitability for fishes under different contaminant regimes. This information might then be integrated into mathematical models designed to assess impacts at the population level. Parallel to the development of ecosystem indicators is research into other new technologies for assessment. For example, more sophisticated application of remote sensing, such as high spatial resolution airborne hyperspectral imagery (led by S. Ustin), could provide quantitative mapping of canopy pigments, water content, and dry standing litter. A value to the collaborative approach in developing indicators is that there may be important links among indicators that would not emerge from the development of each alone.

Trematodes

Using parasites as indicators of ecosystem function is the aspect of PEEIR that I oversee. Trematodes are parasitic worms with complex lifecycles. Several species use the common horn snail as a first intermediate host. There are 17 described species in California, and it is not unusual for half or more of the snails in an estuary to be infected by larval trematodes. The trematodes leave the snail in a free-swimming cercarial stage and (with the exception of a blood fluke) seek out a second intermediate host. This is usually a fish, but it can also be a crab or a mollusk, depending on the species of trematode. Most trematodes encyst inside their second intermediate host, but some encyst on the outside of snails or crabs. Mammals (such as raccoons) and birds become infected when they eat infected second intermediate hosts. Trematodes mature and reproduce in birds and mammals, their eggs being dispersed along with the final host's feces.

Because each trematode species has a unique life cycle that depends on many interacting free-living animals, an estuary with a rich food web of fishes, birds, and invertebrates can support a diverse and abundant community of trematodes. Therefore, the trematode community within a snail population provides, in a glance, the sum effect of several interacting communities of free-living animals. It is relatively easy to sample a population of snails for trematodes, all of which can be identified to species with a practiced eye using a dissecting scope. Because snails and their trematodes are long lived (up to more than 15 years), the community of trematodes in a population of snails provides an integrated history of the free-living animals that have used the estuary on the scale of months or years (depending on the age of snails sampled). This is potentially more satisfying than the single day snapshot surveys that are usually the only possible way to sample birds, fishes, and invertebrates because these are subject to seasonal and, especially for birds, even daily fluctuations in abundance. It also makes trematodes ineffective for assessing rapid changes occurring on short time frames.

An observation of an urban population of horn snails first suggested to me that parasites could indicate habitat function (Lafferty 1993). I was sampling a site

separated from a marsh by a parking lot and bordered by a busy highway intersection. Birds were conspicuously absent (presumably due to the proximity of vehicle traffic), and the snails were completely uninfected compared with a prevalence of 25 percent in the adjacent marsh, suggesting that degradation had reduced trematode prevalence. Other authors have also speculated that the prevalence of trematodes in snails corresponds to the degree of habitat degradation (reviewed by Lafferty 1997). Cort and others (1960) made the first such comparison in Michigan. They found that larval trematode diversity and species richness had declined since studies conducted 20 years before. They also noted an increase in human disturbance and a reduction in the shorebird population.

With Todd Huspeni, I have used trematode communities to assess the success of restoration at Carpinteria Salt Marsh. As one would expect, degraded areas showed significantly reduced diversity and abundance of trematodes compared with reference areas. While trematode communities sampled from reference sites did not vary much from year to year, those in the degraded area rapidly increased in prevalence after restoration. Newly created habitat produced trematode communities similar in prevalence to reference sites. Still, at present, the reference sites and the created sites are not yet identical in their species diversities or compositions; restored areas have relatively more trematodes that use mollusks as intermediate hosts and relatively few trematodes that use fishes (Huspeni and Lafferty, unpublished manuscript). This underscores previous studies that indicate that newly restored estuarine habitat is not automatically the same as natural estuarine habitat. To make this approach broadly useable will require the additional ground-truthing of methods and their eventual publication and dissemination.

Conclusion

In summary, there are several ways that we can describe estuaries when we seek to better understand their function. The most appropriate method varies with the goals and expertise of the evaluator. It is important to understand that there are a variety of types of estuaries that have unique properties, and these may be inappropriate to directly compare with one another. For example, when choosing an estuary or estuaries to act as a reference site, it would be important to be sure that size and tidal regime were similar to the target estuary. The horn snail makes an excellent indicator of regular tidal flushing. Because sampling a single taxon will likely provide an incomplete picture of an estuarine community, attempting a variety of assessments is important. New technologies and ideas may provide innovative methods to assess estuary biota. A description of a larval trematode assemblage is a single measure that captures the ability of an estuary to support a rich and functioning community of invertebrates, fishes, birds, and mammals. However, sampling must be consistent in methodology, and effort must be comparable among sites.

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Up, Down, or Stable: Populations of Endangered Birds in Beach and Estuarine Areas in Southern California¹

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Abstract

The coastal beach-dune ecosystem in California supports two federally listed threatened or endangered species: California least tern (*Sterna antillarum browni*) and western snowy plover (*Charadrius alexandrinus nivosus*). This ecosystem has become highly stressed due to shoreline development, invasion of exotic plants, beach stabilization, and heavy recreational use. Least tern populations have increased significantly since the 1980s. Snowy plover populations, however, show continued decline along California's coast. Management practices to protect least tern nesting colonies appear to be successful for terns but do not offer protection for plovers. More research is needed to monitor reproductive success and survival of snowy plovers in order to improve management practices and preservation of nesting areas. Impacts to estuarine ecosystems have been severe and include loss, degradation, and fragmentation. The most imperiled species within this system is the endangered light-footed clapper rail (*Rallus longirostris levipes*). Rail populations have ranged from a low of 142 pairs in 1985 to a high of 325 pairs in 1996 during the 22-year period they have been monitored. Most alarming is that only one estuary consistently supports more than 50 percent of California's rails, and only three sites support more than 80 percent. Although Belding's savannah sparrow (*Passerculus sandwichensis beldingi*) is not federally listed as endangered, populations in estuaries are stable or declining, but monitoring is erratic at best. Belding's savannah sparrows are area-sensitive, and reproductive success appears to be low in fragmented marshes. Research on productivity and survival of rails and sparrows is needed. Habitat enhancement and creation should be the highest priority for beach and estuarine birds as well as migratory shorebirds, but predator management and restrictions on recreation beach use are also necessary.

Key words: Belding's savannah sparrow, California least tern, endangered, estuarine, light-footed clapper rail, western snowy plover

Introduction

The beach and estuarine ecosystems of southern California have suffered significant degradation and loss of natural habitats. Beach ecosystems are altered by heavy recreational use, urban development, beach stabilization efforts, river channelization, and non-indigenous plant species (Federal Register 1993, Page and Stenzel 1981, Powell 1998, U.S. Fish and Wildlife Service 1985, Veirs and others 1998). Loss of beach habitats resulted in declines of beach-nesting birds, including the California least tern. In 1970, the California least tern was listed as federally endangered, with the California population estimated at 600 pairs (U.S. Fish and Wildlife Service

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1985). More recently, in 1993, the Pacific Coast population of western snowy plover was federally listed as threatened (Federal Register 1993).

California has lost an estimated 91 percent of its wetlands since pre-settlement times, and remaining estuaries are fragmented. Estuarine systems in southern California have been highly altered by urban development, filling, river channelization, changes in freshwater flow, and invasion of exotic species. Loss of total wetland area and degradation of remnant estuaries have caused many wetland-dependent species to be listed as *special concern* by the State and Federal governments (Veirs and others 1998). These include the light-footed clapper rail, federally listed as endangered in 1970 (U.S. Fish and Wildlife Service 1979), and the Belding's savannah sparrow, listed as endangered by the State of California in 1974 (State and Federal endangered and threatened animals of California and their listing dates, unpublished report, State of California, 1994).

What do we know about the populations of these bird species that depend on beach and estuarine ecosystems? How are resource agencies using population information to manage these endangered and threatened birds? Although three of the four species mentioned above were listed more than 25 years ago, information on population status varies in quality, quantity, and availability. This paper summarizes the current knowledge of the four species' populations in the south coast ecoregion of California. In addition, I include recommendations for future management and research for each species.

California Least Tern

Migratory California least terns are present in California from the Mexican border north to San Francisco Bay only during their breeding season, which is mid-April through September. Since being listed as endangered in 1970, management actions have included fencing colonies, limiting access to nesting areas, and, after the mid-1980s, managing predators. Monitoring of least tern colonies to track changes in population trends and productivity began in 1973; efforts to cover all areas have increased over the past 20 years (Patton 2002). Population monitoring, however, is not uniform at each colony, and methods range from non-invasive surveys of terns on nests to intensive efforts that include marking each nest and banding chicks. Monitoring is conducted by State and Federal personnel at some sites and by biological consultants at others. There has been statewide coordination of population data compilation since the mid-1970s (Ron Jurek, California Department of Fish and Game, personal communication).

The California least tern population was estimated at 600 breeding pairs in 1970 (Fancher 1992). For removal from the endangered species list, there must be 1,200 breeding pairs distributed among at least 20 coastal areas and an average over 5 years of one fledgling produced per breeding pair per year (U.S. Fish and Wildlife Service 1985). The population of California least terns has increased dramatically since 1988, growing from approximately 1,000 pairs to more than 4,000 pairs within 10 years (*fig. 1*). Least terns nest at approximately 34-39 sites in southern California, and the number of breeding pairs has exceeded 2,000 since 1992 (Keane 2001, Patton 2002). Although estimates of fledgling production have fluctuated, particularly in El Niño years (Massey and others 1992), the total number of fledglings produced

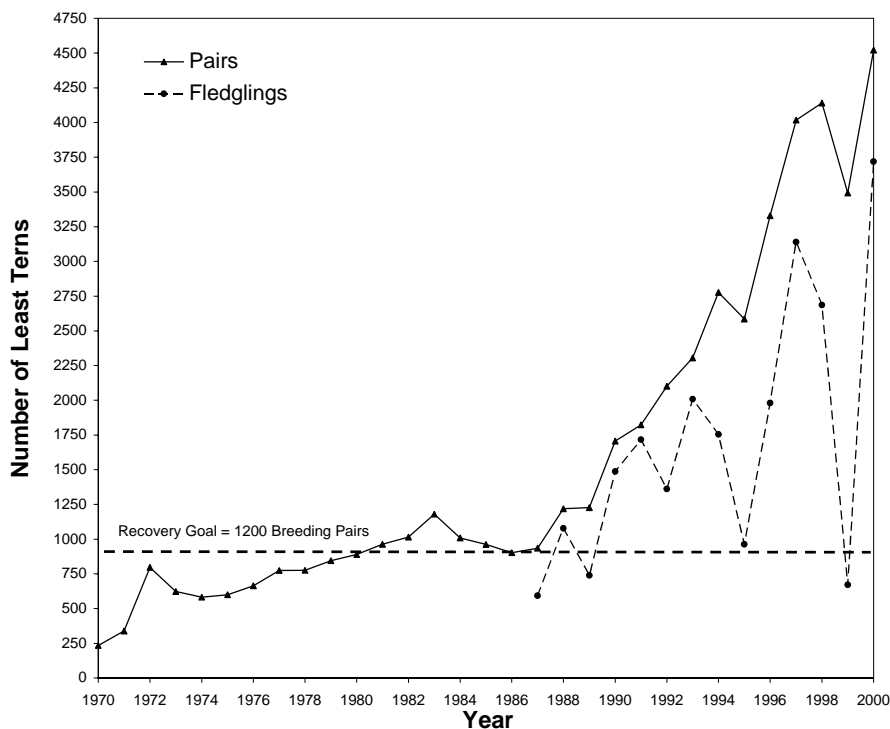


Figure 1—Number of breeding pairs and fledglings of California least terns in California, 1978-2000. Data are from Keane (1998) and from unpublished data on file from California Department of Fish and Game, Sacramento, CA.

increased in the same time period (*fig. 1*). However, dividing the estimated total fledglings by the estimated number of pairs per year reveals that the recovery goal of one fledgling per pair is not being met (mean fledglings/pair = 0.68 ± 0.21 SD, years 1987-2000). It is unknown what proportion of the population and productivity increases can be attributed to increased monitoring efforts over the same time period.

Regardless, increased breeding populations and productivity have been attributed to protection of nesting colonies and predator management (Fancher 1992). Fencing varies from site to site and may exclude people or both people and mammals. Predators are managed by exclusion and direct removal; however, information on the numbers of predators removed is difficult to obtain. Predators include, but are not limited to, common raven (*Corvus corax*), American crow (*C. brachyrhynchos*), American kestrel (*Falco sparverius*), peregrine falcon (*F. peregrinus*), burrowing owl (*Athene cunicularia*), coyote (*Canis latrans*), domestic cat (*Felis catus*), gray fox (*Urocyon cinereoargenteus*), long-tailed weasel (*Mustela frenata*), and raccoon (*Procyon lotor*). In addition, increased monitoring efforts facilitate adaptive management of tern colonies (Keane 1998, Patton 2002). Of the four species described in this paper, we know the most about California least tern populations, which have increased exponentially since 1988.

Western Snowy Plover

Although snowy plover habitat overlaps with the habitat of California least terns, there are several important differences in the biology, management, and population

status of these two species (Powell 1998, 2001). Unlike least terns, snowy plover populations in California are a mixture of migratory and resident birds (Powell and others 2002, Stenzel and others 1994); thus conservation is an issue year-round. In winter, snowy plovers from northern California migrate to southern California. In addition, a proportion of southern California breeders overwinter in the same region. Snowy plovers begin nesting in early March, well before least terns arrive from their wintering grounds in mid-April.

There are large information gaps about snowy plovers that breed and winter in southern California. The Pacific Coast population of western snowy plovers was federally listed as threatened in 1993 because statewide surveys showed overall declines in breeding and wintering populations (Federal Register 1993). Until 1994, data on numbers of plovers, productivity, and survival in the south coast region was sporadic at best. Page and others (1991) estimated the number of individual breeding plovers in California in 1989 (1,386) was 89 percent of the number found from 1977 to 1980 (1,565). Coastal lagoons in southern California historically supported breeding snowy plovers, but habitat loss and alteration of water flows have degraded these sites; they now only sporadically support breeding pairs. Snowy plovers no longer breed within Los Angeles County, and only one nesting area, Bolsa Chica Lagoon, remains in Orange County.

Most of what is known about breeding populations of snowy plovers in Ventura, Santa Barbara, and San Luis Obispo counties comes from “window” surveys conducted approximately every three years by the Point Reyes Bird Observatory. These surveys take place during a specific “window” of time, usually 1-2 days during peak nesting (last week of May). The most recent window survey in 2002 found 1,379 adult plovers in California (unpublished data on file, Point Reyes Bird Observatory, Stinson Beach, CA). The largest numbers of breeding plovers found in 1991, 1995, 2000, and 2002 were at Vandenberg Air Force Base (AFB; 242, 213, 106, and 179, respectively), the Channel Islands (199, 196, 89, and 79), San Francisco Bay (176, no data for 1995, 96, and 78), and northern San Diego County (48, 49, 63, and 80) (unpublished data on file, Point Reyes Bird Observatory, Stinson Beach, CA.). In addition, Point Reyes Bird Observatory has long-term data on snowy plovers in the Monterey Bay area. Their data indicate that the average number of fledglings per adult ranged from 0.85-0.86 annually, but after nests were actively protected from people and predators in 1992, fledging rates increased to over 1 fledgling per adult (unpublished data on file, Point Reyes Bird Observatory, Stinson Beach, CA). A comprehensive study on the population dynamics of snowy plovers in San Diego County was initiated in 1994 and continued through 1999 (Powell and others 2002), and the U.S. Fish and Wildlife Service began monitoring snowy plovers at Bolsa Chica Lagoon in Orange County in 1997. On average, 50 percent of all snowy plovers in San Diego and Orange counties nested at one site, Marine Corps Base Camp Pendleton. Overall reproductive success was low, with estimated nest success in San Diego County typically less than 55 percent with fewer than 0.5 fledglings produced per nest (Powell and others 2002).

The creation of nesting habitat for least terns from dredged materials has been a popular component of habitat restoration to partially compensate for wetland loss in southern California. Five new nesting areas were created at Batiquitos Lagoon in 1994 and 1995. This restoration project provided a unique opportunity to study natural recolonization and subsequent success of snowy plover populations from 1994 to 1998 (Powell and Collier 2000). Snowy plovers traditionally nested at the

lagoon along its perimeter (5 nests in 1994 prior to construction). After the creation of new least tern nest sites, snowy plovers began to use these areas immediately. Although the number of nesting attempts at Batiquitos Lagoon increased from 5 in 1994 to a high of 38 in 1997, fledge rates and nest success declined after peaking the first year the created sites were used, suggesting that the area attracted nesting plovers but ultimately became a habitat sink (Pulliam 1988). Predation pressure and quality of habitat were important in determining habitat use and reproductive success on the newly created areas. As more birds, including least terns, used the created sites, more predators were observed there. In addition, the amount of cover on the created sites may have contributed to lowered nest and chick survival. Areas devoid of cover provided little visual or thermal protection, while other areas became covered with invasive weeds, which made sites less attractive to nesting plovers (Powell and Collier 2000). In summary, snowy plovers easily colonized newly created sites and were highly productive immediately after colonization. However, productivity decreased with time and was related to habitat quality and predation pressure.

More monitoring and research on the effects of California least tern management on snowy plovers is needed in the region. Plovers are more vulnerable to human disturbance than least terns. In addition, estimating population growth by monitoring nests or pairs of breeding plovers is not enough to determine population status, because some areas may serve as population sinks (Pulliam 1988). It is necessary to obtain information on annual productivity in addition to number of breeding plovers. No area in San Diego County or Orange County produces enough snowy plovers to be considered a source population, and knowledge about survival and productivity of snowy plovers north of these counties is sparse.

Light-Footed Clapper Rail

In the United States, this subspecies of clapper rail is a year-round resident of salt marshes from Tijuana Estuary on the Mexican border north to Santa Barbara County (U.S. Fish and Wildlife Service 1985). Considerable research has been done on habitat requirements and behavior of light-footed clapper rails (Massey and others 1984, Massey and Zembal 1987, Zembal and Fancher 1988, Zembal and others 1985, 1989). In addition, genetic analysis of the subspecies indicated there was low genetic variability and a metapopulation with local populations that experienced extirpation, recolonization, and limited dispersal (Fleischer and others 1995).

Light-footed clapper rail populations have been monitored annually since 1980. Marshes that potentially support clapper rails are visited in spring, and clapper rail calls are counted. Clapper rails use several distinct calls during the breeding season that can be used to distinguish single males, single females, and mated pairs (Massey and Zembal 1987). During a census, people walk slowly through the marsh at dawn or dusk and mark locations of calls on a map. In addition, taped calls may be played to elicit responses (Zembal 1998). Each year a breeding survey report is submitted to the California Department of Fish and Game. In 1980, the first year of the survey, the light-footed clapper rail population consisted of an estimated 203 breeding pairs; a high of 325 breeding pairs was counted in 1996. The number of estimated pairs has varied around the 22-year mean of 231 pairs, but there has been no overall pattern of decline or increase during this period (*fig. 2*).

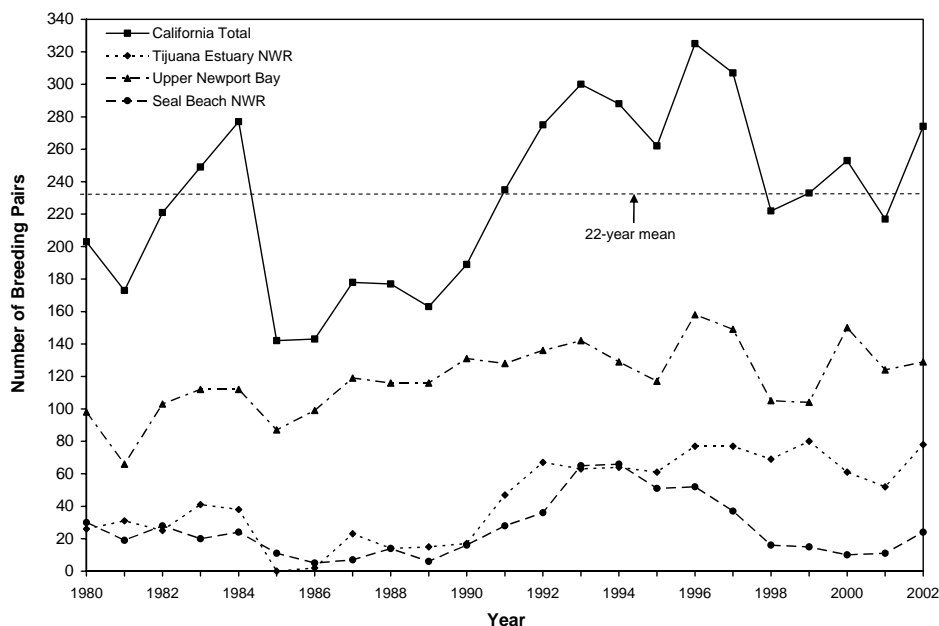


Figure 2—Number of breeding pairs of light-footed clapper rails in California, 1980-2002. Data are from Richard Zembal, U.S. Fish and Wildlife Service, personal communication, unpublished data on file, California Department of Fish and Game, Sacramento, CA.

Predator management to remove non-native red foxes (*Vulpes vulpes*) resulted in growth of the population at Seal Beach National Wildlife Refuge (NWR) from a low of 5 pairs in 1986 to 65 pairs in 1993 (Zembal and others 1998). In addition to predator management, nesting rafts have been deployed at this site to increase nest site availability since the late 1980s. However, the population at Seal Beach appears to be lower (range 5-24 pairs) from 1995-2002 than in the early 1990s (fig.2). It is postulated that rafts may increase the incidence of raptor predation on clapper rails at this site (Zembal and others 1998).

Upper Newport Bay Ecological Reserve consistently supported more than 50 percent of California's light-footed clapper rails, and together three sites (Upper Newport Bay Ecological Reserve, Tijuana Estuary NWR, and Seal Beach NWR) supported more than 80 percent of breeding pairs in any given year. These three estuaries are the second, third, and fourth largest in size within the range of the clapper rail. Mugu Lagoon, the largest wetland, supported on average only four pairs of rails. Of the remaining 21 sites where light-footed clapper rails are found, none supported more than 4 percent of the metapopulation, and 15 each supported less than 1 percent of the metapopulation.

Light-footed clapper rails are associated with cord grass (*Spartina foliosa*) habitats within coastal marshes in southern California (U.S. Fish and Wildlife Service 1979). Although it is unlikely that new estuaries will be created in this region, it is possible to improve and expand cord grass coverage in existing marshes. Foin and Brenchley-Jackson (1991) suggested that cord grass habitat improvement within existing marshes could potentially triple the rail population. Despite the severe limitation of available habitat, there are captive breeding and reintroduction efforts

currently being initiated (unpublished data, California Department of Fish and Game, Sacramento, CA). It has been well documented that the key predictors of successful translocations are habitat quality and the number of animals released. In general, endangered species translocations are unsuccessful more than 50 percent of the time (Griffith and others 1989). Likewise, if animals are released into habitats that are in poor condition or have insufficient area, they are unlikely to persist (Wolf and others 1996, 1998). Fleischer and others (1995) cautioned that translocations of light-footed clapper rails should be avoided until there is documentation that inbreeding depression is a problem for this species. Finally, more information is needed on natural recruitment into light-footed clapper rail subpopulations. Given the small number of light-footed clapper rails remaining in southern California and the limited and degraded condition of estuarine habitat, efforts to increase populations should emphasize habitat creation and enhancement rather than costly translocations with low potential for success.

Belding's Savannah Sparrow

Like light-footed clapper rails, Belding's savannah sparrows are non-migratory and endemic to southern California salt marshes. Unlike rails, however, Belding's savannah sparrows are associated with pickleweed (*Salicornia* sp.) habitats, which are much more expansive than cord grass habitats (Powell 1993). Pickleweed habitats have been degraded by changes in tidal flow and freshwater inputs, invasion of non-indigenous plants, and fragmentation by trails and roads. Restoration of this habitat type is difficult and may not result in suitable nesting habitat for sparrows (Keer and Zedler 2002).

Belding's savannah sparrows are censused in spring by counting singing males and observing breeding pairs. They have been censused sporadically in 26 to 30 coastal salt marshes in southern California, and intensity of efforts to count them varied among wetlands and years. All 30 marshes were surveyed in 1986, 1991, 1996, and 2001, and the total estimated number of breeding pairs ranged from 1,844 to 2,902 (Zemba and Hoffman 2002, Zemba and others 1988). Mugu Lagoon, the largest salt marsh in southern California, supported the largest subpopulation of sparrows, followed by Tijuana Estuary NWR, Upper Newport Bay Ecological Reserve, and Seal Beach NWR. Except in Mugu Lagoon, these sites also supported the largest subpopulations of light-footed clapper rails despite the differences in habitat associations of the two species.

There is evidence that Belding's savannah sparrow has limited dispersal and exists as a metapopulation with extirpation and recolonization of local populations (Bradley 1994, Burnell 1996, Zemba and others 1988). Like grassland savannah sparrows (*P. sandwichensis*), Belding's savannah sparrows are area-sensitive: there is a positive relationship between size of wetland and indices of population size, and sparrows are unlikely to occur in marshes less than 10 ha in size (Powell and Collier 1998). Recent research on reproductive success of Belding's savannah sparrows in different-size wetlands suggested that small, isolated salt marshes supported breeding birds but functioned as population sinks because they supported little or no productivity at those sites (Powell and Collier 1998). Finally, recent work on breeding biology of Belding's savannah sparrows indicates that the effective population size is likely much smaller than the number of males present; less than 50

percent of males establish territories, and only 43 percent of the territorial males manage to attract mates (Burnell 1996).

Ecosystem Importance

There is considerable overlap of the estuaries and associated beaches most important to these four species, and many of the important areas are on federal or State lands (*table 1*). Mugu Lagoon, for example, is among the top five breeding areas for both snowy plovers and Belding's savannah sparrows, and Santa Margarita River estuary and beach areas are critical breeding areas for California least terns and snowy plovers. Both Mugu Lagoon and the Santa Margarita River estuary are within Federal lands managed by the military (Mugu Naval Air Station (NAS), Camp Pendleton MCB). Vandenberg AFB supports the largest number of breeding snowy plovers in southern California. Other important federal lands include National Wildlife Refuges (Tijuana Estuary NWR, Seal Beach NWR, and Bolsa Chica Lagoon) and National Park Service (Channel Islands) lands. Upper Newport Bay, which is managed as an Ecological Reserve by the California Department of Fish and Game, supports the most light-footed clapper rails in the state as well as being the third most important site for Belding's savannah sparrow.

Table 1—*Top five sites, listed in descending order of population size, for breeding California least terns, western snowy plovers, light-footed clapper rails, and Belding's savannah sparrows in southern California.*

Species	Site	Management ¹
California least tern	Santa Margarita Estuary	Camp Pendleton MCB
	Venice Beach	CDFG
	Huntington Beach	CDPR, City of Costa Mesa
	Coronado	NAB Coronado
	Mission Bay	City of San Diego
Western snowy plover	Vandenberg	Vandenberg AFB
	Channel Islands	NPS, TNC
	Santa Ynez River	USAF
	Mugu Lagoon	Mugu NAS
	Santa Margarita Estuary	Camp Pendleton MCB
Light-footed clapper rail	Upper Newport Bay	CDFG
	Tijuana Estuary	NWR, CDPR
	Seal Beach	NWR
	Kendall-Frost Reserve	Univ. of California
	Carpenteria Marsh	Univ. of California, CDPR
Belding's savannah sparrow	Mugu Lagoon	NAS
	Tijuana Estuary	NWR, CDPR
	Upper Newport Bay	CDFG
	Seal Beach	NWR
	Bolsa Chica	FWS

¹ AFB = Air Force Base, CDFG = California Department of Fish and Game, CDPR = California Department of Parks and Recreation, FWS = U.S. Fish and Wildlife Service, MCB = Marine Corps Base, NAB = Naval Amphibious Base, NAS = Naval Air Station, NPS = National Park Service, NWR = National Wildlife Refuge, TNC = The Nature Conservancy, USAF = U.S. Air Force.

In addition to providing habitat to these four threatened and endangered species, these sites are important to wetland-dependent birds in general, particularly migratory species such as shorebirds. For example, Mugu Lagoon supports more than 65,000 shorebirds during spring migration and more than 10,000 in fall (Page and Shuford 1999). Seal Beach NWR, Bolsa Chica Lagoon, and Upper Newport Bay Ecological Reserve all support more than 5,000 shorebirds in fall and winter, and Santa Margarita River estuary and Tijuana Estuary NWR each hold more than 1,500 shorebirds during parts of the year (Page and Shuford 1999). The beaches associated with these wetlands provide habitat for snowy plovers, least terns, and other species of shorebirds. Restoration, enhancement, and creation of habitat at these sites and all remaining coastal wetlands will support biodiversity of beach and estuarine birds within the region.

Conclusions

Habitat degradation includes increased rates of predation related to human causes. Nonnative red foxes have expanded their ranges and populations in California and impact coastal ecosystems (Lewis and others 1999). There is evidence that common raven (*Corvus corax*) populations have increased substantially in California since the 1960s (Boarman and Berry 1995). Likewise, the proliferation of feral and domestic cats in urban areas has a significant impact on native birds (Ogan and Jurek 1997). A predator management plan is necessary to identify problem areas and control predation rates.

In addition, the dense human population in southern California coupled with popular recreational beach use has led to high levels of human disturbance within breeding and foraging areas for terns and plovers and surrounding marshes. Humans can impact bird populations through direct (for example, destruction of nests by trampling, vehicles, and vandalism) and indirect disturbance (for example, causing birds to abandon nests, separating parent birds from their young, bringing pet dogs into nesting areas, leaving trash that attracts predators). Limiting human access to nesting areas during the breeding season is essential for the conservation of these species.

Habitat preservation and enhancement of both beach and estuarine systems are essential for both long-term persistence of endangered birds and biodiversity along the southern California coast. Estuaries are natural islands of habitat, and principles of island biogeography and conservation biology should be applied to planning and management efforts. Light-footed clapper rail and Belding's savannah sparrow populations have experienced isolation and local extirpations, and the smallest and most isolated marshes are unlikely to contribute to productivity or overall recruitment for either species. Degradation and loss of surrounding native habitats have likely affected survival and productivity by increasing predation rates and limiting dispersal of these wetland birds. Nevertheless, these sites may still attract birds and thus behave as ecological traps.

To date there has been no organized effort to characterize existing estuaries across the region according to habitat type, patch size and shape, connectivity, and isolation (Zedler 1996). This information is critical, especially for the management of the year-round residents (light-footed clapper rails and Belding's savannah sparrows). Both subspecies are metapopulations endemic to southern California and Baja California, Mexico, and should be managed as such. Planners and managers

need to ask the following questions before designing habitat restoration and enhancement projects: (1) Are wetlands large enough to support self-sustaining populations over time? (2) Are patches of specific habitat types (for example, cord grass or pickleweed) large enough to support self-sustaining populations over time? (3) Are poor dispersers able to move between wetlands (will source/sink populations even out) over time? Restoration and management planners need to consider these issues to maximize habitat quality and reduce the potential for creating ecological traps.

Finally, a regional approach to wetland restoration is needed to enhance metapopulations of sparrows and rails as well as migratory species such as snowy plovers, least terns, and other shorebirds. For example, given the limited overall area within each wetland, increasing cord grass habitat to benefit clapper rails may be at the expense of pickleweed habitats required for Belding's savannah sparrows and vice versa. Converting salt pan or dredged areas to salt marsh may reduce the amount of habitat available to least terns, snowy plovers, and other shorebirds. Considerations should be giving to the status of the target species, probability of success of habitat restoration, and overall ecosystem functioning.

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Considerations for the Management of Vernal Pool Faunal Communities¹

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Abstract

The faunal community of California's vernal pools is less obvious and has been less studied than the floral community but is similarly diverse, endemic, and endangered. Species richness and composition vary between pool types, between pools of a given type, and within individual pools between years and through the season. The physiology, life history, and ecology of the pool organisms contribute to this complexity. Management considerations must take into account a large number of factors including maintaining pool hydrology and water chemistry, avoiding crushing cysts in the soil, avoiding the input of toxins, and maintaining genetic variability. Decisions must be made at the landscape level and focus on functioning communities, not just individual species or single pools.

Key words: crustacean communities, management, restoration, vernal pools

Introduction

California's diverse climate and topography support a wide variety of ephemeral wetlands. Among these are the vernal pools of the Central Valley and southern coastal mesas. These pools are inherently biphasic. In most areas, the pools are dry for the majority of the year, but they are temporarily converted into aquatic habitats when they fill from winter rains or spring snow melt. The pools then support a diverse flora and fauna, specifically adapted to their oscillating extremes.

The floral communities of California's vernal pools are quite well known (for example, Bauder 1987, Holland 1978, Holland and Jain 1988, Hoover 1937, Stone 1990, Zedler 1987); however, the faunal communities have been less studied. Although amphibians and waterfowl are quite visible, the much smaller invertebrates are not. These include crustaceans, rotifers, insects, worms, and snails.

The crustacean contingent is the more visually apparent of the invertebrates and includes branchiopods (fairly shrimp, tadpole shrimp, clam shrimp, and water fleas), ostracods (seed shrimp), and copepods. These obligately aquatic organisms survive the terrestrial phase of the pool as desiccation resistant, diapausing propagules (cysts, embryos, or eggs) in the soil. Upon hydration, they hatch, quickly develop, mate, and produce new propagules. The life cycle is compact because the pools are ephemeral. In some areas pools may last for months; in others they may last a few weeks or sometimes just days.

Ephemeral pools only exist in areas that are relatively flat and underlain by impermeable soils. Generally, the pools occur in clusters or complexes, creating a

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spatial patchwork across the landscape. Unfortunately these are also the areas utilized for agriculture and urban development. It is currently estimated that for these reasons, 90 percent of the pools have been lost statewide (Holland 1978, Stone 1990). In rapidly growing areas such as San Diego County, the estimates are upwards of 97 percent (Bauder and Wier 1990). This loss of vernal pools and their associated populations has resulted in the listing of several species of vernal pool plants and animals as endangered (Federal Register 1980, 1991, 1992, 1993a, 1993b, 1994, 1997). Unfortunately, a lack of information regarding obligate vernal pool invertebrates complicates this problem. Many more organisms are taxonomically undescribed and may merit listing as well, but their distribution, ecology, and life history are not well known. Only a very few have had primary research targeted toward them specifically. Furthermore, symbiotic interactions within the community and roles of community members in ecosystem cycles are poorly understood. Consequently, decisions regarding management, protection, restoration, and recovery have been difficult.

Here, I briefly discuss a few key findings from the research on vernal pool organisms (focusing on crustaceans) and suggest some of the implications which are relevant to management decisions. The majority of the research to date concerns branchiopods, but most of the implications for management are expected to extend to other taxa as well.

Key Research

Diversity and Endemism

California's vernal pool invertebrate communities exhibit quite high alpha (within site) and beta (across space) diversity.

- Single pools may have as many as 27 species of crustaceans, which exceeds the diversity seen in most permanent lakes (King and others 1996).
- Pools of different types (due to location and soil chemistry) can differ significantly in the species that are present (King and others 1996, Simovich 1998) (*table 1*).
- Within a pool complex, the faunal community can vary in richness (number of species) and species composition (which species) between pools (King and others 1996, Ripley and Simovich unpublished data, Simovich 1998).
- Many species appear to be highly endemic and are limited to one or a few types of pools (Eriksen and Belk 1999, King and others 1996).
- Sampling over a six-year period has shown that the same pool can differ in richness and composition between years and over the season within a year (Ripley and Simovich unpublished data). Similar variability is seen in ephemeral pool plants (Holland 1987). Thus, richness and composition vary spatially and temporally.

Table 1—Summary of crustacean diversity for two surveys. Only three species were found in both studies.

	North/Central Calif. (King and others 1996)	Southern Calif. (Simovich 1998)
# sites	14	1
# pools	58	66
# species	67	27
Range of # species per sites	4-39	NA
Range of # species in single pools	1-27	2-22

Physiology and Life History

Work done with the more visible vernal pool crustaceans, the anostracans or fairy shrimp, points to differences in physiological tolerance and life history associated with the species distributions.

- Some species appear to be broadly tolerant of a variety of water chemistry conditions. Others however, are restricted in their temperature, pH, alkalinity, turbidity, and salinity tolerance (Alexander 1976, Belk and Cole 1975, Belk and Nelson 1995, Bernice 1972, Brendonck 1996, Brown and Carplan 1971, Donald 1983, Eng and others 1990, Forro 1989, Gonzalez and others 1996, Hartland-Rowe 1972, Horne 1967, 1971, Lanway 1974, Moore 1967, Prophet 1963, Sam and Krishnaswamy 1979, Thiéry 1991, or see Eriksen and Belk 1999 for a review). This restricts the elevation (temperature) and location (soil chemistry) of the pools in which they can occur (*table 2*).
- Some species take several weeks to grow, mature, and reproduce while others can do so in as little as 10 days (Eng and others 1990, Hamer and Appleton 1991, Hamer and Sawchyn 1968, Hathaway and Simovich 1996, Mura 1991, Patton 1984, Pennak 1989, Rettalack and Clifford 1980). These life history characteristics restrict species' distributions to areas where precipitation and pool size/depth result in pool longevity consistent with their needs. Although precipitation (and consequently pool duration) can vary among years, pools must last long enough, often enough for reproduction. These factors contribute to endemism, beta diversity, and the differences within pools over time and among years.
- Some vernal pool organisms do not spend their entire life in the pool. Insect pollinators and amphibians are dependent on surrounding uplands for most of their life cycle.

Table 2—A comparison of three species of fairy shrimp with differing habitat requirements (data reviewed in Eriksen and Belk 1999).

Hatching temp. °C	TDS ppm	Pool duration	Example species
0-15°	<300	>3 weeks	<i>Eubbranchipus serratus</i>
5-20°	<600	>3 weeks	<i>Branchinecta conservatio</i>
17-30°	300-600	<3 weeks	<i>Thamnocephalus platyurus</i>

Incomplete Hatch

In areas where precipitation is extremely variable, pools fairly frequently may fill and dry before some species can reproduce. If all the propagules in the soil hatched in such a filling, the species would be extirpated.

- As an apparent adaptation to such occurrences, fairy shrimp species in unpredictable habitats exhibit incomplete hatch (al-Tikrity and Graninger 1990, Belk 1977, Belk and Nelson 1995, Brendonck 1996, Brendonck and Persoone 1993, Dexter 1973, Hildrew 1985, Mossin 1986, Philippi and others 2001, Simovich and Hathaway 1997). As a hedge against failure, only a portion of the cysts hatches in a given pool filling. As predicted by theory (Cohen 1966, 1967, 1968) and demonstrated in the lab (Philippi and others 2001, Simovich and Hathaway 1997), this portion approximates the proportion of time the pool fills sufficiently for reproduction; in other words, the probability of success. Thus, a cyst bank in the soil is crucial to the persistence of the population over time.
- There are several theoretical consequences of incomplete hatch. For example, if a number of cysts are transported to a new pool, only a small portion will hatch. When these reproduce, their offspring (cysts) will dominate the cyst bank, thus dominating the subsequent gene pool. Essentially there are fewer actual founders of the population than cysts transported. This can contribute to genetic drift and inbreeding.

Population Genetics

Vernal pools generally occur in clusters or complexes. Distances between pools within a complex are generally on the order of meters. Distances between complexes are commonly on the order of kilometers.

- As vernal pool crustaceans are obligately aquatic, they must rely on external means of dispersal. Within a complex, cysts may move between pools via overland water flow in high rainfall years. For dispersal between pools in drier years, or between complexes, the species must rely on vectors. The cysts can be transported on the legs of grazing animals or through the digestive tracts of waterfowl and amphibians (Bohonak and Whiteman 1999, Krapu 1974, Maguire 1963, Proctor and others 1967, Reid and Reed 1994). Thus, these species are distributed spatially as metapopulations, numerous subpopulations linked by varying levels of migration and gene flow.
- Genetic studies have shown evidence of low gene flow and consequently high differentiation between populations (Bohonak 1998, Boileau and Her-

bert 1988, Crease and others 1990, Davies and others 1997, Fugate 1992, 1998; Hann and Herbert 1986, Herbert 1974, King 1996). The narrowly endemic San Diego fairy shrimp (*Branchinecta sandiegonensis*) shows low genetic variability (allozymes) within subpopulations and high differentiation between populations, even over short distances ($F_{ST} > 0.50$ at less than 50 km) (fig. 1) (Davies and others 1997). A similar result was found for a Rocky Mountain species (*Branchinecta coloradoensis*) (Bohanak 1998). A more detailed analysis shows the differentiation by distance relationships of the two species to be almost identical (Bohanak and Simovich unpublished data).

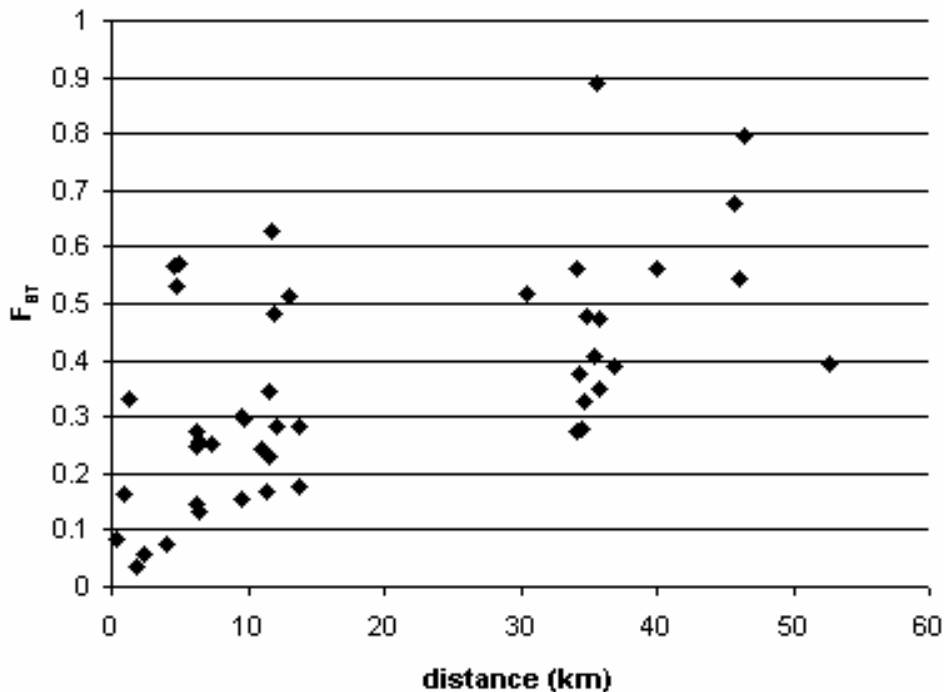


Figure 1—Isolation by distance. F_{ST} versus physical distance for populations of *Branchinecta sandiegonensis* in San Diego County, California (data from Davies and others 1997). F_{ST} can be considered an indicator of differentiation due to genetic drift. $r=0.57$

Missing Knowledge and Missing Species

Although some physiological and ecological information is available for some fairy shrimp species, these data are largely missing for most vernal pool crustaceans and other invertebrates.

- It appears that approximately 50 percent of California's vernal pool crustaceans are undescribed species about which essentially nothing is known (King and others 1996, Simovich 1998).
- Habitat loss models estimate that approximately 30 percent of California's vernal pool crustacean species have already been lost (King 1998).
- Very little is known about the food web, symbiotic relationships, and nutrient and energy cycles of vernal pools. The algae, plants, and invertebrates are food for birds and amphibians (Bohanak and Whiteman 1999, Krapu 1974,

Morin 1987, Proctor and others 1967, Simovich and others 1991). Some anostracans consume mostly algae while others are predators (see for review Parsick 2002). However, there are no studies available for most vernal pool invertebrates.

Additional information

- Anostracan cysts crush very easily, especially when wet (Hathaway and others 1996).
- Commonly used chemicals such as Malathion can kill vernal pool crustaceans (Davis and others 2001).
- At least some cysts (Wells and others 1997) and seeds (Cox and Austin 1990) in pools survive after fire.

Management Implications

These findings have important implications for management including habitat preservation, habitat restoration, and species relocation efforts.

Diversity and Endemism

- Pools at different sites or of different types differ in richness and composition. Therefore, preserving pools at one site as mitigation for losses at another may not preserve all of the same species.
- Pools within a site differ. Therefore, preserving a few pools at a site while losing the others may not preserve all species.
- Pools can differ between years in richness and composition. Therefore, more than one season of pre-manipulation surveying is necessary to establish base-line conditions, and several years of post-manipulation monitoring are necessary to establish success.

Physiology and Life History

- Many species, particularly the narrow endemics that are generally the species of concern, have very specific requirements for water chemistry, temperature, and pool longevity. Thus restoration or habitat creation must result in pools with appropriate chemistry and hydrology that mimic the range and variation of natural pools.
- Any manipulation involving the transport or introduction of organisms must consider the appropriate source. Organisms from different areas or pool types will probably not be appropriate and may not establish populations.
- Preservation of vernal pool communities requires preservation of the surrounding uplands for watershed and for amphibian, pollinator, and vector habitat.

Incomplete Hatch

- Although incomplete hatch provides a hedge against cycles with low reproduction, this life history strategy complicates simple management decisions. For example, after inoculation of a created or restored pool with soil, shrimp could hatch over several hydrations from the cysts in the inoculum. However, if the pool did not last long enough or hydrate often enough for sufficient reproduction, the cyst bank would not be replenished. Thus, initial monitoring would suggest a successful restoration, while in reality the cyst bank was being depleted to extirpation. Consequently, successful reproduction must be documented over several years to establish success.
- Incomplete hatch of the cysts used to inoculate pools may result in lower genetic variability of the new population due to genetic drift. This can have adverse effects on population fitness and evolutionary potential over time. Use of inocula with low cyst density may compound the problem.

Population Genetics

Particularly with narrow endemics, such as the San Diego fairy shrimp (*B. sandiegonensis*), genetic variation within populations and gene flow among populations (as indicated by allozymes) is apparently low.

- Populations should be surveyed in order to preserve those with higher genetic variability, which could, and may now, serve as source populations for gene flow and colonists for other populations.
- Increased isolation of pools will reduce visitation by vector organisms. This will further reduce gene flow and subsequently result in further reductions in genetic variation. This would be expected to put the species in jeopardy of reduced fitness due to inbreeding depression. It would also be expected to reduce evolutionary potential and the ability of the species to adapt over time and to reduce the possibility of rescue (re-colonization) if a population is extirpated or reduced. Consequently, preservation efforts must be considered at the landscape level rather than pool by pool. Sufficient buffer and corridor access must remain to encourage the usage of the area by potential distribution vector species.

Missing Knowledge and Species

- If an organism is undescribed, it is difficult to make decisions necessary to preserve and protect it. Taxonomic description, surveys, and natural history studies to establish species' distributions and resource requirements are critical.
- Any management or manipulations must focus on the entire community, not simply a single species. If a species' food is missing, or for plants, if a pollinator is missing, the species simply will not survive long.

Additional information

- Vehicles should be kept out of pools.
- Pollution run-off from surrounding areas is a potential problem.
- Fire should not be excluded from fire-type habitats, but excessive unnatural fuels in a pool (weeds) may increase fire temperatures and be a problem for cyst survival.

Summary

When trying to preserve communities about which little is known, careful decisions based on the best scientific knowledge available and a clear understanding of population ecology and genetics are necessary. Preservation decisions must be at the landscape level and consider functional communities, not just individual species or single pools. For restoration attempts, a careful, scientific approach documenting pre- and post-restoration conditions and based on well-reasoned experimental design is critical. This can best be accomplished by closely linking research and management. Finally, results must be published, to increase our knowledge, increase the probability of making good decisions, and decrease the probability of repeating poor ones.

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Biodiversity of Mycorrhizal Fungi in Southern California¹

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Abstract

Mycorrhizal fungi are a diverse group of organisms and form an integral link between plants and soil. These symbiotic fungi provide most of the soil resources to the plant in exchange for energy. However, their very diversity means that they can play many different roles and serve as indicators of changing ecosystem dynamics. There are probably more than a hundred mycorrhizal fungi associated with coast live oak alone in southern California. Data indicate that both the composition and functioning of these fungi change with the changing regional environment. Further, as regulators of ecosystem processes, changes in mycorrhizal composition and activity can ramify through the entire community. Understanding mycorrhizal and soil microbial dynamics and incorporating this understanding into management strategies will be crucial for sustaining viable preserves.

Key words: diversity, ecosystem, fungi, global change, mycorrhiza

Introduction

Biodiversity is a broad and general term used to describe the variety of organisms inhabiting a geographical or topological region of interest. For the most part, the emphasis of biodiversity focuses on listing or describing organisms of interest for protection or utilization, or the extent of this variation in terms of species number and abundance (Sisk and others 1994). However, there are vast arrays of organisms about which we know very little. According to recent estimates, we have described around 50 percent of vertebrates, but only 5 percent or less of insects and fungi (for example, Fröhlich and Hyde 1999, Hughes and others 2000). For prokaryotic organisms, we don't even know how to classify kingdoms, much less the concept of species. Of those we know, many are threatened with extinction, often before we even know who they are or their roles in ecosystems (Hughes and others 1997).

Fungi make a useful test group for understanding the concept of biodiversity and, in turn, understanding the environmental changes likely to affect the entire biota of a system (E. Allen and others 1995, M. Allen and others 1995). Fungi are found in every terrestrial environment and are directly and indirectly exposed to every perturbation. They range in scale from microfungi growing in solitary colonies on a single root tip to a macroorganism, such as *Hydnangium carneum*, that extends across an entire plant stand (Allen and others 1993). They also perform many

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essential roles in ecosystems, such as decomposing detritus and providing much of the nutrients needed by plants for photosynthesis. Thus, they are susceptible to every form of environmental change.

Of the vast array of fungi, mycorrhizal fungi represent a tractable group that is also sensitive to environmental perturbations. Mycorrhizae are mutualistic associations between plants and fungi that are localized within the root or root-like structures (Allen 1991). These fungi extend not only outward into the soil to extract nutrients and water, but they also extend into the plant roots where they exchange those resources for carbon. The only terrestrial plants not forming mycorrhizae are a limited number of weedy annuals in a few families such as the Chenopodiaceae or Cruciferae (Allen 1991). Thus, any environmental factor that affects plants can also affect these fungi. Likewise, each change in the substrate that could influence mycorrhizal fungi will also affect the host plants.

Mycorrhizal fungi are interesting and important in themselves. Many are commonly collected mushrooms for culinary purposes. They also make an important contribution to the diets of many mammals, especially rodents. Truffles are common, and searching for them is largely based on finding animal diggings. The hyphae of mycorrhizal fungi also provide much of the soil structure by producing glycoproteins called glomalin, which may make up as much as 25 percent of the soil organic matter and bind soil particles into macroaggregates (Rillig and others 1999, Treseder and others 2003). This structure protects nutrients and increases porosity and water-holding capacity. Finally, mycorrhizal fungi are responsible for much of the nutrient turnover and most of the transport dynamics that move resources around plants and between patches.

We have been studying mycorrhizal fungi in southern California vegetation types for over a decade. Such studies are vital because southern California is a designated hot spot for biodiversity conservation (Myers and others 2000), and the region is subject to intense perturbation from a variety of anthropogenic sources. Our observations have demonstrated some unique patterns (described below), but, of greater importance, they have indicated the need for long-term observations before definitive trends can be conclusively determined. We have focused on observations extending through precipitation cycles and across edaphic gradients at a variety of scales and on experiments evaluating responses to changing environments. Based on these data and the measured environmental change already observed by physical scientists, we believe that southern California ecosystems are likely beginning to undergo important and quantifiable change in microbial communities. Here, we focus on measurable responses of mycorrhizal fungi. These data can form a baseline against which future changes can be measured.

Mycorrhizal Fungi in Southern California: Biodiversity of a Group

Mycorrhizal fungi are diverse in southern California. Little is known about some key variables that would be involved in any program to describe and conserve biodiversity in mycorrhizal fungi. Although seven groups of mycorrhizal fungi are recognized, we focused largely on two major groups of mycorrhizal fungi. The first are ectomycorrhizal fungi found in symbiosis with coast live oak (*Quercus agrifolia*), pines, some other trees, and a few shrubs; ascomycetous and basidiomycetous fungi

form these mycorrhizae. The second are arbuscular mycorrhizal fungi (Glomales) associated with other trees, forbs, most shrubs, and grasses.

Structure of Diversity in Fungi

Diversity is richness and evenness of species, genomes, and functions. Fungi are different from higher plants and animals in that variation can occur and be measured within an individual as well as between individuals, populations, species, and clades. This variation can be detected at the scale of a small patch of ground (cm²) as well as at larger land units. Variation can also occur through time. As environmental pressures change, not only species but also the relative genetic composition of an “individual” mycelium can change.

Characterizing both the current and anticipated changes in fungal diversity with environmental perturbation is challenging. Fungi have multiple, haploid (1N) nuclei. In zygomycetous and glomalean fungi, no cross-walls exist. Thus, groups of nuclei can be found scattered throughout a developing mycelial fan. In ascomycetous and basidiomycetous fungi, most cells contain two separate 1N nuclei. The hyphae expand as individual cells multiply and elongate. However, when two compatible hyphae meet, they anastomose, forming a single mycelial network. As the mycelial network extends outward and multiple hyphae connect, a single connected “individual” mycelium can contain many different nuclei, and an individual connected hypha can contain cells with different functional and sometimes incompatible genes.

Ectomycorrhizal Fungal Diversity

Ectomycorrhizal (EM) fungi are a highly diverse group. Based on a decade of collecting from San Diego State University mycology classes, we have identified 74 species associated with coast live oak groves. Nevertheless, how diversity is characterized is as important as the data collection itself. To better evaluate this diversity, we have utilized a number of approaches. Because the real extent of demographic units in mycorrhizae is essentially unknown, as is the frequency of occurrence of metapopulations, we used geographically and ecologically stratified samples to evaluate patterns of both species and population diversity.

Our experimental research has been undertaken largely at Lopez Canyon, in the Western Riverside County Multispecies Reserve, and consists of evaluation of fungal diversity at the morphological and molecular level. Our first assessment was to plant oak seedlings in association with mature individuals (> 100 years old). At the end of the growing season, we harvested seedlings and estimated the number of morphotypes. Morphotypes are morphologically distinct mycorrhizal root tips that can be distinguished on the basis of characteristics such as texture, color, and hyphal types. Morphotypes sometimes correspond to fungal taxa, although there can be more than one fungal taxon per morphotype. Because of this ambiguity, we also employed molecular differentiation of tips that were morphologically similar. DNA was then extracted and amplified from roots of some seedlings using the polymerase chain reaction (PCR) of the internal transcriber region (ITS) of the small subunit of the ribosomal DNA. This part of the DNA chain was cut using endonuclease enzymes, leaving distinctive small units of DNA. These were run on gels that showed the size patterns of these DNA fragments, called *restriction fragment length polymorphisms* (RFLPs). These size units are distinctive to species and thus can be used to assess

diversity of mycorrhizal fungi at each individual root tip scale (Gardes and Bruns 1996, Karen and others 1997). RFLP comparisons allowed us to assess the numbers of actual mycorrhizal fungal taxa per tree based on the composition of the DNA.

During the winter rainy season of 2001, we found that the richness of EM morphotypes per seedling associated with mature coast live oak averaged 10; however, the richness at the stand level was expected to be much greater. There is considerable variability in the EM composition of seedlings from different oak patches resulting in much greater stand richness. Our initial findings showed that it was common for only a few EM morphotypes to be the dominant colonizers on an individual seedling. Furthermore, not only was there variability in the EM composition between seedlings from different patches, but also in which EM morphotypes were the dominant colonizers.

When we expanded to the RFLP analysis, a greater number of types emerged. For comparative purposes, an average of seven morphotypes per seedling were found, in contrast with an average of 12 RFLP taxa per seedling and a maximum of 20 RFLP taxa per seedling. The same pattern as morphotypes per stand emerged, though. A few dominant taxa could be found, with many infrequent species.

This finding is similar to EM community studies of pinyon pine (*Pinus edulis*) in Arizona (Gehring and others 1998) and New Mexico (Allen and others 2002). Pinyon pine trees act as isolated islands in which an individual tree has an average richness of 5 morphotypes but a stand of 8 trees has a richness of 20 to 30. Similarly, in coast live oak, only a few dominants per tree were found, but there was a great deal of variability among trees. As we sampled across the landscape, there was a continued replacement of species demonstrating a high level of β diversity (Allen and others 2002).

Our final effort was to investigate the diversity of species identified by sporocarps and the relationship between diversity and a stochastic measure of the rate of change in mycorrhizal diversity on a per area basis. At Camp Pendleton, we undertook a 4-year study monitoring the EM fungi fruiting in plots under stands of coast live oak and Engelmann oak. During this period, we identified 58 species of EM fungi. The species increment curve demonstrated a leveling off, suggesting that we had identified most of the sporulating fungi for those sites.

We estimated the land area for sampling, allowing us to calculate a z-value that describes the rate of change in diversity in relation to sample area size (from $s=ca^z$, where s is the number of species, or richness, c is a constant, and a is the area, Rosensweig 1995). Although we recognize that there are many means to assess diversity, the z-value is independent of size and allows comparisons to be made among habitats with varying areas. Since we are only able to assess mycorrhizal fungal responses to environmental change on small plots, this relationship provides some insights into how our region and mycorrhizal fungi might be affected.

Our results show that the z-value may be appropriate for comparison. For the individual seedling studies at Lopez Canyon, the z-value for root-tip morphotypes was 0.57 with an r^2 for the species area curve of 0.96. For the Camp Pendleton sporocarp assessment, the z-value was 0.58, with an r^2 of 0.975. These values are high compared with vertebrates, but they resemble the high values found in insect communities. Given that this z-value is high at the scales of patches and sites, then as the entire range of coast live oak is examined, the diversity of fungi has the potential to become extraordinarily high. This suggests that there probably are, in reality, up to

several hundred taxa associated with coast live oak alone, as has also been found for other mycorrhizal plants (Allen and others 1995, Sanders and others 1995, Sharples and others 2000,). Thus, the potential biodiversity of EM fungi and richness of valuable sources of genetic variation for a group of organisms important to the survival of this tree are extraordinary.

Chamise (*Adenostoma fasciculatum*) normally forms arbuscular mycorrhizae with all genera found in the region. However, during wet years (El Niño), we found EM associated with its roots and EM fungi in the stands (Allen and others 1999b). There was a high diversity of fungi ranging from *Cenococcum* and *Balsamia* spp. (ascomycetes) to a variety of basidiomycetes such as *Pisolithus* sp., *Cortinarius* spp., and *Hysterangium separabile*. We also found a new species of *Rhizopogon*: *R. menzei* (Allen and others 1999a). This is an important finding, since all other known species of *Rhizopogon* are associated with conifers. In addition, we sequenced the dominant fungus found on the root tips of chamise, and this fungus was an unknown species of ascomycete, most closely related to *Sarcocypha emarginata* (97 percent similarity in the sequence alignment of the 5.8S region, 63 percent similarity in ITS1, and 59 percent similarity in ITS2), a common fire-following fungus. There are clearly plant/fungal symbiotic combinations that we do not understand and have yet to explore.

Although we have focused on coast live oak and chamise, it must be noted that there are many other EM plants in southern California. These include all other species of oaks, all members of the Pinaceae, and chinquapin (*Chrysolepus semper-virens*). In our region, these never have been surveyed comprehensively.

Endomycorrhizal Fungal Diversity

Almost all other plants in southern California form endomycorrhizal associations. Most common is the arbuscular mycorrhizal (AM) type found in grasslands and shrublands. The fungal symbiont is a monophyletic group consisting of two distinct clades (phylogenetically-related species), the Glomaceae and the Gigasporaceae, which split with the earliest land plants (Redecker and others 2000, Morton and Redecker 2001). These different clades have some quite distinct characteristics important to mycorrhizal functioning and response to changing environments. Thus, while they are monophyletic, and species diversity is low (approximately 170 species are described worldwide), the different families diverged so long ago (350-400 million years) that functional differences have resulted (Hart and others 2001).

We conducted two relevant types of surveys. In the first, we examined the AM fungi associated with basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) throughout its distribution. This subspecies can be found throughout western North America, ranging north from Baja California in Mexico to British Columbia in Canada and eastward as far as North Dakota and New Mexico. Using this large spatial scale, we found that species richness of AM fungi increased with greater area sampled (fig. 1). However, most of the diversity of AM fungi associated with the Mojave ecotype of big basin sagebrush could be accounted for in just seven sites (fig. 2), because evenness actually declined as more sites were surveyed.

If we examine the pattern of distribution, there are several fungi—*Glomus aggregatum*, *Scutellospora calospora*, and *Paraglomus occultum*—that are widely distributed and found throughout the range. Others, such as *Sclerocystis rubiformis*,

Glomus tortuosum, *Archaeospora gerdemannii*, *Scutellospora pellucida*, and *S. heterogama*, are narrowly distributed, being found in only a few locations. In expanding to all 99 sites where basin big sagebrush exists, the total richness (number of AM fungal taxa) doubles, but the diversity continues to decline due to a lowered evenness. Clearly, each area has its specific combination of AM fungal species. The plant likely adapted to the local AM fungi but probably did not carry the AM fungi with it as it dispersed.

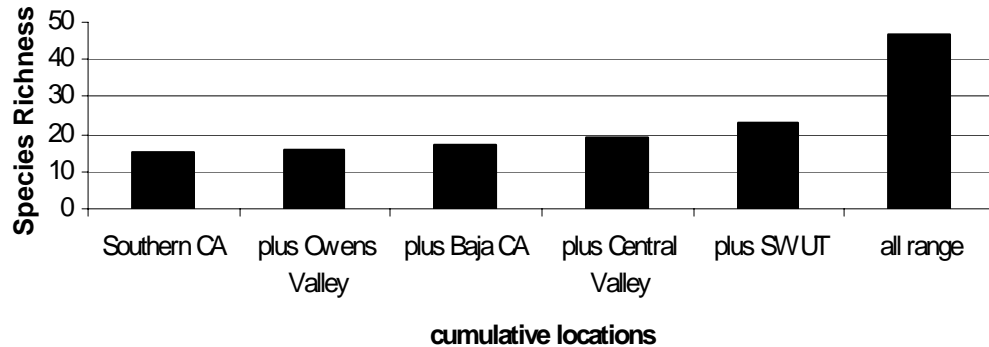


Figure 1—Richness of AM fungi associated with basin big sagebrush from southern California across its range into central California, Baja California, and across the Great Basin.

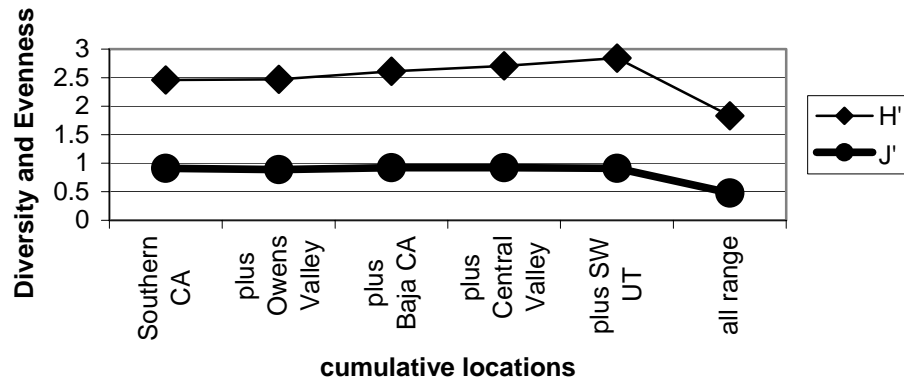


Figure 2—Diversity (H') and evenness (J') of AM fungi associated with basin big sagebrush from southern California expanding across its range into central California, Baja California, and across the Great Basin.

Just as importantly, the same genera and most of the same species diversity can be found associated with California sagebrush (*Artemisia californica*) and probably most other shrublands (Egerton-Warburton and Allen 2000). We do not yet have a large-scale sampling of AM fungi associated with forblands and only limited sampling in perennial *Stipa* grassland. However, in an undisturbed *Stipa* grassland, we found species of *Glomus*, *Acaulospora*, and *Scutellospora* (Allen unpublished data).

We know that, with few exceptions, AM fungi are not species-specific, but rather function as generalists and tend to infect whatever plant is nearby. We also know that there are growth responses that occur preferentially between specific combinations of plants and fungi (Klironomos and others 2000). This leads to increasing stand productivity and plant diversity in response to increasing AM fungal diversity (Klironomos and others 2000, van der Heijden and others 1998). However, the specific combinations that are crucial to a native plant community remain elusive.

Projections of Environmental Change: CO₂, N Pollution, Temperature, and Precipitation

Our global environment is changing dramatically and rapidly. This change translates to direct effects on our local environments and the need for retaining and managing for biodiversity on the remaining open space reserves. The clear changes are in atmospheric CO₂ and in NO₃ and NH₄ deposition. Less clear but potentially important are changes in temperature and precipitation (Rillig and others 2002).

CO₂ has risen dramatically since the industrial revolution, largely in response to increasing human demands for energy and increasing conversion of forest to agricultural lands globally (Houghton 1997). During the last ice age, atmospheric CO₂ was below 200 ppm (parts per million). By the beginning of the industrial revolution, atmospheric CO₂ was around 250 ppm. In the 1970s, it was up to 350 ppm and has rapidly increased, being currently about 370 ppm. Global projections range from 550 to 750 ppm over the next century. CO₂ has direct effects on plant dynamics in that the need for a C sink increases to handle the increasing fixation. Further, nutrients become more limiting to photosynthesis, especially N and P. Finally, with elevated CO₂, water-use efficiency rises.

Increased N deposition is also dramatic but concentrated at the regional rather than global scale. In southern California N largely comes from **denitrification** associated with dairy cattle and vehicular exhaust. Although the levels and forms are changing dramatically (see E. Allen and others, this volume), the amount remains important. Within the Los Angeles basin, deposition can range from 30 to 45 kg ha⁻¹y⁻¹, values equal to agricultural fertilization levels.

Temperature and precipitation changes are much less predictable. However, only small changes can have dramatic impacts. Further, these can remain within the bounds of evolutionary history and still affect the regional biota. According to most of the global circulation models (GCM), our region of southern California may be in the area of maximum climate and vegetation change (Watson and others 1997). Virtually every GCM shows increasing precipitation in southern California as a function of general warming caused by the greenhouse effect. With the heating of the oceans associated with the greenhouse effect, the model predicts increasing precipitation in a manner similar to the observed increases associated with El Niño phenomena. In this scenario, Neilson and colleagues (1998, and 2001 pers. comm.) note a significant increase in both winter and summer precipitation. This increase is coupled to increased water-use efficiency of desert plants associated with elevated CO₂. Consequently, their projections suggest that this increasing precipitation would result in increasing grasslands and mixed forest and decreasing shrublands and deserts.

Responses of Fungi to Change in Southern California

Although all of these projections fail to include all relevant processes, clearly there are enough indicators for us to be concerned with retaining our current biodiversity and managing for the diversity that can protect species of concern. Mycorrhizal fungi are only one group of organisms on which the ecosystem depends. Likely, there is more diversity in these fungi than absolutely required for oaks and similar critical species to survive. However, we are not very good at predicting which might be the crucial species. Below, we note some changes that we can see from our on-going experiments.

Diversity

Diversity and composition responded to changing perturbations. In experimental studies, the total amount of AM increased in response to elevated CO₂, and the increase was largely associated with the Gigasporaceae (Klironomos and others 1998, Treseder and others 2003; *fig. 3*). The amount of Glomaceae did not change even as CO₂ increased from 250 ppm to 650 ppm. At 750 ppm CO₂, the entire belowground system collapsed, and we do not understand the possible mechanisms. Conversely, in response to N deposition, sporulation in the Gigasporaceae disappeared, although some vegetative hyphae remained in association with roots (Egerton-Warburton and Allen 2000). However, the Glomaceae remained relatively constant; moreover, some species of *Glomus* increased in abundance following N enrichment. These findings indicate that N deposition promotes editing of the existing mycoflora, not an invasion. It should be remembered that AM fungi evolved during a period when atmospheric CO₂ was much higher than today (Allen 1996). CO₂ *per se* is not likely a detrimental factor for AM fungi. However, N has generally been the major limiting element in most terrestrial ecosystems, and N fertilization can have rather dramatic effects on AM fungal dynamics (see E. Allen and others, this volume).

There is little field experimental evidence on the interactions of CO₂ and N deposition and the composition of the AM fungal community. In the only data set to date, we find that there was a shift from the normal mix of AM fungi to the fine-endophyte form, *Glomus tenue* (Rillig and others 1999a). This may be a direct effect or a response to changing soil pH.

The abundance of ectomycorrhizae initially increased in response to N fertilization over a single growing season at Lopez Canyon. This area has not received long-term high levels of N deposition, as has the Los Angeles Basin. The z-values were 0.57, 0.68, and 0.60 (not significantly different) for control, N-fertilized, and weeded oak seedlings, respectively. In part, this demonstrates that in this region N remains the most limiting nutrient. N fertilization increased plant survival and growth, allowing a greater rate of both tip and EM formation. Also, these data demonstrate the need for long-term data on the effects of perturbations such as N deposition.

To our knowledge, no data on responses of EM fungal communities to elevated CO₂ have been published. This is important because increasing CO₂ could push ecosystems in high N depositional regions back to C/N equilibrium or propel the ecosystem along an entirely new trajectory.

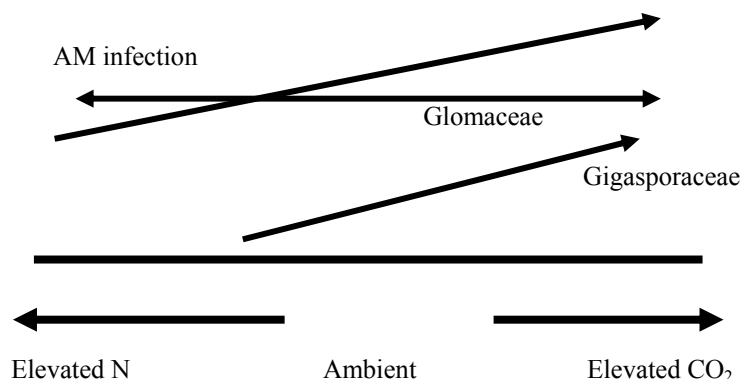


Figure 3—Changing AM activity along an atmospheric change gradient, ranging from elevated N (N deposition) to elevated CO₂. Data come from Egerton-Warburton and Allen (2000), Rillig and others (1999a), and Treseder and others (2003).

Mycorrhizal Activity

CO₂ and N have many impacts on mycorrhizal fungi and the functioning of soil ecosystems. CO₂ in particular has a very subtle effect on arbuscular mycorrhizae. In studies of newly disturbed soil, or pot cultures, AM fungi always appear to increase (Treseder and Allen 2000). However, in *in situ* studies, the total hyphal lengths per soil volume do not change (Allen in preparation). The hyphal lengths in soil aggregates and allocation of new C to soil via aggregates does increase as measured using both isotopic data and glomalin concentrations (Rillig and others 1999b, Treseder and others 2003). These data indicate that more C is allocated to mycorrhizae but that the turnover also increases. The residual C in the form of recalcitrant carbon builds up but probably not at the same rate as the increasing atmospheric levels that we are currently experiencing.

There are no data on the effects of elevated CO₂ on oak mycorrhizae from southern California. However, in a similar climate in Italy, ectomycorrhizal activity tends toward increasing cycling rates in a manner observed for AM (Cario and Allen in preparation).

N fertilization has mixed effects on total mycorrhizae. In N deficient situations, N fertilization can actually increase mycorrhizae. However, N can rapidly saturate shrublands and forb communities, causing a decline in the abundance of mycorrhizae often within three years following the onset of N enrichment (Egerton-Warburton and Allen 2000).

In forest ecosystems, there is a large capacity for absorbing N. We contrasted N cycling in oaks, comparing two sites: the first was the Sky Oaks Field Station, managed by San Diego State University, near Warner Springs, CA (N limited and low deposition); second was the San Dimas Experimental Forest (USDA Forest Service) (high deposition). The $\delta^{15}\text{N}$ data from San Dimas shows that N cycling has changed markedly since the experiment station was established in the 1930s. The values from San Dimas in 1935 (-2 percent) are equivalent to Sky Oaks, suggesting that Sky Oaks N-cycling patterns are less impacted by recent N deposition. Current leaf $\delta^{15}\text{N}$ is -4 percent. The values for the EM sporocarps for Sky Oaks and San Dimas average 6.9 percent and 6.8 percent, respectively. These data suggest that the

functioning of the mycorrhizal fungi (utilizing NH_4^+ and organic N) may not have changed but that depositional N is taken directly by the plant. In oak stands, initial evidence suggests that the oaks are not N saturated and mycorrhizal fungi remain active. How long this will persist and whether the fungal composition changes as the plants depend less on mycorrhizae for N are open questions.

Exotic Fungi

Pisolithus tinctorius is a widespread fungus associated with many host plants. Because it is so widespread, it was also widely used in reforestation efforts and in urban plantings (Marx and others 1984). (It is important to note that when this project began, it was considered a single species, but recent systematic studies are in the process of dividing *P. tinctorius* into several new species.) We studied the diversity of several sporocarps of *P. tinctorius*. Of relevance to us, this fungus is associated with oaks in California, pines in the southeastern US, and eucalyptus in Australia. We wanted to determine whether the fungus associated with cultivated trees was different from fungus associated with eucalyptus or from the native oaks.

On the basis of morphology, the sporocarps were virtually indistinguishable, and the spores ranged in size from 9.3 to 10.3 μm in diameter. However, the median spore diameter did vary significantly among the different isolates. The ITS region was also examined to determine whether the molecular structure could be distinguished. Even without further RFLP analyses it was possible to discern three ITS size categories: 610, 635, and 650 base pairs. When the spore size and ITS regions are examined together, the different sporocarps could be broken into six distinct groups (*table 1*). Importantly, there are four groups of sporocarps primarily found with exotic trees, two in the city of San Diego, one at the Santa Margarita Ecological Reserve (planted in 1974 as part of a biomass production study), and a third mixed planting near the Sky Oaks site with eucalyptus. There are two distinct genotypes found with native trees. The first was found in southern California with *Quercus agrifolia* and with *Q. turbinella* in New Mexico. This second is found in association with many native plants and stands scattered across California.

The important issue here is that there appear to be two native groupings and four likely introduced exotic fungi, which may switch hosts. Although we focused on *P. tinctorius*, there are many other exotic mycorrhizal fungi found in eucalyptus groves, including *Hydnangium separabile* from Tasmania, a fungus in the *Laccaria amethystina* group from Australia (Allen and others 1993). At this time, we do not know the implications of this invasion, but in other studies, switching can result in a less effective, or even detrimental, symbiosis for the plant.

Implications for Southern California Ecosystems

Mycorrhizal fungi are absolutely critical components of all terrestrial ecosystems in southern California and globally. These organisms provide the majority of nutrients to the plants, stabilize soils, sequester carbon, provide food for animals, and serve as the predominant microbial C sink for fixed photosynthate. They are extremely diverse with the differing fungi undertaking slightly different roles in the highly spatially variable semiarid to arid ecosystems of our region. Most global change models predict that our region will likely experience profound changes, potentially within our lifetimes.

Table 1—Differentiation of taxa of *Pisolithus tinctorius* from collections in Southern California based on spore size and ITS size fractions.

Group	Isolate	Host	ITS (bp)	Spore size (um)	Location
I	Pt 4	<i>Eucalyptus</i> sp.	610	9.3	SMER (Riverside County)
	Pt 2	<i>Eucalyptus</i> sp.	610	9.6	SMER (Riverside County)
	Pt 22	<i>Pinus radiata</i>	610	9.6	San Diego State University
II	Pt 16	<i>Eucalyptus</i> sp.	610	9.8	Sky Oaks (San Diego Co.)
	Pt 17	<i>Eucalyptus</i> sp.	610	9.8	Lake Skinner (Riverside Co.)
III	Pt 24	<i>Quercus turbinella</i>	635	9.2	Seville LTER, NM
	Pt 7	<i>Quercus agrifolia</i>	635	9.4	Boden Field (Sky Oaks, San Diego Co.)
IV	Pt 23	<i>Eucalyptus</i> sp.	635	9.6	San Diego State University
V	Pt 11	<i>Quercus agrifolia</i>	635	9.7	Sky Oaks (San Diego Co.)
	Pt 1	<i>Chrysopsis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 3	<i>Chrysopsis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 6	<i>Chrysopsis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 14	<i>Quercus agrifolia</i>	635	10	Sky Oaks (San Diego Co.)
	Pt 18	<i>Adenostoma fasciculatum</i>	635	10	Lake Skinner (Riverside Co.)
	Pt 10	<i>Quercus agrifolia</i>	635	10.1	Boden Field (Sky Oaks, San Diego Co.)
	Pt 13	<i>Quercus agrifolia</i>	635	10.3	Sky Oaks (San Diego Co.)
VI	Pt 19	<i>Eucalyptus</i> sp.	650	9.4	San Diego State University
	Pt 8	<i>Eucalyptus</i> sp.	650	9.6	SMER (Riverside County)
	Pt 15	<i>Quercus agrifolia</i>	650	9.6	Sky Oaks (San Diego Co.)
	Pt 20	<i>Eucalyptus</i> sp.	650	9.7	San Diego State University
	Pt 9	<i>Eucalyptus</i> sp.	650	9.9	SMER (Riverside County)
	Pt 21	<i>Eucalyptus</i> sp.	650	9.9	San Diego State University
	Pt 5	<i>Eucalyptus</i> sp.	650	10	SMER (Riverside County)
	Pt 12	<i>Quercus agrifolia</i>	650	10	Sky Oaks (San Diego Co.)

According to GCMs, our region generally will experience increasing precipitation (IPCC 1998). The impacts of this potential change can be seen in the effects of El Niño years on ecosystem dynamics. Moreover, the changing precipitation interacts non-linearly with N deposition, elevated CO₂, human population growth, and increasing development in many and complex ways. Our ability to manage the diversity and integrity of wildland ecosystems may depend on our understanding the microbial groups such as mycorrhizal fungi and sustaining their diverse and differing needs (Daily and others 2000).

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A New Look at Coastal Sage Scrub: What 70-Year-Old VTM Plot Data Tell Us About Southern California Shrublands¹

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Abstract

This is a preliminary report on a project to characterize the historic species composition of coastal sage scrub vegetation in southern California using plot data collected between 1929 and 1934 by the USDA Forest Service's Vegetation Type Map (VTM) survey. Records and maps from a large historic data set collected for the VTM survey were converted into a digital database and GIS coverage. Historic data for 1481 shrub plots were combined with climate, modern land use, and land cover data. Preliminary analysis found patterns of species composition and geographic distribution in coastal sage scrub considerably more detailed than have been described in previously published regional descriptions. Coastal sage scrub associations described in local studies are here shown to occur over larger areas in the southern California region than the areas within which they were originally described. Maps of the regional distributions of these coastal sage scrub associations were produced. Summer precipitation, elevation, and minimum winter temperature best predicted relative differences in abundance of *Eriogonum fasciculatum* and *Artemisia californica*. *Salvia apiana* preferred interior, higher elevation sites with high annual precipitation and an extremely continental climate. *Salvia mellifera*'s distribution was not well predicted by any environmental factors measured in this study. Rates of coastal sage scrub conversion were estimated by county and regionally for a number of species associations.

Key words: classification, climate, coastal sage scrub, gradient analysis, ordination, vegetation associations

Introduction

Coastal sage scrub is a drought-deciduous, soft-leaved shrub plant community frequently dominated by *Artemisia californica*, *Eriogonum fasciculatum*, and/or *Salvia* species (Mooney 1988). This vegetation has been drastically reduced in extent and highly fragmented by conversion to agricultural, industrial and residential land use, grazing pressure, altered fire regimes, and air pollution. How much coastal sage scrub has been lost is a matter of some contention. Westman (1981a) estimated that perhaps 10-15 percent of the original distribution remained. Minnich (1998) maintains that the Los Angeles basin contained very little of this vegetation at first Spanish contact and suggests that a much higher fraction remains extant today. Freudenberger and others (1987) concluded that the Los Angeles basin was once a mosaic of shrublands and grasslands, suggesting a number somewhere between

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Westman's and Minnich's opinions. O'Leary (1995) cited consultant Michael Brandman Associates' estimate that as of 1991, 44 percent of historic coastal sage scrub remained. All agree that large cumulative losses of coastal sage scrub occurred during the 20th century and that loss is ongoing.

The remnants provide habitat for nearly 100 species of plants and animals currently classified as *rare*, *sensitive*, *threatened* or *endangered* by Federal and State agencies (Davis 1994). Since 1990, coastal sage scrub in coastal areas from Los Angeles to San Diego has been the target of intensive conservation planning and management activities (O'Leary and others 1992). There is an immediate practical need for accurate information on the distribution and composition of coastal sage scrub (O'Leary 1990, 1995).

The Natural Communities Conservation Program (NCCP) is a regional multi-agency effort to conserve biological diversity across southern California through directed scientific research, regional land use planning, and mitigation banking (O'Leary and others 1992). The coastal sage scrub preservation plan was the NCCP's first pilot project. The project area corresponds roughly to San Diego, Orange, western Riverside and western San Bernardino counties. The NCCP region represents the geographic extent of research described in this report.

The Vegetation Type Map (VTM) survey was a Depression-era public works project conducted between 1929 and 1934 by the California Forest and Range Experiment Station (USDA Forest Service), Berkeley, California (Wieslander and others 1933). Survey teams mapped vegetation (at 1:64,000 to 1:125,000 scale) across about one third of California, including all of coastal southern California exclusive of the Los Angeles basin. They also collected quantitative data on dominant plant species cover from about 18,000 plots, including several thousand shrubland plots. The shrub plots were 0.1 acre (0.04 hectare) in extent, 33.0 feet (10.1 meters) by 132.0 feet (40.2 meters). Tree plots were twice that size. They allocated about 75 plots per 15-minute map, equal to a sampling density of about 1 plot per 2000 acres (800 hectares). The plots were subjectively placed in locations intended to represent typical stands of the qualitatively determined vegetation associations indicated on the vegetation maps. The plots were allocated fairly evenly over non-desert areas that were undeveloped at the time. The data were collected at a rather early point in the explosive urban development of southern California; thus they constitute a valuable historical snapshot of California plant communities when they were still much more intact and expansive than they are today. Between 1930 and 2000 the population of San Diego County went from 210,000 to 2,814,000, doubling about every 14 years (U.S. Census Bureau 2003).

Axelrod (1978) and Westman (1981a, 1981b, 1983) described geographic limits of generalized coastal sage scrub types. These pioneering studies represent a starting point for further research on regional distributions of coastal sage scrub species and species associations. Axelrod's work was based on a qualitative analysis of VTM vegetation maps, weather station data and other data. Westman's work was based on quantitative analyses of data from 99 vegetation plots subjectively placed in coastal sage scrub stands from El Rosario in Baja California, Mexico, to Contra Costa County, California, including 28 plots in the NCCP region. Both researchers described an interior type of coastal sage scrub called *Riversidian* and coastal associations called *Venturan* and *Diegan*. Axelrod's (1978) *Diegan* association reaches its northern limit near Torrey Pines State Park. Westman's (1983) *Diegan* coastal sage scrub association extends north along the coast all the way to the Los

Angeles County line. Species associated with the two authors' coastal sage scrub types are roughly comparable.

Although coastal sage scrub is generally recognized as a highly diverse plant community, it is often dominated by just one or a few species when viewed at a scale of a few meters to tens of meters (Mooney 1988). Substantial floristic variation exists at scales larger than individual stands. In other words, coastal sage scrub seems to have moderate alpha diversity, but higher beta and gamma diversity (Whittaker 1978). Westman (1981a) noted that this property of coastal sage scrub makes it necessary to sample a relatively large number of sites to characterize the full range of floristic variation in the vegetation type. He noted that his own sampling effort was distinctly inadequate to this task and encouraged further study. Nevertheless, 22 years later most coastal sage scrub conservation planning is still based on Westman's very general regional characterizations of the resource (Holland and Keil 1986), although more detailed sub-regional characterizations have been published (DeSimone and Burk 1992, Kirkpatrick and Hutchinson 1977, White and Padley 1997).

Access to coastal sage scrub stands on private lands has only gotten harder since Westman did his field work, making the task of collecting a modern regional data set increasingly problematic. For example, White and Padley (1997) were only granted permission to conduct surveys on 4 percent of the coastal sage scrub in their Riverside County study area. The VTM survey certainly does not represent a complete inventory of prehistoric California vegetation. But VTM data are still very useful because so much land has been developed since it was collected and because many of the cumulative impacts of various anthropogenic disturbance regimes have become more pronounced over time.

This report presents preliminary findings of a regional study of coastal sage scrub in southern California based on VTM plot data. I used a newly created spatial database of VTM plot data to examine general organizing principles of shrubland plant communities in southern California at a regional scale, with a focus on coastal sage scrub. Geographic patterns of species distribution, floristic composition of major species associations, and environmental correlates with species distributions in coastal sage scrub were examined in a regional context with a large, systematically allocated data set.

Preliminary research questions can be stated as follows:

- To what extent is coastal sage scrub really a floristically distinct plant community separate from contiguous chaparral plant communities?
- How strong are the relative contributions of climatic factors and disturbance history in determining the chaparral-coastal sage scrub boundary?
- What types (associations) of coastal sage scrub are evident among the VTM plots? How do these coastal sage scrub associations compare to classifications and habitat preferences reported by other authors from other data sources?
- How are these coastal sage scrub associations distributed geographically? Do coastal sage scrub associations previously described in detailed, sub-regional studies occur beyond the boundaries of those studies?
- How have regional development patterns impacted the coastal sage scrub associations?

Methods

The original researchers recorded VTM plot data on paper forms and maps that are currently archived at U. C. Berkeley. All remaining plot records collected south of the greater Los Angeles area were photocopied and entered into a Paradox database (Borland 1996). Extensive error checking and data proofing were undertaken to create a reliable database from the handwritten notes on the historic paper forms. Although the data are generally of high quality, many classes of errors were discovered, including redundant, ambiguous or undefined species codes, occasional reported occurrences of taxa in completely implausible locations (sometimes resolvable as typographic errors or misread handwriting), codes miscopied from one part of data sheets to another, mistakes in counting occurrences on data sheets, and mislabeled data sheets. Many were correctable after careful examination, but about 50 occurrence records (=0.04 percent of the total) had to be deleted because they could not be reliably resolved. Most of those were ground-layer species with low frequency. Archaic taxonomy was updated according to the new Jepson manual (Hickman 1993). Using a geographic information system (ESRI 1999), plot locations were digitized from archived VTM plot maps based on 15-minute USGS topographic maps originally published in 1898. About 1,600 plot locations were indicated on the maps, but a few were never sampled and some plot data sheets have been lost. The result was a database of 1,481 plot records and about 275 species with about 12,000 records of individual species occurrences.

VTM surveyors divided each plot into a 5 by 20 array of 100 square cells, 6.6 feet (2.0 meters) on a side. For each cell, they recorded which shrub species had the greatest absolute cover. If total plant cover was less than 50 percent they recorded the cell as bare. The number of cells dominated by each species was its percent absolute cover in the plot. They also often noted a number of additional subdominant and ground-layer species that did not appear in the cover summary, characterizing their absolute cover on an ordinal scale of 1 to 3 (“occasional, frequent, or abundant”) (Wieslander and others 1933). I converted the ground-layer scores to plausible quantitative absolute cover values based on Braun-Blanquet cover classes (1=3 percent, 2=15 percent, 3=38 percent) and combined them with cover data for dominant species. For some analyses, all quantitative data were converted to presence/absence data. All results presented in this paper are based on untransformed absolute cover values.

Plots were sorted based on their species compositions by means of several ordination and classification methods, using methods for gradient analysis developed by Whittaker (1978). To increase the robustness of conclusions, several different ordination and classification programs were used. Programs included TWINSpan (a divisive, polythetic, hierarchical classification program) (Gauch and Whittaker 1981, Hill 1979), Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), Non-metric Multidimensional Scaling (NMS) (Clarke 1993), and an agglomerative cluster algorithm (McCune and Mefford 1998). Forest and woodland plots were deleted by inspection. Chaparral plots that were extreme statistical outliers were also deleted, reducing the data set to 1,252 shrub plots with 203 species. As Westman (1983) found, deleting records of all species with fewer than five occurrences resulted in a great reduction of data (reduced the species list to 97) without affecting ordination and classification results noticeably. This preliminary analysis identified 529 plots

representing coastal sage scrub vegetation. Additional ordination and classification studies were conducted with this subset of plots.

Excellent detailed reviews of ordination methods include Whittaker (1978), Greig-Smith (1983), Clarke (1993) and McCune and Grace (2002). A brief summary of ordination and classification methods follows.

Non-metric Multidimensional Scaling (NMS, MDS, NMDS, or NMMDS) is an ordination method that is well suited to data that are non-normal or on arbitrary, discontinuous, or otherwise problematic scales. It is based on ranked distances, so it is robust with regard to the “zero truncation problem” that plagues most ordination methods for ecological data. It has been widely applied in disciplines including sociology, psychology, and, more recently, ecology. NMS is an iterative search for a ranking and placement of plots in species space in relatively few dimensions that minimizes the stress of the full multidimensional configuration. “Stress” is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original multidimensional space and distance in the reduced, relatively few-dimensional ordination space.

TWINSPAN stands for *Two Way Indicator Species Analysis* because it simultaneously classifies species and samples. The classification program was written at Cornell University for ecological data. TWINSPAN is a divisive algorithm that iteratively splits a set of plots into smaller and smaller groups by most efficient dividing of a reciprocal averaging ordination space. It iteratively sorts plots based on the indicator species value of the species and then sorts species based on indicator species value of plots. Recent improvements to code remove instability problems of earlier versions (McCune and Mefford 1998). It is good at representing a single environmental gradient but performs poorly when multiple, more or less independent gradients exist. It produces a two-way table with plots and species sorted by similarities in overall composition. It is often useful as a “first cut” analysis of a large data set, especially for identifying meaningful subgroups of similar plots for further analysis.

Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) is an eigenanalysis ordination technique for ecological data also based on reciprocal averaging (RA). Like RA and TWINSPAN, DCA ordines both species and samples simultaneously. It removes two known artifacts from RA ordination by dividing the first axis into segments and rescaling the results. RA is equivalent to an eigenanalysis of distances in a space defined by the chi-squared distance metric. Recent improvements to code remove instability problems of earlier versions (McCune and Mefford 1998).

DCA has been quite popular in ecology. Recently it has been found to be less robust than NMS in a number of circumstances. In the course of the current research, DCA tended to seek and find unimodal species distributions in data sets while NMS tended to represent the most abundant species as unimodal and produce bimodal distributions of less abundant species. DCA is generally more sensitive to outliers than NMS.

Cluster analysis classifies items into groups based on their similarities. Cluster algorithms in PC-ORD are hierarchical, agglomerative, and polythetic. *Hierarchical* means that large clusters are composed of smaller clusters. *Agglomerative* means that the analysis proceeds by joining clusters rather than dividing them (as TWINSPAN does). *Polythetic* means that many attributes of the items are used to decide the

optimum way to combine or divide clusters. Analyses presented in this report were based on a relative Sorensen's-distance matrix and a furthest-neighbor-linkage rule (McCune and Grace 2002, McCune and Mefford 1998).

Agglomerative cluster analysis was used in this study to further reduce the data set and make general observations about the composition and distribution of many sites with similar species composition. A well-defined cluster of plots serves as a meaningful and objective way to describe different types (associations) of coastal sage scrub. This level of aggregation is useful to compare groups of plots and their geographic distributions to published descriptions of coastal sage scrub species assemblages.

The most ecologically meaningful levels of hierarchical clustering can be determined by a series of Indicator Species Analyses and Monte Carlo tests for statistical significance as suggested by Dufrene and Legendre (1997). Their method combines information on the concentrations of species abundance in particular groups and faithfulness of species occurrences in groups. It produces indicator values for each species in each group. These values are tested for statistical significance using a Monte Carlo technique. If groups are too finely divided then indicator values will be low. On the other hand, if groups are too large, then internal heterogeneity reduces indicator values. Indicator values peak at some intermediate level of clustering that varies by species. An appropriate level of clustering that maximizes meaningful natural breaks between groups of plots in a data set is the goal.

In this study, a hierarchical cluster analysis was performed. Indicator Species Analysis (McCune and Mefford 1998) was performed for each cluster across many levels, and Monte Carlo tests of randomized plot data were performed for each indicator species and each cluster at each level to distinguish groups with statistically significant indicator species. P-values for all clusters across each level of the cluster analysis were tabulated, and cluster levels with the largest numbers of highly predictive indicator species were identified. Finally, graphical and geographic analyses of cluster groups were undertaken. Species and groups of plots with similar species composition were mapped to examine their geographic distribution. Similarly, cluster groups were mapped in ordination space.

Other sources of spatial data were collected, including climate data (Franklin 1998), modern land use, and land cover data for San Diego (SANDAG 2000), Orange, and western Riverside counties (data from USGS, Carlsbad CA, 2000). Point-in-polygon and grid-identity operations in Arc Info (ESRI 1999) were used to extract additional attribute data for each plot location from these data sources. Summary statistics for land use conversions of VTM plots were tabulated. Several indices of continentality (Tuhkanen 1980) were calculated from climate data. As a simple estimate of relative insolation, an index of north-ness was calculated from slope and aspect attributes (Borchert and others 1989). Correlations between environmental parameters, and patterns of species composition represented by cluster groups were assessed using Pearson and Kendall's correlation coefficients.

Results

The Berkeley archive contained plot records for 1,481 shrub plots in the NCCP region. A total of 58 plot records have been lost, most of them in Riverside County. These maps and plot records have been missing at least since 1974 (Rich Minnich,

personal communication). Gaps in the plot distribution showed the extent of agricultural and urban development in the early 1930s (*fig. 1*). These areas are delimited even more clearly for some areas on the published VTM vegetation maps. General patterns of shrubland biogeography documented by other authors could be seen. Coastal sage scrub and chaparral were quite intermixed when viewed at a regional scale, with coastal sage scrub generally occupying more coastal and lower elevation areas. In a portion of central San Diego County from La Jolla to Oceanside, chaparral came down to the sea. Otherwise it generally occurred at higher elevation. Many more VTM plot locations have been developed in San Diego County than in Orange or Riverside counties. Most of the developed plot locations contained coastal sage scrub, not chaparral. Of 529 coastal sage scrub plots in 1931, only 332 (63 percent) remained substantially undeveloped in 1995. The highest remaining numbers of undeveloped coastal sage scrub plots occurred on the Camp Pendleton Marine Base in northern San Diego County, at Crystal Cove State Park in Orange County, and on (mostly) private land in the Perris Plain of western Riverside County.

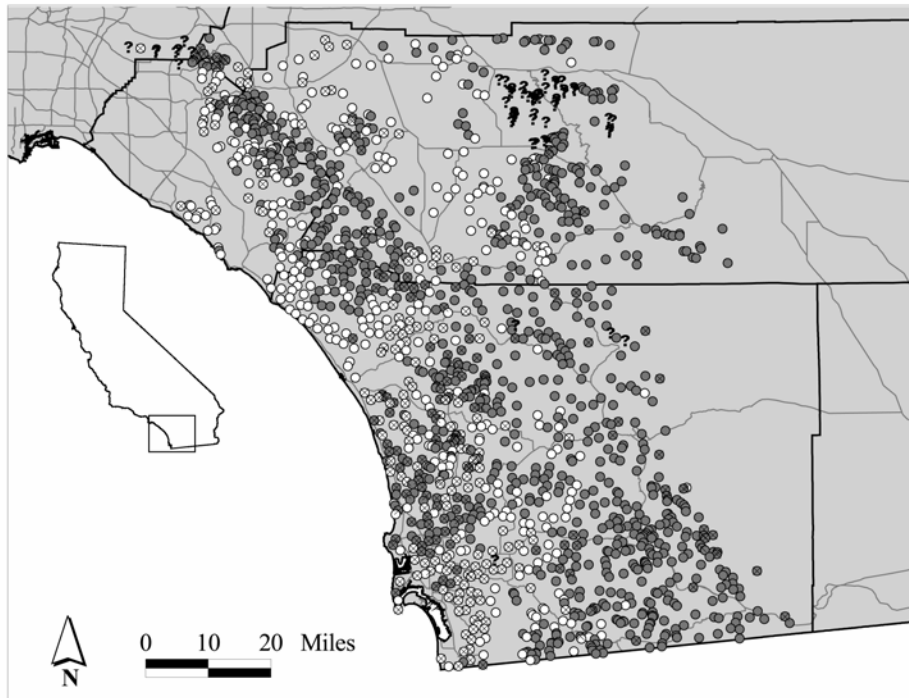


Figure 1—VTM plots in the NCCP area. ○=coastal sage scrub about 1931, ●=chaparral about 1931, ×=developed by 1995, ?=plot record missing.

An ordination and a divisive classification of plots showed convergent results (*fig. 2*). Plots displayed along the first two synthetic axes of an NMS ordination based on similarities in species composition clearly divided into two major groups. There was a high correlation between membership in these groups and membership in groups of plots determined by a first level split in TWINSpan (eigenvalue = 0.5530). Species composition showed the two groups were coastal sage scrub and chaparral vegetation types, as described in community ecology literature (Hanes 1988, Mooney 1988). Indicator species for the first TWINSpan split included *Artemisia californica* (+), *Adenostoma fasciculatum* (-), and *Quercus berberidifolia* (-). Positive preferentials (associated with coastal sage scrub) included *Eriogonum fasciculatum*, *Lotus scoparius*, *Malosma laurina*, *Poaceae* spp., and *Salvia apiana*. Negative preferentials

(associated with chaparral) included *Arctostaphylos tomentosa*, *Ceanothus crassifolius*, *Ceanothus greggii* var. *perplexans*, *Ceanothus leucodermis*, *Ceanothus tomentosus*, *Cercocarpus betuloides*, and *Rhus ovata*. Taxonomy follows Hickman (1993). When ordered by floristic composition, coastal sage scrub and chaparral appeared as distinct, separate communities intergrading only slightly.

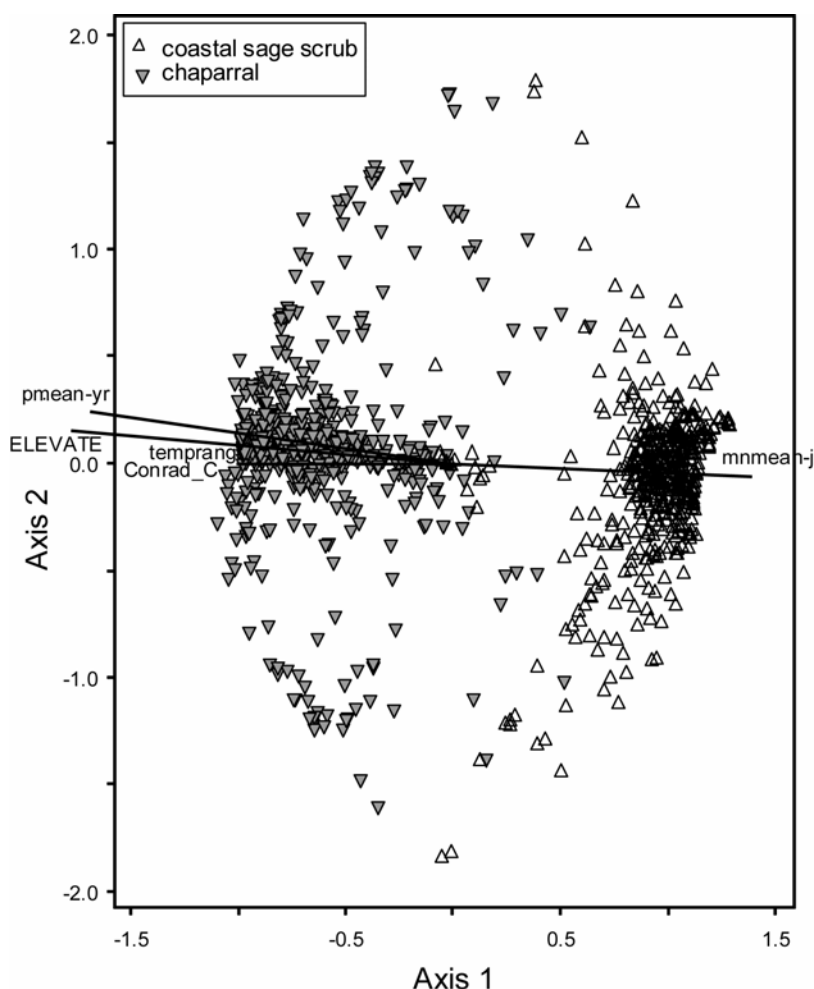


Figure 2—Coastal sage scrub and chaparral plots in NMS (non-metric multidimensional scaling) ordination space with joint plots of environmental factors. Plots ordered according to floristic composition measured as relative Sorensen's distance. Coastal sage scrub and chaparral plots distinguished by first level TWINSpan split. Joint plots show direction and relative magnitude of correlation between environmental factors and synthetic ordination axes. ELEVATE=elevation ($r^2=0.22$), pmean-yr=mean annual precipitation ($r^2=0.20$), mnmean-j=mean minimum January temperature ($r^2=0.17$), Conrad_C=Conrad's continentality index ($r^2=0.13$), temprang=mean annual temperature range ($r^2=0.12$).

Several environmental factors were significantly correlated with the environmental gradient that distinguishes chaparral from coastal sage scrub (fig. 2). Chaparral was positively correlated with (and coastal sage scrub was negatively correlated with) mean annual precipitation, elevation, and two indices of continentality: mean annual temperature range and Conrad's C. Conrad's C is the most widely used index

of continentality. It is based on annual temperature range and seeks to remove effects of latitude (Tuhkanen 1980). Conrad's C is:

$$C = (1.7 * A / \sin[\phi + 10^\circ]) - 14 \quad [1]$$

Where A=mean annual temperature range, ϕ =latitude. Chaparral was negatively correlated with (and coastal sage scrub was positively associated with) mean minimum January temperature. A continental climate has colder winters and greater evapotranspirative stress in summer; it apparently favors chaparral over coastal sage scrub.

An indirect gradient analysis of the dominant species in chaparral and coastal sage scrub was conducted to explore general patterns of community organization. Running averages of absolute cover for the five most widespread and abundant species in all shrub plots were plotted along the primary NMS ordination axis. Dominant species had generally unimodal distributions in this indirect gradient analysis, with the exception of *Salvia mellifera*, which was somewhat bimodal (fig. 3).

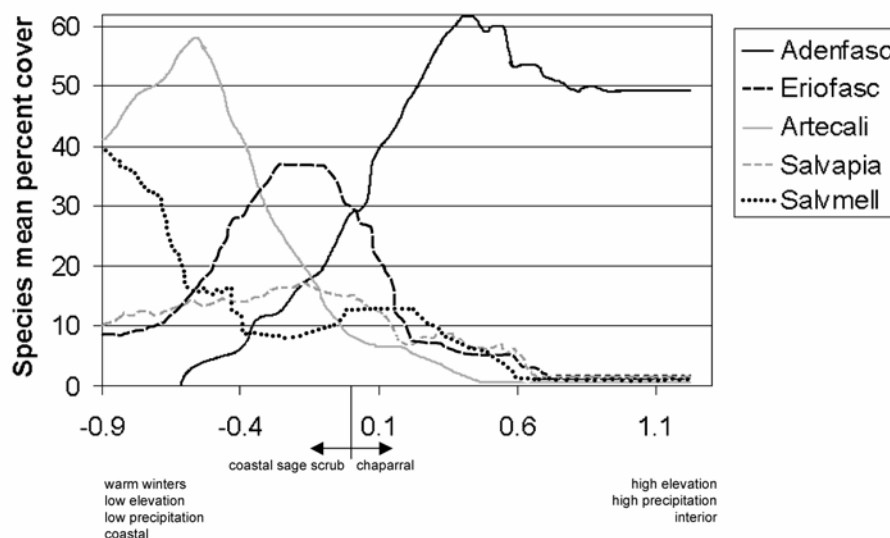


Figure 3—Mean cover values of dominant shrub species and coastal sage scrub-chaparral boundary along an NMS ordination axis correlated with several environmental gradients. Adenofasc=*Adenostoma fasciculatum*; Eriofasc=*Eriogonum fasciculatum*; Artecali=*Artemisia californica*; Salvapia=*Salvia apiana*; Salvmell=*Salvia mellifera*.

The 529 plots identified as coastal sage scrub in the initial classification (white plots in figs. 1 and 2) were examined more closely by ordination and agglomerative clustering (fig. 4). The plots are displayed along the first two synthetic axes of another NMS ordination. Distance between plots is a function of their similarity in species composition. Clusters of plots having greater within-group similarities in floristic composition than between-group similarities are restricted to more or less discrete areas of the space defined by the synthetic ordination axes. Total precipitation, which was a fairly strong predictor of distributions for chaparral and coastal sage scrub, had no significant predictive power for floristic patterns within coastal sage scrub. The relative distribution of *Artemisia californica* and *Eriogonum fasciculatum* was

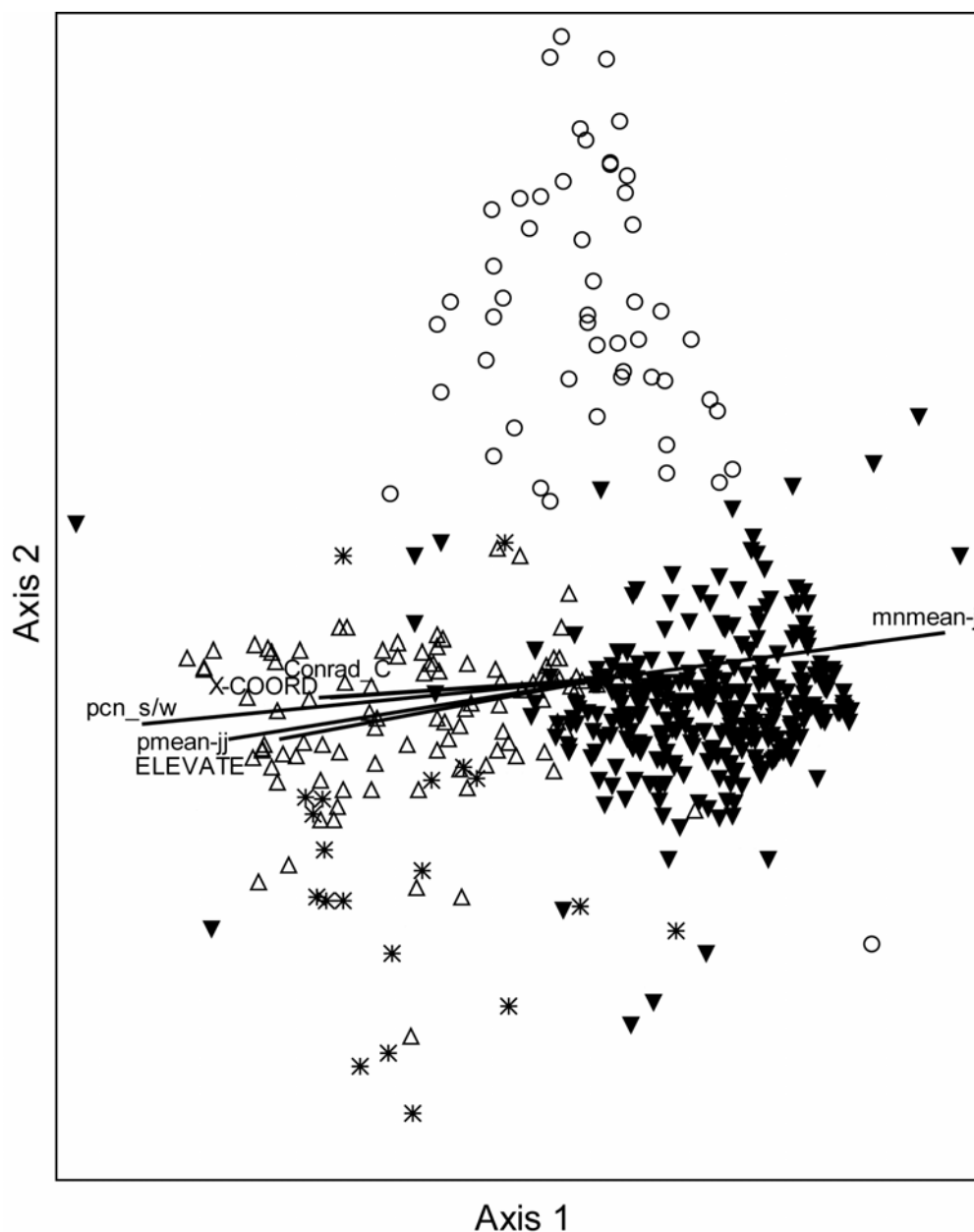


Figure 4—NMS (non-metric multidimensional scaling) ordination of 535 coastal sage scrub plots with joint plots of environmental factors. Plots ordered by floristic composition measured as relative Sorensen's distance. Axis 1 captured 41.6 percent total variance. Axis 2 captured an additional 36.1 percent of total variance (cumulative total=77.7 percent). Axes are 99.7 percent orthogonal. Joint plots show direction and relative magnitude of correlations with environmental factors.

Symbols show most frequently occurring coastal sage scrub associations, classified by agglomerative cluster algorithm using relative Sorensen's distance and furthest neighbor linkage. Δ=*Eriogonum fasciculatum*-dominant type, ▼=*Artemisia californica*-dominant type, ○=*Salvia mellifera*-dominant type, *=*Salvia apiana*-dominant type). pcn_s/w=ratio of summer precipitation to winter precipitation (Pearson correlation coefficient $r^2=0.30$); pmean-jj=mean precipitation June-Sept. ($r^2=0.25$); ELEVATE=elevation ($r^2=0.21$); mnmean-j=mean minimum January temperature ($r^2=0.22$); Conrad_C=Conrad's continentality index ($r^2=0.19$); X_COORD=easting ($r^2=0.18$).

correlated with summer precipitation, elevation, distance from the coast, mean minimum annual temperature, and the continentality index Conrad's C. The variation in mean annual summer precipitation over the range of *E. fasciculatum* was only 10-12 mm. No measured environmental factors were significantly correlated with the second ordination axis, which was determined by the relative distributions of *Salvia mellifera* and *S. apiana*.

Of all dominant species, *Artemisia californica* (the single most widespread and abundant coastal sage scrub species in this study) was geographically distributed most like Westman's (1981a) Venturan coastal sage scrub (fig. 5), with markedly coastal, low elevation preferences. A few other strictly coastal species (*Rhus integrifolia*, *Encelia californica*) shared this general distribution.

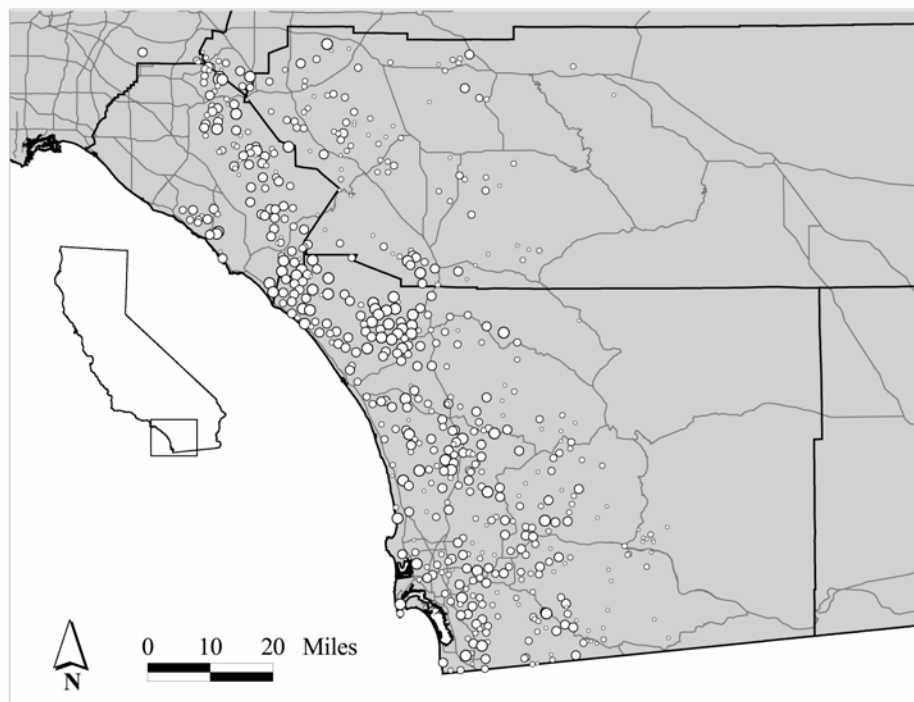


Figure 5—Regional distribution of *Artemisia californica* in VTM plots. Symbol size proportional to absolute cover.

The second most abundant species, *Eriogonum fasciculatum*, had a broad distribution that ranged from near the coast to far inland (fig. 6). It occurred from near sea level to considerably higher elevations than *Artemisia californica* could apparently tolerate.

The third most abundant species, *Salvia mellifera*, was broadly distributed but also somewhat patchy (fig. 7). It generally co-occurred with *Artemisia californica*, but each species also occurred abundantly in a few gaps in the distribution of the other. *S. mellifera* was better represented than *A. californica* in Riverside County. Its distribution was not significantly correlated with any of the environmental factors measured in this study.

Classification and ordination routines tended to form groups defined by dominance of the most common species. Their geographic distributions were similar to those of the dominant species that define them (fig. 8). The four most common

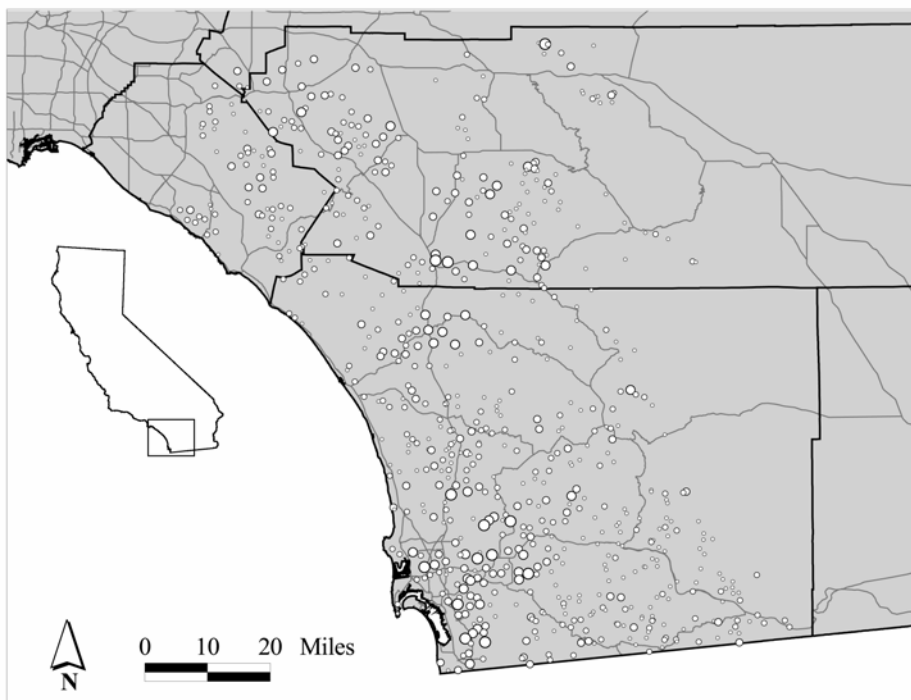


Figure 6—Regional distribution of *Eriogonum fasciculatum* in VTM plots. Symbol size proportional to absolute cover.

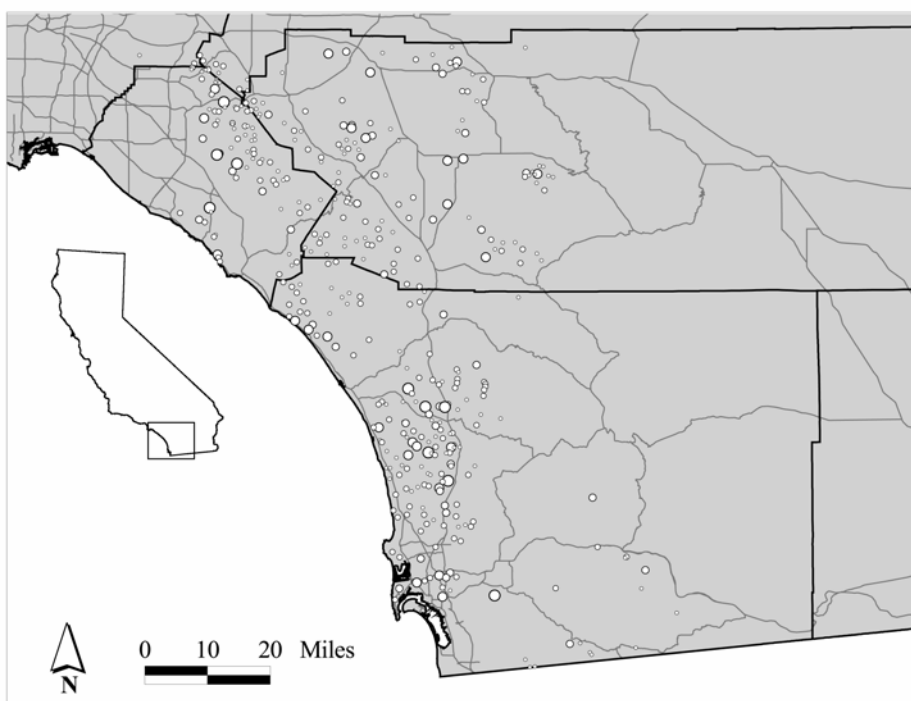


Figure 7—Regional distribution of *Salvia mellifera* in VTM plots. Symbol size proportional to absolute cover.

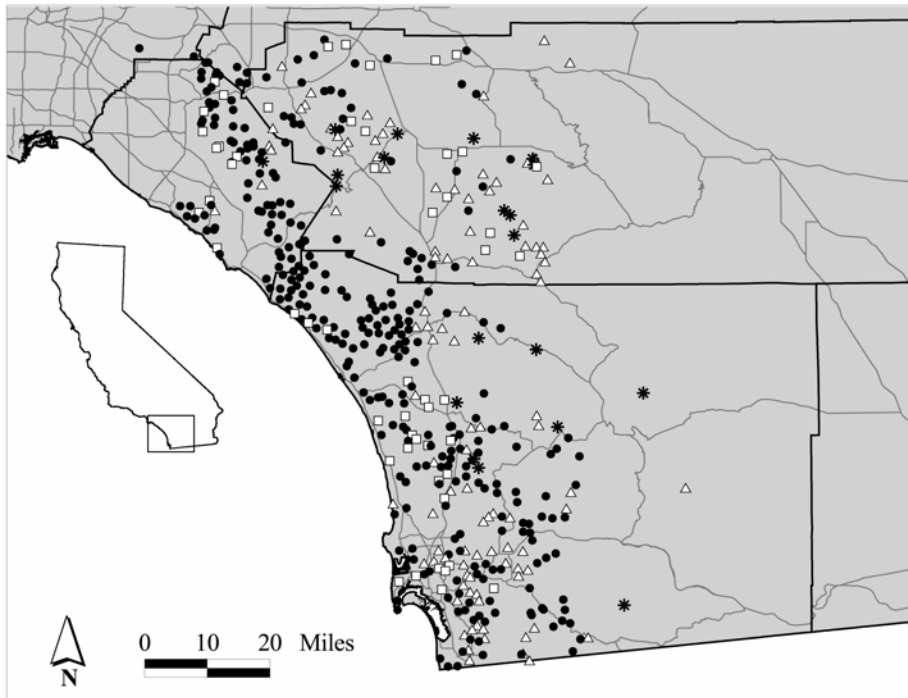


Figure 8—Regional distribution of common coastal sage scrub associations in VTM plots. •=*Artemisia californica*-dominant; Δ=*Eriogonum fasciculatum*-dominant; □=*Salvia mellifera*-dominant; *=*Salvia apiana*-dominant

cluster groups, dominated by *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia mellifera* and *Salvia apiana*, respectively, were quite a bit more intermixed in geographic space than they appeared in floristically-defined ordination space.

A few other clusters represented less common coastal sage scrub associations with more restricted geographic distributions (fig. 9). A group of plots dominated by a regionally distinctive association of *Rhus ovata*, *Salvia apiana*, and *Keckiella antirrhinoides* var. *antirrhinoides* was restricted to a small portion of western Riverside County. Another group of plots dominated by *Eriogonum fasciculatum* var. *foliolosum* was restricted to Riverside and Orange Counties. That group's distribution reflected the distribution of its dominant subspecies, which was quite different than the widespread regional representation by *Eriogonum fasciculatum*.

Another group of plots dominated by *Eriogonum fasciculatum*, *Salvia apiana*, and *Artemisia californica* with a distinct but minor element of *Adenostoma fasciculatum* was largely confined to San Diego County. VTM surveyors noted no higher incidence of recent disturbance for these plots than for other similar plots.

All of the common coastal sage scrub associations were broadly similar to associations described by one or more other published studies (table 1). Some of the less widespread groups appear to be unlike anything previously described.

Approximately 63 percent of coastal sage scrub sites sampled by VTM surveyors about 1931 were still undeveloped in 1995. Since VTM plots were fairly evenly allocated over undeveloped areas in 1931, this should be a fairly good estimate of relative amounts of coastal sage scrub lost in different parts of the NCCP

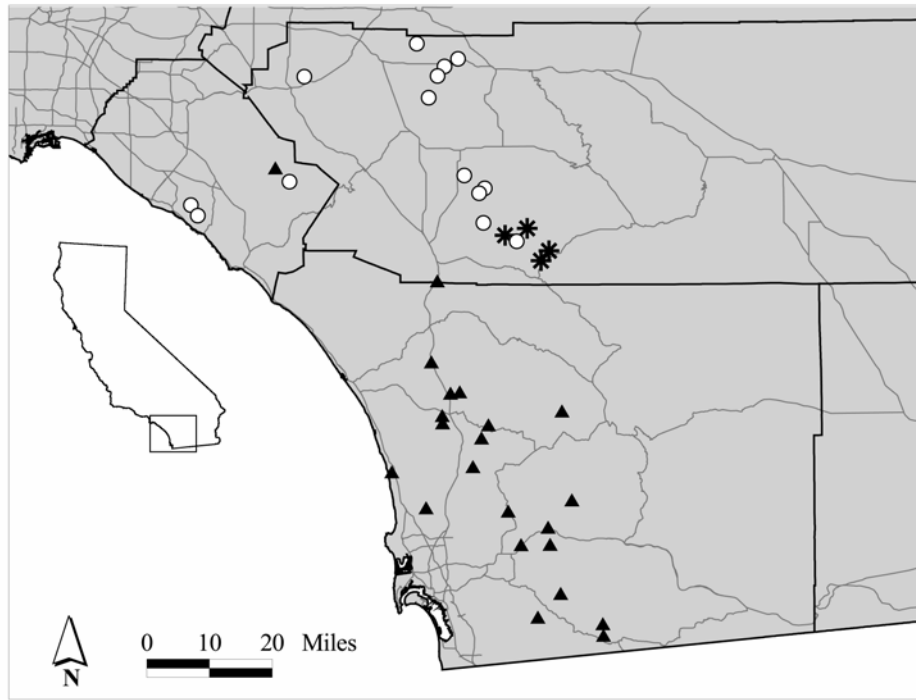


Figure 9—Regional distribution of other coastal sage scrub associations in VTM plots. ▲=*Artemisia californica*, *Eriogonum fasciculatum*, *Adenostoma fasciculatum*-dominant. ○=*Eriogonum fasciculatum* var. *foliolosum*-dominated. *=*Rhus ovata*, *Salvia apiana*, *Keckiella antirrhinoides* var. *antirrhinoides*-dominant.

Table 1—Coastal sage scrub associations (plot clusters) compared to broadly similar, floristically-defined associations of coastal sage scrub described in other published studies.

Coastal sage scrub associations (cluster groups)	Sawyer & Keeler-Wolf (1995)	White & Padley (1994)	DeSimone & Burk (1992)	Kirkpatrick & Hutchinson (1977)	Davis & others (1994)
<i>Artemisia californica</i>	1 (+3)	1	1 (+1)	1 (+1)	2
<i>Eriogonum fasciculatum</i>	1	1	-	1	1
<i>Salvia mellifera</i>	1	1	1	2	3
<i>Salvia apiana</i>	1		1		2
<i>Artemisia californica</i> , <i>Eriogonum fasciculatum</i> , <i>Adenostoma fasciculatum</i>	-	X	-	-	X
<i>Eriogonum fasciculatum</i> var. <i>foliolosum</i>	-	-	-	-	X
<i>Rhus ovata</i> , <i>S. apiana</i> , <i>Keckiella antirrhinoides</i>	-	-	-	-	-

This table shows how many floristically-defined associations of coastal sage scrub described by other published studies (in rows) are broadly similar to associations defined in the current study (in columns, named by dominant indicator species). X = series overtly excluded by site selection criteria or analysis in a published study. The terms “association” (Kirkpatrick and Hutchinson 1977), “subassociation” or “group” (DeSimone and Burk 1992), and “series” (White and Padley 1994, Sawyer and Keeler-Wolf 1995) are roughly equivalent. Davis and others (1994) defined “species assemblages” based on frequently occurring dominant species in larger (>1km²) mapping units than the other studies.

region since that time. Fractions of VTM coastal sage scrub plots developed during that time period varied by county (*table 2*).

The fraction of VTM plots that were lost to land development between 1931 and 1995 was different for different associations of coastal sage scrub (*table 3*). In several cases losses were disproportionate to a type's total representation in the plant community. This reflected regional patterns in initial distribution of the plots and regional patterns of land use conversion.

Table 2—*Fractions of VTM coastal sage scrub plots developed 1931-1995, by county.*

County	Orange	Riverside	San Diego	Total
Number of plots sampled in 1931	91	123	315	529
Number of plots undeveloped in 1995	71	91	170	332
Percent of plots remaining	78	74	54	63

Discussion

It is important to note that large amounts of coastal sage scrub were lost to agriculture (and to a lesser extent, urbanization) before the VTM plot data set was collected. VTM vegetation maps show large areas of urban and agricultural land use. Various researchers believe those developed areas were formerly occupied by native grasslands, coastal sage scrub and other shrublands, or lost native forb communities, in unknown proportions. Most undeveloped areas sampled by the VTM crews had been subjected to repeated burning, grazing, and other types of disturbance, with imprecisely known effects on vegetation. The VTM survey cannot answer many questions about what happened in the preceding decades and centuries. The survey does provide a large sample of consistent, quantitative observations of this vegetation about 1931. These data can be used to characterize vegetation patterns at that time and to assess how vegetation has changed since that time.

Table 3—*Fractions of major coastal sage scrub species associations developed, 1931-1995.*

CSS associations (cluster groups)	Number of plots about 1931	Number of plots still undeveloped in 1995	Pct plots remaining, 1995
<i>Rhus ovata</i> , <i>Salvia apiana</i> , <i>Keckiella antirrhinoides</i> var. <i>antirrhinoides</i>	4	4	100
<i>Eriogonum fasciculatum</i> var. <i>foliolosum</i> -dominated	14	11	77
<i>Salvia apiana</i> -dominated	20	14	70
<i>Artemisia californica</i> - dominated	303	193	64
<i>Artemisia californica</i> , <i>Eriogonum fasciculatum</i> , <i>Adenostoma fasciculatum</i>	22	13	59
<i>Salvia mellifera</i> -dominated	53	29	55
<i>Eriogonum fasciculatum</i> - dominated	105	53	50

The rate at which VTM coastal sage scrub plots were lost between 1931 and 1995 is plausibly consistent with the previously published overall estimates of coastal sage scrub loss (63 percent of the VTM sites remained compared to Michael Brandman Associate's estimate that 44 percent of original coastal sage scrub remained). Since 1931, much more shrubland in general (*fig. 1*) and coastal sage scrub in particular (*table 2*) has been lost in San Diego County than has been lost in Orange and Riverside Counties. This is partly because Orange and western Riverside Counties converted much more land to agriculture than San Diego County did prior to 1931. Urban development throughout the region generally occurred on flat agricultural lands first and adjacent hillsides second. In San Diego, 20th century development moved onto hillsides (where coastal sage scrub still existed) to a much greater extent than in the other two counties.

Camp Pendleton and Crystal Cove State Park contain almost all the remaining coastal shrublands in the NCCP region. Without the large areas preserved at Camp Pendleton, the loss would be even greater in San Diego County.

Ordinations and classifications are generally driven by common species. This is true in ordinations of coastal sage scrub and chaparral, since stands of these plant communities are generally dominated by just a few species. Coastal sage scrub and chaparral are floristically distinct and easily distinguishable by a variety of ordination and classification methods (*fig. 2*).

Several correlated environmental factors related to seasonal water availability make up an environmental gradient that separates coastal sage scrub and chaparral communities. Although chaparral tends to receive more annual precipitation, it also endures more extreme evapotranspirative stress in the summer. The fact that winter minimum temperatures are more strongly predictive of chaparral and coastal sage scrub distributions than summer maximum temperatures may partly be a reflection of wintertime temperature limits on efficient photosynthesis and growth for coastal sage scrub, which grows more actively during the winter months than does chaparral.

One of the longest standing discussions in plant community ecology concerns the relative merits of a community unit model of vegetation (Clements 1916) versus an individualistic (continuum) model (Gleason 1926). Over the years, a number of researchers have tested predictions of these two models against data from various sources (Hoagland and Collins 1997, Keddy 1987, McIntosh 1967, Whittaker 1975). Whittaker (1975) referred to the abundance curves of many species measured along an environmental gradient as a *coenocline*, which he used as a way to visualize plant community structure. A coenocline of dominant shrub species in southern California shrublands along the most influential environmental gradient in those communities produced a typically ambivalent result (*fig. 3*). Species responses appeared more or less individualistic, but there was also some sense of a synchronous species turnover at the chaparral-coastal sage scrub boundary. Coastal sage scrub species occurred at the low precipitation, coastal end of the environmental gradient, and chaparral (represented by *Adenostoma fasciculatum*) occurred at the high precipitation, continental climate end of the axis, as has been reported in literature (Hanes 1988, Mooney 1988). Most species exhibited a more-or-less unimodal distribution as predicted by Whittaker (1978), even when ordinated by NMS, which does not assume unimodal distributions for species.

The general observation that *Eriogonum fasciculatum* prefers a more continental climate than *Artemisia californica* is clear. The somewhat bimodal distribution of

Salvia mellifera is probably artifactual, since that species was not found to be significantly correlated with these environmental factors (see *fig. 4*). The major coastal sage scrub species persist at low cover levels well into the portion of the coenocline dominated by chaparral species (represented in *fig. 3* only by *Adenostoma fasciculatum* for clarity). *A. californica* is more restricted in distribution than the other species. The resolution of these species distribution curves was much higher than in other published accounts (see Westman 1981b, page 447), but even with hundreds of additional observations, this analysis did not produce a great amount of additional insight.

Analysis of coastal sage scrub plots suggested that summer precipitation may possibly be an important environmental factor in determining the regional distribution of *Eriogonum fasciculatum* and *Artemisia californica*, but not of *Salvia mellifera* and *S. apiana*. It seemed unlikely that the relationship would be causal, since summer rainfall anywhere in the coastal sage scrub zone is generally infrequent, unreliable, and scant (John O'Leary, personal communication). That was the strongest regional signal in this ecological data set, however (*fig. 4*). Summer rainfall patterns were invoked by Axelrod (1978) to explain the distribution and composition differences between Diegan (south of Torrey Pines State park in San Diego County) and Venturan coastal sage scrub (north of same). However the regional patterns of summer precipitation that he described (more summer precipitation south of Torrey pines in coastal San Diego County) were not evident in this data set.

The geographic distribution of *Artemisia californica* and the *A. californica*-dominated coastal sage scrub type (*fig. 8*) corresponded more or less to the distribution of Westman's (1983) Diegan association (*fig. 5*). Other dominant species including *Eriogonum fasciculatum* (*fig. 6*), *Salvia mellifera* (*fig. 7*), *S. apiana* and coastal sage scrub associations (floristically-determined groups of plots) dominated by these species (*fig. 8*) generally did not conform very well to the boundaries of regional coastal sage scrub types defined by Westman (1983) or Axelrod (1978). There were general similarities between the distributions of these coastal sage scrub associations and maps of species assemblages derived from the California GAP database (Davis and others 1994). These similarities were, to some extent, circularly referential because both studies were based at least in part on VTM data (plot data or vegetation maps derived from those data).

In general, the most abundant floristically-defined groups of plots showed less distinct patterns when viewed in geographic space (*fig. 8*) than they did when viewed in species-attribute space (*fig. 4*). It appears that the geographic distribution of coastal sage scrub species associations evident in the VTM plot data are primarily determined by environmental variation occurring at a scale considerably smaller than that of the NCCP region. Field observations by DeSimone and Burk (1992) support my own observations that stands of coastal sage scrub vary considerably in species composition at spatial scales on the order of tens to hundreds of meters. When plot data are aggregated over the NCCP region, slope and aspect are poor predictors of species distributions, even when combined as an index of "north-ness." These factors might have more predictive power if subsets of plots from smaller geographic areas were analyzed, because slope and aspect often appear to control local distributions of shrub species. Both DeSimone and Burk (1992) and the current study recognized a *Salvia mellifera*-dominated coastal sage scrub type, and neither study found any measured environmental factor that was correlated with its distribution. *Salvia mellifera*'s distribution may possibly be controlled by biological or historical factors of site disturbance or site colonization not documented in these studies.

Sample size and sample allocation methods clearly explain some differences in published accounts of regional coastal sage scrub variation. Since the VTM survey sampled about 18 times as many coastal sage scrub sites in the NCCP area as Westman (1983) did, it is no surprise that VTM plot data revealed a more complex picture of coastal sage scrub associations. The main plot groups (coastal sage scrub associations) that emerged from this study's classifications were generally determined by the dozen or so most frequent and dominant species. The main associations (cluster groups) appear to be dominated in turn by each of the most dominant species. Thus it appears that the methods of the California GAP analysis (describing vegetation cover by noting triplets of dominant species) may be a reasonably good way to make general characterizations of variation in coastal sage scrub associations (Davis and others 1994).

Some of the compositionally determined groups of plots found in this study resemble species associations described by Kirkpatrick and Hutchinson (1977), DeSimone and Burk (1992), and other more intensive studies of smaller areas (table 1). The amount of variation found when studying coastal sage scrub is partially a function of sampling intensity, either in a regional study like the VTM survey, in a mid-scale study (Kirkpatrick and Hutchinson 1977, White and Padley 1997), or in an intensive local survey (DeSimone and Burk 1992). Axelrod's (1977) and Westman's (1983) generalized regional species associations begin to break down as sample size of a study increases, especially when sampling strategy aims to capture the full range of compositional variation (as in the VTM Survey) rather than sampling only sites typical of the most abundant types.

Previous studies (Kirkpatrick and Hutchinson 1977, 1980; Westman 1983) found that some understory species showed greater habitat specificity than the dominant shrub species did. There is no evidence of this in the VTM plot data. But since VTM crews took only cursory, and sometimes incomplete, notes on understory species, these findings should not be taken as definitive on this count.

In summary, this regional scale study has largely substantiated findings of previous local studies of coastal sage scrub. Coastal sage scrub associations described in local studies are here shown to occur more broadly than the areas within which they were originally described. Generalized maps of the regional distributions of coastal sage scrub associations were produced. An intermediate coastal sage scrub-chaparral type with *Adenostoma fasciculatum* was found that did not appear to be dependent upon recent site disturbances. Several occurrences of a narrowly distributed coastal sage scrub type dominated by *Rhus ovata*, *Salvia apiana*, and *Keckiella antirrhinoides* var. *antirrhinoides* were found on private land in western Riverside County. A new coastal sage scrub type dominated by *Eriogonum fasciculatum* var. *foliolosum* is described that was not described by previous authors, although it appears to occur in areas where they would have had opportunities to detect it. This may possibly reflect variable levels of attention to taxonomic details in previous surveys. It also highlights the importance of collecting samples for a large number of sites when describing floristic variation in a diverse and patchy plant community.

Coastal sage scrub characteristically is dominated by only a few species. The strong control of community organization by the few most dominant species is one of the most striking attributes of the community. Despite the widespread impression that coastal sage scrub is a highly diverse community, most of the species occur infrequently and in rather low abundance.

The biggest regional trend observable in the dominant species is a transition from *Eriogonum fasciculatum* dominance at interior sites to *Artemisia californica* near the coast. Of the environmental factors measured in this study, summer precipitation, ratio of summer to winter precipitation, and minimum winter temperature are most important in predicting the relative differences in abundance of *E. fasciculatum* and *A. californica*. *Salvia apiana* prefers interior, higher elevation sites with high annual precipitation and an extremely continental climate. *Salvia mellifera*'s distribution is poorly predicted by any environmental factors measured in this study.

Different associations of coastal sage scrub were lost in varying amounts. Coastal sage scrub associations occurring frequently in coastal San Diego County and at low elevations suffered the highest rates of conversion, while those found in Orange and Riverside Counties, or at high elevations throughout the region, remained more intact. Associations of coastal sage scrub that have experienced high rates of loss (*Eriogonum fasciculatum* and *Salvia mellifera*-dominated associations, table 3) ought to be considered high priorities for inclusion in the NCCP preserve system. Regionally distinct and geographically restricted associations (shown in fig. 9) may warrant additional study as candidates for inclusion in a regional conservation plan. It would be useful to compare the proportions of coastal sage scrub associations currently included in preserves to these statistics to see how representative the current preserve system is of the diversity that existed in 1931 and the remaining diversity existing today.

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Air Pollution and Vegetation Change in Southern California Coastal Sage Scrub: A Comparison with Chaparral and Coniferous Forest¹

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Abstract

The coastal sage scrub (CSS) vegetation of southern California is rapidly converting to annual grasslands, perhaps in part because of air pollution. By contrast, chaparral and coniferous forest are subject to equally high levels of air pollution but are relatively stable. A comparative analysis of ozone and nitrogen deposition on plants of CSS, exotic annual grassland, chaparral, and coniferous forest shows these vegetation types have different susceptibilities to each pollutant. Historically high concentrations of ozone in the local mountains weakened pines, contributing to tree mortality. Native shrub seedlings had decreased growth in chambers with current-day levels of 150 ppb ozone. Under natural field conditions the shrubs may escape ozone injury by being physiologically active early in the season when ozone concentrations are below phytotoxic levels. Summer-active pines are more susceptible to ozone than summer-deciduous CSS shrubs and senescent annual grasses. Nitrogen deposition has different impacts from ozone because N accumulates on leaf and soil surfaces during the summer. Conifers are more susceptible to leaf-deposited nitric acid because they are physiologically active in summer, while chaparral may be less so because of thick cuticles and reduced summertime activity. Deciduous CSS and senescent grasses are less susceptible to direct leaf damage. However, N becomes available for root uptake after the first fall rains. Soil accumulations up to 87 µg/g extractable N have been measured in surface soil of CSS shrubland, levels that have caused mortality in the greenhouse. Grasses may escape the deleterious effects of high soil N levels because of their annual habit. Coniferous forest may have a higher threshold for N damage because of high stand biomass, high N immobilization in soil organic matter, and watershed N runoff. The resistance of chaparral to high N is less well understood, but may be due to higher biomass and slower growth rates than CSS and also high leachate losses of N.

Key words: chaparral, coastal sage scrub, coniferous forest, exotic annual grassland, nitrogen deposition, ozone

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Introduction

We are currently witnessing a rapid vegetation type-conversion of the coastal sage scrub (CSS) of southern California to exotic annual grassland, a change that has been occurring over the past three decades (Allen and others 1998, Minnich and Dezzani 1998). Local botanists report that mountainsides, such as the Box Springs Mountains and Mount Rubidoux, that were covered with CSS only 20-25 years ago are now dominated by less diverse stands of Mediterranean annual grasses and forbs. In other areas where shrubs still occur they have exotic-dominated understories, and the native herbaceous species that used to occur have largely been replaced. This directional change in vegetation composition has been attributed to such factors as urbanization, fragmentation and corridors that increased weed movement (Zink and others 1995), and historic domestic livestock grazing that removed native species and facilitated weed seed dispersal (Burcham 1957). Frequent fire is creating a positive feedback of increased dominance of highly flammable annual grasses, compared to CSS shrubs that burned on a 25-30 year fire cycle (Minnich and Dezzani 1998). Air pollution, which has less often been considered a factor in vegetation change in CSS, is the focus of this review. Understanding the impact of air pollution for conservation of CSS is critical because it impinges upon vegetation even in those reserves that have been protected from other impacts. Air pollution is greatest in areas dominated by Riversidean sage scrub (Westman 1981), so this CSS association will be emphasized.

As part of this discussion, we compare the type-conversion of CSS to annual grassland with the comparatively stable vegetation in two other major vegetation types of southern California, chaparral and mixed coniferous forest. CSS harbors some 200 sensitive species and is the least widespread of these three vegetation types (Sawyer and Keeler-Wolfe 1995, Skinner and Pavlik 1994). It is the most impacted not only because of air pollution but also because of its location in the most favorable low-elevation private lands planned for development. By contrast, much chaparral and coniferous forest is protected in public lands. However, all three vegetation types are subject to air pollution, both ozone and nitrogen deposition that originate from automobile emissions. Up to 45 kg N/ha/yr are deposited in San Bernardino mixed coniferous forests (Fenn and others 1998) and 30 kg/ha/yr in chaparral in the San Dimas Experimental Forest (Bytnerowicz and others 1987, Riggan and others 1985). All three vegetation types have been impacted by ozone as well, with historical monthly averages as high as 350 ppb (parts per billion) in 1975 (*fig. 1*).

However, ozone levels have declined with increasing regulation and pollution control; summertime peak concentrations above 150 ppb occur infrequently. In this analysis we hypothesize that ozone and N deposition have affected vegetation of southern California historically and currently, but CSS, exotic annual grassland, chaparral, and coniferous forest have different sensitivities to the two forms of air pollutants.

To help elucidate the impacts of N on CSS, we present the preliminary results of an N fertilization experiment in CSS vegetation. Anthropogenically deposited nitrate, the dominant form in Riversidean CSS (Padgett and others 1999), is formed from nitrogen oxides, which co-occur with ozone. The concentrations of ozone and nitrogen oxides increase simultaneously along rural to urban gradients of air pollution. To separate the confounding effects of ozone and N, a fertilization experiment was done in a rural area with relatively clean air, at Lake Skinner in the Western Riverside County Multispecies Reserve. The objective of this experiment was to evaluate the

long term effects of N on CSS plant species composition in a controlled field setting, and we present results from the first 8 years of fertilization.

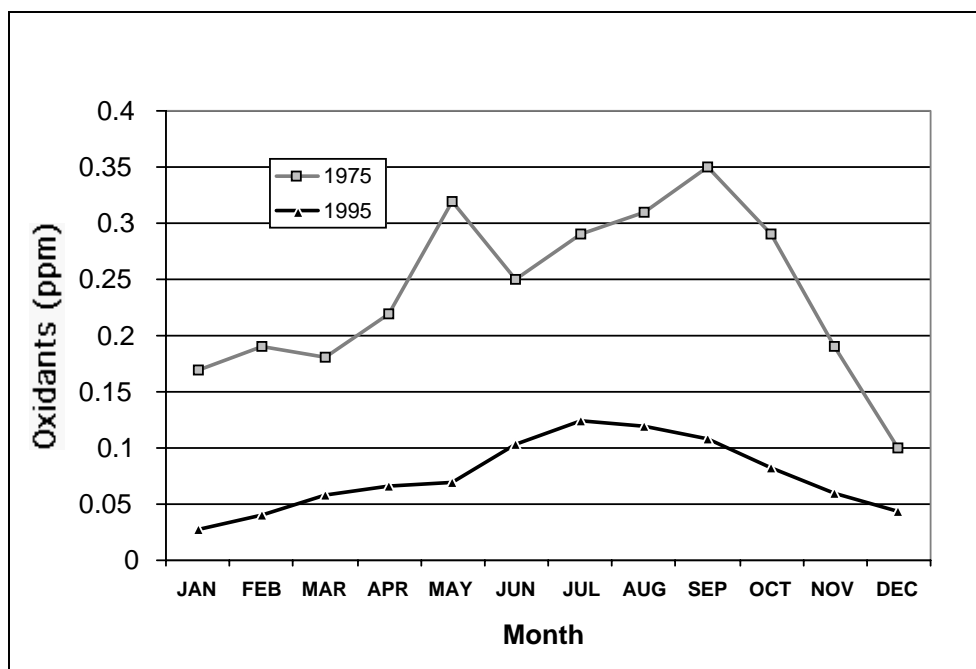


Figure 1—Mean monthly high concentrations of ozone in 1975 and 1995 in Riverside (daily hourly peak values averaged over the month). Different analytical methods were used in 1975 that detected total oxidants, but are corrected to give approximations of ozone (AQMD).

Comparative Air Pollution Effects in CSS, Chaparral, and Coniferous Forest

Ozone

Pinus ponderosa and *Pinus jeffreyi* develop visible ozone damage at daily average levels of 50-60 ppb (Miller and others 1997). The ozone sensitivity of pines was known early from the studies of Miller and others (1963) when levels of ozone were extremely high in the Los Angeles Basin and surrounding mountains. The high concentrations of past decades (*fig. 1*) contributed to conifer mortality in the mountains, in part coupled with drought, bark beetle and other stressors (Miller and others 1997). The dead trees from the 1960s and 1970s were often harvested, eliminating the evidence of ozone-induced mortality (Arbaugh and others 1999, Miller 1992). At current reduced levels of ozone, tree mortality does not seem to be a short-term response (Arbaugh and others 1999), but ozone is nevertheless affecting the physiology of trees in the field (Grulke and others 1998, Takemoto and others 2000, Temple and Miller 1994). For instance, at Camp Paivika in the San Bernardino Mountains, ponderosa pine retains 1-2 years of needle growth, rather than the typical 5 years (Grulke and Balduman 1999, Miller and others 1997). The ground at this site is littered with a deep cover of undecomposed needle litter.

The few available studies of ozone effects on native CSS and chaparral shrubs indicate that visible injury occurs at levels of ozone 2 to 10 times higher than for pines. For instance, seedlings of *Adenostoma fasciculatum*, *Ceanothus leucodermis*,

Arctostaphylos glauca, and *Quercus dumosa* experienced visible damage at the relatively high levels of 100 to 500 ppb ozone (Stolte 1982). Well-watered seedlings of *Salvia mellifera* and *Eriogonum cinereum*, common CSS shrubs, experienced leaf drop and reduced flowering after fumigation in the greenhouse with 100-200 ppb ozone (Westman 1990). One interesting observation that Westman (1990) reported was that the exotic grass *Bromus madritensis* ssp. *rubens* had an ecotype less sensitive to ozone in areas of the Los Angeles basin with high air pollution in the early 1980s.

We have observed mortality of CSS shrubs in the field, especially in urban areas (Allen and others 1998, 2000), but the cause of death is not clear and has not been quantified across the landscape. CSS shrubs are summer-deciduous and are physiologically active mainly in winter and spring (fig. 2), when mean daily high ozone levels are below 60 ppb (fig. 1). Thus they may avoid extensive ozone injury by dropping leaves before high ozone exposures occur. Westman (1990) observed that CSS shrubs experienced considerable ozone damage in the Santa Monica Mountains, but his work was done in the mid 1980s when springtime, growing season ozone levels were much higher than today. Maximum hourly summer high ozone levels were 180-390 ppb ozone in the Santa Monica Mountains in 1986 (Westman 1990). Nevertheless, we should not discount the long-term, low level effects of current springtime mean daily high exposures of 50-60 ppb, although short-term chamber studies have shown no acute effects at these levels (Preston 1986).

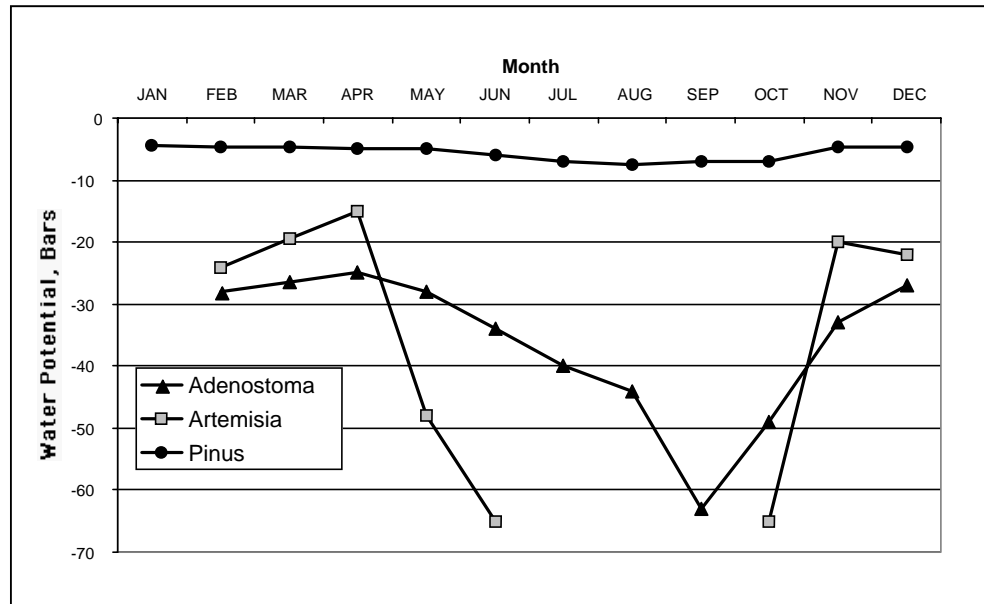


Figure 2—Xylem water potentials of three dominant species of coniferous forest (*Pinus ponderosa*), chaparral (*Adenostoma fasciculatum*) and CSS (*Artemisia californica*). Soil moisture is available during the summer in the coniferous forest where deep-rooted trees tap fractured rocks. *Artemisia* and other species of CSS are partially or wholly deciduous in summer, while *Adenostoma* and other chaparral shrubs have small sclerophyllous leaves that close their stomates in response to dry soil. Data from Poole and Miller (1975), Coyne and Bingham (1982).

Chaparral may also be less sensitive to present-day levels of ozone than ponderosa pine and Jeffrey pine. The sclerophyllous leaves of the chaparral dominant *Adenostoma fasciculatum* close their stomates in response to summer drought (Hanes 1965, Poole and Miller 1975) and so are also unlikely to absorb a great deal of ambient ozone in summer at present day levels. By contrast, pines have deep roots that seek water in rock fractures (Hubbert and others 2001a) and may continue to photosynthesize and absorb ozone all summer long (Coyne and Bingham 1982, Hubbert and others 2001b). Photosynthesis is lower in summer than spring resulting in lower rates of ozone uptake (Temple 1996), but considerable amounts of ozone may still be absorbed under high summertime ambient concentrations. The phenological differences among these three vegetation types may explain why pine is so sensitive to the high summertime levels of ozone. In 1975 even the springtime ozone levels were as high as 150 ppb (*fig. 1*). Had regulations not been enforced to reduce ozone to present day levels, coniferous tree mortality would have continued. The ozone damage symptoms that Westman (1990) observed in CSS shrubs in the mid-1980s would be more widespread, with unknown consequences on mortality. Further reductions in ozone are needed to improve the health of pine forests in locations that currently receive high exposures such as the western San Bernardino Mountains.

Nitrogen

Most of the N deposition in southern California occurs as dryfall in the form of $\text{HNO}_3/\text{NO}_3^-$ originating from automobile exhaust, and about 10-20 percent arrives as $\text{NH}_3/\text{NH}_4^+$ from agricultural origins (Fenn and others 1998, Padgett and others 1999) or more depending on proximity to local dairy farms (Fenn and others 2000). The proportion of agricultural input is expected to decline as agriculture moves from the south coast and Inland Empire counties to the Central Valley and the deserts. While neither form of N input is desirable, $\text{NH}_3/\text{NH}_4^+$ acidifies the soil more than $\text{HNO}_3/\text{NO}_3^-$, as documented in the Netherlands where up to $90 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of $\text{NH}_3/\text{NH}_4^+$ are deposited annually (Bobbink and Willems 1987). CSS soils accumulate up to $87 \text{ }\mu\text{g/g}$ of extractable N during summer near Riverside. These soils are not more acid than soils in reserves that have less air pollution, such as Lake Skinner with a maximum of about $20 \text{ }\mu\text{g/g}$ extractable soil N in the dry season (Padgett and others 1999). Nitrate has been increasing in soils downwind of urban areas over the past 40 years, with different effects on native and invasive exotic vegetation, as described below.

While historic air concentration data for $\text{HNO}_3/\text{NO}_3^-$ are not available as for ozone, NO_x emissions have been calculated since 1938 (*fig. 3*). These emissions reached a high of nearly 3,000 T daily (dy^{-1}) in 1972 in the Los Angeles Basin and declined to present day levels of 1,300 T dy^{-1} , except for a rise in 1999 that may be related to La Niña stagnant air conditions. NO_x is converted to NO_3^- in the atmosphere, more so under hot and sunny summer conditions. Most of the N deposition occurs as dryfall during the summer (Padgett and others 1999), although areas with foggy seasons, as occur in some pine forests in the San Bernardino Mountains, may have high N deposition at that time of year (Fenn and others 2000). Summer-deposited nitrate accumulates on soil and leaf surfaces and becomes available for plant uptake during the following winter rainy season when it is leached into the soil. Because HNO_3 is sufficiently acidic to cause leaf lesions at high concentrations, dryfall of HNO_3 actually has two separate effects, one to fertilize the

soil and a second to damage the leaf. Some direct uptake of leaf-deposited N occurs also. These different effects of N are considered separately.

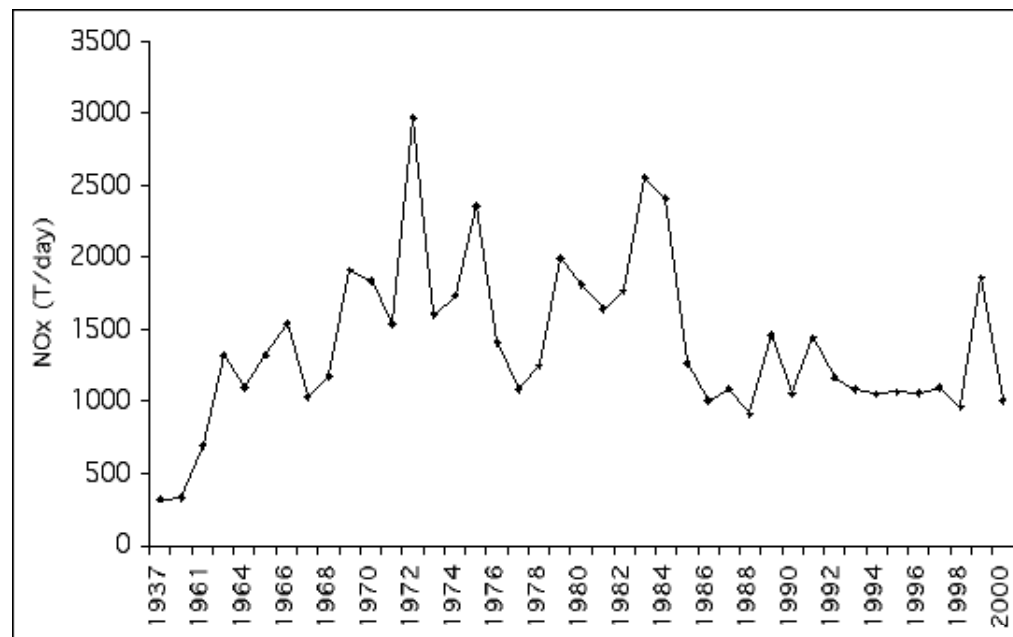


Figure 3—Emissions of NO_x in the South Coast Air Basin, 1937-2000 (Alexis and others 2000).

Epicuticular leaf lesions, visible using the electron microscope, may be induced by deposition of atmospheric HNO₃ in California black oak and ponderosa pine (Bytnerowicz and others 1998, 1999). Lesions may be accompanied by structural changes of epicuticular waxes around the stomates. HNO₃ concentrations of 50 ppb for 12 hours were sufficient to cause damage to pine, but oak damage was observed at the higher dosage of 200 ppb. Cuticular damage was observed at ambient levels of 30 ppb HNO₃ in pine and oak under longer exposures (Parry 2001), although long-term impacts on plant growth still need to be evaluated. The latter study showed the importance of transcuticular uptake of HNO₃, indicating that even physiologically inactive plants with closed stomates may be subject to damage from HNO₃ deposition. CSS shrubs drop most of their leaves in summer and may be largely unaffected by leaf-deposited HNO₃/NO₃⁻. Chaparral shrubs may be protected from extensive nitric acid damage because most of these species have sclerophyllous leaves with thick cuticles, but this is a hypothesis to be tested.

While HNO₃ may cause damage to the leaf surface, it also acts as a fertilizer. As much as one-half of the leaf-deposited N is taken up directly by the stomates into the mesophyll (Bytnerowicz and others 1999). The N that remains on leaf and other plant surfaces may enter the soil via throughfall and stem flow and become available for uptake by roots. In vegetation with a low leaf area, such as Riversidean CSS, some of the N will deposit directly on the soil, also increasing the N available to plants. We have done a series of N fertilization experiments to determine whether exotic grasses and forbs have a greater growth response to soil NO₃⁻ than native CSS plants. In greenhouse and field studies, ¹⁵NO₃⁻ was taken up at greater rates by individual *Bromus madritensis* than *Artemisia californica* (Yoshida 1999, Yoshida and Allen

2001). Three exotic species (*Bromus madritensis*, *Avena fatua*, *Hirschfeldia incana*) had luxury consumption levels of N in their tissues and increased biomass as well (Padgett and Allen 1999). Three native shrub species (*Artemisia californica*, *Eriogonum fasciculatum*, *Encelia farinosa*) had continued growth response with increased soil N up to 80 µg/g, but without luxury uptake, that is, with constant levels of tissue N. These experiments were based on comparisons of individual shrubs with individual weeds, but in the field the weeds are prolific seeders and individual shrub seeds or seedlings are overwhelmed by competition from many individual weedy plants (Eliason and Allen 1997). Additional long-term experiments showed that *Artemisia* and *Encelia* suffer mortality if soil extractable N is maintained at 30-50 µg/g for 6 or more months (Allen and others 1998; Padgett, unpublished data). These concentrations probably only occur in surface soils during the dry season in the field, so we do not know whether shrubs may be dying from high levels of N in N-polluted sites in the field. However, exposure to high levels of fertilizer may shorten the lifespan of native plants, as has been shown in botanic gardens (Keator 1994). The annual grasses escape long-term nutrient stress by having a short lifespan with high seed production.

Ongoing N fertilizer studies in the San Bernardino Mountains show that ponderosa pine is responding to N additions of 50 kg/ha with increased diameter growth even in sites that currently receive high N deposition of 45 kg/ha/yr (Fenn and Poth 2001). Levels of excess N are so high that NO₃⁻ in streamwater is the highest in North America from wildland watersheds (Fenn and Poth 1999). Even so, the available soil N is apparently still limiting during the spring and summer when plants are physiologically active. N fertilization of chaparral caused a small increase in branch length of *Adenostoma fasciculatum* and *Ceanothus greggii*, indicating N deficiency (McMaster and others 1982). This research was performed at the Sky Oaks Field Station, east of Mount Palomar, in an area that is relatively free of air pollution even today. Plants of chaparral have lower CO₂ uptake and lower growth rates than CSS shrubs (Hanes 1988, Mooney 1988) and would not be expected to respond to nutrient additions with rapid growth. In contrast, fertilized CSS shrubs increased their growth and took up N at equivalent or only slightly lower rates than annual weeds, as discussed above (Padgett and Allen 1999, Yoshida and Allen 2001). The loss of shrub cover in CSS is surprising considering the shrubs respond so well to N, so we initiated a field N fertilization experiment to study the interactions of exotic annuals with native shrubs.

Nitrogen Fertilization Experiment in CSS

The effects of N deposition on vegetation can be determined by examining the cumulative effects of long-term changes along an N deposition gradient and also by conducting N fertilizer experiments in an area that receives low N deposition. Changes in the N gradient along the Riverside-Perris Plain (described in Padgett and others 1999) are confounded by multidimensional changes as for any natural gradient. The covariance of ozone with nitrogen oxides is the primary concern, but local differences in soil type and fire history also occur, even though sites have been chosen to be as similar as possible. We hypothesized that N deposition or fertilization induces an increase in annual grasses and weeds and a decrease in shrub cover. The opportunity to begin these studies arose after the November 1993 fires that burned about 4000 ha of the Western Riverside Multispecies Reserve. We initiated N fertilizer plots on the north shore of Lake Skinner in the Reserve, where the edge of

the fire had burned, and included burned and unburned sites. The unburned CSS vegetation showed very little measurable growth response to N fertilizer, so data from these plots will not be shown here, but the burned site had several notable responses to N fertilization.

Fertilization began in winter/spring 1994 with the application of NH_4NO_3 twice each growing season at 30 kg N ha^{-1} for a total of $60 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This rate was chosen to double the highest known deposition in shrublands at the San Dimas Experimental Forest in the San Gabriel Mountains of $30 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Riggan and others 1985). The fertilizer was applied to 10 plots of 5x5-m, which were interspersed in a block design with 10 unfertilized controls. During the first several years, when the plots were dominated by herbaceous vegetation, percent cover data were collected in small 0.25x0.5-m quadrats. Cover was estimated to the nearest 1 percent by species within a gridded quadrat frame. When shrubs began to get larger, their percent cover was measured using 20 m of line transects within each 5x5-m plot, and individual shrub species were counted in the plots to estimate their density. Forb data were collected in April each year when the forbs were at maximum cover, and shrub data were collected in June or July when they had achieved their maximum cover for the year. To calculate grass biomass, a double-sampling technique was used where grasses in additional 0.25x0.5-m quadrats were clipped following percent cover estimates. A regression equation was used to calculate the biomass of the unclipped plots.

Exotic grass cover was significantly higher in the fertilized than the unfertilized plots during most years between 1994 and 2001 by 10 to 18 percent, becoming similar in the dry spring of 1999 when cover of all species declined greatly (*fig. 4*). The species composition of exotic grasses varied somewhat each year, but included *Bromus madritensis*, *B. diandrus*, *B. hordeaceus*, *Avena fatua*, *Vulpia myuros*, and *Schismus barbatus*. For exotic grasses we also harvested biomass, which was considerably higher in fertilized than unfertilized plots during wet years (*fig. 5*). The biomass data were a more sensitive indicator of grass response because percent cover did not detect productivity changes that are related to height.

Exotic forb cover was not significantly different in fertilized and unfertilized plots in any year (*fig. 4*). The most abundant exotic forbs were *Erodium cicutarium* and *Hypochaeris glabra*. The native forbs responded to N with increased cover during the first year after the fire, but this trend reversed by 1998 ($P = 0.06$) when they had decreased cover with N. The species of native forbs changed considerably over time, starting with about 26 species of native forbs immediately after the fire and 12 native species by 2001. These are the typical fire-following annuals as reported in other local studies (Carrington and Keeley 1999). There was low cover of both native and exotic forbs during the dry springs of 1996 and 1999. The shrubs followed the opposite pattern from the exotic grasses, having significantly lower cover following fertilization in 1996 and 1997, although no longer significantly lower after 1998. Shrub cover also declined during the dry spring of 1999 and did not recover. Shrub cover was very low during the first two years following fire and was not estimated until the third growing season, 1996 (see *fig. 4* below and on the following page).

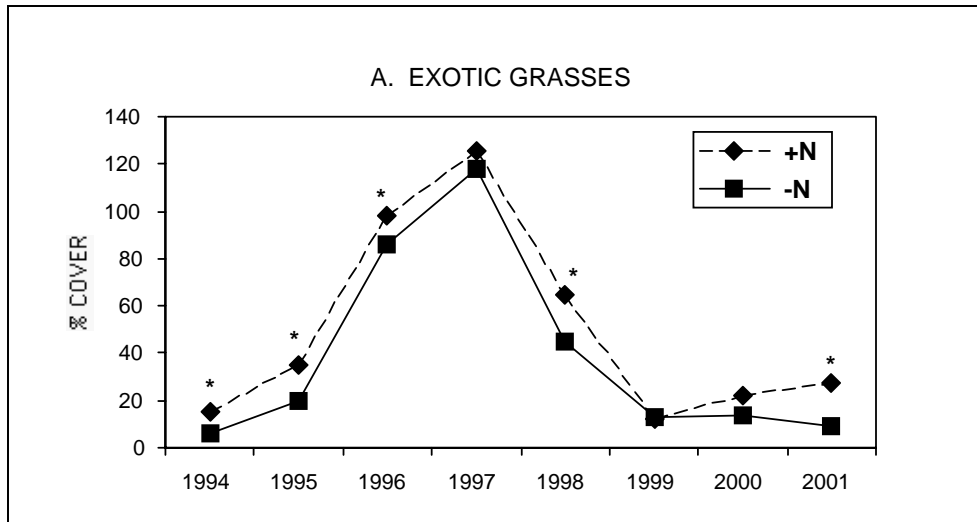


Figure 4—Percent cover of vegetation in plots with and without 60 kg/ha/yr N fertilizer following the 1993 fire at Lake Skinner. Vegetation was analyzed by life form as A. exotic grasses, B. exotic forbs, C. native forbs, and D. native shrubs. *=significantly different at $P=0.05$.

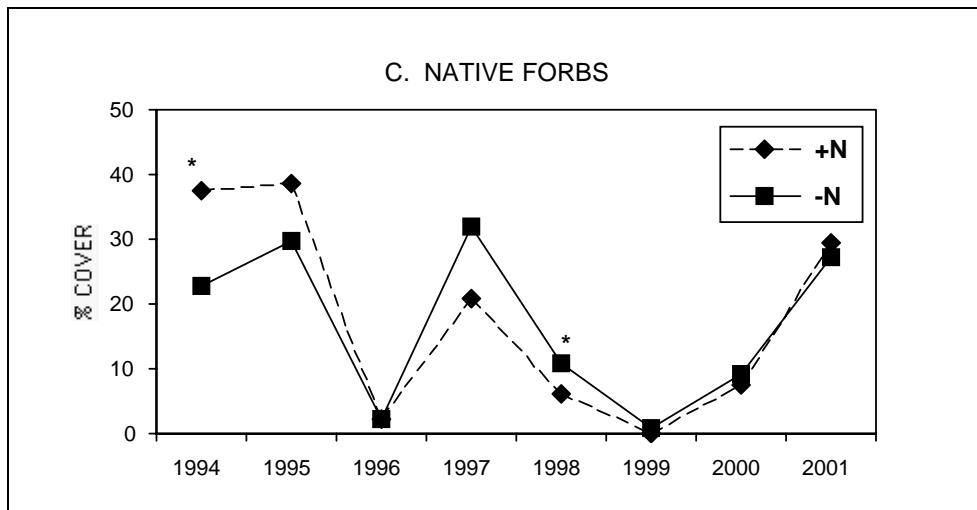
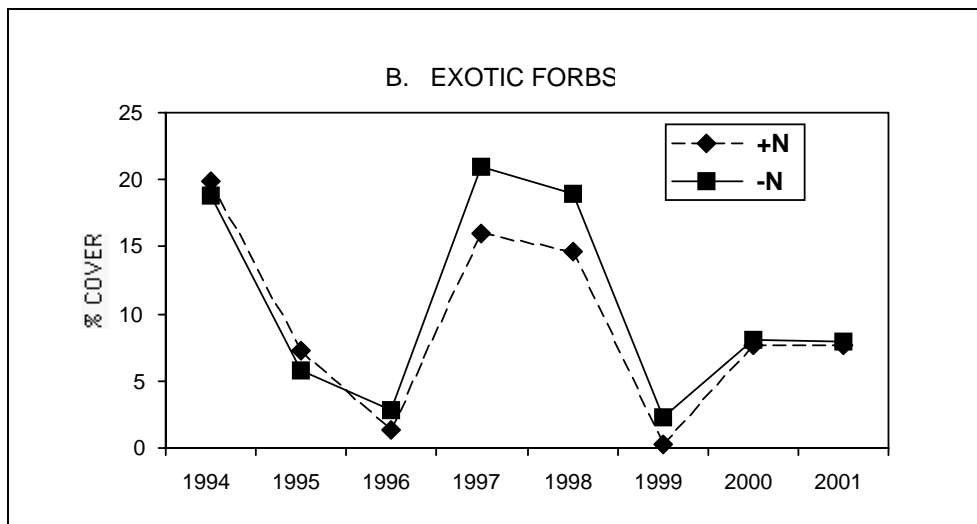


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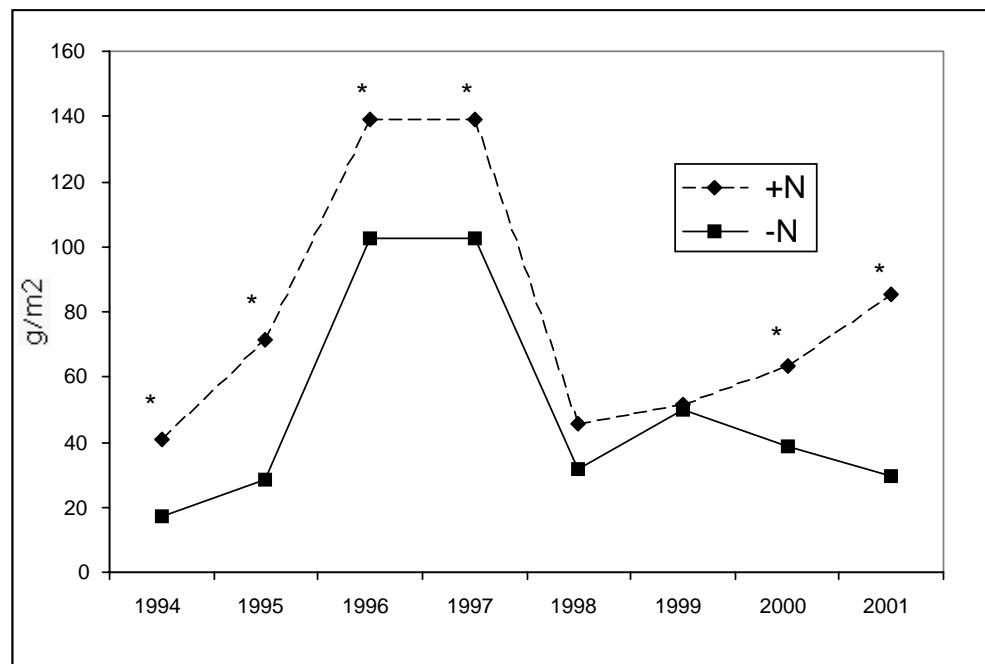
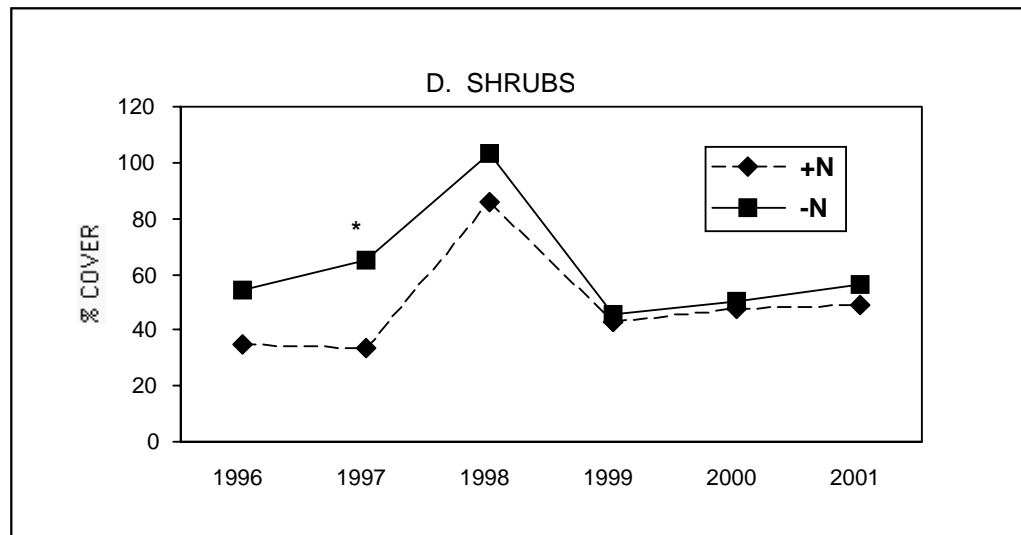


Figure 5—Biomass (g/m^2) of exotic annual grasses calculated from double-sampling a subsample of clipped plots and using a correlation applied to permanent sample plots. *=significantly different at $P=0.05$.

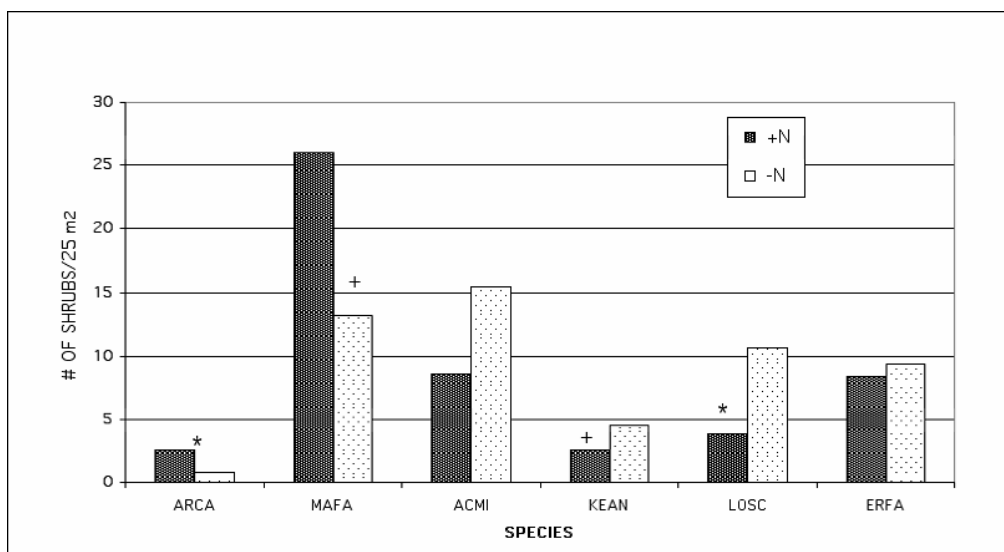


Figure 6—Density of dominant shrubs by species in N fertilized and unfertilized plots. *=significantly different at $P=0.05$, += $P<0.10$. ARCA=*Artemisia californica*, MAFA=*Malacothamnus fasciculatus*, ACMI=*Acourtia microstachys*, KEAN=*Keckiella anthirrhinoides*, LOSC=*Lotus scoparius*, ERFA=*Eriogonum fasciculatum*.

The shrubs were dominated by six species (fig. 6) that each responded differently to N fertilizer. The density of *Malacothamnus fasciculatus* was greatly increased by N fertilization, while that of *Lotus scoparius* was greatly reduced. The only other shrub that responded significantly was *Artemisia californica*, which had increased density with N fertilization. However, *Artemisia* had a relatively low density compared to the two short-lived colonizers *Malacothamnus* and *Lotus*. *Lotus* mortality was highest between 1998 and 1999, accounting for the large drop in shrub cover between those years. Over time the remaining longer-lived shrubs (*Artemisia*, *Keckiella*, and *Eriogonum*) that dominate mature CSS will fill in, most likely by growing larger. Their percent cover was not different between 1999 and 2001, all relatively dry years, but their future rate of growth may be determined by the level of N fertility.

The mechanisms by which N affected growth of the plant species in this stand cannot be determined directly from these field data, but they include a combination of individual plant responses to N and yearly climatic conditions and competitive interactions among groups of species that respond differentially to N. The reduction in *Lotus* with N is expected, because legumes typically respond to N by cessation of N fixation. This makes them less competitive with fast growing neighbors (see Munoz and Weaver 1999). In another study *Artemisia* showed increased growth with N fertilizer in the field both in monoculture and in mixture with grasses (Allen and others 1998). However, it had greatly reduced growth with grass competition in this study, and the N response was too small to overcome the competitive interaction with grasses. The stand studied at Lake Skinner had a relatively high cover of exotic grasses even without N fertilization (fig. 4). The nearby unburned stands have a patchy understory of exotic grasses, suggesting that exotics were present before the 1993 fire. The exotics may have been introduced by domestic grazing animals, which are responsible for dispersing seeds of many species (Malo and Suarez 1995). These lands had been grazed by cattle up to about 20 years prior to the experiment. CSS

shrubland in western Riverside County has been widely invaded by exotic grasses and forbs (Minnich and Dezzani 1998), so a site without exotics probably no longer exists. The most important effect of N deposition is likely to facilitate exotic grass dominance. Drought interacted with N fertilizer in our experiment, so that there was no measurable response to N in dry years with low productivity. In addition, the timing of rain may also give an advantage to native forbs, as occurred in the relatively dry 2001 when most rainfall occurred during February. Because the rainfall dynamics have resulted in patterns of plant growth and interactions with N fertilizer, we plan to continue fertilization and observations of these plots for additional years.

Conclusions

The physiological effects of ozone and nitrogen discussed above are summarized in figure 7, which shows that CSS, chaparral, coniferous forest, and annual grassland respond differently to the combined effects of these major pollutants. Ponderosa pine forest has negative growth responses to ozone and leaf-deposited nitrate, but the pines still respond to N fertilization of the soil with increased growth. CSS, on the other hand, may be sensitive to elevated soil N as *Artemisia* and *Encelia* experienced mortality in the greenhouse under high soil N (Allen and others 1998). Alternatively, CSS avoids summertime high levels of ozone and leaf-deposited $\text{HNO}_3/\text{NO}_3^-$ because leaves are deciduous. Chaparral growth response to N has been measured only in an N-limited situation, and it is uncertain how these shrubs respond to high levels of N deposition. It is likely that chaparral would not respond to N fertilizer as well as CSS shrubs, as they are comparatively slow growing (Hanes 1988, Mooney 1988). Based on these slower growth rates, we would not expect large changes in productivity in N-impacted chaparral, although controlled studies still need to be done. CSS shrubs, on the other hand, continued to grow at high rates with unlimited N, water, and other nutrients, but died after 6-9 months (Allen and others 1998, Padgett unpublished data, Padgett and Allen 1999, Yoshida and Allen 2001).

Vegetation type	O ₃	NO ₃ soil	NO ₃ leaf dep.
Coastal sage scrub	0	↓	0
Chaparral	0	0?	0
Pine forest	↓	↑	↓
Annual grassland	0	↓	0

Figure 7—Responses of dominant species of four vegetation types to air pollution stresses. Large and small up and down-oriented arrows represent large or small responses to pollutants; 0=no or minimal response. Response arrows are based on physiological responses of individual dominant species (see text for references).

The overall “winner” in this race against pollutants is the exotic annual grassland, which is replacing CSS but not chaparral or pine forest. The annual grasses have a high response to N fertilization, and they escape ozone and $\text{HNO}_3/\text{NO}_3^-$ leaf damage by summer dormancy. The summary responses of *figure 7* show individual dominant plant growth responses and do not indicate community or ecosystem level changes and feedbacks that may occur. For instance, during competitive interactions between *Artemisia* and *Bromus*, the grass took up N at greater rates (Yoshida 1999). N deposition also changed the species composition of mycorrhizal fungi in CSS along a nitrogen deposition gradient in the Riverside-Perris Plain (Egerton-Warburton and Allen 2000). Loss of certain mycorrhizal fungal species in high N soils caused a reduced growth response by host plant species, indicating the fungi are no longer effective mutualists (Sigüenza 2000). Many other changes are occurring, such as increases in N mineralization and nitrification rates and increased litter build-up in N-impacted sites in the mountains (Fenn and others 1996). The forest may be relatively buffered from the effects of elevated N by having a longer lifespan, higher biomass, and soil organic matter to absorb the N. In addition, the mountains experience yearly flushing of accumulated N in snow meltwater and precipitation run-off (Fenn and Poth 1999). There have been some vegetation changes, such as an increase in *Pteridium aquilinum* in the understory at high N sites in the San Bernardino Mountains, but no known changes in the overstory that can be attributed to N.

The reasons for stability of chaparral after N fertilization are not as clear but may also be related to the open watersheds that experience high levels of N flushing (Fenn and Poth 1999). Chaparral shrubs are long-lived, and many resprout from lignotubers following fire. They have slow growth rates compared to CSS and may not respond to N fertilization with rapid growth. Finally, many stands of chaparral accumulate undecomposed litter except on the steepest slopes, which may enable immobilization of deposited N. Chaparral stands seem to be stable across the landscape (Minnich and Chou 1997), having been affected neither by ozone die-off in the past like pines nor by possible N impacts as in CSS. However, ecosystems may appear healthy until they reach a threshold of N saturation (Aber 1992). A better understanding of chaparral responses to N is needed before we can be certain that it will remain healthy with continued N accumulation. The dramatic type conversion of CSS to annual grassland should be enough evidence that air pollution levels, especially N deposition, need to be reduced to improve the health of the vegetation.

Acknowledgments

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Fire as a Threat to Biodiversity in Fire-Type Shrublands¹

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Abstract

Chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants and thus are of particular conservation concern. Unnaturally high fire frequency has been a leading cause of degradation of chaparral and coastal sage scrub ecosystems. Although these shrublands are fire-adapted, below a certain threshold of fire frequency, resilience is inversely related to the fire return interval: this threshold is 3-5 years in coastal sage scrub and 10-20 years in chaparral, with the higher values more typical of interior sites. High fire frequency depletes the native flora and increases the proportion of non-native herbaceous species. Resilience to different fire regimes varies across growth forms, and thus it is of particular significance that the growth form distribution of rare species is significantly different from the proportions of growth forms in these communities.

Key words: chaparral, endangered species, high fire frequency, resilience, sage scrub

Introduction

The California landscape has been altered in many ways, with the potential for profound impacts on biodiversity and ecosystem functioning (Keeley and Swift 1995). Other than direct development, one of the more important changes in shrubland ecosystems has been the anthropogenic alteration of the natural fire regime. Despite a long-standing policy of fire suppression, the primary impact has been a dramatic acceleration of fire occurrence (Keeley and Fotheringham 2002, Keeley and others 1999, Moritz 1997). Although species in these shrublands are “fire adapted,” they are not adapted to all fire regimes, and one can distinguish species differences and broad growth form differences in resilience to increased fire occurrence. This is of particular concern because both chaparral and coastal sage scrub communities have a disproportionately high number of rare and endangered plants.

Shrubland Biodiversity

The California Native Plant Society (CNPS) list of rare and endangered plant species (Skinner and Pavlick 1994) places chaparral first in number of taxa that are of concern (*table 1*). Although coastal sage scrub ranks fifth, both shrub communities have a much higher number of rare taxa than expected based on their area occupied. If all the rare and endangered taxa in the top five habitats were distributed randomly,

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Table 1—*Top-ranking habitats of California's rare plants according to all CNPS lists (data from Skinner and Pavlik 1994). These observed values are contrasted with the values expected based upon the amount of land area occupied by each habitat (data from Jones and Stokes 1987).*

Rank	Habitat	Taxa	
		Observed	Expected
1	Chaparral	516	432
2	Lower coniferous forests	359	294
3	Cismontane woodland	311	362
4	Valley/foothill grassland	247	431
5	Coastal scrub	211	132

$(p < 0.001; \Pi^2 = 164.2 \gg \Pi^2_{0.999[3]} = 16.3)$

one would expect chaparral to top the list based just on areal extent of this vegetation, but chaparral contains 18 percent more species than expected. Coastal sage scrub contains nearly 40 percent more taxa than predicted by its areal extent.

In both chaparral and coastal sage scrub, herbaceous perennials, typically geophytes, top the list of growth forms that are rare or endangered (Skinner and Pavlick 1994). If we contrast these numbers just for southern California chaparral and coastal sage vegetation with those expected, based on extensive surveys of postfire peak of diversity (Keeley 1998a), we see that rarity is not randomly distributed across growth forms (*table 2*). Annuals are very under-represented. If rarity were randomly distributed with respect to growth form we would expect three times as many annuals as observed in the lists. On the other hand, there are three times as many herbaceous perennials as expected and double the number of shrub species.

Resilience to different fire regimes varies across growth forms (Keeley 2000), and thus it is of interest to consider rarity in terms of fire specialization. Fire is a frequent ecological factor and has played an obvious evolutionary role in these communities. Most non-woody plant species reach their greatest population sizes, and thus greatest potential for spread, in the postfire environment. However, not all species or even all growth forms are equally specialized towards fire. Annuals comprise a rich diversity of species that range from extreme specialization—strictly fire-stimulated germination (Keeley and Fotheringham 1998)—to generalized opportunistic species that occupy many types of disturbance. cursory examination of the rare annuals listed in Skinner and Pavlick (1994) indicates they are not highly restricted to burned sites. Herbaceous perennials, particularly geophytes, in these shrublands lack obvious specialization to fire, and their life cycle is not substantively different from that of geophytes in other less fire-prone habitats (Rundel 1996). At the time of fire most geophytes are dormant and nearly all have transient seed banks that do not require specialized fire cues (Keeley 1991). Thus, most rare herbaceous species do not appear to be highly specialized for postfire recruitment.

This pattern is not evident in the rare shrubs, where a large proportion are species of *Ceanothus* and *Arctostaphylos* that have seedling recruitment strictly tied to postfire conditions (Keeley 1998b). Thus, it is to be expected that the direct effects of alterations in fire regime would affect some components of the rare plant flora more than others.

Table 2—Growth form distribution of CNPS rare and endangered taxa in southern California chaparral and coastal sage scrub (data from Skinner and Pavlik 1994). Expected values based on distribution of growth forms following fire in 90 0.1 ha sites in southern California (Keeley 1998a)

	Annual	Herbaceous perennial	Suffrutescent	Subshrub/ shrub/tree
Observed	43	79	17	63
Expected	131	27	16	28
$(p < 0.001; \Pi^2 = 202.5 \gg \Pi^2_{0.999[2]} = 13.8)$				

This is well illustrated by the extreme event of back-to-back wildfires studied by Zedler and others (1983). At four *Adenostoma fasciculatum* dominated sites, postfire frequency of this shrub increased following a fire in mature vegetation but decreased dramatically following the second fire. The impact was most profound on the non-resprouting shrub *Ceanothus oliganthus*, which was present from seed in three-fourths of the plots after the first fire but nearly absent after the second fire. In contrast, these repeat fires had little impact on the herbaceous perennials *Calochortus weedii* and *Dichelostemma pulchella*.

Fire suppression has been frequently cited as a major threat to fire type rare species, for example, the rare locoweed *Astragalus brauntonii* that is restricted to sites around the Los Angeles Basin (Skinner and Pavlick 1994). This idea is a logical extension of the well-documented threat of fire suppression in many western coniferous forests (SNEP 1996). However, fire records show that in southern California fire suppression has not effectively excluded fire (Conard and Weise 1998, Keeley and others 1999). Indeed, urban mountain ranges such as the Santa Monica Mountains in Los Angeles and Ventura Counties have a fire rotation interval of less than 15 years, and this is likely many times shorter than the natural regime (Keeley 2002a). Lack of fire is not likely a threat to the persistence of these shrublands or rare species within them. A far greater threat in many areas, particularly the Los Angeles Basin, is habitat degradation due to increased fire frequency.

Fire-Induced Habitat Degradation

Unnaturally high wildfire frequency has long been a leading cause of degradation of chaparral and coastal sage scrub ecosystems, second only to land development. While these shrublands are fire-adapted, below a certain threshold of fire frequency resilience is inversely related to the fire return interval. This threshold is probably about 3 years in coastal sage scrub (but longer for interior sage scrub sites) and 10-20 years in chaparral (Keeley 2000). Generally speaking, as fire frequency increases, herbaceous vegetation is favored over woody growth forms (Sauer 1975, Wells 1962). Numerous studies have shown that unnaturally high fire frequency depletes the native flora and increases the proportion of non-native herbaceous species (Haidinger and Keeley 1993, Zedler and others 1983). In California it is quite likely that, except on fine-textured argillaceous soils, grasslands are degraded shrubland sites (Cooper 1922, Keeley 1990, 1993; Wells 1962), and even grasslands on certain argillaceous soils may have been dominated by the shallow rooted summer-deciduous coastal sage scrub (Kirkpatrick and Hutchinson 1980, Wells 1962).

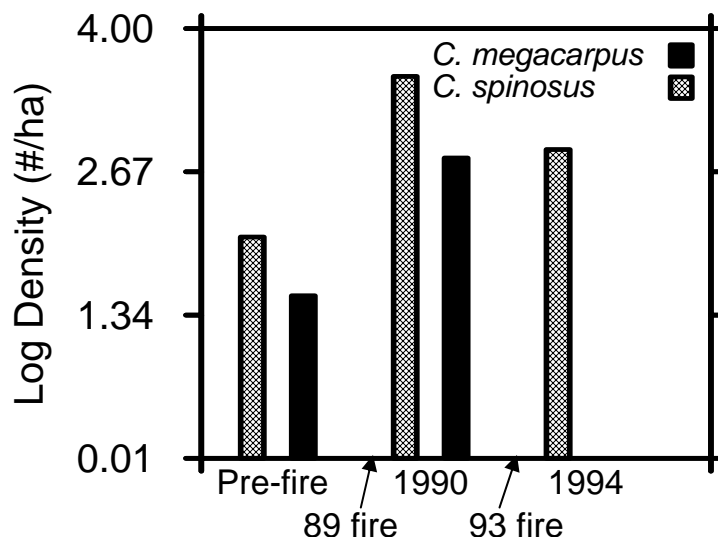


Figure 1—Effect of repeat fires on the populations of an obligate-seeding shrub, *Ceanothus megacarpus*, and a facultatively-seeding shrub, *C. spinosus*, in the Santa Monica Mountains. The first fire occurred in mature chaparral in 1989, the second in 1993 (from Keeley 2000).

The impact of frequent fires on the native shrub populations is well illustrated by the back-to-back wildfires that Zedler and others (1983) discussed, above. This extreme event resulted in the near extirpation of one obligate-seeding shrub population, and this can occur with even longer intervals between fires. *Figure 1* shows the extirpation of a non-sprouting shrub with fires four years apart, whereas a resprouting congener survived this high fire frequency, albeit at a lower density.

As native shrub cover is reduced due to high fire frequency, there is typically a type conversion to an herbaceous community dominated by non-native species. This is illustrated in the study by Haidinger and Keeley (1993) showing vegetation changes on adjacent sites experiencing different fire regimes. For example, two fires in six years reduced shrub populations of *Adenostoma fasciculatum* and *Salvia mellifera* but favored the suffrutescent *Lotus scoparius* (*fig. 2*). Three fires in six years were detrimental to most natives but conducive to the spread of non-native invasives such as *Brassica nigra* and species of *Bromus*. The results of this chronosequence study are corroborated by similar observations on a single site over time (*fig. 3*). In this study a mature coastal sage scrub site burned in 1993, and over the following three growing seasons the exotic cover declined as the native shrubs recovered. Following a second fire in 1996 the exotics exploded; within two years they dominated the site.

Such type conversions of shrublands to grasslands are not always the result of wildfires but have long been a goal of prescription burning programs (CDF 1978, Sampson 1944). Sometimes these are done for “range improvement,” to increase deer and livestock range, but other times for reducing fire hazard. These herbaceous (grassland) associations generate far less intense fires than shrub associations, and these grassland fires are more safely suppressed than chaparral fires (Keeley 2002a).

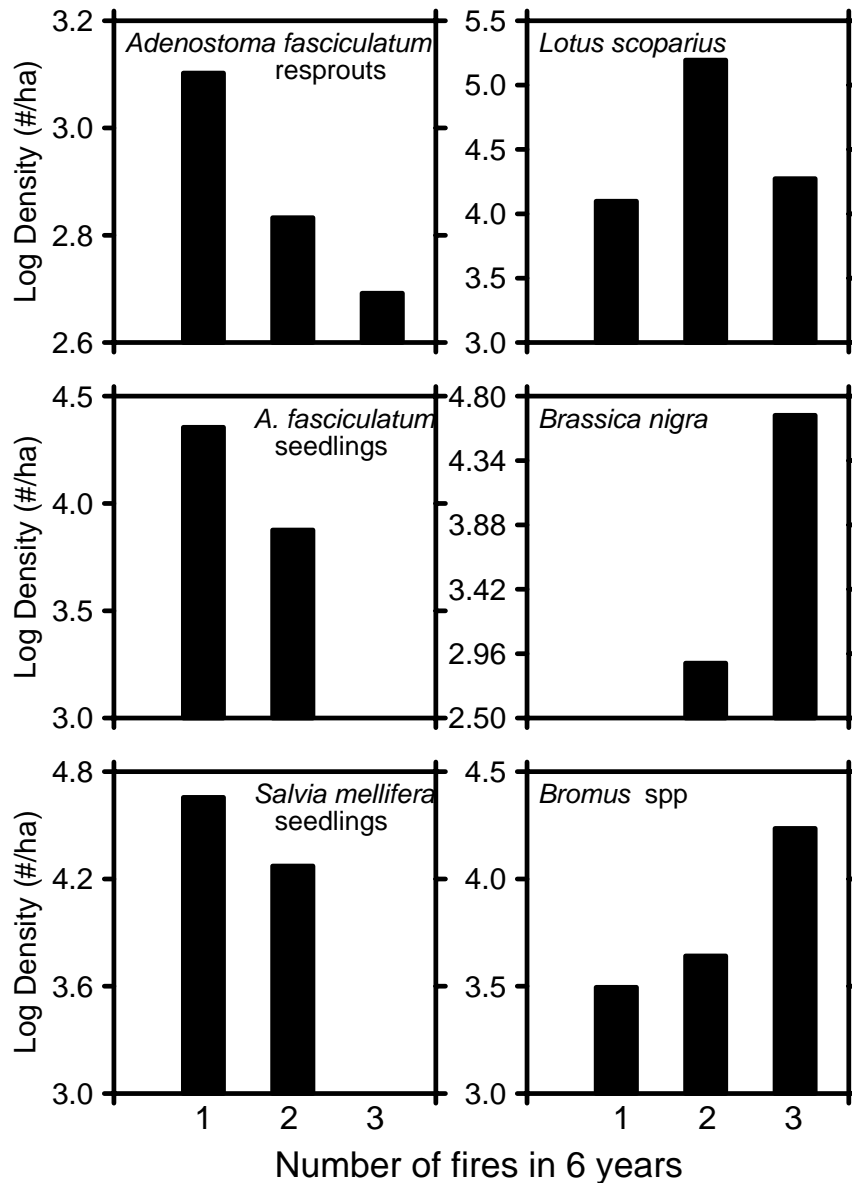


Figure 2—First growing season shrub and herb density in adjacent stands of mixed chaparral and coastal sage scrub burned once, twice, and three times in 6 years (redrawn from Haidinger and Keeley 1993).

Type conversion not only alters fire intensity, but also it often leads to increased fire frequency (Keeley 2002a). This results from several factors. These herbaceous species dry rapidly during the late spring and thus greatly expand the seasonal window of opportunity for fire. In addition, they constitute fine fuels that ignite readily and spread fire both horizontally through the stand and vertically into the shrubs with little wind. As the extent of herbaceous cover increases, it sets the stage for repeat fires in a self feed-back process where more fires thin the shrub overstory and increase the presence of a persistent herbaceous layer. Over time, repeating this process will type-convert shrublands to annual grasslands dominated by non-native species, which in turn alters the fire regime by increasing further expansion of

the seasonal window for fire because non-native species dry earlier in the spring than most native herbaceous species (Keeley and Fotheringham 2003).

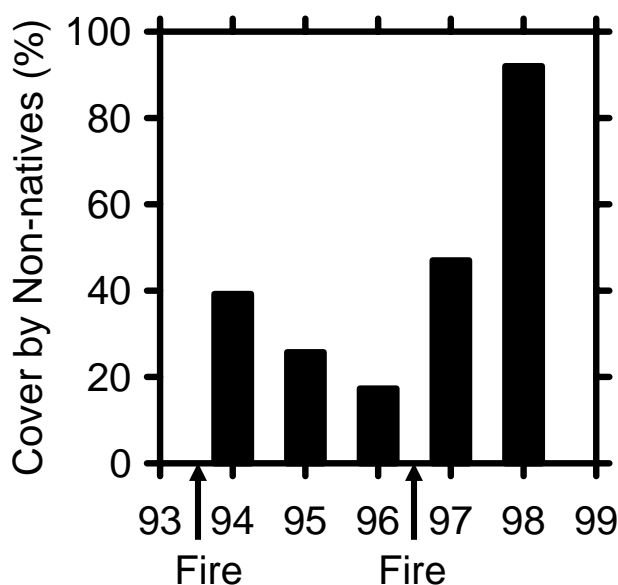


Figure 3—Percentage ground surface covered by non-native species on a coastal sage scrub site in the Santa Monica Mountains burned at 21 years of age in 1993 and reburned three years later in 1996 (data from Keeley and Fotheringham, unpublished data).

Sites differ greatly in their propensity for repeat fires. In general, interior sites are far more vulnerable to frequent fires than coastal sites due to the slower rate of shrub recovery (*fig. 4*). In another study of 90 sites burned during the same week in 1993, total herbaceous cover was positively correlated with parameters such as distance from the coast, soil phosphorous, organic matter, and sand content (*table 3*). Postfire herbaceous cover was negatively correlated with stand age prior to the fire and estimated annual insolation. In short, herbaceous cover sufficient to carry a repeat fire is most likely when fires occur in young stands on fertile sites in the interior.

History of Type Conversion

Cooper (1922) believed there was abundant evidence, based upon his observations in the Coast Ranges, to say that burning by Indians accounted for a shift from woody vegetation to grasslands. He contended that this process of type conversion continued with the colonization by Europeans. Bauer (1930) believed the same applied to the grasslands of the Tehachapi Mountains farther south and cited examples of relictual patches of shrubland as evidence.

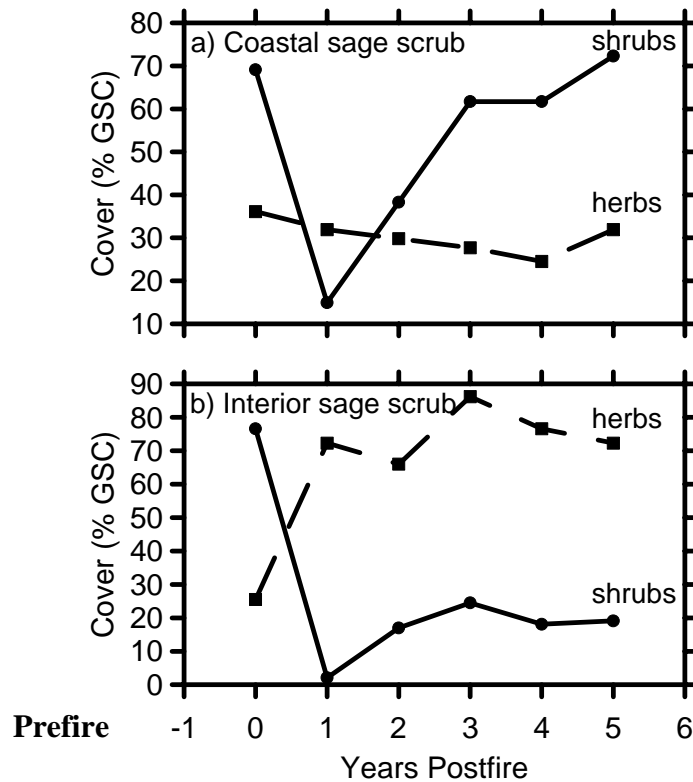


Figure 4—Foliar cover before and after fire at coastal and interior sage scrub sites (redrawn from O’Leary and Westman 1988).

Today the coastal ranges south of San Francisco have 25 percent of their landscape dominated by alien grasses, and there is reason to believe this derives from shrubland type conversion beginning with Native Americans (Keeley 2002b). Brown and Show (1944) recounted the history of rural land use in California, which included the use of fire to convert “useless” brush to “more productive” grasslands. This type conversion process accelerated in the latter part of the 19th century with increasing competition for suitable grazing land. During the latter part of the last century such type conversion was officially sanctioned by the issuing of brush burning permits for “range improvement” by the California Division of Forestry (CDF 1978). Throughout the 20th century, type conversion of shrublands occurred from other types of disturbance as well (Stylinksi and Allen 1999).

Presently, we have relatively limited information on the extent of such type conversions. However, there are reasons to believe this was done on a massive scale. One is the extensive distribution of non-native grasslands in the Coast Ranges of central California and the lack of any obvious correlation with environmental parameters such as soil type or slope exposure (Wells 1962). Another is the widespread distribution of grasslands in the foothills east of San Francisco and the demonstration of their rapid conversion to woody vegetation upon cessation of grazing (McBride and Heady 1968). Finally, quantitative measures of type conversion in southern California coastal sage scrub indicate that over the past 60 years more than half of the vegetation has been partially or completely type converted to grassland (Minnich and Dezzani 1998).

Table 3—*Stepwise multiple regression of postfire herbaceous cover vs. environmental variables at 90 sites of coastal sage scrub and chaparral (from Keeley and Fotheringham unpublished data).*

$r^2 = 0.42 \quad P < 0.001$	
	2-tail <i>P</i>
Positively correlated:	
Distance from coast	0.000
Percentage sand	0.002
Soil phosphorus level	0.003
Soil organic matter	0.009
Negatively correlated:	
Prefire stand age	0.002
Annual solar insolation	0.033

Conclusions

Besides human development, the greatest threat to biodiversity in Mediterranean-climate shrublands of California is changes in the natural fire regime. Fire suppression alters the fire regime by increasing the fire return interval and potentially threatens the persistence of species with fire-dependent recruitment. However, this impact is offset by the abnormally high number of fire occurrences due to human-caused ignitions. Consequently, the fire return intervals in southern California shrublands are higher than was historically the case, and the greatest threat to the persistence of these vegetation types is type conversion to herbaceous species more resilient to and more conducive to frequent fires. In general, non-native grasses and forbs are most favored by the current fire regime of frequent fires.

In general the majority of rare herbaceous species show no specialized response to fire. However, areas heavily affected by human-induced acceleration of fire return intervals may not be suitable sites for these natives because of the intense competition from non-native invasives that are favored by high fire frequency.

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Recovery Research for the Endangered Pacific Pocket Mouse: An Overview of Collaborative Studies¹

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Abstract

The critically endangered Pacific pocket mouse (*Perognathus longimembris pacificus*), feared extinct for over 20 years, was “rediscovered” in 1993 and is now documented at four sites in Orange and San Diego Counties, California. Only one of these sites is considered large enough to be potentially self-sustaining without active intervention. In 1998, I gathered a team of biologists to initiate several research tasks in support of recovery planning for the species. The PPM Studies Team quickly determined that species recovery would require active translocations or reintroductions to establish new populations, but that we knew too little about the biology of *P. l. pacificus* and the availability of translocation receiver sites to design such a program. Recovery research from 1998 to 2000 therefore focused on (1) a systematic search for potential translocation receiver sites; (2) laboratory and field studies on non-listed, surrogate subspecies (*P. l. longimembris* and *P. l. bangsi*) to gain biological insights and perfect study methods; (3) studies on the historic and extant genetic diversity of *P. l. pacificus*; and (4) experimental habitat manipulations to increase *P. l. pacificus* populations. Using existing geographic information system (GIS) data, we identified sites throughout the historic range that might have appropriate soils and vegetation to support translocated *P. l. pacificus*. Reconnaissance surveys of habitat value were completed in all large areas of potential habitat identified by the model. Those sites having the highest habitat potential are being studied with more detailed and quantitative field analyses. The surrogate studies helped us design individual marking and monitoring methods and will be used to test translocation methods before applying them to *P. l. pacificus*. Genetic results suggest that *P. l. pacificus* populations were naturally fairly isolated from one another prior to modern development, that genetic diversity will continue to erode in the small populations that remain, and that individuals from extant populations could probably be mixed if maximizing genetic diversity in any newly established populations is an important recovery goal. Local populations should be increased *in situ* before they can supply donor animals for translocations. Experimental habitat management (shrub thinning) at one occupied site yielded a short-term, positive, behavioral response of mice to thinned habitat plots. However, the overall population seems to be in decline, and long-term population responses to habitat manipulations are not yet evident. The approach of the PPM Study Team has been to proceed cautiously and scientifically to obtain critical information and to design a translocation program, but we are prepared to recommend swift action to prevent extinction despite “insufficient data.” At this point, political and economic obstacles to species recovery seem larger than obstacles presented by scientific uncertainty.

Key words: endangered species, Pacific pocket mouse, *Perognathus longimembris pacificus*, recovery, reintroduction, translocation

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Introduction

Recovery planning for endangered species requires a pragmatic use of science that recognizes we cannot always expect significant sample sizes or fully informed decisions. In recovery research, the goal of sustaining and increasing populations must sometimes overrule clean experimental design, and decisions must often be made based on untested hypotheses, lest we observe extinction while we await more data. The overall guiding principal should be to proceed cautiously with good science, but be prepared to act swiftly and decisively to avoid extinction, using whatever imperfect information you have.

Recovery planning for the Pacific little pocket mouse (*Perognathus longimembris pacificus*, commonly referred to as PPM) offers a useful example of this approach. This paper briefly summarizes background information on the species, its history of decline, and initial studies in support of species recovery. I then review methods and preliminary results of some recent research tasks coordinated under the informal umbrella of the “PPM Studies Program.” Finally, I review current status of these studies and summarize future directions for the program.

Background

Perognathus longimembris pacificus is the smallest subspecies of the little pocket mouse (*Perognathus longimembris*), a nocturnal, burrow-dwelling, mostly granivorous, heteromyid rodent species restricted to arid southwestern North America (Hall 1981, Williams 1986, Williams and others 1993). It is unusual as the only subspecies or species of *Perognathus* found on the Pacific coast, rather than in arid inland deserts and grasslands. Historically, this subspecies occurred on fine, sandy soils within about 4 to 6 km of the Pacific coast of southern California from near the Mexican border to El Segundo in Los Angeles County (Grinnell 1933, Meserve 1976, Patten and others 1998, von Bloeker 1931). Since the 1930s, most historic habitat has been removed or fragmented by urban development and agriculture, with the last known population being extirpated by development in Newport Beach during the early 1970s (Patten and others 1998). After approximately 20 years, during which time the species was not detected, a small population (tentatively estimated at 25-36 individuals) was rediscovered on the Dana Point Headlands in 1993 (Brylski 1993).

The subspecies was emergency listed as endangered by the U.S. Fish and Wildlife Service (USFWS) in 1994 due to immediate threats to this tiny, remnant population (USFWS 1998). Subsequently, three additional population sites have been discovered on Marine Corps Base Camp Pendleton, San Diego County (Ogden 1995, 1997; MBA 1997). Despite extensive survey efforts throughout the range, these four sites (*fig. 1*) represent the full extent of the current known subspecies range (USFWS 1998, Spencer and others 2000a, 2000b).

Criteria for species recovery include permanent protection of ten independently viable populations (USFWS 1998). Currently, three of the four occupied sites (Dana Point, San Mateo North, and San Mateo South) are less than 12 ha each in size, and their populations are thought to number under 50 individuals each (Spencer and others 2000a, 2000b). Such small sizes predispose these populations to extirpation by stochastic events, catastrophes, inbreeding depression, or other factors (Noss and Csuti 1997). At present these three sites cannot confidently be called viable. The

fourth and largest site (Oscar One/Edson Range) approaches 900 ha in total area (a mosaic of occupied, suitable patches and generally unoccupied, unsuitable matrix) and supports hundreds of individuals (Pavelka personal communication, Dodd and Montgomery 1998, Spencer and others 2000a). Although the Oscar One/Edson Range site is also vulnerable to extirpation, it is considered sufficiently large to be sustainable over at least the near term, barring catastrophe.

Initial Studies and Founding of the PPM Studies Program

Since the listing of the species, various studies were initiated to monitor *P. l. pacificus* populations, improve field study methods, evaluate potential project impacts, and improve understanding of the species' biology. The USFWS has been studying the *P. l. pacificus* population, monitoring methods, and microhabitat selection at the Oscar One/Edson Range site since 1997, and S. Dodd and S. Montgomery

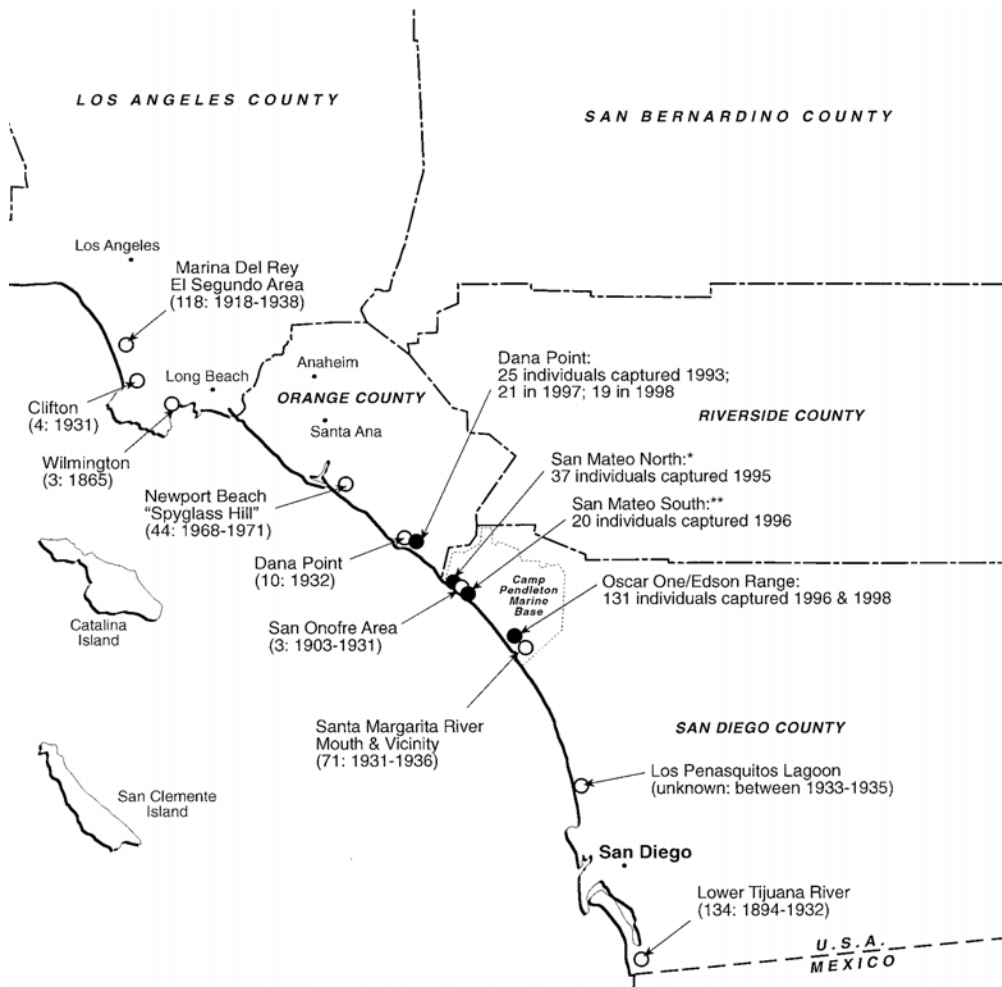


Figure 1—Historic (open circles) and extant (closed circles) locations occupied by *P. l. pacificus*. For historic locations, parentheses indicate the number of specimens in museum collections and the years of their collection. For extant populations, the numbers of individuals captured in recent years are shown. No capture-recapture estimates of population size are yet available.

have performed yearly population monitoring at Dana Point since 1997. Dodd and Montgomery (1998) also investigated effects of trap spacing and trapping duration on monitoring effectiveness at the Oscar One site.

In 1997, the Foothill/Eastern Transportation Corridor Agencies entered into a Memorandum of Agreement (MOA) with the USFWS and California Department of Fish and Game to fund several research tasks specifically called for by the species' Recovery Plan (USFWS 1998). In response, I assembled a team of biologists (including C. Schaefer, S. Montgomery, and S. Dodd), which in July 1998 initiated four specific research tasks called for by the MOA: (1) evaluate the feasibility of translocating *P. l. pacificus* to establish new populations, (2) determine dispersal characteristics of *P. l. pacificus*, (3) evaluate effects of Argentine ants on *P. l. pacificus*, and (4) develop a *P. l. pacificus* translocation protocol. We also assembled a scientific peer review committee to review progress reports and study designs throughout the process. Participants on the committee have included Drs. James Patton, William Longland, Jay Diffendorfer, Howard Shellhammer, Nicholas Holler, Michael Wooten, and Richard Reading.

During 1998, the study team reviewed existing literature pertaining to the four initial research tasks, interviewed scientific experts, and performed very limited pilot studies. Based on this information, we concluded (Spencer and others 2000a) that (1) a translocation or reintroduction program is probably necessary to achieve species recovery in the long term, but we knew too little to attempt such a program in the short term; (2) knowledge of *P. l. pacificus* dispersal characteristics would be useful, but a study specifically designed to answer dispersal questions would be prohibitively expensive, technologically impractical, and might do more harm than good to extant populations; (3) Argentine ants are unlikely to be a major limiting factor on *P. l. pacificus* due to differing habitat affinities (Argentine ants require moist ground conditions and are generally associated with irrigated landscapes in southern California [Suarez and others 1998, T. Case personal communication], whereas *P. l. pacificus* require well-drained and open vegetation communities); and finally, (4) we felt we could not design a translocation program until critical information gaps were filled.

Table 1 summarizes information on *P. l. pacificus* available in 1998 relative to the information needed to design a translocation program, according to Nielsen (1988) and USFWS (1998). The information gaps evident in *table 1* were used to define several research tasks deemed of highest immediate priority to further recovery: (1) a systematic review of potential translocation receiver sites based on habitat suitability and land uses; (2) a controlled laboratory study using a non-listed subspecies of *P. longimembris* to derive a preferred individual marking technique; (3) an intensive, multiyear study of a non-listed subspecies to test field techniques, before using them on *P. l. pacificus*, to gain basic biological information on the species and to test potential translocation methods; and (4) a population genetics study to establish baseline measures of genetic diversity within and between extant and historic *P. l. pacificus* populations. Once results of these studies make it possible to perform more intensive field studies on *P. l. pacificus* that would do more good than harm, we recommended (5) an intensive multiyear study of *P. l. pacificus* to obtain essential demographic and other natural history data. Finally, (6) we also recommended experimental habitat management, particularly controlled burning or shrub thinning, to improve habitat quality and *P. l. pacificus* population sizes at one or more occupied sites.

Table 1—Translocation feasibility considerations for *P. l. pacificus* as of 1998 based on USFWS (1998) and Nielson (1988). A “yes” under “sufficient information?” indicates sufficient information exists to assess whether translocations are necessary or feasible, but does not imply that information is sufficient to design a translocation program.

Consideration	Sufficient information?	Notes and comments
Reason for translocation	Yes	Recovery criteria probably cannot be met without a translocation/reintroduction program.
Status of wild populations	Yes	Severely in danger of extinction. Most potential habitat has been surveyed: four known occupied locations, representing three or four isolated populations. All remaining populations small.
Biology	No	Insufficient information on habitat requirements, demographics, space-use, dispersal patterns, and so forth. Sparse information available on related subspecies.
Size and density of wild populations	No	Rough estimates (individuals captured within a single season) available for four sites: Oscar One/Edson Range=131 ¹ ; San Mateo South=20; San Mateo North=37; Dana Point=21 to 36. No capture/recapture population estimates.
Movements and distribution	No/Yes	Little available information on movements of <i>P. l. pacificus</i> or related subspecies. Geographic distribution fairly well established.
Male: female ratio	Yes	Dana Point: 1.1:1 to 1.4:1; San Mateo North: 0.8:1.
Annual recruitment	No	No information on <i>P. l. pacificus</i> ; limited information on related subspecies.
Mortality rate and causes	No	No information on rates; some causes known or suspected from limited observations.
Health and condition of populations	No	Little information besides external observation of wild-caught specimens in hand. Most individuals appear healthy and free of external parasites.
Genetic variability and integrity	No	No information. To be determined by this study.
Status of remaining habitat	No	Although it is known that few potential habitat areas remain, systematic review needed to identify potential translocation receiver sites (this study).
Depredation rates in target areas	No	Limited information on presence or abundance of predators in potential receiver sites.
Translocation strategy	No	To be determined by this study.
Capture technique and technology	Yes	Capture methods in donor sites are relatively simple to define.
Number and location of release sites	No	Systematic review of potential receiver sites is needed to determine adequacy (this study). Recovery criteria will be used to define number and relative distribution of desirable sites.
Post-release support of translocated animals	No	To be determined by this study.

¹ Includes 111 unique captures on Oscar One (USFWS 1998) plus 20 unique individuals on Edson Range (Montgomery and Dodd 1998 unpublished data). Additional captures represent an unknown number of additional individuals because they were not marked to identify recaptures.

The remainder of this paper focuses on methods and preliminary results of those primary research tasks conducted to date, focusing on the translocation receiver site study, laboratory-marking study, field marking study, population genetics study, and shrub thinning study.

Methods

Translocation Receiver Site Study

The search for sites to receive translocated populations uses a coarse-filter/fine-filter approach. We first developed a simple habitat evaluation model based on existing geographic information system (GIS) data layers to identify, at a coarse scale, large areas near the coast having appropriate combinations of soil and vegetation to possibly support translocated *P. l. pacificus*. S. J. Montgomery and S. Dodd then surveyed these areas in the field to better rank habitat conditions using a quick evaluation method developed for this purpose (coarse filter). Those sites having the highest rankings based on the field reconnaissance will be subject to more intensive, quantitative studies (fine filter). These efforts are restricted to coastal Orange and San Diego Counties, because soils maps are not available for Los Angeles County, and remaining native coastal areas there seem generally unsuitable for establishing new *P. l. pacificus* populations due to inappropriate soils, habitat degradation, abundant exotic species, and other factors (W. Spencer, personal observations; P. Behrends, S. Montgomery, and M. Pavelka, personal communications; Ogden and Dames and Moore 1999).

The GIS habitat model was used to screen out areas of Orange and San Diego Counties that are clearly unsuitable for *P. l. pacificus* reintroduction and to identify areas deserving field evaluation. The model was therefore designed to be conservative, tending to overestimate potential habitat value for *P. l. pacificus* to minimize chances of missing a suitable site. This conservative approach recognizes that available digital information for soils and vegetation is coarse in scale relative to *P. l. pacificus* habitat selection and may have inaccuracies.

The model ranks *P. l. pacificus* habitat potential based on three criteria: distance from the Pacific coast, soil type, and vegetation type. Nearly all historic observations of *P. l. pacificus* are within 4 km of the Pacific coast, with a few as far as 6 km, so inland limits of the study area were conservatively set at 8 km of the coast (measured from the main shoreline or the eastern shore of larger bays).

W. Spencer and M. Pavelka—in collaboration with Dr. Robert Graham, Professor of Soil Mineralogy and Pedology at U.C. Riverside—ranked all soil types mapped within this study area (USDA 1973, 1978) as having very high, high, low, or no potential to support *P. l. pacificus* based on surface horizon texture, soil depth, and other factors (for example, presence of a hardpan or high gravel or cobble content). Care was taken to consider all physical factors likely to affect burrowing or foraging abilities of *P. l. pacificus*, as well as the potential for higher quality soils to exist as inclusions within lower-ranked soil polygons. The highest-ranking soils were classified based on results of detailed soils analyses performed by the USFWS at occupied versus unoccupied microhabitats at the Oscar One *P. l. pacificus* site (Pavelka, Winchell, and Graham, unpublished data). Those results suggest that *P. l. pacificus* are very discriminating of soil characteristics at a finer scale (measured on 20 x 20-m grids) than that of existing soils maps, and that they strongly select for

deep (>30 cm), fine-grained, loamy sands (not sandy loams) having less than about 7 percent by volume of clay and less than 4 percent by weight of gravel and rock.

Vegetation types were ranked as having high, low, or no potential to support *P. l. pacificus* using regional GIS vegetation maps (SANDAG and Ogden 1997 for San Diego County; Orange County Planning and Development Services Department 1993 for Orange County). *P. l. pacificus* historically have been associated with open coastal scrub and grassland habitats having a diversity of annual herbs, so these vegetation communities were ranked high. *P. l. pacificus* probably cannot persist in denser shrub communities, wetlands, or woodlands. However, the regional vegetation maps are coarse in scale, and some upland areas mapped as generally unsuitable natural vegetation may contain small areas of open scrub or grassland. Therefore all natural vegetation types were considered to have at least a low potential to support *P. l. pacificus*. Areas mapped as *agriculture, developed, disturbed, rock, or open water* were ranked as having no potential.

The soil and vegetation rankings were combined to create overall habitat rankings within 8 km of the coast (table 2) based on the following logic: Evidence to date suggests that soils are the primary determinant of habitat quality, at least within areas of natural vegetation near the coast. As long as the soils are highly suitable to support *P. l. pacificus*, low suitability vegetation (e.g., chaparral) may reduce *P. l. pacificus* habitat potential somewhat, but vegetation management (e.g., burning or thinning) might be used to increase habitat quality. Therefore, the presence of low quality vegetation on high quality soils only slightly reduces the overall habitat potential to support *P. l. pacificus*. However, if the soils are low quality for *P. l. pacificus*, the vegetation community type or vegetation management will probably have little effect on *P. l. pacificus* habitat potential; consequently, the overall rating reflects the soil potential (low). If either soils or vegetation are inappropriate (e.g., clay soils or agricultural fields), the site has no *P. l. pacificus* potential.

Once maps of the overall habitat potential rankings were created, relatively large (> 20 ha) blocks of moderate to very high habitat value were outlined as field evaluation sites. S. J. Montgomery and S. Dodd then evaluated these sites in the field during 1999-2000 using a rapid evaluation data sheet to record vegetation, soil, and other site characteristics. The 5-10 sites receiving the highest scores during these coarse-level field evaluations are currently subject to more intensive, quantitative (fine-filter) study to determine their potential to support translocated *P. l. pacificus* populations.

Table 2—Habitat potential to support *P. l. pacificus* based on soils and vegetation. See text for how soils were ranked (a complete list of soil rankings is available from W. Spencer upon request). For vegetation suitability, all coastal scrub, grassland, and dune vegetation communities were ranked high; all other natural vegetation communities were ranked low; all developed, disturbed, agricultural, rock, and open water areas were ranked none.

Vegetation suitability	Soil suitability			
	Very high	High	Low	None
High	very high	high	low	none
Low	high	moderate	low	none
None	none	none	none	none

Laboratory Marking Study

We tested four permanent, individual marking methods on a captive population of a non-listed subspecies, *P. l. longimembris*: (1) subcutaneous passive integrated transponder (PIT) tags, (2) toe clipping, (3) tiny, custom-designed ear tags, and (4) color-coded surgical sutures. *P. l. longimembris* was chosen as a logical surrogate for *P. l. pacificus* due to close phylogenetic and body-size relationships and its non-sensitive status. S. Dodd captured 36 *P. l. longimembris* in Sherman live traps near Yucca Valley, San Bernardino County, California—28 during June 1999 and 8 more during May 2000. The animals were housed individually in 19 x 21 x 32-cm plastic cages supplied with natural desert soils in a room having a skylight (for natural day/night cycles) and an air filter.

Captive animals were assigned to one of the four marking techniques or to a control group by random draw. Marking was done with the assistance and oversight of a veterinarian (Dr. Anthony Michael). Six animals were marked in one ear with custom-designed aluminum ear tags bearing 3-digit numbers etched into their surface. Six animals were marked with a 2-digit toe clip code (one digit on a front paw and one on a rear paw) using the standard mammalogical method (Baumgartner 1940, Melchior and Iwen 1965). Toes were clipped distal to the ultimate toe joint, only far enough back to remove the nail and the cells producing nail growth, using either a baby nail clipper or surgical scissors. Six animals were marked with two color-coded monofilament sutures (size 4-0 monofilament nylon surgical sutures, one black, one blue) stitched through the loose skin on the nape of the neck, tied with a triple surgeon's knot, and cut to leave 1.0 to 1.5 cm of loose thread projecting from the knot. Seven animals were tagged subcutaneously between the scapulae with PIT tags that measure 11.5x2 mm. Six tags were injected using a 12-gauge hypodermic needle, and one tag was inserted by hand via a surgical incision across the nape after shaving a patch of hair. Nine animals served as unmarked controls. They were removed from cages, weighed, and examined according to the same schedule as the marked animals.

After marking, the test and control groups were regularly weighed and examined for adverse health effects or behaviors. The examination schedule was every other day for the first two weeks, then weekly for ten more weeks, and at least monthly thereafter.

Field Marking Study

The study team initiated a field surrogate study during 1999-2000 to investigate long-term mark retention and health effects in the wild, collect basic natural history and demographic data, and to test various translocation techniques (for example, use of enclosure fences, artificial burrow design). We established two permanent study grids near the village of Snow Creek in the Coachella Valley, Riverside County, California (San Bernardino Base and Meridian; USGS 7.5' White Water Quadrangle, Section 21 of Township 3 South, Range 3 East). Habitat on the site is relatively homogeneous creosote- (*Larrea tridentata*) dominated desert scrub on a north-sloping bajada, which is densely occupied by the non-listed subspecies *P. l. bangsi*.

Two trapping grids (Grids A and B) were established approximately 80 m apart, with inter-trap spacing initially set at 5 m for Grid A and 7 m for Grid B based in part on the trap-spacing study for *P. l. pacificus* performed by Dodd and Montgomery (1998). Grid A consisted of 14 x 14 trap stations (196 total stations) and Grid B of 10 x 10 trap stations (100 total stations). The area trapped by each grid was thus 0.49 ha

(70 x 70 m), assuming a ½-trap-space perimeter strip around each grid. Each station was set with two traps to reduce trap saturation by non-target species (especially kangaroo rats, which often enter traps early in the evening). Thus, Grid A contained 392 traps at 196 stations and Grid B contained 200 traps at 100 stations, for a total of 592 traps per night.

The grids were trapped for eight consecutive nights from 27 July to 3 August 1999 to mark residents and search for an asymptote in capture of new individuals. We also trapped the grids for two nights on 1 and 2 September 1999 to observe health and mark retention on previously marked individuals, and to see if the mice were still active above ground so late in summer (seasonal timing and influences for entering and leaving aestivation/hibernation are poorly understood in *P. longimembris*). All captured individuals were marked by a unique, 2-digit toe-clip combination. A subset of the mice was also marked by attaching a uniquely numbered ear tag to the left ear or a PIT tag inserted subcutaneously using the hypodermic needle technique. Toe clipping provided a redundant mark for animals also marked with ear or PIT tags, in case these tags were lost.

We recorded the following data for all captures: sex, weight, reproductive condition, age (young of the year or adult, by pelage appearance), location, recapture status, and notes on animal condition and condition of any previously applied marks. Reproductive condition was based on the position of the testes for males and condition of the vagina and size of mammae for females.

Trapping was continued during 2000—for five nights in April and four nights in July—with both grids trapped at the 5-m (14 x 14) trap spacing. We began marking individuals with either toe clipping or a PIT tag, but discontinued ear tagging due to high loss rates for ear tags.

Population Genetics

James Patton and Andrea Swei at UC Berkeley analyzed geographic genetic structure within and among the five subspecies of little pocket mice in southern California (*P. l. bangsi*, *brevinasus*, *internationalis*, *longimembris*, and *pacificus*) by examining haplotype variation in their mitochondrial cytochrome *b* gene (Swei and others 2003). The 111 total *P. longimembris* samples they analyzed included 48 *P. l. pacificus* specimens collected in 1995-2000 (by pulling hairs or clipping toe tips from live-caught individuals) and 12 *P. l. pacificus* museum skins collected in the 1930s (from 2 x 2-mm skin snips). Full 810-base pair (bp) sequences were obtained from the live-caught specimens, and 430-bp fragments were amplified from the museum specimens. To date the following live-caught *P. l. pacificus* samples have been analyzed: Dana Point (N=27), San Mateo South (N=10), San Mateo North (N=5), and Oscar One (N=6). The historic museum specimens were collected from El Segundo (N=1), Oceanside (N=6), and Tijuana Estuary (N=5). Swei and others (2003) applied a variety of analytic and statistical measures to describe phylogenetic and population genetic structure within and among the five subspecies and to infer population genetic processes affecting *P. l. pacificus* populations historically and today (see Swei and others 2003, and citations therein, for complete laboratory and analytical methods).

Shrub Thinning Experiment

A variety of theoretical and empirical evidence suggests that vegetation has become too dense at some of the occupied *P. l. pacificus* sites for optimal habitat condition, and that thinning the vegetation by fire or other means might increase habitat value and *P. l. pacificus* population sizes. Experimental habitat thinning was therefore initiated within the Dana Point *P. l. pacificus* reserve during 1999. It was not possible to obtain permission for a controlled burn at the site, so shrub cover was thinned by hand on experimental plots.

Eleven trapping grids (40 traps arranged in 4 x 10 arrays with 3-m spacing) were established and trapped during the spring and summer of 1999 (pre-thinning) and 2000 (post-thinning): three control grids and eight experimental grids. The three control grids were established in known, occupied *P. l. pacificus* habitat having relatively low shrub cover; the eight experimental grids were established in areas of dense shrub cover not known to harbor *P. l. pacificus* but having appropriate soils. The experimental grids overlapped four roughly rectangular shrub-thinning plots of about 30 x 60 m each, such that half of each of the experimental grids was in an area to be thinned and half in an area not to be thinned (hereafter, thinned and unthinned subgrids).

Before thinning, shrub canopies on the experimental plots covered a mean of about 83 percent (range 75-87 percent), measured at 21-60 cm aboveground using point-intercept transects. During January 2000, shrub cover was thinned on the four plots to a mean of 32 percent (range 26-36 percent). Thinning was done by removing individual shrubs at ground level, using chainsaws and pruning tools to avoid soil disturbance. Concentrations of woody duff and litter were also lightly raked to uncover mineral soils.

Trap lines were run for seven consecutive nights, once during spring (late April-early May) and once during summer (mid August). Captured *P. l. pacificus* were individually marked by clipping hair and using indelible colored markers (during 1999) or by toe clipping (during 2000). Use by *P. l. pacificus* of the control, thinned, and unthinned grids was compared between the pre-thinning (1999) and post-thinning (2000) periods using Chi-square. Spring and summer trapping sessions were pooled within each year, and the sample frequencies were calculated as the cumulative sum of all unique individuals captured on a grid. Thus, a recapture of an individual on the same grid was not counted as an independent observation, but a recapture on another grid was, because individuals could choose to move from one grid (for example, a control grid) to another (for example, a thinned grid) during the study.

Results

Translocation Receiver Site Study

Figures 2 and 3 illustrate output of the GIS habitat suitability model for the northern and southern halves of the study area, respectively. The maps also indicate general areas investigated in the field for their potential to support translocated *P. l. pacificus*. These maps surely overestimate the actual extent of high and very high quality habitat, due to the conservative model assumptions and the gross nature of the digital map information relative to the scale at which *P. l. pacificus* select habitats. Although the model correctly identified all extant *P. l. pacificus* population sites as having very

high habitat quality, it missed some areas of apparently high suitability due to inaccuracies in the soils data. Nevertheless, the maps proved useful in focusing field efforts in areas with the highest likelihood of having suitable soils and vegetation to support translocated *P. l. pacificus*. Reconnaissance surveys indicate that six or seven sites may have sufficient acreage of fine, sandy soils and appropriate vegetation to support translocated *P. l. pacificus* populations.

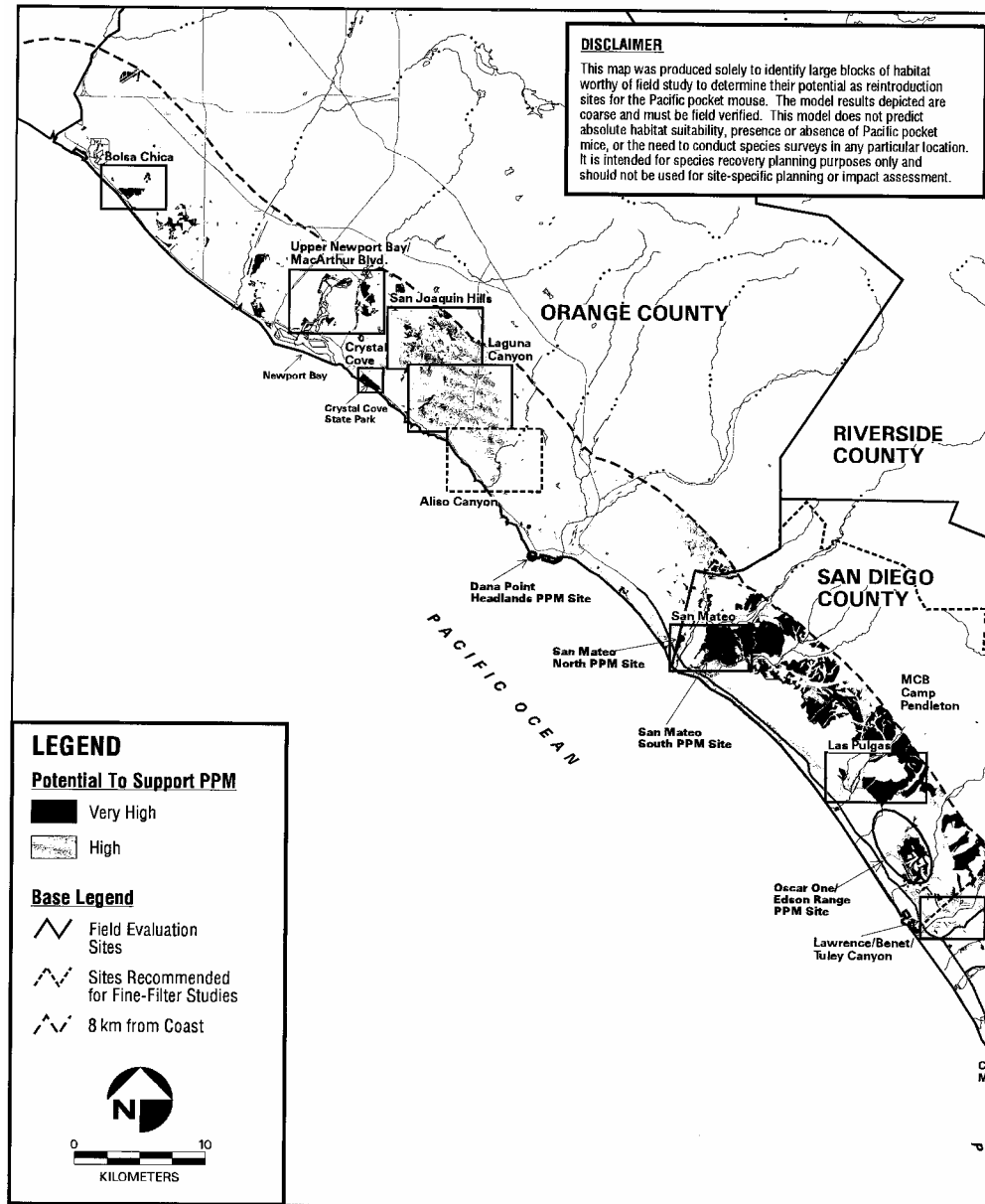


Figure 2—Areas in Orange County and Northern San Diego County having potential to support translocated *P. l. pacificus* populations, based on the GIS habitat suitability model. Boxes indicate general areas assessed in the field. Note that these maps greatly overestimate actual habitat suitability in many areas due to conservative model assumptions and coarse data input scales. They may also miss areas of potential due to inaccuracies in model input data.

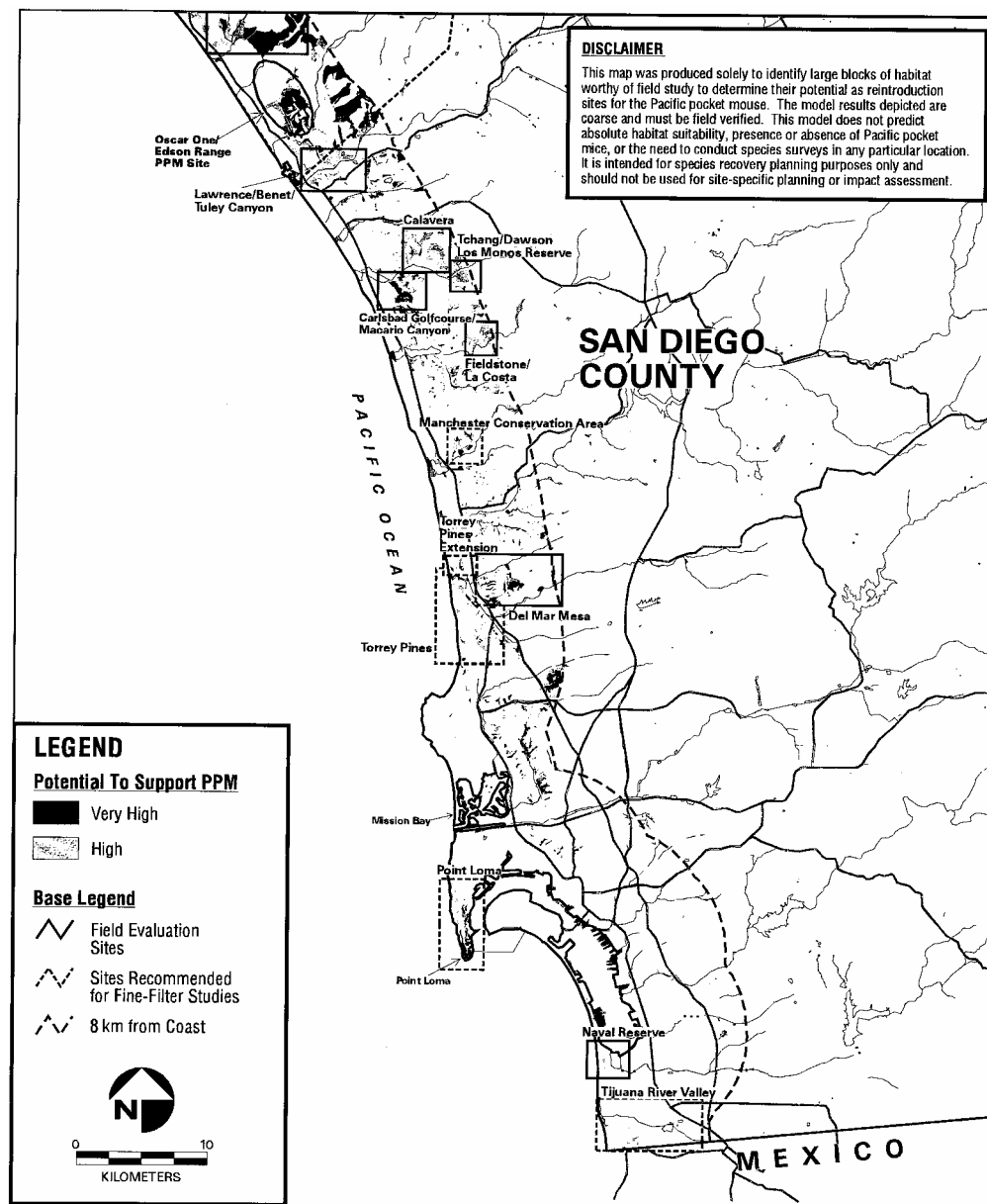


Figure 3—Areas in San Diego County south of Camp Pendleton having potential to support translocated *P. l. pacificus* populations, based on the GIS habitat suitability model. Boxes indicate general areas assessed in the field. Note that these maps greatly overestimate actual habitat suitability in many areas due to conservative model assumptions and coarse data input scales. They may also miss areas of potential due to inaccuracies in model input data.

Laboratory Marking Study

Of the various marking techniques tested, toe clipping seemed clearly the least harmful and possibly the most reliable for uniquely identifying animals over their life span. The suture technique and ear tags resulted in high rates of tag loss (100 percent and 50 percent, respectively) and other complications, and they are not recommended

for further testing. PIT tags seem promising and are recommended for further testing on surrogates. However, the puncture wound for tag insertion is large for such small animals, and once inserted, PIT tags sometimes migrate under the skin or cause rumpling of the skin and hair. PIT tags would offer substantial benefits over toe clipping if they could be made smaller to reduce potential adverse health effects; they are not recommended for use on *P. l. pacificus* in their currently available dimensions.

Field Marking Study

Table 3 summarizes captures of male and female *P. l. bangsi* on the two grids in 1999 and 2000. Sex ratios recorded on grids using 5-m trap spacing (Grid A during both years and Grid B during 2000) did not differ significantly from each other nor from 1:1 ($\chi^2=0$ to 0.5; $df=1$; $P> 0.25$ for all comparisons). However, during 1999, when Grid B used 7-m inter-trap spacing, few females were captured and the recorded sex ratio strongly favored males (24 males:9 females=2.67:1). This ratio almost differed significantly from that recorded on the same grid using the 5-m spacing in 2000 ($\chi^2=3.79$; $df=1$; $P=0.051$), and it did differ significantly from an even ratio ($\chi^2=6.82$; $df=1$; $P< 0.01$). These results support a hypothesis that the 7-m spacing may have under-sampled females on Grid B during 1999 (compare the low number of females captured in this treatment relative to all others in table 3). Although we recognize that this conclusion is weak due to a lack of grid replication, reduced female captures at greater trap spacing would be expected if females move less extensively than males, which is true in most pocket mice (review in Jones 1993).

Captures on both grids more than doubled between summer 1999 and summer 2000. This reflects a large reproductive output in 2000, with 126 of 162 aged individuals (78 percent) identified as young of the year during summer 2000. In contrast, we identified all individuals captured during April 2000, and all but one individual captured during July-August 1999, as over-wintered adults. The reproductive season seemed near a peak during April 2000, with most individuals showing signs of sexual activity, including descended testes in males or perforate vaginas in females. By July-August of both years, few individuals showed signs of sexual activity, and we were able to distinguish three age classes: adult, subadult, and juvenile.

Table 3—*P. l. bangsi* captures at the Snow Creek study grids during 1999 and 2000.

Trap Session	Sex		Total
	Male	Female	
Grid A			
Summer 1999	22	22	44
Spring 2000	15	20	35
Summer 2000	53	40	97
			(4 not sexed)
Grid B			
Summer 1999 ¹	24	9	33
Spring 2000	17	15	32
Summer 2000	37	32	71
			(2 not sexed)

¹ Traps on Grid B used 7-m inter-trap spacing in summer 1999; otherwise, all traps had 5-m inter-trap spacing.

When both years are pooled, 248 individuals were toe clipped, 34 were PIT tagged, and 50 were ear tagged. All ear tags were applied in 1999, because a high rate of tag loss caused us to discontinue this method in 2000. By the end of the first 1999 trap session, at least a third of the ear-tagged individuals exhibited various levels of ear inflammation and redness, ripping around the tag insertion hole, or drooping ears. One individual had lost its ear tag when it was recaptured 7 days after marking. At least seven more ear tags were lost by the second trapping session (4-5 weeks after tagging).

Toe clipping was the fastest and easiest marking technique under field conditions and seemed to have little or no adverse effects on animal health. Clipped toes exhibited no or little bleeding (one or a few drops) that ceased within minutes; and recaptured animals rarely showed inflammation or redness of the wound. Nevertheless, toe clipping is not without problems, as evidenced by about 25 problem incidences (out of 248 toe-clipped individuals) due to natural causes or human error: (1) ten cases of naturally missing, deformed, or injured toes, which would make toe clipping potentially confusing; (2) six or seven cases where field workers apparently read the wrong code on a previously toe-clipped animal; (3) three or four cases where the toe tip grew back, apparently due to not clipping far enough back; (4) and four cases where two individuals were mistakenly given the same toe clip code. In addition, the number of unique toe-clip codes is finite (depending upon the number of digits clipped), which poses problems for population monitoring in a fairly long-lived species (up to at least 6 years, with about 30 percent over-winter survival; Bailey 1939, Behrends personal communication, Chew and Butterworth 1964).

The hypodermic insertion PIT-tagging procedure worked well in the field with practice. Most mice seemed to experience minor inflammation, scabbing, and sensitivity to touch at the insertion wound. Tags appeared to migrate under the skin, which exhibited bulging on some individuals. Unfortunately, recapture rates were too low (there were no over-winter recaptures of PIT-tagged individuals) to ascertain health effects of PIT tagging in the field.

Population Genetics

Swei and others (2003) found that all *P. l. pacificus* haplotypes analyzed to date are unique to that subspecies, and all are closely linked genealogically. *P. l. pacificus* has apparently been diverging from its geographically closest relatives (*P. l. brevinasus*, *bangsi*, *internationalis*, and *longimembris*) for some time, although none of these subspecies is reciprocally monophyletic (i.e., no subspecies has a common ancestor not shared with any other subspecies).

Pooling all extant populations of *P. l. pacificus*, the subspecies exhibits similar levels of nucleotide and haplotype diversity as other southern California subspecies of *P. longimembris*, although the sample from Dana Point has markedly low haplotype diversity in comparison to all other subspecies or populations. Of the total genetic variation among samples of *P. l. pacificus*, about 39.1 percent is variance among individuals within populations, 54.4 percent is between populations within a time period, and 6.5 percent (which is not significantly different from zero) is between modern and historic samples. Thus, the pattern of haplotype differentiation suggests that historical populations (in the 1930s) were already largely isolated from one another, and that current patterns of genetic diversity are due largely to natural isolation of these populations prior to the modern urbanization of coastal California.

Indeed, the genetic signatures measured by Swei and others (2003) suggest that although populations of *P. l. pacificus* were somewhat isolated in recent evolutionary time, they do not yet reflect a loss of genetic diversity due to habitat losses in modern times. Swei and others (2003) concluded that 40 to 70 years of habitat reduction at locations like Dana Point are insufficient to override the population's deeper genetic history, but that we can confidently predict future losses of genetic diversity unless current population declines are reversed.

Measures of gene flow between populations of *P. l. pacificus* are quite low, both in historical and current times. This stands in sharp contrast to higher levels of gene flow measured across greater geographic distances in the Mojave Desert for *P. l. longimembris*. Measures of gene flow between the Dana Point population and all other *P. longimembris* populations are especially and uniformly low. The Dana Point population also has the lowest haplotype diversity of any sample of *P. longimembris* (only 9 unique haplotypes recovered from 27 individuals). Together, these results suggest that the Dana Point population has been relatively small, as well as isolated, for some time. Slightly higher gene flow measures and haplotype diversity were recorded among the three sites on Camp Pendleton (San Mateo North and South and Oscar One).

Swei and others (2003) concluded that, given current levels of fragmentation and low population sizes, genetic diversity will continue to erode within *P. l. pacificus* populations. This suggests that mixing of individuals from different sites may be necessary to meet the recovery goal (USFWS 1998) of maintaining the full remaining genetic variability of the subspecies. Although the haplotypes of extant *P. l. pacificus* populations are largely apportioned among populations, they are all genealogically closely related, and genetic variability seems to be governed by neutral (rather than selective) genetic processes. It is possible that there are selective differences among these populations that are more likely to be expressed in nuclear than mitochondrial genes, but this seems unlikely given the small geographic range of the subspecies and similarities in ecological conditions at occupied sites. Thus it appears that mixing individuals from different *P. l. pacificus* populations during translocations should not have any deleterious genetic effects (for example, "outbreeding depression").

Shrub Thinning Experiment

P. l. pacificus seemed to respond quickly and positively to the shrub thinning by redistributing themselves into the newly thinned habitat areas. During 1999 (pre-thinning), 11 individual *P. l. pacificus* were captured, yielding 12 independent grid observations (one individual was captured on two grids)—9 observations (9 individuals) were on the known occupied control grids, 2 were on subgrids to be thinned (including 1 individual that also used a control grid), and 1 on a subgrid not to be thinned. In contrast, during the year 2000 (post-thinning), 10 individual mice were captured for a total of 18 unique observations—4 on control grids, 11 on thinned subgrids, and 3 on unthinned subgrids. This shift in the distribution of captures is statistically significant ($P=0.026$), largely due to the great increase in captures on the thinned subgrids. During the year 2000, 6 of 10 individuals were captured only on thinned subgrids (5 were captured on only one subgrid, but 1 male was captured using three different thinned subgrids). Of the 4 individuals captured on control grids, 3 also were captured on thinned subgrids. No individuals were captured

only on unthinned subgrids—all three individuals captured on unthinned subgrids were also captured using the adjacent thinned subgrid. In fact, all captures on unthinned subgrids were less than 6 m (two trap distances) from the thinned area that these individuals also used. Moreover, all capture locations on unthinned subgrids were connected to the thinned plots via natural inter-shrub openings.

Thus, the pattern of captures before and after the thinning suggests a strong shift in distribution to the newly thinned habitat areas or their edges. This reinforces observations that *P. l. pacificus*, like other species of *Perognathus*, are most abundant in fairly open habitats, although they may prefer to forage in microhabitats in or near shrubs (Brown and Lieberman 1973, Harris 1984, Meserve 1976, Price 1978, Reichman and Price 1993). Although *P. l. pacificus* may forage under shrubs near openings, they do not seem to frequent interior portions of closed-canopy shrub cover, especially when other options are available.

Unfortunately, intensive trapping at the Dana Point site during May-June 2001 captured only four *P. l. pacificus* (2 female, 2 male; USFWS unpublished data). This sample is too small to reveal any patterns relative to the shrub-thinning experiment. Moreover, these results reinforce a general pattern of population decline at Dana Point since the population's discovery in 1993. Whether or not shrub thinning may positively influence population size at this or any other site is, therefore, not yet determined.

Discussion

The informal collaborative process followed by the PPM Studies Team—with frequent re-evaluation of priorities, methods, and results—has thus far proved effective in addressing the most urgent questions bearing on species recovery. We benefited greatly from an active peer input and review process that helped keep the program focused and scientifically valid while allowing for flexible, pragmatic responses to new information. We have proceeded with a realization that statistical certainty, while desirable, isn't always possible or necessary when prudent actions must be taken to recover rare species.

During 1998, the study team concluded that *P. l. pacificus* translocations were necessary to achieve species recovery, but that existing information was insufficient to design a translocation program. We therefore refocused our research to answer those questions considered most critical to designing a *P. l. pacificus* translocation program. We now feel we have gained sufficient information to begin designing the program as one essential recovery tool. Please note that our goal is translocations to establish new *P. l. pacificus* populations, and thereby to help rescue the species from the brink of extinction. No one should interpret our intent as translocation to mitigate proposed take over of *P. l. pacificus* or their habitat by development projects.

In the future, we hope to comprehensively update our evaluation of translocation feasibility, design a framework translocation program based on the updated information, and design experiments to test translocation methods (for example, use of release enclosures and artificial burrows) prior to implementing the program. At this point in the process, I am confident that continued research and common sense could sufficiently answer the most pressing biological questions bearing on species recovery. Less certain, however, are methods of overcoming political and economic obstacles. For example, subsequent to the drafting of this document, the U.S. Marine

Corps denied requests from the PPM Studies Team to continue *P. l. pacificus* studies on Camp Pendleton, due apparently to concerns that the results might constrain military training and readiness. This has postponed indefinitely our ability to answer remaining questions and further species recovery. Such non-scientific obstacles must now take center stage if we are truly to recover populations of this charismatic little mouse.

Acknowledgments

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Herbaceous Responses to Livestock Grazing in Californian Oak Woodlands: A Review for Habitat Improvement and Conservation Potential¹

Barbara Allen-Diaz and Randall D. Jackson²

Abstract

Livestock grazing effects on herbaceous vegetation diversity and ecosystem function are summarized from peer-reviewed literature. Ecosystem responses are linked to grazing management via residual dry matter (RDM), which is alternatively called *litter* or *mulch*. Residual dry matter is the dead herbaceous aboveground biomass remaining on a site at the time of autumn germination in annual grassland and oak woodlands. RDM is known to play an important role in nutrient cycling, soil erosion prevention, and herbaceous species production and composition the following year. Minimum RDM guidelines are used to ensure forage sustainability and protect ecosystem resources. Recent work has indicated that *maximum* RDM standards may be necessary to meet wildlife habitat requirements at both site (for example, burrowing owls) and landscape (for example, kit fox) scales and may be useful for fire-fuels management. Livestock grazing can be a useful conservation tool because managers can control the type, abundance, and spatial and temporal distribution of grazers to meet desired goals. Furthermore, political and economic considerations are rendering prescribed fire, hand mowing, and large native herbivore reintroduction increasingly difficult tools to apply. We review herbaceous vegetation responses to grazing management so that they might be translated to advantages and disadvantages for specific ecosystem and habitat conservation goals on a case-by-case basis.

Key words: annual grassland, biodiversity, conservation, grazing, habitat improvement, livestock, oak woodlands

Introduction

Oak woodlands and savannas occupy 3 million ha in California (Bolsinger 1988, Griffin 1977). Seven series and 57 subseries have been described within the oak community type (Allen and others 1991). Oak types occupy 52 of California's 58 counties and are widely distributed west of the Sierra Nevada (*fig. 1*). Oak savannas and woodlands generally occur from 60 to 700 masl (meters above sea level), between annual grassland at lower elevations and mixed conifer forests at higher elevations (Barbour and Major 1988). The climate is Mediterranean, with

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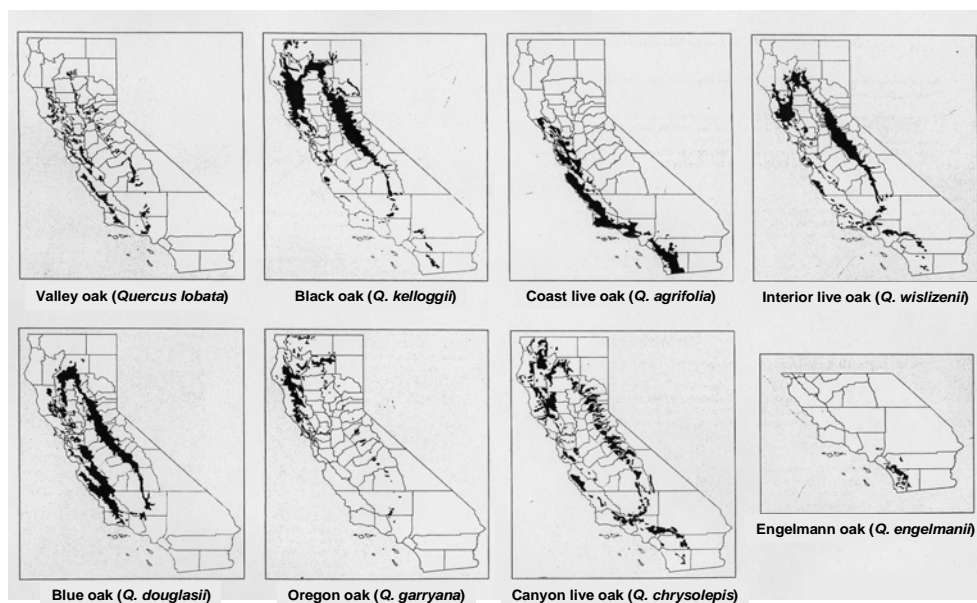


Figure 1—Distribution of eight native oak trees in California (modified from Pavlik and others 1991).

precipitation occurring primarily as rain between October and May. Summer drought results in 3 to 5 months of water deficit (Major 1977).

Dominant trees in the oak woodland include blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), interior live oak (*Q. wislizenii*), coast live oak (*Q. agrifolia*), Oregon white oak (*Q. garryana*), and Engelmann oak (*Q. engelmannii*). These species occur in monospecific to mixed stands (Allen-Diaz and others 1999). Ninety percent of California's oak woodlands are privately owned (Ewing and others 1988). Over 300 species of vertebrates live in oak habitats, including ~80 mammals, 160 birds, 25 amphibians, and 40 reptiles (Standiford and Tinnin 1996). Livestock grazing is the primary agricultural use of oak woodlands, but other economic products include firewood, wildlife, water, and recreation (McClaran and Bartolome 1985, Standiford and Tinnin 1996).

Annual grassland is the major oak understory vegetation, although shrubs and perennial grasses may be an important component in some areas. Native perennial grasses are scattered throughout California (Bartolome and Gemmill 1981, Beetle 1947) and found interspersed within a matrix of annual grasses, forbs, and legumes that are mostly native to the Mediterranean region (Jackson 1985).

Here we review the scientific basis for livestock grazing management on the herbaceous component of California's oak woodlands. The status of this ecosystem over the last 25 years has been addressed in a series of symposia (Pillsbury and others 1997, Plumb 1979, Plumb and Pillsbury 1986, Standiford 1990, Standiford and others 2002), the proceedings of which contain numerous studies of grazing and other management effects on the regeneration of oaks, in addition to many other topics. We do not attempt to review or duplicate this literature. Instead, we emphasize the herbaceous plant communities of oak woodlands and their responses to management so that they might be translated to advantages and disadvantages for specific ecosystem and habitat conservation goals on a case-by-case basis. As much as possible we rely on literature specific to oak woodlands, but with their annual

grassland understory, some references to open grasslands are applicable and cited. Finally, we discuss two approaches for managing and understanding complex systems—Residual Dry Matter guidelines and State-Transition models—that have gained wide use in the field of rangeland resource science as rational approaches to ecosystem management.

Pre-European-settlement Herbaceous Flora

Dominant herbaceous vegetation in California prior to European contact is unknown. Many believe native perennial grasses, particularly the bunchgrass *Nassella pulchra*, once enjoyed a more widespread distribution (Clements 1934, Heady 1977). Hamilton (1998) has argued rather convincingly against overuse of this paradigm, citing over-extrapolation of Clements's climax community concept and the dogma that has derived from it. He suggested that native annuals were once dominant, especially in drier parts of the grassland. Holstein (2001) suggested the rhizomatous perennial grass *Leymus triticoides* dominated the pre-agricultural Central Valley floor. However, his analysis relied on the relict method for which he and others criticize Clements, along with observational accounts of European explorers and settlers.

We know of only two studies providing physical evidence of pre-European settlement composition. Bartolome and others (1986) found greater abundance of distinctive opal phytoliths, silica bodies that are resistant to decay with shapes specific to certain taxonomic groups, at soil depths corresponding to greater than 150 years past. The shapes these phytoliths took were specific to those found in perennial grasses, indicating their greater abundance in the past at that particular site (Jepson Prairie).

The second paper offering some physical evidence of pre-European flora is Mensing and Byrne (1998). They examined preserved pollen in sediment cores from the Santa Barbara channel and determined that the presence of the exotic annual *Erodium cicutarium*—now ubiquitous in much of California—pre-dated European settlement and livestock introduction. They show patterns suggesting it invaded from Baja California prior to the Mission Period in California's history.

Controls on Herbaceous Community Structure

Factors at many spatial and temporal scales interact to control herbaceous productivity in California's annual grasslands, although these factors may be modulated by the presence of oak canopy. In annual grasslands, peak standing crop (aboveground biomass at late spring seed set) varies interannually as a function of the timing and amount of precipitation, temperature (Bentley and Talbot 1948, George and others 1988, Heady 1958, Talbot and others 1939), and edaphic and topographic characteristics (Jackson and others 1990). A typical yearly production curve for the annual grassland understory (*fig. 2*) includes the onset of autumn germination with the first rains over 2.5 cm occurring within a 1-week period. Slow winter growth progresses as temperatures decline, followed by rapid spring growth as soil temperatures increase concurrent with adequate soil moisture. Peak standing crop of the herbaceous vegetation generally occurs between 1 April and 15 May, followed by the death of the annual plants. Standing dead biomass slowly decomposes as summer

drought slows microbial activity, until the ensuing autumn rains stimulate decomposition concurrent with annual plant germination (Jackson and others 1988).

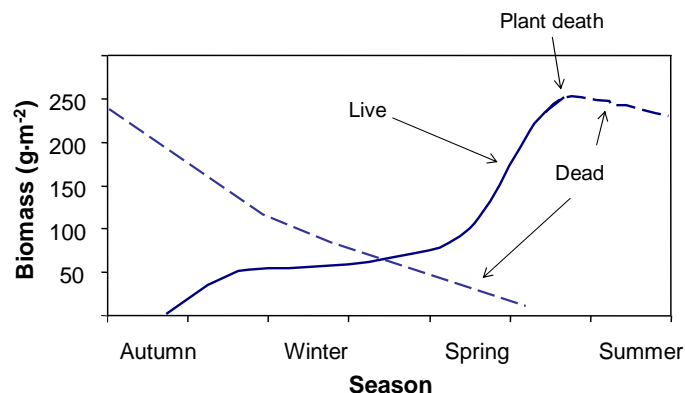


Figure 2—Typical herbaceous production for the University of California's Sierra Foothill Research & Extension Center (SFREC), a blue oak woodland site NE of Sacramento.

Herbaceous understory production is primarily controlled by interannual weather variability (Connor and Willoughby 1997, Frost and others 1991); however, several workers have demonstrated that tree canopy cover exerts a proximate but variable influence on peak standing biomass depending on regional location, tree density, and tree type (Bartolome and others 1994, Frost and McDougald 1989, Ratliff and others 1991). Relative to open grasslands, canopy cover inhibits herbaceous production in areas of California receiving >50 cm annual precipitation (McClaran and Bartolome 1989), suggesting light reduction as a mechanism. The inverse relationship generally holds for drier portions of the state, where canopy cover serves to attenuate drought stress. From a livestock production perspective, Frost and others (1997) found that an increase in tissue and litter quality per unit biomass under oak canopy in drier regions more than compensated for reduced herbage mass. Nutrient concentrations differed as a result of species composition differences rather than some change in individual plant nutrient use efficiencies.

Species composition differences between oak understory and open grassland have been demonstrated by several authors (Borchert and others 1991, Jackson and others 1990, Marañón and Bartolome 1993, Saenz and Sawyer 1986). Some species appear to be strongly controlled by this dichotomy, but generalizations for California's oak woodlands are tenuous. A given species may be strongly associated with canopy cover at one site but with open grassland at another. For instance, *Nassella pulchra* is thought to be an open grassland species, but we have observed it scattered under relatively high oak canopy cover in the Sierran foothills (B. Allen-Diaz, unpublished data). Alternatively, *Cynosurus echinatus* is rare in open grassland but common beneath oak canopy throughout the state. Rice and Nagy (2000) sought the mechanism for the spatial separation of *Bromus diandrus* (found under canopy) and *Bromus hordeaceus* (found in the open), showing that interspecific competition was important in the high resource oak canopy soils, but only *B. hordeaceus* could tolerate the harsher conditions of open grassland; there was little evidence of competition between these species in the open. Working in blue oak woodlands of the Sierran foothills, Shlisky (2001) found that aspect, measured at the 10- to 100-m² scale, was a more important determinant of species composition than canopy cover.

Hence, species composition in the herbaceous understory is a complicated mix of time, site, abiotic, and biotic interactions; generalizations are tenuous.

Plant species diversity (measured as species richness) was shown to be highest at intermediate herbaceous biomass levels (Heady and others 1992, Marañón and Bartolome 1994) following the model of Grime (1979) and discussed by Marañón and García (1997) and García and others (1993). Marañón and Bartolome (1994) listed optimum biomass levels for maximum species diversity on California annual grassland/oak woodlands at 35 to 57 g m⁻². They also showed that maintaining an oak overstory component provides for maximal landscape diversity owing to different plant assemblages in canopy and the open.

Grazing Effects on Herbaceous Vegetation

Grazing animals have been part of California grassland, savanna, and woodland ecosystems for thousands of years (Edwards 1992). Before European contact and the establishment of widespread cattle and sheep grazing (Burcham 1957), large herds of pronghorn antelope, tule elk, mule deer, and rodents grazed California grasslands, savannas, and wetlands (Edwards 1996). Many grassland species have evolved habits (for example, prostrate growth) and structures (for example, basal meristems) to avoid or tolerate aboveground tissue loss (Briske 1991).

Grazing animals may influence plant composition and community structure both directly via physical means and indirectly via biogeochemical and biotic feedbacks. McBride and Heady (1968), for example, found that trampling by cattle prevented the encroachment of native coyote bush (*Baccharis pilularis*) into the grasslands of the Berkeley hills. Some evidence exists that high grazing levels promote invasion of undesirable plant species via biological feedbacks (D'Antonio and others 1999); that is, grazers alter the competitive balance of natural communities by interrupting nutrient cycles, altering soil organic matter quality, and creating gaps for colonization, in effect creating an alternate ecosystem more conducive to the invader. However, this model assumes equilibrium-type conditions where biotic interactions play a significant role in shaping the plant community (Wiens 1984). California's Mediterranean climate, with its high interannual rainfall variability, does not lend itself to equilibrium conditions where competitive interactions among plants are allowed sufficient time to affect community structure. From one year to the next, community structure is primarily determined by abiotic constraints associated with autumn germination (Bartolome 1979, Evans and Young 1989).

Evidence for the well-known Intermediate Disturbance Hypothesis (IDH) (Connell 1978, Sousa 1979) is inferred from Marañón and Bartolome (1994) and Bartolome and others (1980), who showed diversity maximized at intermediate levels of aboveground biomass. If intermediate levels of grazing disturbance leave intermediate levels of biomass, these results should apply. However, these results were from coast live oak (non-deciduous) woodlands on the Coast Range (Marañón and Bartolome 1994) and from various open grassland sites (Bartolome and others 1980). The scientific basis for IDH as a mechanism in deciduous blue oak woodlands is lacking. Fehmi and Bartolome (2002) showed that a possible tradeoff between livestock and rodent herbivory exists in these grasslands. In their study, rodents appeared to preferentially locate burrows (thereby disturbing vegetation) in areas where livestock were excluded, that is, high cover sites. Hence, any response of diversity to livestock grazing regime changes may be cancelled by rodent activity.

Similar results were noted by Dyer and Rice (1997). Keeley (2002) found slightly reduced herbaceous species richness in livestock-excluded areas compared to grazed areas of blue oak woodlands of the southern Sierran foothills. Nonetheless, these zones maintained greater plant diversity than adjacent mixed-conifer zones at higher elevations irrespective of grazing management, but the oak woodlands were more highly invaded.

Spring-fed wetlands and riparian areas are often the only sources of water in oak woodlands and are especially heavily utilized by grazing animals. However, light to moderate, autumn/winter grazing had little effect on Sierra Nevada foothill spring-fed vegetation after 6 years of treatment (Allen-Diaz and Jackson 2000). Continued monitoring of these systems under experimental treatments has shown that by years 7 through 10, moderate grazing reduced herbaceous cover, light grazing had minimal effect, and grazing removal significantly increased cover (Jackson 2002). These increases in cover resulted in an undesirable accumulation of plant litter that suppressed subsequent plant productivity. Studies examining grazing effects on vegetation structure in riparian systems other than spring-fed wetlands are few. High intensity grazing can negatively affect water quality, plant biodiversity, productivity, wildlife habitat, wildlife species biodiversity, and nutrient cycling in riparian areas in regions with continental-type climates (Belsky and others 1999, Clary 1995, Fleischner 1994, Kauffman and Krueger 1984, Kauffman and others 1983). However, extrapolation of these results to Mediterranean-type regions should be made very cautiously (Gasith and Resh 1999, Larsen and others 1998). Effects of moderate to light grazing on ecosystems of these regions tend to be overwhelmed by larger scale environmental fluctuations (Allen-Diaz and Jackson 2000, Allen-Diaz and others 1998).

Many studies have sought to determine management techniques for enhancing native perennial grasses, namely grazing, burning, and grazing removal. If target perennial grasses are not present on a site, these treatments will not be effective. However, if present on a site, native perennial grasses have been shown to respond favorably to disturbance treatments, but the particular combination of treatments depends on geography and possibly weather patterns. Bartolome and Gemmill (1981) rejected the notion that *N. pulchra* represents relictual dominance and hypothesized that it likely is a disturbance-adapted species that finds refuge in spaces where light is less limiting than belowground resources. Their hypotheses were largely confirmed by experimental findings of Dyer and Rice (1999). Dyer (2002) found that *N. pulchra* seed from grazed and/or burned individuals germinated and survived at higher rates than seed from undisturbed plants. He invoked *maternal provisioning* as the mechanism by which this advantage is conferred.

Working in Coast Range grassland, Bartolome and others (unpublished data) found a positive response of *Nassella* under post-treatment grazing removal, but not during the grazing removal treatment, indicating some residual effect of their seasonal grazing treatments that was magnified by removal of the disturbance. This aligned with Dyer's and Rice's (1997) work in Valley grassland showing that *N. pulchra* abundance increased only when released from diffuse competition with neighboring annual grasses and forbs.

The studies cited above illustrate the importance of rangeland management based upon scientifically produced information that is applicable to appropriate sites and scales (Bartolome 1989). Range managers control grazing animal type, abundance, spatial distribution, and temporal distribution (season of use). Each of

these singular or interacting factors can produce disparate effects on various ecosystems and ecosystem components. Therefore, grazing efficacy should not be assessed as an “either-or” proposition (in the sense used by Belsky and others 1999).

Grazing Effects at the Ecosystem Level

Grazing can affect ecosystem processes as well as ecosystem structure, though this topic has received considerably less attention in oak woodland understory than open annual grasslands. In general, grazing accelerates carbon and nutrient cycling by effectively bypassing the microbial decomposition pathway. Livestock mineralize plant organic material and return it to the soil and atmosphere as feces, urine, and gas much more quickly than microbes. In perennial grasslands of the Midwest, accelerated nutrient cycling is credited for stimulating net primary productivity (Frank and Evans 1997, Frank and McNaughton 1993, Frank and others 1994). However, similar grazing effects on nutrient dynamics in California annual grassland were not evident (Dahlgren and others 1997, Davidson and others 1993). Nitrogen quickly cycles within annual-dominated ecosystems, where plant species possess low nutrient use efficiencies and high litter qualities irrespective of herbivory (Davidson and others 1990, Jackson and others 1989, Schimel and others 1989).

Dahlgren (1997) describes soils beneath oak canopy as “islands of fertility” because of greater carbon, nitrogen, and phosphorous stocks compared to adjacent open grasslands sites. The patchiness of oak woodland canopy may be enhanced by the ability of oaks to garner water and nutrients from beyond the canopy perimeter, from the open grassland spaces between them and their neighbors, and then preferentially returning leaf litter below the existing canopy, thereby redistributing ecosystem resources. However, this process would constitute a positive feedback that would be unsustainable in the long-term, depressing herbaceous production in the open; this effect is not evident. An untested hypothesis is that herbivores provide a check on this effect by harvesting herbaceous resources from beneath the canopy and redistributing them relatively more homogeneously across the landscape.

Camping and others (2002) found little effect of grazing on soil chemical properties in blue oak woodland of northern Sierran foothills. Dudley and others (2002), working at the San Joaquin Experimental Range, found higher soil bulk densities in areas with moderate to heavy grazing intensities compared to historically ungrazed areas, indicating deleterious effects on soil physical properties.

Spring-fed wetlands provide many important functions within oak woodland landscapes; livestock grazing modifies these functions. Much of the water exiting oak woodland watersheds passes through these highly productive zones at the terrestrial-aquatic interface (Huang 1997). Wetland vegetation in these zones, typically cattails (*Typha* spp.), sedges, rushes, and perennial grasses, likely acts as a nutrient filter (primarily nitrate) as waters emerge at the soil surface. Jackson (2002) has determined with a paired-plot grazing removal experiment that nitrate concentrations in surface waters where grazing was discontinued for only 2 years were as much as five times greater than grazed counterparts. Furthermore, ungrazed concentrations far exceeded the U.S. Environmental Protection Agency’s maximum standard for surface waters of 714 μm (Fan and others 1987).

that while some species may respond to RDM manipulations in some years, overall plant community composition is relatively insensitive to these changes. Composition seems to be entrained by annual weather patterns producing nonequilibrium conditions that render overall community manipulation via livestock grazing futile. However, this is not to say that a single species such as a native perennial grass or diversity (in the sense of Meyer and Schiffman 1999) cannot be managed for by manipulating the type, intensity, or distribution of grazing (Hatch and others 1999).

Table 1—Minimum residual dry matter guidelines ($\text{g}\cdot\text{m}^{-2}$) for livestock grazing management in Californian annual grassland.

Precipitation regime (yearly total in cm)	Slope class		
	Lower or flat	Average or gentle	Upper or steep
< 25	22	28	39
25-100	45	67	90
>100	84	112	140

RDM is now the preferred criterion for measuring grazing management effectiveness on California's rangelands. Livestock operators estimate RDM using various methods including harvesting a known area, dry weight rank, and visual estimation (Harris and others 2002). Desired RDM levels are determined based on combinations of slope and average total rainfall (*table 1*). Experiments are currently underway to produce RDM guidelines for oak woodlands where overstory litter complicates the matter. The University of California Cooperative Extension publishes scorecards indicating minimum RDM levels that should sustain system productivity in the face of fluctuating weather conditions. Guidelines like these should be developed for various conservation management objectives.

State-transition Models for Adaptive Management

The emphasis throughout this paper has been on uncertainty and hedged statements about environmental and management effects on grassland understory in oak woodlands. Unraveling of the complexity inherent in this system is occurring, albeit slowly. This is attributable to the plodding pace of the scientific method combined with the context-dependent nature of responses in Mediterranean ecosystems (Gasith and Resh 1999). Experimental information is needed from applied treatment combinations under the range of climate patterns for each setting.

Complex phenomena such as these beg for an organizing framework where results are catalogued and testable hypotheses generated. One such organizing tool, state-transition models, has been espoused for over a decade by rangeland ecologists working in the inherently variable and difficult-to-manage arid and semi-arid regions of Australia and North America (Brown 1994, Filet 1994, Taylor and others 1994, Westoby and others 1989, Whalley 1994). Applications vary, but all state-transition models are simple box-and-arrow diagrams of actual ecosystem states (defined by combinations of vegetation, soils, fauna, and so forth) and transitions among states related to all possible factors—anthropogenic or otherwise (*fig. 4*). Observed and/or hypothetical transitions among states are catalogued, their causes to be tested and

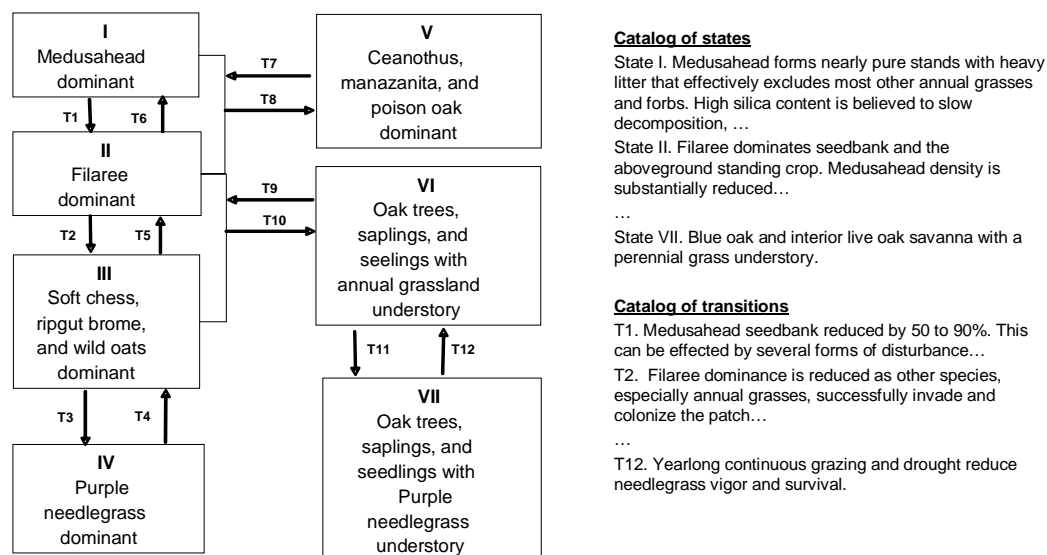


Figure 4—Example of a state-transition model for a Sierran foothill blue oak woodland site. Models such as these could be developed for ecosystem conservation as a means of organizing information and generating testable hypotheses about management induced effects. Note that this model, adapted from George and others 1992, has been simplified; it is shown here only for demonstration of state-transition model structure.

validated or rejected. State-transition models have since been applied to California's oak woodlands (Huntsinger and Bartolome 1992) and annual grasslands in various forms (George and others 1992, Jackson and Bartolome 2002). However, these applications usually summarize data or hypotheses under relatively restrictive conditions; they seldom allow for filling in gaps in information. More useful models would exhaustively identify as many different weather scenarios and management goals as possible, explicitly differentiating reliable knowledge from hypotheses and conjecture. Publication of this information would minimize redundancy and allow for refinement of research questions.

State-transition models are especially useful where system response is complex and dynamic and therefore should gain wide use in conservation management. They are most useful when data-driven by spatially and temporally explicit results acquired through monitoring and adaptive management.

Livestock Grazing Alternatives

Alternatives to livestock grazing for vegetation management include non-commercial grazing, prescribed fire, herbicidal application, and hand weeding. All are ecologically effective at some scale, yet all possess significant drawbacks. Fire has great potential as a vegetation management tool as it is generally more effective than grazing at removing aboveground biomass. Successful applications include control of yellow starthistle (DiTomaso and others 1999), barbed goatgrass (DiTomaso and others 2001, Hopkinson and others 1999), and medusahead (Murphy and Lusk 1961). However, it is ultimately cost-prohibitive to many managers and agencies because of the high costs associated with maintaining emergency personnel on site during "burn

windows.” Burn events are prone to postponement and cancellation as ideal environmental conditions are sought to maximize the burn’s efficacy while minimizing air pollution. Finally, catastrophe may result from the inevitable escaped prescribed burn.

Potential side effects of herbicide treatment render it a politically as well as an ecologically unsound alternative over extensive areas. Furthermore, long-term efficacy of such treatments tends to be poor (Allen-Diaz and Bartolome 1998). Combinations of herbicidal spraying and livestock grazing are currently being tested for efficacy of yellow starthistle control in northern California. Finally, hand-weeding and non-commercial grazing by waterfowl, goats, and the like for conservation management are effective, politically feasible measures, but at local scales only. Regional, landscape, and even site scales are not manageable by these means.

Future Research

We do not propose livestock grazing as a panacea—a vegetation management tool whose application will help meet every conservation goal. When managed improperly, livestock cause damage to riparian and upland systems and alter habitat, affecting other species. On the other hand, there is a renewed interest in using livestock to achieve specific conservation objectives (Meyer and Schiffman 1999, Pykala 2000, Stolzenburg 2000). This presumes that researchers and managers understand enough about the structure and function of the ecosystem to implement grazing management that will effect the desired response.

Future studies must continue elucidating the relationships between a wide range of grazing intensities and ecosystem responses. Experiments must continue assessing grazing gradients from none to light to moderate to heavy. Furthermore, research should focus on uncovering mechanisms controlling system dynamics in the hope that general principles might evolve. Overgrazing, defined as grazing intensity which will not sustain the desired state of an ecosystem, should not be compared to grazing removal; information from such studies does not advance our understanding but serves to further polarize complex ecological, political, and management issues.

Managing grazing for conservation objectives will require more than the simple RDM scorecards for simultaneously maximizing herbage removal and regrowth used by livestock producers now. Optimal timing and distribution of grazing as well as the type of grazer and grazing intensity will differ for each site and/or species of interest, necessitating monitoring and adaptive management until ecosystem responses under controlled situations can be assessed. Resource consultants are beginning to use remotely sensed RDM estimates in grazing management plans (Standiford and others 1999). Linking geographic information systems to direct management is necessary so that these tools can enjoy wider application. Monitoring efforts should be aimed at multiple spatial and temporal scales for state-transition model development that will lead toward heuristic and even serendipitous knowledge and away from the dogma that surrounds much of rangeland ecology today.

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Management Tools

Residual Dry Matter (RDM) Manipulation

To maintain long-term livestock production, range managers must cope with the vagaries of California climate. While location and yearly weather patterns limit herbaceous productivity in Californian annual grasslands, it has long been known that the amount of mulch remaining at summer's end influences the coming year's peak standing crop (Heady 1956, 1965; Hedrick 1948). Bartolome and others (1980) demonstrated that within a range of residual dry matter (RDM) levels representative of typical grazing intensities, RDM at the time of autumn germination had a positive relationship to peak standing crop of the ensuing year (*fig. 3*). This relationship was roughly consistent along a rainfall gradient from southern San Joaquin Valley to the northern Coast Ranges and has been validated for open grassland at a Sierran foothills site (Aimee Betts, unpublished data). The relationship was weakest at sites with <20 cm total annual rainfall.

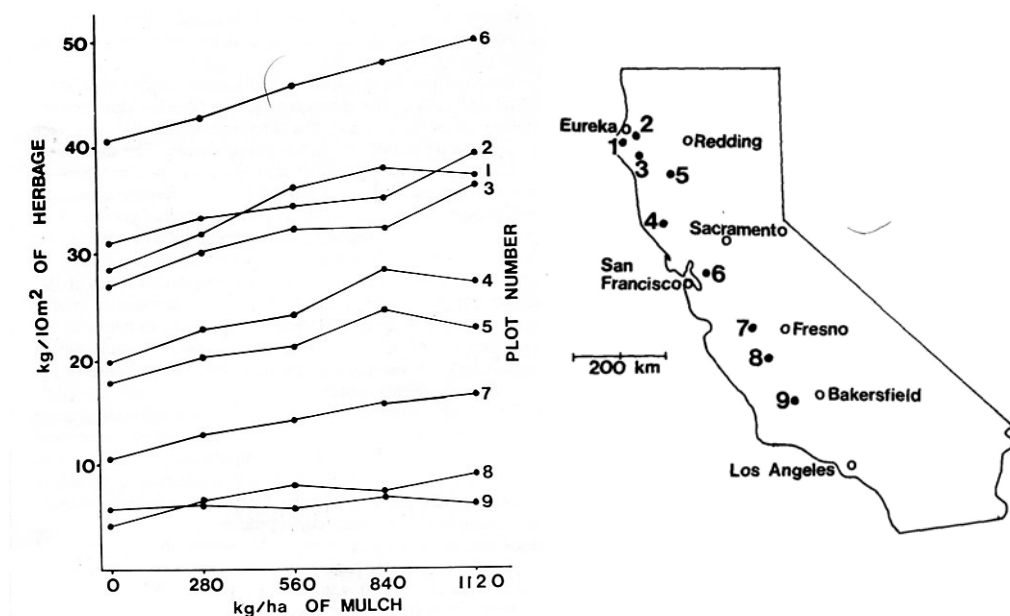


Figure 3—Herbaceous production response to residual dry matter manipulations at nine sites along a N-S rainfall gradient (modified from Bartolome and others 1980).

Mechanisms for this relationship have not been elucidated but are believed to be a favorable combination of light, space, nutrient, and water modifications by moderate levels of RDM. The effects of litter on vegetation in general were reviewed by Xiong and Nilsson (1999). The high RDM extreme, which was not tested by Bartolome and others (1980), probably inhibits production via these same parameters (J.W. Bartolome, unpublished data). Stemming from this work has been an effort to develop minimum RDM guidelines for grazing management in annual grasslands (Bartolome and others 2002, Clawson and others 1982, George and others 1985).

Residual dry matter has been shown to influence species composition on a Mendocino County site (Heady 1965, Pitt and Heady 1978), but recent analysis of the species composition component of the Bartolome and others (1980) data set indicates

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Air Pollution Impacts in the Mixed Conifer Forests of Southern California¹

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Abstract

Air pollution, principally in the form of photochemical ozone and deposition of nitrogen compounds, has significantly affected mixed conifer forests in the mountains of southern California. Foliar injury, premature needle abscission, crown thinning, and reduced growth and vigor have been well documented, particularly for ponderosa (*Pinus ponderosa* Laws.) and Jeffrey (*P. jeffreyi* Grev. and Balf.) pines on the western side of the pollution deposition gradient in the San Bernardino Mountains. Tree mortality of the more ozone-susceptible ponderosa and Jeffrey pines has led to alterations in stand composition, in favor of increased dominance by more ozone-resistant species such as incense cedar (*Calocedrus decurrens* [Torr.] Florin), white fir (*Abies concolor* [Gord. & Glend.] Lindl.), and sugar pine (*P. lambertiana* Doug.). Increased rates of litter deposition, alterations in C/N ratios in litter and soil, and reductions in fine root biomass of trees have also altered the dynamics of biogeochemical processing in stands impacted by ozone and excess N deposition. Research into the effects of atmospheric deposition across the mixed conifer forests of the San Bernardino Mountains continues to provide insights into the complex interactions among anthropogenic and natural stresses in a forest ecosystem.

Key words: air pollution, forest health, nitrogen deposition, ozone, San Bernardino National Forest, water quality

Introduction

For the past 40+ years, mixed conifer forests in the mountains of southern California have been exposed to the highest levels of oxidant air pollution and the highest levels of nitrogen deposition of any ecosystem in North America (Miller and McBride 1999, Takemoto and others 2000). These high concentrations of air pollutants arise as a consequence of a unique set of topographic, climatological, and social factors characteristic of the Los Angeles (LA) air basin. First, the Transverse Ranges, including the Santa Monica, San Gabriel, and San Bernardino Mountains to the north, and the Peninsular Ranges, including the San Jacinto and Santa Rosa Mountains to the east, are barriers to the westward flow of oceanic breezes, particularly during the summer months. The stagnant air masses and strong radiational heating contribute to the formation of a subsidence inversion layer, typically beginning at about 500 m (Edinger 1973). The inversion layer limits vertical mixing, which traps air pollutants at its base, leading to increased pollutant concentrations near ground level. Second, increased industrialization of the region during and after World War II, rapid population growth, and increased reliance on the automobile as the basic and

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necessary form of transportation across the region contributed into the atmosphere massive amounts of precursor pollutants in the form of hydrocarbons from gasoline and oxides of nitrogen from auto exhaust. Photochemical processes converted the precursor molecules to ozone (O_3), peroxyacyl nitrates (PANs), aldehydes, nitric acid, and other highly oxidative compounds (Finlayson-Pitts and Pitts 1986). These photochemical air pollutants, principally O_3 , have had significant adverse effects on the vegetation of the region, from agricultural crops near the coast to the mixed conifer forests of the San Bernardino Mountains.

Historical Trends of Air Quality in the San Bernardino Mountains

Tropospheric O_3 forms by the action of ultraviolet radiation (UV) on oxides of nitrogen, principally NO_2 . The photolysis of NO_2 produces NO and singlet O, which quickly reacts with molecular O_2 to produce O_3 . This reaction is rate-limited by the decomposition of O_3 and its reaction with NO, so that in the absence of other air pollutants, the concentration of O_3 produced by the photolysis of NO_2 is relatively low (Finlayson-Pitts and Pitts 1986). However, in the presence of reactive hydrocarbons, such as those from gasoline and auto exhaust, a series of complex catalytic reactions reduces the concentration of NO, leaving very little NO to react with O_3 and permitting the concentration of O_3 to greatly increase. The amount of surface ozone formed by these reactions depends upon time of day, amounts of precursor pollutants, and meteorological conditions. In the morning, large amounts of precursors are produced by morning rush hour traffic, but the concentration of O_3 is low. Ozone concentrations increase during the day as photochemical reactions continue. Concentrations also increase along a gradient from west to east as onshore breezes transport the polluted air mass eastward. In addition, the height of the inversion layer also increases from west to east as elevations increase from the coastal plain to the mountains and as temperatures increase from the coast to the interior. As a result, the highest O_3 concentrations in the LA Basin are typically found not in the valleys, but in mountain slopes facing LA at 1200 to 1500 m, near the base of the inversion layer. Afternoon heating of the mountain slopes also vents the highly polluted layers up and over the mountain ridgeline by upslope flow (Edinger 1973). The inversion layer may also serve as a reservoir for ozone in the evening. The lack of vertical mixing as the air mass cools and stabilizes reduces contact of ozone with scavenging processes such as deposition to ground surfaces and reaction with NO molecules. As a consequence, high concentrations of O_3 persist in the evening and early morning hours in forested areas of the mountains, while O_3 concentrations in the valleys typically decrease rapidly as the sun sets (Edinger and others 1972). Thus the mixed conifer forests on the western slopes of the San Bernardino Mountains (SBM) have been subjected not only to high concentrations of O_3 during mid to late afternoon but in the early morning as well, when humidity is relatively high and physiological activity of the trees is also at its peak.

Monitoring oxidant concentrations in the SBM began in 1968 with the placement of a Mast ozone meter at Rim Forest/Sky Forest (NRC 1977). Data from this instrument and correlated data from a monitoring station in San Bernardino indicated a continuing upward trend from 1963 in both peak ozone concentrations and in numbers of hours of elevated O_3 in the mountains. These trends culminated in 1974, when maximum hourly O_3 concentrations at Sky Forest exceeded 0.33 parts

per million (ppm) on 46 days. The highest hourly concentrations averaged 0.38 ppm, and the highest hourly concentration ever recorded was 0.60 ppm on June 28, 1974 (NRC 1977). Peak and mean O₃ concentrations in the mountains remained relatively constant throughout the 1970s, with growing season (May to September) means frequently exceeding 0.10 ppm for 10 or more hours daily (Miller and McBride 1975). However, in response to concerted air pollution control activities, O₃ levels have declined steadily since the 1980s (Miller and others 1997). Growing season ozone means in the late 1990s have declined to 0.05 to 0.06 ppm, and recent peak concentrations have rarely exceeded 0.22 ppm in the areas most severely impacted by ozone (CARB 1999).

A network of ozone analyzers located across the SBM was established in the 1970s. Data from these instruments showed that O₃ concentrations decreased along a gradient from west to east and from south to north across the mountain range (Miller and others 1986). Highest concentrations were found at sites facing the LA Basin, such as Crestline, Lake Gregory, and Sky Forest. Ozone concentrations decreased gradually until Barton Flats, and then they more rapidly approached baseline levels at Big Bear, Heart Bar, and Holcomb Valley. A more recent survey of air quality in the SBM indicated that a similar trend continues today, although current O₃ levels are significantly lower than those recorded in the 1970s (Watson and others 1999).

It is more difficult to establish historical trends for nitrogen deposition in the SBM because systematic monitoring for total N deposition has been conducted only relatively recently (Fenn and Poth 1999a). However, NO_x emissions in the south coast (Los Angeles) air basin decreased by 13 percent from 1985 to 1995 and NO₂ concentrations have decreased by 39 percent since 1980 (Alexis and others 1999), suggesting that N deposition has been decreasing since the 1980s. Deposition of reduced N forms (NH_x) in the western SBM is expected to decrease in the next 10 to 15 years as dairy operations in the Chino/Norco area, the major source of reduced N forms in the atmosphere (Luebs and others 1973), move north to central California.

Measurements of N in throughfall, dry deposition, and fog demonstrate that the gradient of N deposition is steeper than that of O₃ (Fenn and Bytnerowicz 1993). Total N deposition, based on throughfall data, is estimated to average 31 kg ha⁻¹ y⁻¹ in the western SBM and 5 kg ha⁻¹ y⁻¹ at Barton Flats, located at approximately the median of the O₃ gradient (Fenn and others 2000). Spatial variability in N deposition is high due to heterogeneous canopy cover and varying exposure to air pollution. Nitrogen deposition in microsites with high leaf area index is greater than plot-level average values. In the western SBM, it is estimated that total N deposition is greater than 50 kg ha⁻¹ y⁻¹ in sites with complete canopy cover and direct exposure to incoming pollutant masses. Nitrogen deposition in fog is also high in the western SBM, constituting about a third of total annual N deposition (Fenn and others 2000b), due to extremely high concentrations of N compounds in fog and effective fog interception by canopy surfaces. Wet and dry deposition of N pollutants is also much higher than previously expected in the SBM during the winter months (Fenn and Bytnerowicz 1997), the season when, compared to summer, ozone concentrations are extremely low.

Effects of Ozone on the Mixed Conifer Forest

Physiological Responses

Ozone is a gaseous air pollutant with a molecular weight similar to that of carbon dioxide (CO₂), and it follows the same diffusive pathway as CO₂ from the air surrounding a plant to intercellular air spaces. The primary mode of entry of gases into leaves is through the stomata, and the rate at which this gas exchange occurs is known as *stomatal conductance*. All the physiological and environmental factors that control stomatal conductance, such as light intensity, temperature, relative humidity, and soil moisture, also affect the rate at which O₃ enters the leaf (Runeckles 1992). Stomatal conductance is also determined by intrinsic genetic factors often correlated with the rate of growth of the plant. In general, fast growing annual species and agricultural crops have higher rates of stomatal conductance than perennials, shrubs, and trees. Plants with deciduous leaves have higher rates of conductance than those with evergreen foliage. Species adapted for growth under dry conditions have lower rates of stomatal conductance and, in general, are less affected by ozone than those growing under favorable soil moisture conditions. These broad correlations among plant growth rates, stomatal conductance, and ozone response are generally useful in predicting patterns of ozone effects across the landscape, but they cannot be used to predict individual species responses to ozone.

Once inside the leaf, O₃ diffuses through intercellular leaf spaces, following the diffusive pathways of CO₂, to areas of highest cellular physiological activity. The precise intercellular pathways and mechanisms by which O₃ is absorbed into plant cells and the biochemical mechanisms of O₃ toxicity to intercellular components are not well understood (Heath and Taylor 1997). Ozone, or the free radical by-products of its initial reactions at the cell surface, may react with components of the cell membrane, altering active transport of ions such as Ca²⁺ and K⁺ (Castillo and Heath 1990). This change in membrane polarity will also affect the pH gradient across the membrane, leading to a chain of events that include specific enzyme activation and deactivation and altered gene transcription (Heath 1987). If the amount of O₃ absorbed exceeds cellular detoxification and repair mechanisms, membrane function is irrevocably compromised, and normal biochemical activity ceases. One of the first indications of O₃ toxicity at the cellular level is loss of the enzyme responsible for carbon fixation, RUBISCO (ribulose biphosphate carboxylase/oxygenase; Pell and others 1994). This response is reflected at the whole-leaf level by a reduction in the rate of photosynthesis of leaves exposed to O₃. This reduction is reversible at first, but as the length of exposure or O₃ concentrations increase, the loss of photosynthetic capacity, accompanied by a loss of chlorophyll, becomes permanent. The first visible signs of foliar O₃ injury are chlorotic areas on the upper leaf surface, which reflect the permanent loss of photosynthetic capacity in the chloroplasts of the underlying cells. In broad-leaved plants these lesions usually are sharply defined by the network of leaf veins and veinlets, producing a chlorotic stipple over the leaf surface. In conifers, particularly in pines, the injury is more diffuse, producing a characteristic O₃ injury pattern known as *chlorotic mottle*. As O₃ injury accumulates, the leaf appears to age prematurely, leading to accelerated senescence and abscission of older leaves. The reduction in both rate of photosynthesis and amount of photosynthetic tissue in plants exposed to O₃ can lead to significant reductions in total amounts of carbon fixed over the course of the growing season, with concomitant reductions in carbohydrates available for repair, growth, reproduction, and defense (Heath and Taylor 1997).

Ecological Responses

The first indication that air pollution was having an effect on trees in the mixed conifer forest of the SBM was the observation in 1953 of significant needle chlorosis, necrosis, and premature needle abscission on ponderosa pine (*Pinus ponderosa* Laws.) in the vicinity of Crestline-Lake Gregory (Miller and McBride 1975). Possible scale insect or pathogenic disease etiologies were investigated, but observations of similar injury symptoms on grapes growing in the San Gabriel Valley suggested that an air pollutant might have been involved. Laboratory and field exposures of ponderosa pine branches to high concentrations of O₃ elicited injury symptoms similar to those observed in the field, and the chlorophyll content of needles exposed to O₃ was less than that of controls, as was also observed in the field (Miller and McBride 1975). Monitoring of pollutant concentrations in the Crestline area also revealed concentrations of oxidants similar to those that had elicited pine needle injury in the lab, confirming the identification of O₃ as the causal agent. Similar foliar injury symptoms were observed on a variety of plant species in the SBM, including Jeffrey pine (*P. jeffreyi* Grev. & Balf.), California black oak (*Quercus kelloggii* Newb.), sycamore (*Platanus racemosa* Nutt.), big-leaf maple (*Acer macrophyllum* Pursh), and several other trees, shrubs, and perennials (Richards and others 1968). Among conifers native to the SBM, ponderosa and Jeffrey pines were the most susceptible to O₃ injury, followed in order of increasing resistance by Coulter pine (*P. coulteri* D. Don), white fir (*Abies concolor* [G. & G.] Lindl.), big-cone Douglas-fir (*Pseudotsuga macrocarpa* [Vasey] Mayr), knobcone pine (*P. attenuata* Lemmon), incense cedar (*Calocedrus decurrens* [Torr.] Florin), sugar pine (*P. lambertiana* Doug.), lodgepole pine (*P. contorta* ssp. *murrayana* [Grev. & Balf.] Critch.), and limber pine (*P. flexilis* James) (Miller and McBride 1975).

By the late 1960s observations of the extent of oxidant injury to the mixed conifer forest from Crestline to Lake Arrowhead showed that over 46,000 ac of forest had heavy foliar injury, 54,000 ac had moderate amounts of injury, and 61,000 ac had light to no injury (Wert and others 1970). Estimates of tree mortality in the most heavily polluted areas of the forest suggested that over 25 percent of the pines might have died as a result of severe O₃ injury in combination with other causes (Miller and McBride 1975). Pines weakened by O₃ were particularly susceptible to attack by pine bark beetles (*Dendroctonus* spp.). Ozone-injured pines apparently emitted α -pinene, a bark beetle attractant (Stark and others 1968). The weakened pines produced less sap, the primary defense against bark beetle emergence. Tree mortality of ponderosa pines in the heavily damaged areas of the SBM due to increased intensity of bark beetle attacks was estimated to be up to 24 percent during a 3-year period in the late 1960s (Cobb and Stark 1970). Severely O₃-injured pines also did not recover from periods of drought stress as did uninjured trees (Miller and McBride 1975). Thus, pine mortality in the SBM was due to severe O₃ injury acting in combination with other biotic and abiotic stressors.

Historical Trends in Ozone Injury to the Mixed Conifer Forest

In the early 1970s, a series of 18 permanent observation plots were established in the mixed conifer forest of the SBM along the air quality gradient from west to east (fig. 1). At each plot, 50 ponderosa and/or Jeffrey pines >30 cm in diameter were permanently tagged; stem diameter of each was measured, and the amount of O₃

injury on the tree crowns was evaluated. Ozone injury was measured using a scale called the *FPM Score*, which recorded the youngest annual whorl with visible O₃ injury symptoms (FPM=Forest Pest Management; Miller and others 1996). In this scale, low numbers indicate higher O₃ injury. All other trees on the plots >10 cm DBH (diameter at breast height) were also measured and evaluated for O₃ injury (Taylor 1973). Elevation, slope, aspect, precipitation, available soil water, and estimated O₃ dose were also recorded at each plot. Tree condition of pines was measured annually from 1973 until 1978 and at a sub-set of these plots at 4-year intervals from 1978 until 1994. Measurements of crown conditions in 1974 clearly showed a trend for decreased amounts of O₃ injury from plots on the western edge of the forest closest to Los Angeles to those in the northeast. Remeasurements of those same trees in 1988 showed general improvements in crown conditions at all plots except Camp Paivika, the plot with the highest amount of O₃ injury and the highest input of ambient O₃ (Miller and Rechel 1999). Data from remeasurements of a smaller subset of plots in 1994 showed that pines at Camp Paivika showed no improvement in O₃ injury scores over the 20-year period and that the condition of trees at Camp Angeles and Heart Bar had only slightly improved (*fig. 2*). Despite the relatively high O₃ injury scores and high rates of foliar senescence and abscission of ponderosa pines at Camp Paivika, many of these trees have greater relative growth rates and higher standing biomass than ponderosa pines growing in less polluted areas (Grulke and Balduman 2000). The high rates of N deposition at the western end of the gradient appear to compensate for, or indeed override, the adverse effects of O₃ in this area.

Although the FPM injury score showed only slight improvement over the 20-year period from the 1970s until the 1990s, other measures of tree health indicated that severely injured pines were capable of recovering in response to lower ambient O₃ in recent years (Miller and Rechel 1999). Measurements of the number of annual whorls retained on a sample of over 200 ponderosa pines at Dogwood campground, near Blue Jay, showed that in 1973 most pines held only two to three annual whorls (*fig. 3*). By 1992 many more pines retained four to five annual whorls (*fig. 3*), and 43 percent of all the pines showed improvements in crown condition as indicated by increased needle retention (Miller and Rechel 1999). Increased needle retention has been reflected in increased tree growth in recent years in the same area (Arbaugh and others 1999). Tree ring width data from increment borings of 166 ponderosa pines at Dogwood campground were converted to increments of basal area.

Growth patterns of ponderosa pine from the 1880s to the present can generally be divided into three phases (*fig. 4*). Growth gradually increased from the 1880s until about 1945, but over the next 30 years basal area incremental growth declined, reaching its lowest point in the mid-1970s. After 1975, tree growth increased rapidly, reaching rates similar to those seen before the 30-year growth decline. Although the post-war decline in tree growth and the subsequent recovery roughly corresponded to changes in ambient O₃ air quality over the same time interval, it is likely that long-term patterns of annual precipitation in the forest were the primary factor controlling tree growth. A century of annual precipitation data from Big Bear dam indicates that the period 1925 to 1949 was the wettest on record, 1950 to 1974 the driest, and 1975 to 1991 again was a wet period (Arbaugh and others 1999). However, analysis of tree ring patterns of individual trees suggested that some pines with significant amounts of O₃ injury might have been less able to recover from the drought stress than healthy trees. A similar pattern of growth in response to O₃ and drought stress also has been

observed in bigcone Douglas-fir growing along the O₃ gradient in the SBM (Peterson and others 1995).

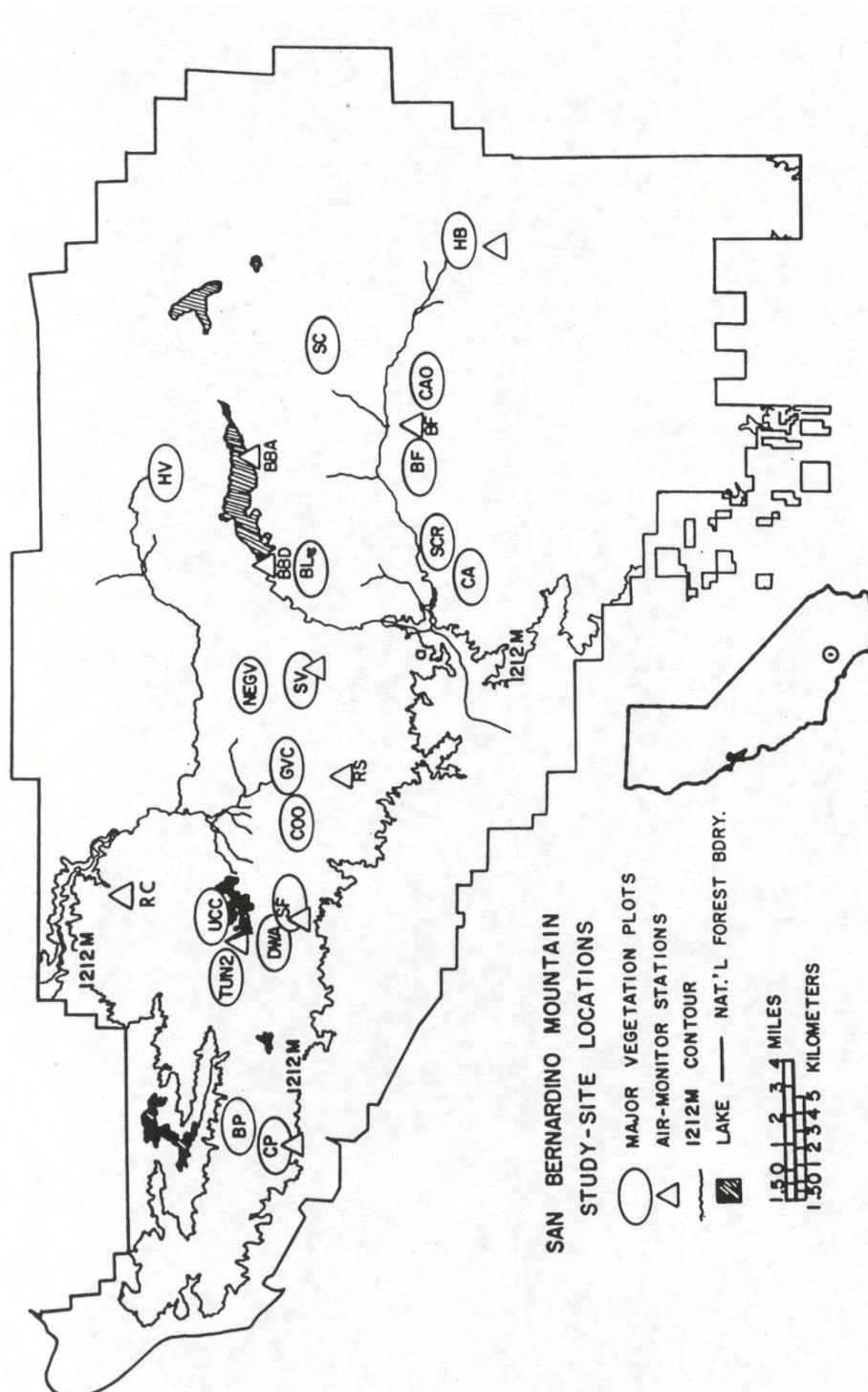


Figure 1—Location of permanent forest plots in the San Bernardino National Forest, established in 1972 to monitor long-term effects of ozone on ponderosa and Jeffrey pines and other dominant tree species in the plots. (Adapted from Miller and Rechel 1999)

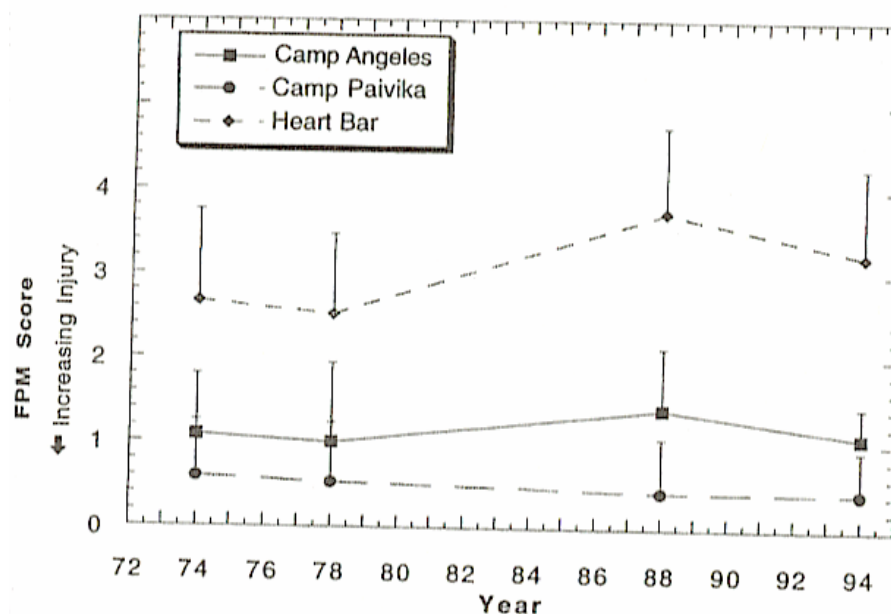


Figure 2—Changes in ozone injury scores from 1974 to 1994 for ponderosa and Jeffrey pines at three plot locations in the San Bernardino Mountains, based on a average of 50 trees per plot. Camp Paivika is in the high ozone area, Heart Bar is a relatively clean site, and Camp Angeles is intermediate. (Adapted from Miller and Rechel 1999)

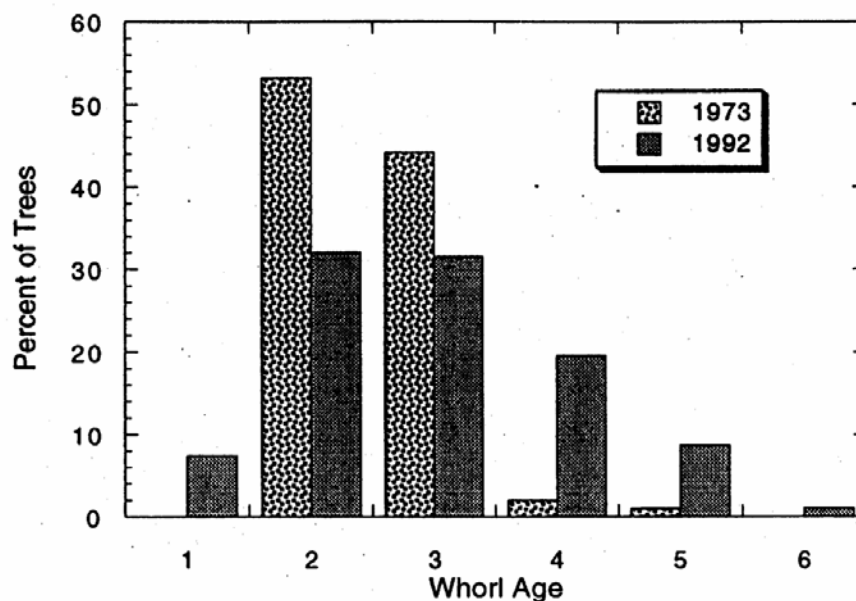


Figure 3—Average number of annual needle whorls retained by ponderosa pines (n=219) in an area of high ambient ozone in 1973 and in 1992. The higher number of annual whorls retained in 1992 is an indication of improved tree health. (From Miller and Rechel 1999)

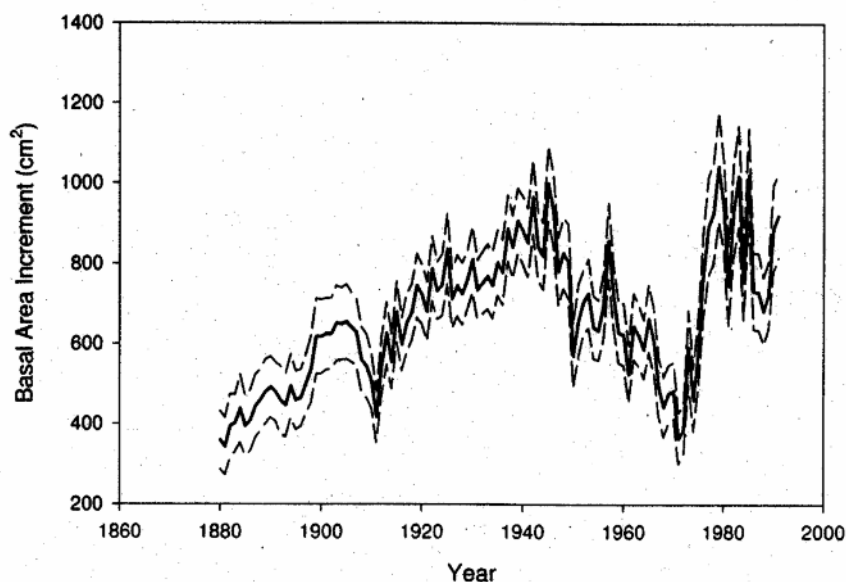


Figure 4—Average annual basal area increments of ponderosa pines ($n=40$ to 166 , based upon tree age) growing near Lake Arrowhead, San Bernardino Mountains. Dashed lines are 95 percent confidence limits. (From Arbaugh and others 1999)

Ozone and Drought

The interaction between O_3 and drought stress is complex and may involve both synergistic and antagonistic reactions (Grulke 1999, Temple and Miller 1998, Temple and others 1993). Trees exposed to O_3 under conditions of drought stress will generally show less O_3 injury than those growing under favorable soil-water conditions because of reduced rates of gas exchange in the drought-stressed trees. This interaction between O_3 and drought has been observed both under experimental conditions (Temple and others 1992, 1993) and in the field (Temple and Miller 1998). However, if the mechanism of stomatal closure is impaired because of O_3 injury (Grulke 1999, Patterson and Rundel 1989, Torsethaugen and others 1999) the trees may be more vulnerable to drought stress because of slow or incomplete stomatal closure. Reduced root biomass in ponderosa pine trees chronically stressed by O_3 may also predispose O_3 -injured trees to increased susceptibility to drought stress (Grulke and others 1998). Severely O_3 -injured pines may also increase rates of stomatal conductance on remaining foliage to compensate for the loss of older annual whorls (Beyers and others 1992, Coyne and Bingham 1982). This increase in the rate of gas exchange may render these needles more susceptible to O_3 injury than needles from uninjured trees. It is also possible that those individual pines that are particularly susceptible to O_3 may have intrinsically higher rates of stomatal conductance than more resistant trees, although the evidence for this is currently tenuous (Coyne and Bingham 1982, Grulke 1999).

Seasonal and annual patterns of precipitation will also alter tree responses to O_3 . In the SBM, where almost all soil water is contributed by winter precipitation, the total amount of available water in the upper soil column at the beginning of summer will control the physiological activity, length of growing season, and thus the total

amount of seasonal O_3 flux for most trees in the mixed conifer forest. Significantly greater amounts of O_3 will be absorbed into leaves following a wet winter than during a dry year, even if ambient O_3 concentrations are the same in both years (fig. 5) (Gulke 1999, Temple and Miller 1998). As an additional complication, the morphology and physiology of pine needles are altered by the environmental conditions under which they develop. Leaves developing during periods of favorable moisture conditions tend to be larger, longer, and have greater intrinsic rates of stomatal conductance than those produced during drought years. Those larger needles will develop greater amounts of O_3 injury than the smaller ones, even when exposed to similar ambient O_3 concentrations (Temple and Miller 1998). Ponderosa and Jeffrey pines will retain greater numbers of annual whorls of needles during periods of drought. But in the first wet year following a drought, the great increase in the amount of O_3 injury on older pine foliage leads to accelerated senescence and premature abscission of older age classes of needles. As a consequence, litter accumulation in the high O_3 areas of the mixed conifer forest increases greatly in the year following a drought (Temple and Miller 1998).

Effects of Ozone on Species Composition

The mixed conifer forest of today in the SBM differs greatly from the forest found by the original European settlers. The original forests were subjected to frequent low-intensity fires that burned grasses, shrubs, and competing understory trees. The forest landscape was dominated by large-diameter pines and other fire-resistant species in open, irregularly distributed stands. Following a century of intense logging of old-

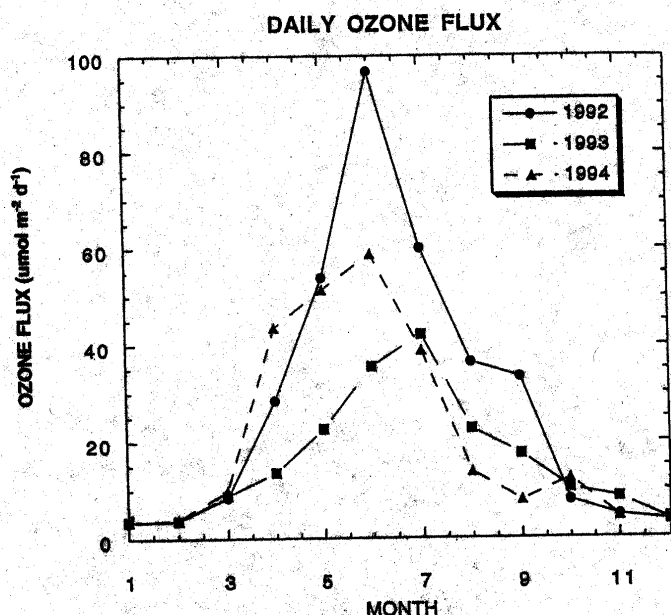


Figure 5—Mean daily ozone flux to 1-year-old needles of mature ponderosa and Jeffrey pines growing at Barton Flats, San Bernardino Mountains, from 1992 to 1994. Higher fluxes in 1992 reflected improved growing conditions in 1991-1992, following several previous years of drought. (Adapted from Temple and Miller 1998)

growth trees, stand-replacement fires, bark beetle infestations, salvage logging, strict fire suppression tactics, O₃ damage, and nitrogen deposition, the forest has been transformed. In the western, more mesic areas of SBM, the open growth, fire-resistant pine-dominated forest has become a closed-canopy forest dominated by dense stands of incense cedar and white fir (Minnich 1999). While fire-suppression policies have played a major role in this transformation, the impacts of air pollution should not be minimized. Ponderosa and Jeffrey pines are significantly more susceptible to O₃ than are incense cedar and white fir (Miller and McBride 1978), and they suffered far greater damage due to O₃. Salvage logging removed over 25 percent of mature pines damaged by combinations of O₃ and bark beetle infestations in the 1970s (Miller and McBride 1975). Measurements of basal diameter growth of all trees >30 cm in diameter in plots along the O₃ gradient from west to east showed that in high O₃ areas ponderosa pine basal area growth was reduced relative to incense cedar and white fir (Miller and others 1997). Measurements of tree seedling mortality and establishment also showed increased success of incense cedar and white fir seedlings and saplings, relative to that of pines (McBride and Laven 1999). Ozone injury to pines also greatly increased the amount of leaf litter on the forest floor in high O₃ areas of the forest, because of accelerated senescence and abscission of O₃-injured pine needles (Arkley and others 1980). Rates of leaf litter accumulation and decomposition may also be significantly increased by the higher rates of N deposition at these plots on the western side of the SBM (Fenn 1991). The thick litter layer discourages the establishment of pine seedlings, which is an additional factor in the transformation of the mixed conifer forest from open-growth pine stands to a closed canopy, dense incense cedar/white fir-dominated forest.

The effects of O₃ in altering species composition and community dynamics of forest understory species are less well known. Ozone injury symptoms have been noted since the 1950s on understory species such as blue elderberry (*Sambucus mexicana* C. Presl.), wild grape (*Vitis girdiana* Munson), and several woody species of riparian areas such as sycamore (*Platanus racemosa* Nutt.) and big-leaf maple (*Acer macrophyllum* Pursh) (Richards and others 1968). Foliar O₃ injury symptoms also have been observed on a variety of annual and perennial herbaceous plants in the mixed conifer forest (Temple 1999). However, unlike the systematic study of O₃ effects on injury and growth of overstory trees, no careful chronological sequence measurements of understory species frequency or density have been conducted along the air pollution gradient in the SBM. Shrub and herbaceous plant cover was measured once along the pollution gradient in 1973 (Taylor 1973), but these observations were not sufficient to establish a causal relationship between ambient O₃ concentrations and changes in community structure or composition. The same species of herbaceous annuals and perennials and woody shrubs recorded in plots in high O₃ areas in 1972 were also present in 1996 (Temple 1999). Some of these species, such as blue elderberry and mugwort (*Artemisia douglasiana* Besser) are also highly susceptible to O₃ (Temple 1999). These observations, while hardly definitive, suggest that O₃ may have had only minor direct effects on understory plant community composition in the SBM in comparison with other factors, such as habitat alteration, fire suppression, invasion by weedy plants, and N deposition (see below).

Most of the rare, threatened, endangered or endemic plant species in the SBM are found to the north and east of high O₃ areas, primarily in the Bear Valley and on the limestone deposits on the north slope of the mountains. However, at least 23 species or subspecies of rare or threatened plants are found in western areas of the forest (Skinner and Pavlik 1994). Scattered observations on some of these species did

not reveal any foliar O₃ injury in recent years (Temple 1999). However, no systematic surveys of O₃ injury have been conducted on these plants, so no conclusions can be drawn regarding the impacts of O₃ on threatened and endangered plant species in the SBM. Epiphytic lichen communities in the San Bernardino Mountains have been dramatically reduced both in species diversity and in numbers both historically and relative to comparable habitats with little air pollution (Nash and Sigal 1999). However, the role of O₃ in this reduction, relative to other factors such as N deposition or other pollutants, has not been determined.

Nitrogen Deposition in the Mixed Conifer Forest

Nitrogen Cycling in Forest Ecosystems

Nitrogen is the mineral nutrient most limiting to growth of forest trees. Most N in forest ecosystems is stored in the soil in the form of organic N, not readily assimilable by plant roots. Mineralization of organic N and nitrification convert N to forms readily available to plants. Because mineral N is generally present in limiting amounts in forest ecosystems, these systems have evolved tightly-coupled processes to conserve N through the cycle of litter decomposition, mineralization, bacterial and fungal associations, and internal N cycling (Chapin 1980). Conifers in particular are adapted to nutrient-poor soils, and they have evolved efficient mycorrhizal associations for nutrient uptake from the soil and internal retranslocation of N from senescent foliage prior to abscission (Chapin 1980). Because of this tight coupling of N deposition, mineralization, and uptake, cycling of N through forest ecosystems is generally highly efficient, and in a healthy ecosystem leaching of mineral N is low (Johnson 1992). Mixed conifer forests of California are no exception, and trees respond with increased growth to added N (Kiefer and Fenn 1997). Thus, increased rates of deposition of atmospheric N may actually increase tree growth if other nutrients and particularly water are not also limiting. However, if N deposition from atmospheric sources is in excess, normally conservative processes of N cycling and N retention within the ecosystem can be disrupted, producing a condition referred to as N saturation (Aber and others 1995).

Nitrogen Deposition in the San Bernardino Mountains

Recent studies in the mixed conifer forest in the SBM have suggested that western sections of the forest are currently experiencing N-saturated conditions (Fenn and Poth 1999a). Rates of N deposition, primarily in the form of dry deposited nitrate, ammonium, and nitric acid and N deposition in fog, can exceed 30 kg ha⁻¹ y⁻¹ as an average near Crestline/Lake Gregory and points west (Fenn and Bytnerowicz 1993). As mentioned earlier, total N deposition is estimated to be as high as 50 kg ha⁻¹ y⁻¹ in sites with complete canopy cover and direct exposure to polluted air masses (Fenn and others 2000). In contrast, total N deposition on the eastern side of the SBM is generally <5 kg ha⁻¹ y⁻¹. Evidence for N-saturation in areas of high N deposition includes increased nitrate concentrations in stream water from contaminated watersheds, elevated nitrate concentrations in soil solution and soil leachate, increased volatilization of N from the soil, decreased C:N ratios in soil and foliage, increased N concentrations and N:P ratios in foliage, nitrate accumulation in foliage of understory and overstory plants, and altered rates of litter decomposition (Fenn and others 1996, Fenn and Poth 1999a, 1999b).

Effects of Excess N Deposition

The direct and indirect effects of excess N deposition on the mixed conifer forest are under investigation. Deposition of nitric acid on plant foliage can alter surface wax structure and chemical composition (Bytnerowicz and others 1998b). In addition, nitric acid deposited on plant leaves may be a source for plant N, both through a transcuticular pathway (Hanson and Garten 1992) and stomatal uptake (Bytnerowicz and others 1998a). Concentrations of N in plant foliage from contaminated areas of the forest are significantly higher than those from areas of low N deposition (Fenn and others 1996). As a result of the combined effects of ozone stress (enhanced foliar senescence and abscission) and nitrogen (greater foliar and branch growth), litter production is increased in the western SBM. Litter with high N concentrations frequently exhibits higher decomposition rates in the short term (Fenn 1991, Fenn and Dunn 1989), but numerous studies show greatly reduced decomposition rates and greater humus accumulation in the later stages of decomposition when litter N content is high (Berg 2000, Fog 1988). Thus, N enrichment as a result of chronic N deposition favors litter accumulation on the forest floor by stimulating litter production and simultaneously causing long-term reductions in litter decomposition rates. The available evidence also suggests that C sequestration also may be greater in these forests influenced by the combined effects of ozone and N, with greater amounts of C stored in the forest floor and in woody biomass.

As noted earlier, the thick litter layer in the western SBM can retard germination of pine seeds, contributing to the change in species composition of the forest. It has not been clearly established whether higher rates of N deposition have increased growth of pines or other trees in the mixed conifer forest, but growth rates are higher in the western high pollution sites than in the less polluted sites to the east, notwithstanding the high O₃ concentrations that co-occur with N deposition (Arbaugh and others 1999, Grulke and Balduman 1999, M.E. Fenn and M.A. Poth, unpublished data). However, other environmental factors such as elevation, precipitation, temperature, and soil characteristics also vary across this gradient, making it difficult to determine the most important factors causing higher growth rates in the high pollution sites. Interactions between O₃, which can inhibit tree growth, and N, which can enhance growth, are complex, particularly as both interact with seasonal and annual variations in soil water availability. However, the higher growth rates in the western SBM suggest that elevated N deposition in areas such as Camp Paivika has acted to ameliorate the adverse effects of O₃ on the growth of ponderosa pine in this area of the forest. The effects of excess N on N-fixation, mycorrhizal associations, N mineralization, insect and disease infestations, and other ecosystem processes need further investigation (Fenn and Poth 1999a).

Nitrogen enrichment of the mixed conifer forest may also play a role in altering species composition and competitive interactions among species (Takemoto and others 2000). Because most native forest species have adapted to an N-limited environment, they may be at a competitive disadvantage to species able to utilize the extra N from atmospheric deposition to enhance growth and reproductive potential. The latter may be particularly true for alien weedy species of grasses that have invaded the mixed conifer forest in recent years. Excess atmospheric deposition of N may have contributed to the recent rapid conversion of coastal sage shrub habitats to annual grasslands dominated by weedy annual species of Mediterranean origin (Allen and others 1998). However, there is as yet no direct evidence that excess N has

contributed to the invasion of the mixed conifer forest in the SBM by weedy species or has altered competitive interactions among native species of annuals, perennials, or woody plants. Bracken fern (*Pteridium aquilinum* [L.] Kuhn), a nitrophilous species with a known capacity to accumulate nitrate in foliage (Fenn and others 1996), is a dominant, vigorously growing understory species at Camp Paivika, an N-saturated site in the SBM. However, it is not known whether long-term N deposition has favored bracken fern or whether bracken fern was already the dominant understory species prior to the occurrence of elevated N deposition.

The clearest response of the mixed conifer forest in the SBM to excess N deposition is the greatly increased concentrations of nitrate in stream water draining areas with high N deposition. Elevated nitrate loss is observable at the watershed scale and is the classic symptom of an N-saturated ecosystem (Fenn and others 1996). Surprisingly, and notwithstanding the N enrichment of soil and foliage in the western SBM, the bole diameter growth of ponderosa pine and California black oak trees at Camp Paivika increased significantly after three years of N fertilization at 50 or 150 kg ha⁻¹ yr⁻¹. It is not yet clear how the forest can export large quantities of excess N in stream water and as gaseous N emissions from soil and yet the production of woody biomass is still N-limited. Earlier studies indicated that foliar biomass production in ponderosa pine was not N-limited at Camp Paivika, but it was N-limited in low pollution sites in the SBM and San Gabriel Mountains (Kiefer and Fenn 1997). Further studies are underway to address this phenomenon. The interactive effects of high N deposition and ozone on conifer growth and carbon allocation are also under active investigation. Early results indicate that O₃ injury and N deposition can interact to increase rates of foliage loss and reduce fine root growth of ponderosa pine (Grulke and Balduman 2000). The consequences of this interaction in relation to drought stress and seasonal patterns of soil water availability are currently under investigation.

In a 3-year study of 19 streams across the SBM, a strong relationship was found between N deposition rates and nitrate concentrations in stream water (Fenn and Poth 1999b). Stream nitrate concentrations generally peaked in mid-winter, in response to large volume winter storms, although extremely high peak summertime concentrations also occurred following summer thundershowers in some streams draining the San Geronio Wilderness. Asynchronies between periods of maximum availability of mineralized N and biological demand contribute to increased leakage of N from the system (Fenn and Poth 1999a, 1999b). This temporal asynchrony is a function of the Mediterranean climate, characterized by major runoff periods in the winter, while plant N demand is expected to be greatest in the warm, dry spring and summer seasons. Another critical factor contributing to the highly open N cycling nature of these N saturated systems is the high nitrifying potential of the soil. Laboratory and field studies of N mineralization and nitrification show that ammonium is rapidly and completely nitrified in soil. This means that all the mineralized N is rapidly converted to nitrate, a highly mobile form of N, for which there are no effective retention mechanisms in soil except for microbial and plant uptake. The possibility that high concentrations of nitrate in stream water may be toxic to aquatic organisms during sensitive periods in their reproductive cycle will be investigated in future studies (Fenn and others 2000a).

Nitrate concentrations in streams of the SBM and San Gabriel Mountains are the highest reported for wildland ecosystems in North America. Peak concentrations approaching 400 µEq L⁻¹ (fig. 6; Fenn and Poth 1999b, Riggan and others 1985) are

not unusual during high runoff periods. In the more severely N saturated watersheds in the SBM, nitrate levels in streams and springs remain elevated ($>70 \mu\text{Eq L}^{-1}$) year-round. By comparison, in relatively undisturbed forested watersheds, peak nitrate levels are typically $5\text{--}10 \mu\text{Eq L}^{-1}$ or lower, and baseline values are beyond detectable limits.

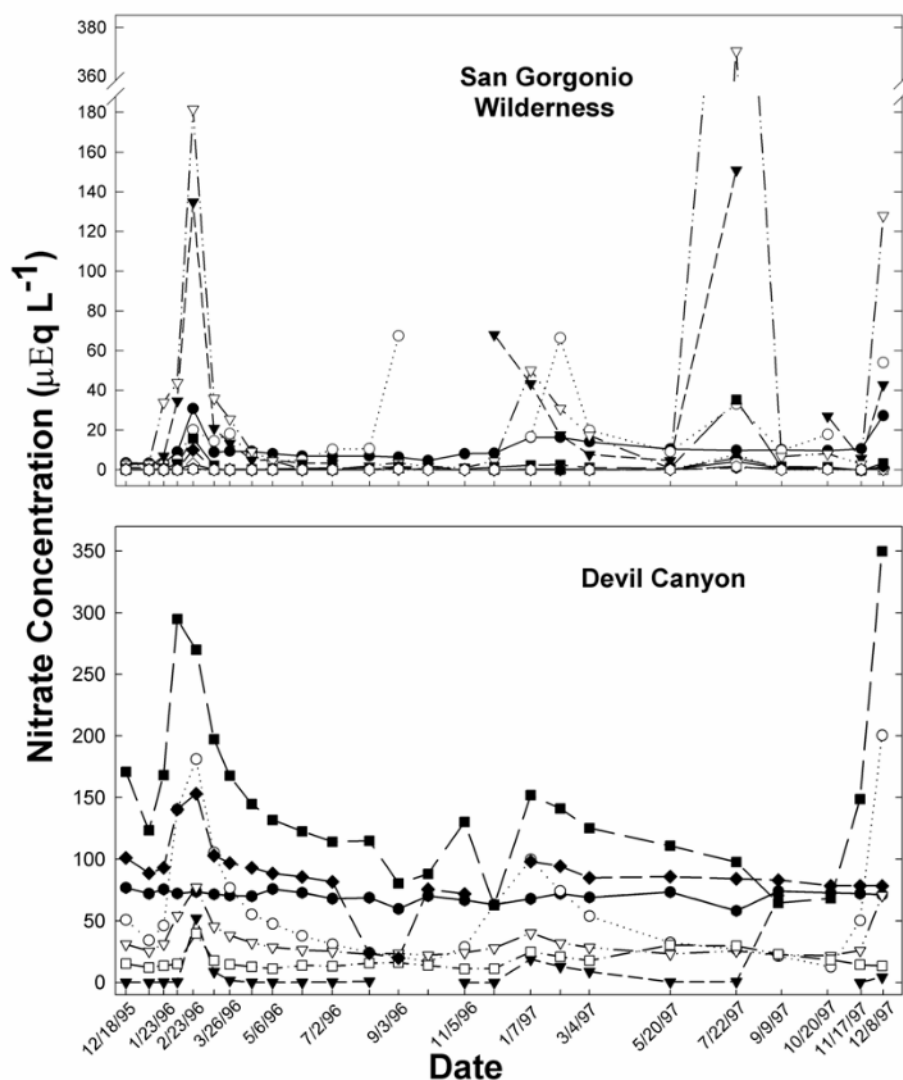


Figure 6—Nitrate concentrations in streamwater draining from areas of high nitrogen deposition (Devil Canyon) and low to moderate deposition (San Gorgonio Wilderness) in the San Bernardino Mountains, 1995 to 1997. (Adapted from Fenn and Poth 1999)

Summary

Montane forests in southern California have been subjected to high levels of ozone air pollution and deposition of nitrogen compounds for several decades. Severe O_3 injury to ponderosa and Jeffrey pines and other forest tree species was observed

beginning in the late 1950s. By the early 1970s, over 25 percent of the pines growing on the west side of the San Bernardino Mountains had died because of O₃ damage in combination with bark beetles, drought, and other natural stressors. The selective removal of pines in association with fire-suppression policies has contributed to the change in species composition of the mixed conifer forest, from open, pine-dominated stands to dense, closed stands dominated by incense cedar and white fir. Ambient O₃ concentrations in the mountain forests are now significantly lower than in previous decades, and crown conditions and growth rates of pines have improved in recent years. However, O₃ injury to pines and other species of native annuals, perennials, and woody plants of the mixed conifer forest continues to be observed on slopes and ridge-tops facing Los Angeles, and O₃ continues to have significant adverse impacts on these forests.

The effects of excess N deposition on the mixed conifer forest have only recently been investigated. Evidence has accumulated that the westernmost areas in the SBM are N-saturated, with consequences for biogeochemical cycling of N, tree growth, C sequestration, and export of N from the forest ecosystem. Both N deposition and ozone toxicity interact with seasonal and annual variations in precipitation and in soil water availability. The effects of excess N deposition in the mixed conifer forest on productivity, biogeochemical cycling, and soil and stream water hydrology are areas of continuing investigation.

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Sensitive Species of Snakes, Frogs, and Salamanders in Southern California Conifer Forest Areas: Status and Management¹

Glenn R. Stewart², Mark R. Jennings³, and Robert H. Goodman, Jr.⁴

Abstract

At least 35 species of amphibians and reptiles occur regularly in the conifer forest areas of southern California. Twelve of them have some or all of their populations identified as experiencing some degree of threat. Among the snakes, frogs, and salamanders that we believe need particular attention are the southern rubber boa (*Charina bottae umbratica*), San Bernardino mountain kingsnake (*Lampropeltis zonata parvirubra*), San Diego mountain kingsnake (*L.z. pulchra*), California red-legged frog (*Rana aurora draytonii*), mountain yellow-legged frog (*R. muscosa*), San Gabriel Mountain slender salamander (*Batrachoseps gabrieli*), yellow-blotched salamander (*Ensatina eschscholtzii croceater*), and large-blotched salamander (*E.e. klauberi*). To varying degrees, these taxa face threats of habitat degradation and fragmentation, as well as a multitude of other impacts ranging from predation by alien species and human collectors to reduced genetic diversity and chance environmental catastrophes. Except for the recently described San Gabriel Mountain slender salamander, all of these focus taxa are included on Federal and/or State lists of endangered, threatened, or special concern species. Those not federally listed as Endangered or Threatened are listed as Forest Service Region 5 Sensitive Species. All of these taxa also are the subjects of recent and ongoing phylogeographic studies, and they are of continuing interest to biologists studying the evolutionary processes that shape modern species of terrestrial vertebrates. Current information on their taxonomy, distribution, habits and problems is briefly reviewed and management recommendations are made. Further research is needed to elucidate their biological status and needs and to provide the basis for appropriate management programs. Programs must be monitored to ensure that desired objectives are achieved.

Key Words: collecting, degradation, endangered species, ensatina, extinction, extirpation, fragmentation, fuel wood, habitat loss, mountain kingsnake, off-highway vehicle, red-legged frog, riparian, rubber boa, salamander, special concern, threatened species, yellow-legged frog

Introduction

Our area of concern in this paper is limited primarily to the conifer forest and included riparian habitats above 1,230 m in roughly the southern two-thirds of the southern California mountains and foothills assessment region described by

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Stephenson and Calcarone (1999). This elevation break generally corresponds to the lower limit for conifer forest habitats at this latitude. The area includes the south coast ranges (Sierra Madre, San Rafael, Santa Ynez, and Topatopa Mountains and Pine Mountain) in Ventura County, the Mount Pinos area straddling the Ventura-Kern County line, the Piute and Tehachapi Mountains in east-central Kern County, the transverse ranges (Santa Monica, San Gabriel, and San Bernardino Mountains) in Los Angeles and San Bernardino Counties, the peninsular ranges (San Jacinto, Santa Rosa, and Laguna Mountains) in Riverside and San Diego Counties, the Santa Ana Mountains in eastern Orange and western Riverside Counties, and certain isolated mountains in San Diego County. At least 35 species of amphibians and reptiles are known to occur regularly in the area: five salamanders, seven frogs and toads, one turtle, eight lizards, and 14 snakes (*table 1*). Many of these are wide-ranging species that include the mountains within their geographic range, but others are more or less restricted to montane habitats.

Mostly adjacent to the greater Los Angeles-San Diego metropolitan area, with a population of over 15 million people (Stephenson and Calcarone 1999), many of these amphibian and reptile species are impacted negatively by human activities, and 12 have some or all of their populations identified as experiencing some degree of threat (*table 1*). We discuss here three taxa of snakes, two taxa of frogs, and three taxa of salamanders that we believe are in particular need of attention as sensitive species. Although the California red-legged frog generally occurs at lower elevations peripheral to conifer forest areas, and ranges farther north along the coast, it is included because of its critically threatened status and omission from other habitat area discussions in these proceedings.

Southern Rubber Boa *Charina bottae umbratica* Klauber 1943

Description

A small (total length 35-55 mm, Hoyer and Stewart 2000a), rather stout-bodied snake with smooth scales and a blunt head and tail (*fig. 1*; Brown 1997). Adults are light brown or tan in dorsal color with an unmarked yellow venter; juveniles are pale without a distinct margin between dorsal and ventral coloration (Hoyer and Stewart 2000a). The subspecies may be further characterized as follows: frontal scale usually sub-rectangular with a straight or only slightly convex or angular posterior margin, generally 41 or fewer mid-dorsal scale rows, usually 196 or fewer full-sized ventral scales (Rodriguez-Robles and others 2001).

Table 1—Amphibian and reptile species known to occur regularly above 1,230 m in conifer forest areas of southern California. (All names follow Crother 2000.)

Salamanders	
	Ensatina- <i>Ensatina eschscholtzii</i> (SC, FS)*
	Black-bellied Slender Salamander- <i>Batrachoseps nigriventris</i>
	Tehachapi Slender Salamander- <i>Batrachoseps stebbinsi</i> (ST, FS)
	San Gabriel Mountain Slender Salamander- <i>Batrachoseps gabrieli</i> (FS)*
	Arboreal Salamander- <i>Aneides lugubris</i>
Frogs and Toads	
	Pacific Treefrog- <i>Pseudacris regilla</i>
	California Treefrog- <i>Pseudacris cadaverina</i>
	Red-legged Frog- <i>Rana aurora</i> (FT, SC)*
	Mountain Yellow-legged Frog- <i>Rana muscosa</i> (FE, SC)*
	American Bullfrog- <i>Rana catesbeiana</i> (introduced)
	Western Toad- <i>Bufo boreas</i>
	Arroyo Toad- <i>Bufo californicus</i> (FE, SC)
Turtles	
	Pacific Pond Turtle- <i>Clemmys marmorata</i> (SC, FS)
Lizards	
	Coast Horned Lizard- <i>Phrynosoma coronatum</i> (SC, FS)
	Granite Spiny Lizard- <i>Sceloporus orcutti</i>
	Western Fence Lizard- <i>Sceloporus occidentalis</i>
	Common Sagebrush Lizard- <i>Sceloporus graciosus</i>
	Common Side-blotched Lizard- <i>Uta stansburiana</i>
	Western Skink- <i>Eumeces skiltonianus</i>
	Gilbert's Skink- <i>Eumeces gilberti</i>
	Southern Alligator Lizard- <i>Elgaria multicarinata</i>
Snakes	
	Western Threadsnake- <i>Leptotyphlops humilis</i>
	Rubber Boa- <i>Charina bottae</i> (ST, FS)*
	Ring-necked Snake- <i>Diadophis punctatus</i> (FS)
	Striped Racer- <i>Masticophis lateralis</i>
	Gophersnake- <i>Pituophis catenifer</i>
	Common Kingsnake- <i>Lampropeltis getula</i>
	California Mountain Kingsnake- <i>Lampropeltis zonata</i> (SC, FS)*
	Western Terrestrial Gartersnake- <i>Thamnophis elegans</i>
	Two-striped Gartersnake- <i>Thamnophis hammondi</i> (SC, FS)
	Western Black-headed Snake- <i>Tantilla planiceps</i>
	Western Lyresnake- <i>Trimorphodon biscutatus</i>
	Nightsnake- <i>Hypsiglena torquata</i>
	Speckled Rattlesnake- <i>Crotalus mitchellii</i>
	Western Rattlesnake- <i>Crotalus viridis</i>

FE—Federally Listed Endangered Species

FT—Federally Listed Threatened Species

ST—State Listed Threatened Species

SC—State Species of Special Concern

FS—Forest Service Region 5 Sensitive Species

*Species discussed in text



Figure 1—Adult female southern rubber boa from Heaps Peak, San Bernardino Mountains, San Bernardino County, California. Photo by Robert H. Goodman, Jr.

Taxonomy

The infraspecific taxonomy of the rubber boa (*Charina bottae*) has been much debated (Brown 1997, Stewart 1988), with various authors recognizing either three (Klauber 1943, Stebbins 1985), two (Stewart 1977), or no subspecies (Collins 1990, Nussbaum and Hoyer 1974), or suggesting full species status for the southern form (Erwin 1974). While scalation patterns are highly variable within rubber boa populations, and there is considerable overlap among populations, Stewart (1977) noted fairly consistent differences between southern rubber boas (*C.b. umbratica*) and northern rubber boas (*C.b. bottae*). He recommended that these forms be retained as distinct subspecies and regarded populations in the Mount Pinos area and Tehachapi Mountains as intergrades. Recent analyses of mitochondrial DNA by Rodriguez-Robles and others (2001) have shown that the southern rubber boa populations form a clade that separated from all other rubber boa lineages approximately 4.4 to 12.3 million years ago. Together with existing morphological and allozyme data (Weisman 1988), this suggests *C.b. umbratica* could be recognized as a full species. Although the Mount Pinos area and Tehachapi Mountains populations cannot be identified reliably by morphological characters, they cluster with *C.b. bottae* in the mitochondrial DNA analyses (Rodriguez-Robles and others 2001).

Distribution

The southern rubber boa is restricted to the San Bernardino and San Jacinto Mountains (fig. 2) at elevations between about 1,540 m and 2,460 m (Stewart 1988, 1991). It is known from over 40 localities in the San Bernardinos (Stewart 1991) and eight in the San Jacintos (Keasler 1982, Loe 1985). Twenty-six of the San Bernardino localities occur in a 16-km-long strip of habitat in the Lake Arrowhead area between Twin Peaks on the west and Green Valley on the east (Stewart 1988, 1991).

Habitat and Habits

Typical habitat for this snake is mixed conifer-oak forest or woodland dominated by two or more of the following species: Jeffrey pine (*Pinus jeffreyi*), yellow pine (*P. ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and black oak (*Quercus kelloggii*) (Stewart 1988). A relatively open canopy seems to be preferred, at least during the spring months (April and May), and rock outcrops evidently are important as hibernacula (Keasler 1982, Stewart 1988). In the Heaps Peak area near Lake Arrowhead, the boa occurs at rock outcrops in open areas characterized by mixed grasses and bracken fern (*Pteridium aquilinum*) together with variable numbers of shrubs and small trees (Hoyer and Stewart 2000a). Because it is semi-fossorial, primarily crepuscular or nocturnal, and

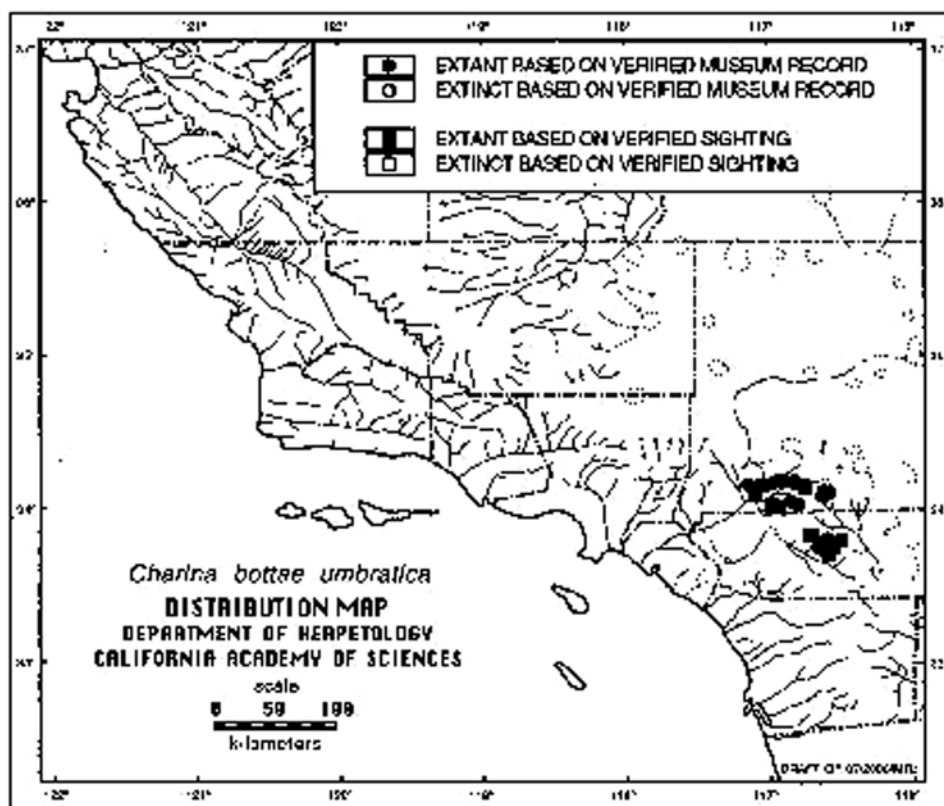


Figure 2—Historic and current distribution of the southern rubber boa

highly secretive, its seasonal activity and habitat use are difficult to determine. Boas are most easily found during the spring months at rock outcrops where scattered surface rocks and wood debris provide movable cover under which to search (Hoyer and Stewart 2000a, Keasler 1982, Stewart 1988,). The snakes essentially disappear during the summer months, though they may emerge for surface activity on humid nights (Alten and Keasler 1978) or after a rain (Stewart pers. observ.). It is likely that some individuals remain at the rock outcrops during the summer and retreat deeper into crevices (Stewart pers. observ.), but others apparently move into cooler, moister forest and riparian habitats (Loe 1985, Stewart 1988). In all habitat types, rock outcrops and surface materials (such as rocks, logs, and a well-developed litter/duff layer) are important habitat components because they provide cover and maintain soil moisture (Loe 1985). Lizards, particularly common sagebrush lizards (*Sceloporus graciosus*) and western fence lizards (*S. occidentalis*), often are associated with the outcrops where southern rubber boas are found. Hoyer and Stewart (2000b) demonstrated that both juvenile and adult boas readily consume lizard eggs, with adults also taking nestling voles (*Microtus* spp.) and shrews (*Sorex* spp.). These snakes are viviparous; Hoyer and Stewart (2000a) recorded a litter size of 2 to 5 in 12 females.

Status and Threats

The southern rubber boa is listed by the State of California as *Threatened* and is a Forest Service Region 5 *Sensitive Species* (Stephenson and Calcarone 1999). While an assessment of the boa's current status is hindered by its secretive behavior, it is continuing to experience significant habitat loss and degradation. Most of the prime habitat in the 16-km strip near Lake Arrowhead is private land subject to residential and commercial development (Stewart 1988, 1991). Elsewhere in the San Bernardino and San Jacinto Mountains, substantial areas of known or potential habitat are on San Bernardino National Forest lands (Loe 1985, Stewart 1991). However, Forest Service-permitted activities, such as personal fuelwood harvesting, off-highway vehicle use, and commercial timber sales, increasingly degrade and fragment what once were large, contiguous tracts of rubber boa habitat (Loe 1985, Stewart 1991). The combined factors of habitat degradation, fragmentation, and loss increase the likelihood of local extirpations and restrict gene flow, potentially leading to reduced genetic diversity and greater vulnerability to chance environmental catastrophes.

Management Recommendations

A Southern Rubber Boa Advisory Committee was established in 1980, and with its assistance the San Bernardino National Forest produced a comprehensive set of habitat management guidelines (Loe 1985). The guidelines seek to maintain habitat quality, minimize negative impacts on Forest Service lands, and coordinate management activities with county and city governments. We recommend continued adherence to these guidelines, with monitoring to insure that objectives are being met. A better understanding of seasonal movements and habitat utilization, obtained through radio telemetry studies, would permit fine-tuning of management to the needs of this snake. Special efforts should be made to establish protective management on a large (30 hectares or more) tract of private property containing boa habitat in the Heaps Peak area (Stewart 1991) and several smaller (10 hectares or so) tracts elsewhere within the boa's range. This could be done through conservation easements with willing landowners and/or by setting up a land-bank system that

developers pay into to get mitigation credits for their habitat impacts. Ideally, these acquired properties should be adjacent to public lands to maximize the size of contiguous habitat areas. Although rubber boa populations in the Mount Pinos area may now be assigned to the northern rubber boa (Rodriguez-Robles and others 2001), similar guidelines should be developed for these populations by the Los Padres National Forest. They are small and isolated (Alten and Keasler 1978, Hoyer and Stewart 2000b), and they provide opportunities for further study of evolutionary processes.

San Bernardino Mountain Kingsnake *Lampropeltis zonata parvirubra* Zweifel 1952

Description

A medium-sized (total length 55-111 cm, Jennings and Hayes 1994a) snake with a tricolor pattern of black, white, and red rings around the body (*fig. 3*; Brown 1997). Diagnosis of the different subspecies of the California mountain kingsnake (*Lampropeltis zonata*) is based almost entirely on color pattern characteristics. The basic color unit is a triad composed of a black ring, partly or completely divided by a red band or ring, and separated from adjacent black rings by a pair of white rings (Rodriguez-Robles and others 1999, Zweifel 1952, 1974). The number of body triads in *L.z. parvirubra* typically is 37 or more, and usually fewer than 60 percent are completely divided by a red ring (Zweifel 1974).



Figure 3—San Bernardino mountain kingsnake from Sawpit Canyon, San Gabriel Mountains, Los Angeles County, California. Photo by Robert H. Goodman, Jr.

Taxonomy

Identification of this taxon is problematic because of the wide range of variation and broad overlap of its color characteristics with other subspecies of *L. zonata*. Examining a large series of specimens representing all seven of the named subspecies, Rodriguez-Robles and others (1999) concluded that color patterns cannot be used to reliably differentiate among them. However, mitochondrial DNA analyses by these authors showed that the San Bernardino mountain kingsnake and San Diego mountain kingsnake (*L.z. pulchra*), together with two other subspecies from northern Baja California, Mexico, form a southern clade that may be distinct from the more northern subspecies (Rodriguez-Robles and others 1999). Resolution of California mountain kingsnake systematics must await the completion of additional morphological and genetic studies. In the meantime, we believe it is important to continue to recognize the named infraspecific taxa of this mountain kingsnake to help ensure that the diversity of the herpetofauna in the southern California mountains is adequately protected.

Distribution

The San Bernardino mountain kingsnake is restricted to the San Gabriel, San Bernardino, and San Jacinto Mountains (fig. 4) at elevations from about 370 m to 2,470 m (Jennings and Hayes 1994a).

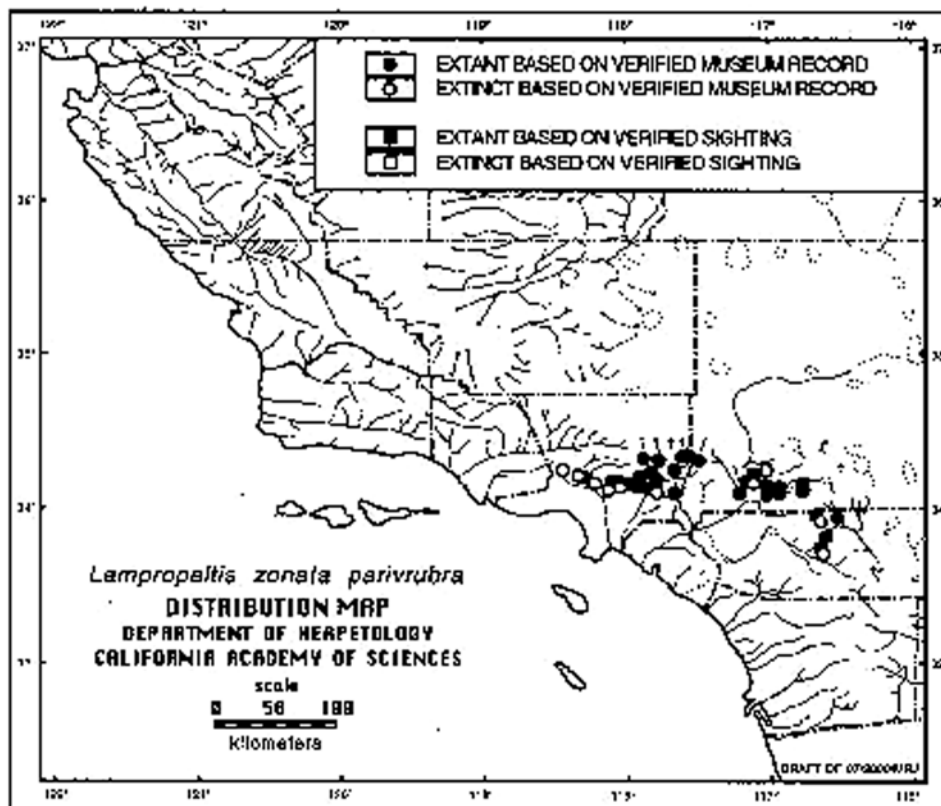


Figure 4—Historic and current distribution of the San Bernardino mountain kingsnake. Modified from Jennings and Hayes (1994a).

Habitat and Habits

This snake tends to occur in well-illuminated rocky canyons in association with big-cone Douglas-fir (*Pseudotsuga macrocarpa*) and various chaparral species at lower elevations and with black oak, incense cedar, Jeffrey pine, and yellow pine at higher elevations (Jennings and Hayes 1994a). Above 1,540 m in the San Bernardino and San Jacinto Mountains, it commonly is found in rock outcrops together with the southern rubber boa (Hoyer and Stewart 2000a, Keasler 1982). Rock crevices and outcrops likely serve as hibernacula and cover, and they also provide potential food sources. Mountain kingsnakes are known to be primarily lizard eaters, most often taking common sagebrush lizards, western fence lizards, and western skinks (*Eumeces skiltonianus*) (Jennings and Hayes 1994a). While secretive and infrequently observed, mountain kingsnakes are more likely to move about on the surface during daylight hours of spring months than are southern rubber boas (McGurty 1988, Stewart pers. observ.). Later in the season and at lower elevations, they may be active after dark (Jennings and Hayes 1994a). As in the case of rubber boas, rock outcrops and a variety of surface materials (rocks, logs, bark) probably are important habitat components in all habitat types (McGurty 1988). Mountain kingsnakes are oviparous and have been reported to produce clutches of 3-9 eggs (McGurty 1988).

Status and Threats

The San Bernardino mountain kingsnake is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and a Forest Service *Region 5 Sensitive Species* (Stephenson and Calcarone 1999). It is impacted by most of the same factors (habitat degradation, fragmentation, and loss) that affect the southern rubber boa. In addition, it is highly prized by reptile fanciers and continues to be collected despite State laws limiting collecting and preventing the sale of native reptiles in California (California Freshwater Sport Fishing Regulations 2002, Jennings and Hayes 1994a). While the impact of habitat alteration and collecting pressures is difficult to assess, it results from the ripping apart of decaying logs and stumps and removal of exfoliating pieces of granite boulders, practices that are prohibited by State law (California Freshwater Sport Fishing Regulations 2002). These microhabitats probably require decades to millennia to develop, but only seconds to minutes to destroy. Their loss may lead to local extirpations and reduced population viability, especially at locations easily accessed by roads.

Management Recommendations

Implementation of management recommendations for the southern rubber boa in the San Bernardino National Forest also benefits the San Bernardino mountain kingsnake. In addition, particular attention should be paid to maintaining surface cover and minimizing human impacts in rocky draws and canyons. Similar management guidelines should be developed for the Angeles National Forest. Because visitors to National Forest lands commonly confuse mountain kingsnakes with venomous coral snakes (Jennings pers. observ.), which also have a tri-color pattern but are not found in California, posters and other educational materials should be provided at convenient locations to counter misinformation about snake identification and biology. Again, radio telemetry studies would provide more

information on the activity and habitat use patterns of the San Bernardino mountain kingsnake and allow for more precise management prescriptions.

San Diego Mountain Kingsnake *Lampropeltis zonata pulchra* Zweifel 1952

Description

A medium-sized (total length 53-108 cm, Jennings and Hayes 1994a) snake with a tricolor pattern of black, white and red rings (*fig. 5*; Brown 1997) similar to the San Bernardino mountain kingsnake. On the average, however, there are fewer body triads and more of the triads have complete red rings (Rodriguez-Robles and others 1999). Zweifel (1974) gave the number of triads as typically 36 or fewer, and the number of triads with complete red rings as usually 60 percent or more.



Figure 5—San Diego mountain kingsnake from Boiling Springs, Cuyamaca Mountain, San Diego County, California. Photo by Robert H. Goodman, Jr.

Taxonomy

Taxonomic comments made for the San Bernardino mountain kingsnake also apply to this subspecies.

Distribution

The San Diego mountain kingsnake occurs in the Santa Monica, Santa Ana, Santa Rosa, and Laguna Mountains. In San Diego County, it also occurs on the more isolated Palomar, Hot Springs, Cuyamaca and Corte Madera Mountains (*fig. 6*). It ranges in elevation from near sea level to about 1,800 m (Jennings and Hayes 1994a).

Habitat and Habits

Much of the information given for the San Bernardino mountain kingsnake is applicable to the San Diego subspecies. In the interior mountain ranges, it occurs primarily in associations of yellow, Jeffrey and Coulter pine (*Pinus coulteri*) and black oak. At lower elevations and in coastal areas, it usually is found in canyon bottoms with western sycamore (*Platanus racemosa*), Fremont cottonwood (*Populus fremontii*), coast live oak (*Quercus agrifolia*) and willows (*Salix* spp.). Rock outcrops appear to be a particularly important habitat element for this snake in San Diego County (McGurty 1988).

Status and Threats

The San Diego mountain kingsnake is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and a Forest Service Region 5 *Sensitive Species*

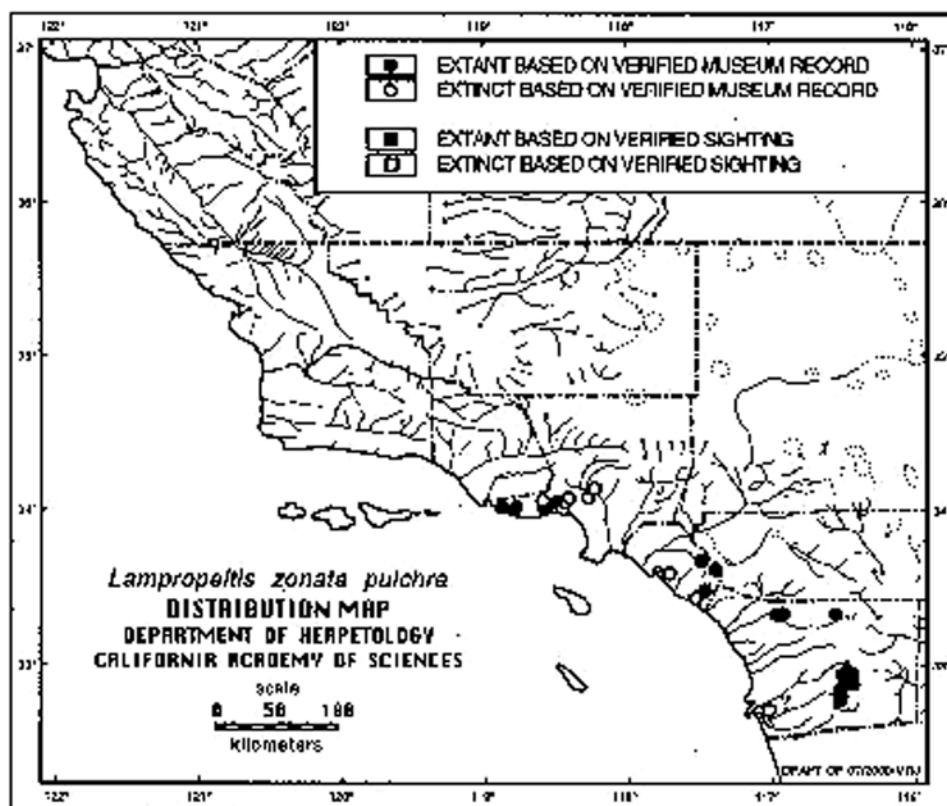


Figure 6—Historic and current distribution of the San Diego mountain kingsnake. Modified from Jennings and Hayes (1994a).

(Stephenson and Calcarone 1999). It is subject to the same anthropogenic impacts as the San Bernardino mountain kingsnake. Due to its tendency to display more red in its color pattern, however, it may be even more highly prized by collectors. McGurty (1988) has noted a local population decline and examples of habitat destruction (dismantling of rock outcrops and shredding of logs and stumps) in San Diego County. These activities continue despite California Department of Fish and Game and U. S. Forest Service regulations prohibiting such habitat alterations (California Freshwater Sport Fishing Regulations 2002, Jennings and Hayes 1994a).

Management Recommendations

All management recommendations made for the San Bernardino mountain kingsnake also apply to the San Diego subspecies and should be developed for the Cleveland National Forest. In addition, a program of systematic habitat monitoring and public education would be particularly important here to ensure that habitat impacts are minimized.

California Red-legged Frog *Rana aurora draytonii* Baird and Girard 1852

Description

A large (adult snout-urostyle length 85-138 mm, Jennings and Hayes 1994a) frog with a dorsal pattern of dark flecks and spots on a brown, gray, or reddish-brown background color (*fig. 7*; Stebbins 1985). The distribution of red or red-orange pigment is highly variable, but usually restricted to the belly and undersurfaces of the thighs, legs, and feet (Jennings and Hayes 1994a). Frogs in southern California often have red only on the undersurfaces of the feet (Jennings pers. observ.). There are prominent dorsolateral folds that are yellow or orange in juveniles (Stebbins 1985). The groin has a distinct black mottling on a white or yellow background. The iris is dark brown with iridophores on the upper and lower portions of the iris (Jennings and Hayes 1994a). Larvae (*fig. 8*) range from 14 to 80 mm long and have two or three upper and three or four lower rows of teeth (Stebbins 1985). Newly hatched tadpoles generally are blackish in color, gradually changing to a brown background color with darker marbling or spots after a week or two of growth (Storer 1925).

Taxonomy

Recent molecular phylogenetic analysis of red-legged frogs (*Rana aurora*) from across their range supports independent morphological (Hayes and Kremples 1986, Hayes and Miyamoto 1984), allozyme (Green 1985, Hayes and Miyamoto 1984), and life history data (Hayes and Miyamoto 1984, Jennings and Hayes 1994a) suggesting that *Rana aurora draytonii* should be considered a full species (Bradley [sic] and others 2000). Further, limited samples indicate that populations south of the Transverse Ranges form a clade distinct from those populations further north in coastal southern and central California (Bradley [sic] and others 2000).



Figure 7—Adult California red-legged frog from the Santa Rosa Plateau Preserve, Riverside County, California. Photo by Mark R. Jennings.



Figure 8—Larval California red-legged frog from Corral Hollow, San Joaquin County, California. Photo by Norman J. Scott, Jr.

Distribution

Historically, *Rana aurora draytonii* was found in Pacific slope drainages from the vicinity of central Mendocino County and Redding, Shasta County (Bradley [sic] and others 2000, Storer 1925) south to the Santo Domingo River drainage in Baja California, Mexico (Linsdale 1932). Isolated populations occurred in four desert drainages in southern California (Jennings and Hayes 1994b). In the area covered by this paper, it was historically found in low to mid-elevations of much of the South Coast Ranges, Tehachapi Mountains, Greenhorn Mountains, Transverse Ranges, Peninsular Ranges, and South Coast Plain between near sea level (Gaviota Creek, Santa Barbara County) and 1,706 m (Crystal Lake in the San Gabriel Mountains, Los Angeles County) (fig. 9). Currently, red-legged frogs still are extant over much of the South Coast Ranges and in drainages north of the Santa Clara River in Los Angeles and Ventura Counties (Jennings and Hayes 1994a). However, south of the Santa Clara River, frog populations appear to have been extirpated, with only two small populations still known in this area. All known populations in the Tehachapi and Greenhorn Mountains now appear to be extinct (Jennings and Hayes 1994a).

Habitat and Habits

The California red-legged frog typically is found in or next to livestock ponds and pools in perennial streams in southern California (Jennings pers. observ.). The most optimal habitat is characterized by dense, shrubby riparian vegetation associated with

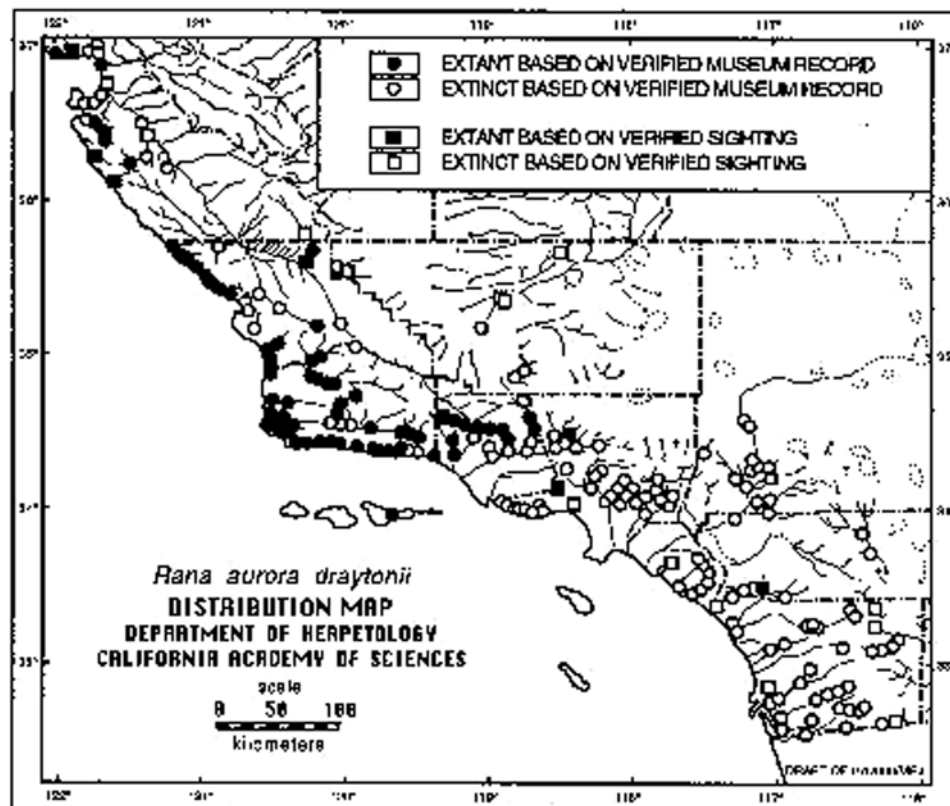


Figure 9—Historic and current distribution of the California red-legged frog in southern California. Modified from Jennings and Hayes (1994b).

deep (>0.7 m), still, or slow-moving water (Hayes and Jennings 1988, Jennings 1988). The shrubby riparian vegetation that structurally seems to be most suitable for this frog is that provided by arroyo willow (*Salix lasiolepis*), although cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.) also can provide suitable habitat (Jennings 1988). Although California red-legged frogs are found in ephemeral streams and ponds, populations cannot be maintained where all surface water disappears (Jennings and Hayes 1994a). This frog is infrequent or absent in habitats where introduced aquatic predators such as green sunfish (*Lepomis cyanellus*), red-swamp crayfish (*Procambarus clarkii*), and bullfrogs (*Rana catesbeiana*) are present (Hayes and Jennings 1986, 1988), probably because its larval stages are susceptible to such predators (Jennings and Hayes 1994b). Subadult and adult California red-legged frogs often include other anurans and small mammals in their diet (Hayes and Tennant 1986). They are highly nocturnal and quite wary (Hayes and Tennant 1986, Storer 1925), but juveniles tend to be much less wary and frequently are active diurnally (Hayes and Tennant 1986). This frog breeds from late November to April, and females attach masses of 2,000 to 6,000 eggs to emergent vegetation in shallow water (Hayes and Jennings 1986, Jennings pers. observ., Storer 1925). Larvae require 4-5 months to metamorphose (Storer 1925) and apparently, under limited circumstances, will overwinter (Fellers and others 2001).

Status and Threats

The California red-legged frog is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and was federally listed as a *Threatened Species* on 23 May 1996, based on a range reduction of approximately 70 percent and continued threats to remaining populations (U.S. Fish and Wildlife Service 1996). Frogs in southern California have declined largely due to habitat loss and the introduction of non-native aquatic predators such as green sunfish, red-swamp crayfish, and bullfrogs (Jennings and Hayes 1994b). It is possible that a pathogen also helped to eliminate frog populations in southern California during the 1970s (Fellers and others 2001). Recent work suggests that nitrate/nitrite pollution (Marco and others 1999) and pesticide drift (Davidson and others 2001, 2002) also may be responsible for frog declines in California. Although California red-legged frogs still are present in some numbers in South Coast Range drainages north of the Santa Clara River, they are virtually extinct south of this location (Jennings and Hayes 1994a). The population in the Las Virgenes Creek drainage in extreme western Los Angeles County numbers fewer than 25 adults (R. Smith pers. comm.). The population at the Santa Rosa Ecological Preserve in western Riverside County was down to only two males in 2001 and no frogs were seen in 2002 (Jennings unpubl. data). Populations at both locations are at risk due to surrounding development, non-native aquatic predators, and native predators such as the raccoon (*Procyon lotor*) (Jennings unpubl. data).

Management Recommendations

Surveys at several sites on the Cleveland National Forest have failed to reveal any California red-legged frog populations (D. Holland pers. comm.), but searches need to continue, focusing especially on private lands in southern California. Known populations need to be protected from threats such as urban development, flood control projects, spread of known frog pathogens, increased raccoon populations, and introduced fishes and bullfrogs. Finally, the genetic diversity of extant populations

needs to be conserved, including breeding of captive populations, for possible reintroduction onto public lands with suitable remaining habitat. The largest pool of frogs for this task appears to be confined to northern Baja California, Mexico.

Mountain Yellow-legged Frog *Rana muscosa* Camp 1917

Description

A medium-sized (snout-urostyle length about 40-80 mm, Jennings and Hayes 1994a) frog with a variable dorsal pattern (*fig. 10*; Stebbins 1985). The markings usually range from discrete dark spots that can be few and large, to smaller and more numerous ones in a mixture of sizes and shapes, to irregular lichen-like patches, or a poorly defined reticulum (Zweifel 1955). Color also is highly variable, usually a mixture of brown and yellow, but often with gray, red, or green-brown (Jennings pers. observ.). The posterior half of the upper lip is weakly light-colored and dorsolateral folds are present but normally not prominent (Stebbins 1985). The throat is white or yellow, sometimes with a mottling of dark pigment (Zweifel 1955). Undersurfaces of the legs and lower belly are pale yellow to sun yellow; the latter color usually present on the largest individuals (Jennings and Hayes 1994a). The iris is gold with a horizontal, black counter-shading stripe (Jennings pers. observ.). Larvae (*fig. 11*) range in length from 10 to 65 mm long and have two to four upper and four lower rows of teeth (Stebbins 1985). Newly hatched tadpoles generally are



Figure 10—Adult mountain yellow-legged frog from Vincent Gulch, San Gabriel Mountains, Los Angeles County, California. Photo by Galen B. Rathbun.

blackish in color, gradually changing to a brassy background color with darker marbling and spots after a week or two of growth (Jennings pers. observ.).

Taxonomy

The mountain yellow-legged frog was originally described as two subspecies of *Rana boylei*, one in the Sierra Nevada and the other in southern California (Camp 1917). On the basis of morphological data, Zweifel (1955) separated these two forms from *R. boylei* and combined them as the distinct species *R. muscosa*. This arrangement was supported by subsequent genetic work (see Jennings and Hayes 1994a). Recent mitochondrial DNA studies indicate that mountain yellow-legged frog populations in all southern California mountain ranges form a clade distinct from the populations in the Sierra Nevada (Macey and others 2001). Further studies may suggest species level recognition for these southern California frogs.



Figure 11—Larval (2nd year) mountain yellow-legged frog from Little Rock Creek, San Gabriel Mountains, Los Angeles County, California. Photo: Norman J. Scott, Jr.

Distribution

In southern California, the mountain yellow-legged frog historically was present in most streams, watercourses, and natural lakes in the San Gabriel, San Bernardino, and San Jacinto Mountains, as well as on Mount Palomar in San Diego County (*fig. 12*). At many locations prior to 1965, the frogs could be extremely abundant (Jennings and Hayes 1994b, Stewart pers. observ.). The elevation range was from

370 m at Eaton Canyon, Los Angeles County, to over 2,290 m near Bluff Lake, San Bernardino County (Jennings and Hayes 1994a, Zweifel 1955). Today, mountain yellow-legged frogs are largely restricted to small watercourses at elevations greater than 1,500 m (Jennings 1993, 1994).

Habitat and Habits

This species inhabits mid- to upper-elevation perennial streams, often in locations with bedrock pools (Jennings 1993, 1994; Jennings pers. observ., Mullally 1959). Adult frogs are diurnal and often observed sitting in shallow pools of water with their back exposed to direct sunlight. Although streams may be partly shaded by riparian vegetation such as white alder (*Alnus rhombifolia*), most streams that contain frog populations are relatively open (Jennings pers. observ.). While life history data for southern California mountain yellow-legged frogs are very limited, the frogs appear to be strictly insectivorous and do not include vertebrates in their diet (Jennings and Hayes 1994a). In the late 1960s, Stewart (pers. observ.) found egg masses in April at 700 m elevation in Bear Creek in the San Gabriel River drainage. Oviposition probably occurs later at higher elevations. Egg masses typically are deposited in shallow water and not attached to objects (Jennings and Hayes 1994a, Stewart pers. observ.). In the Sierra Nevada, larvae are known to overwinter and take between 1 and 2.5 years to metamorphose (Jennings and Hayes 1994a). Overwintering of larvae has been observed at all locations where this species still occurs in southern California (Jennings pers. observ.).

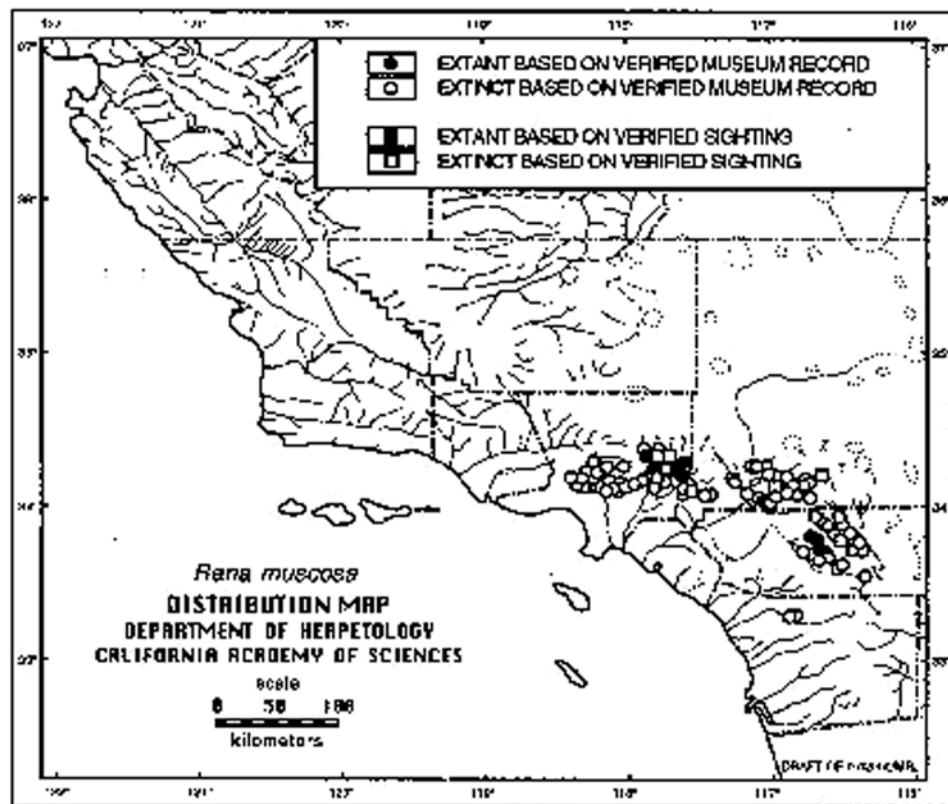


Figure 12—Historic and current distribution of the mountain yellow-legged frog in southern California. Modified from Jennings and Hayes (1994a).

Status and Threats

The mountain yellow-legged frog is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and a Forest Service Region 5 *Sensitive Species* (Stephenson and Calcarone 1999). It is believed to have been extirpated from approximately 99 percent of its historic range in southern California (Jennings 1995a, Jennings and Hayes 1994a), and the southern California population was federally listed as an *endangered species* on 2 July 2002 (U.S. Fish and Wildlife Service 2002). In the San Gabriel Mountains, small populations of frogs exist only in the upper reaches of Little Rock Creek, Big Rock Creek, Devil's Canyon, and the East Fork of the San Gabriel River (Jennings 1993, 1994, 1995b, 1998, 1999; Jennings and Hayes 1994b). In the San Bernardino Mountains, a small population currently exists in a short section of the lower portion of the East Fork of City Creek (Jennings pers. observ., U.S. Fish and Wildlife Service 2002). In the San Jacinto Mountains, small populations of frogs exist only in the upper reaches of the North Fork of the San Jacinto River, Hall Canyon, Dark Canyon, and Fuller Mill Creek (Jennings 1998, 1999). Current estimates put the total number of adult frogs in the nine known populations at fewer than 200 individuals (Jennings 1995a).

All of these populations are extremely vulnerable to extirpation via recreation (U.S. Fish and Wildlife Service 1999), especially when such activities occur on a repeated basis year after year (U.S. Fish and Wildlife Service 2002). For example, the second author has witnessed the children of rock climbers chasing frogs and adults disturbing sunning frogs in the Little Rock Creek drainage; adults hiking directly in and up the streams of Little Rock Creek and the North Fork of the San Jacinto River, disturbing the larval and metamorphosing frogs present; a mother and daughter photographing flowers in the North Fork of the San Jacinto River and disturbing a small population of metamorphosing frogs; and adults and children swimming (and associated litter) in Dark Canyon, Mill Creek, and the East Fork of the San Gabriel River where larvae and subadult frogs were present. Such activities are not limited to areas near roads. For instance, one individual reported hiking directly up a stream containing a known frog population on Mount San Jacinto because he “just wanted to get away from the crowds.”

Other recreational activities which negatively effect frog populations include fishing for trout (*Oncorhynchus mykiss* and *Salmo trutta*) at almost all known frog locations and camping at locations along the North Fork of the San Jacinto River and East Fork of the San Gabriel River where frog populations are still extant. All of these recreational activities greatly increase the chances of pathogen introduction (via shoes, clothing, and fishing equipment) that could decimate the small, isolated populations. Continuing requests for water removal for ski operations in the uppermost reaches of Little Rock Creek also threaten the small frog population there through potential dewatering of the stream (U.S. Fish and Wildlife Service 1999, 2002).

Finally, the negative effects of chance catastrophic events, such as fires, droughts and floods, also greatly endanger these localized populations (U.S. Fish and Wildlife Service 2002). The 1968-69 floods in southern California decimated many of the frog populations that formerly were abundant in the region (Jennings and Hayes 1994a, 1994b).

Management Recommendations

There needs to be a long-term, comprehensive program to determine and monitor the number of adults, juveniles, and egg masses or larvae for each of the remaining populations. This will require careful yearly surveys. Otherwise, most of these populations could become extinct without us knowing it. Additionally, campgrounds in sensitive frog breeding sites need to be closed for a portion of the year or removed. Also, trails near sensitive frog habitats need to be relocated well away from riparian areas. If possible, volunteers should be used to keep recreationists out of the most sensitive frog breeding habitats throughout the summer. Trout stocking should be discontinued in frog habitat, and existing trout populations should be removed. Finally, a captive breeding population of frogs from each southern California mountain range needs to be started to assure that the genetic diversity of this species is preserved for potential reintroduction programs.

San Gabriel Mountain Slender Salamander ***Batrachoseps gabrieli* Wake 1996**

Description

A slender salamander of medium size (snout-vent length 40-50 mm, Wake 1996) with a relatively broad, flattened head that is well demarcated from the neck (*fig. 13*; Wake 1996). It also has long limbs, large feet, a tapered tail, and 18 or 19 costal grooves between the front and hind limbs (Wake 1996). With a complete interlacing of melanophores, the ground color generally is black in this species throughout its range. Individuals from the western part of the range (San Gabriel Canyon, San Gabriel Mountains, Los Angeles County) have a dorsum overlain with a dense layer of coppery iridophores that are more concentrated around the shoulders and pelvic region, forming two short, broad stripes. Salamanders from the central part of the range (San Antonio and Lytle Canyons, San Gabriel Mountains, Los Angeles and San Bernardino Counties) usually have white-to-silvery iridophores in addition to the coppery iridophores. Specimens from the eastern part of the range (Devil and Waterman Canyons, San Bernardino Mountains, San Bernardino County) typically are devoid of any coppery iridophores, but have the white-to-silvery iridophores.

Taxonomy

Batrachoseps gabrieli is a recently described salamander known only from the cismontane side of the San Gabriel and San Bernardino Mountains in southern California (Goodman and others 1998, Hansen and others 2005, Wake 1996). Wake (1996) notes that this species is morphologically and genetically differentiated from all other *Batrachoseps*, with separation from other lineages occurring approximately 8-13 million years ago.

Distribution

The range (*fig. 14*) of *B. gabrieli* is poorly known. Originally, this species was known from only two locations within the San Gabriel Mountains (Wake 1996), but it recently has been collected and/or observed at 11 other sites within the San Gabriel

and San Bernardino Mountains (Goodman and others 1998, Goodman pers. observ.).



Figure 13—Two adult San Gabriel Mountain slender salamanders. The animal on the left is from Waterman Canyon, San Bernardino Mountains, San Bernardino County, California and the animal on the right is from Alpine Canyon, San Gabriel Mountains, Los Angeles County, California. Photo by Robert H. Goodman, Jr.

The distribution apparently is discontinuous, with populations restricted to narrow swaths of suitable habitat in separate drainages, bounded on the west by San Gabriel Canyon and on the east by Waterman Canyon. All specimens have been collected in either the Angeles or San Bernardino National Forests. The elevation range is from approximately 850 m to 2,380 m.

Habitat and Habits

Habitat associations for the new populations of *B. gabrieli* (Goodman and others 1998) are similar to those described by Wake (1996) for the type locality, although generally lower in elevation. Most individuals have been observed in and around talus, under rotting logs, bark, downed branches, downed fern fronds and rocks (Hansen and others 2005). Vegetation components present within and around the talus include canyon live oak (*Quercus chrysolepis*), bigcone Douglas-fir, Jeffrey pine, yellow pine, and chaparral components such as ceanothus (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), mountain mahogany (*Cercocarpus betuloides*) and chaparral yucca (*Yucca whipplei*). Surface activity appears to peak during southern California's winter snow/rain season; individuals have been observed while snow was present (Goodman pers. observ., Wake 1996.). Three other plethodontid

salamanders—the Monterey salamander (*Ensatina eschscholtzii eschscholtzii*), black-bellied slender salamander (*Batrachoseps nigriventris*), and arboreal salamander (*Aneides lugubris*)—are known to occur sympatrically with *B. gabrieli* (Goodman pers. observ., Wake 1996).

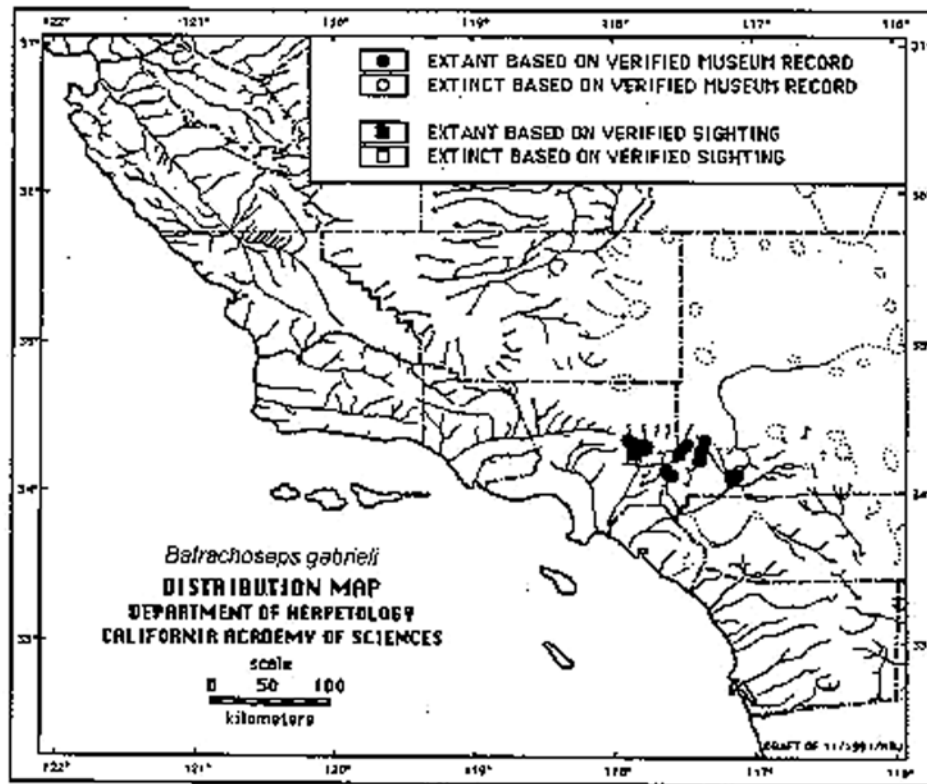


Figure 14—Current distribution of the San Gabriel Mountain slender salamander.

Status and Threats

The San Gabriel Mountain slender salamander currently has no State or Federal status, but it is a Forest Service Region 5 *Sensitive Species* (Stephenson and Calcarone 1999). Fortunately, all populations of *B. gabrieli* occur within national forest boundaries, and because it occurs within and around talus slopes and seems to be surface active only during the winter months, there appear to be no direct threats to it at this time.

Management Recommendations

Since this salamander currently is known from only 13 locations within the central to eastern San Gabriel Mountains and western San Bernardino Mountains, we recommend that it be listed by the State of California as a *Species of Special Concern*. For management purposes, and to obtain a better estimate of its range, further surveys should be conducted throughout the San Gabriel, San Bernardino, and San Jacinto Mountains to locate new populations. In addition, management guidelines should be developed to protect the talus habitat of this species.

Yellow-blotched Salamander *Ensatina eschscholtzii* *croceater* (Cope 1869)

Description

A medium-sized (snout-vent length 48-78 mm, Jennings and Hayes 1994a) salamander with large, irregular, pale, lemon-yellow to yellowish cream blotches on a deep blackish brown to black ground color (*fig. 15*; Stebbins 1985). As in other forms of *Ensatina*, there are 12-13 costal grooves and a noticeable constriction at the base of the tail (Stebbins 1949, 1985).



Figure 15—Adult female yellow-blotched salamander from San Emigdio Mountain, Kern County, California. Photo by Robert H. Goodman, Jr.

Taxonomy

The ensatina (*Ensatina eschscholtzii*) has long been considered a classic example of a “ring species” (Highton 1998, Wake and Schneider 1998). Seven named subspecies are distributed around the Central Valley of California, apparently intergrading in contact areas, but overlapping without interbreeding at the ends of the ring (*E.e. eschscholtzii* and *E.e. klauberi*) in southern California (Stebbins 1949). Behaving as closely related but distinct species, unblotched *eschscholtzii* and blotched *klauberi* are known to hybridize occasionally (Brown 1974, Wake and Yanev 1986), and Highton (1998) advocated species-level recognition with hybrid zones for all the infraspecific taxa within *Ensatina*. However, Wake and Schneider (1998), while ac-

knowledging that the ensatina does not meet all of the criteria for a true ring species, argued against disrupting the long-stable taxonomy of this species complex until further morphological and genetic studies are completed. We follow that policy here.

Distribution

The current known range of the yellow-blotched salamander essentially is restricted to east-central Kern and northern Ventura Counties, extending from the Piute Mountains in the Sequoia National Forest southwestward to the vicinity of Alamo Mountain in the Los Padres National Forest (fig. 16). Northwest of the Piute Mountains, ensatina populations appear to be intergrades between *E.e. croceator* and *E.e. platensis*. Two hundred km east of Alamo Mountain, blotched ensatina collected in the San Bernardino Mountains look like intergrades between *E.e. croceator* and *E.e. klauberi* (Stebbins 1949; fig. 17), with specimens from some localities looking more like one or the other of the two taxa (compare figs. 16 and 19). However, all are genetically closer to the latter (Wake and Schneider 1998). Interestingly, blotched ensatina seem to be absent from the intervening San Gabriel Mountains, an area known as “Bob’s Gap” in reference to Robert Cyril Stebbins who did much of the early work with the species complex. *E.e. croceator* occurs from about 427 m to 2,285 m in elevation (Jennings and Hayes 1994a).

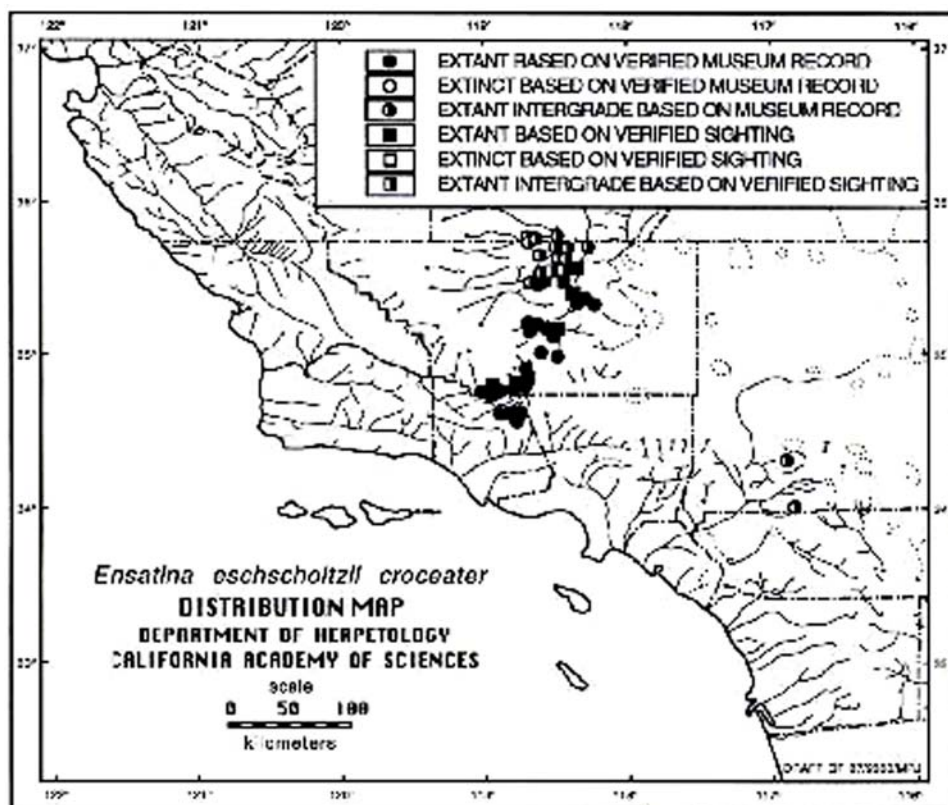


Figure 16—Historic and current distribution of the yellow-blotched salamander. Intergrades indicated in the San Bernardino Mountains look more like *E.e. croceator* than *E.e. klauberi*. Modified from Jennings and Hayes (1994a).

Habitat and Habits

The yellow-blotched salamander occurs in a wide variety of vegetation associations including oak (*Quercus douglasii* and *Q. kelloggii*) woodlands, pine (*Pinus jeffreyi* and *P. ponderosa*) and fir (*Abies concolor*) forests, and open chaparral (Jennings and Hayes 1994a, Stephenson and Calcarone 1999). It typically is found under downed logs, leaf litter and duff, woody debris, and medium-to-large rocks (Goodman pers. observ., Jennings and Hayes 1994a). As with most other southern California salamanders, the habits of this subspecies are poorly known, although surface activity generally peaks during the winter months. Gravid females have been observed in April and May (Jennings and Hayes 1994a).

Status and Threats

This salamander is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and a Forest Service Region 5 *Sensitive Species* (Stephenson and Calcarone 1999). Although it is more widespread and abundant than originally realized, there are concerns about increased development in the Tehachapi Mountains, Cummings Valley, and Bear Valley areas and increased wood harvesting on the Tejon Ranch (Jennings and Hayes 1994a). These activities occur primarily in oak woodlands and may have a direct impact on known and undiscovered salamander populations.



Figure 17—Subadult intergrade between yellow-blotched and large-blotched salamanders from Crystal Creek, San Bernardino Mountains, San Bernardino County, California. Photo by Robert H. Goodman, Jr.

Management Recommendations

Systematic surveys and habitat assessments should be conducted within known populations of the yellow-blotched salamander in order to gain a better understanding of this taxon's natural history. Similar work might then be able to locate populations in areas like the San Gabriel Mountains. If specimens are collected in “Bob’s Gap,” they may yield significant information on the phylogeography of the ensatina species complex (Wake and Schneider 1998). While *E.e. croceator* may be more directly impacted by habitat degradation on private lands than by prevailing land use activities on public lands (Stephenson and Calcarone 1999), we believe that guidelines should be developed by the Sequoia and Los Padres National Forests to prevent over-harvesting of standing trees, downed logs, and wood debris.

Large-blotched Salamander *Ensatina eschscholtzii klauberi* Dunn 1929

Description

A medium-sized (snout-vent length 45-82 mm, Jennings and Hayes 1994a) salamander with large, rectilinear, orange blotches (sometimes spots or bands) on a deep blackish-brown-to-black ground color (*fig. 18*; Stebbins 1985).



Figure 18—Subadult large-blotched salamander from near Julian, Cuyamaca Mountain, San Diego County, California. Photo by Robert H. Goodman, Jr.

Taxonomy

The taxonomic comments made for the yellow-blotched salamander also apply to this subspecies.

Distribution

The known range of the large-blotched salamander is from the San Jacinto Mountains, Riverside County to Cottonwood Creek, San Diego County (*fig. 19*). Its distribution is discontinuous, and as, previously noted, possible intergrades between *E.e. klauberi* and *E.e. croceator* occur in the San Bernardino Mountains (Stebbins 1949; *fig. 17*). Recently, *E.e. klauberi* has been observed in the Sierra San Pedro Martir, Baja California Norte, Mexico (Mahrtdt and others 1998). The elevation range for this salamander is from about 518 m to 1,646 m (Jennings and Hayes 1994a).

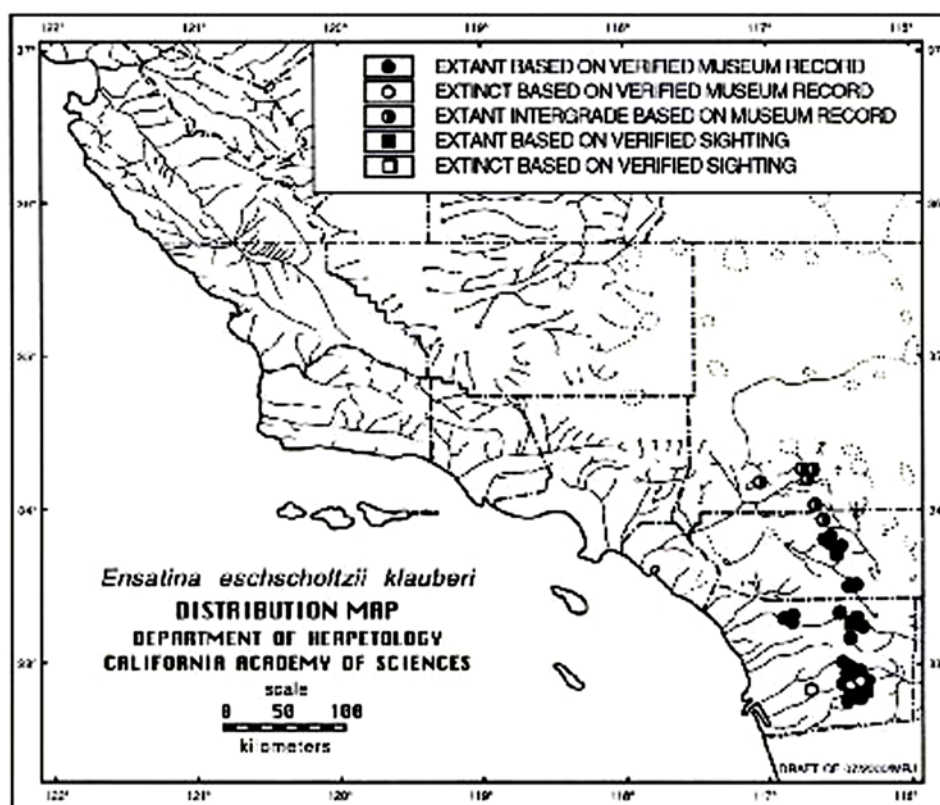


Figure 19—Historic and current distribution of the large-blotched salamander in southern California. Intergrades indicated in the San Bernardino Mountains look more like *E.e. klauberi* than *E.e. croceator*. Modified from Jennings and Hayes (1994a).

Habitat and Habits

Vegetation associations of this subspecies are similar to those of the yellow-blotched salamander, but the oaks are more likely to be *Quercus chrysolepis* and *Q. kelloggii*, and the pines *Pinus coulteri* and *P. ponderosa*, along with incense cedar (Jennings and Hayes 1994a, Stephenson and Calcarone 1999). Again, the salamanders typically

are found under various kinds of surface litter and rocks (Goodman pers. observ., Jennings and Hayes 1994a), and surface activity generally peaks when moisture is present.

Status and Threats

The large-blotched salamander is a State of California *Species of Special Concern* (Jennings and Hayes 1994a) and a Forest Service Region 5 *Sensitive Species* (Stephenson and Calcarone 1999). Even though it also is considerably more common than was formerly believed (Jennings and Hayes 1994a), threats from habitat destruction are increasing. As with the yellow-blotched salamander, the large-blotched salamander may be more impacted by habitat degradation resulting from development on private lands than land use activities on public lands (Stephenson and Calcarone 1999). However, potential impacts to populations from mining exist in the Crystal Creek area of the San Bernardino Mountains (Goodman pers. observ., Jennings and Hayes 1994a).

Management Recommendations

Recommendations discussed with respect to *E.e. croceater* are applicable here. According to D. Wake (pers. comm.), known populations of blotched salamanders from the San Bernardino Mountains are few and disjunct, and more surveys need to be done to locate additional populations for study. To maintain habitat quality for ensatinas, the Cleveland and San Bernardino National Forests should develop guidelines to prevent over-harvesting of trees, logs, and wood debris.

Conclusion

As described in the foregoing accounts, all of these taxa face varying degrees of threat—in some cases, severe threat—from a multitude of anthropogenic factors prevalent in southern California. Lest there be any doubt that these factors can result in extinctions here, the case of the foothill yellow-legged frog (*Rana boylei*) must be mentioned. In the south coast area, this frog historically occurred below the conifer forest habitats in parts of the South Coast Ranges and San Gabriel Mountains from near sea level (Gaviota Creek, Santa Barbara County) to 1,219 m (Indian Creek in the San Rafael Mountains, Santa Barbara County). It has not been observed in this area since before 1978 (H. DeLisle, M. Long, and S. Sweet pers. comm.; Jennings and Stewart pers. observ.), and all of these populations are now believed to be extinct (Jennings 1995a, Jennings and Hayes 1994a).

With their relatively low vagility, all of the taxa discussed in this paper face threats from habitat degradation, fragmentation, and loss. These may lead directly to extinction in the short term for those already reduced to very small, isolated populations or to a more gradual extinction process involving local extirpations, restricted gene flow, reduced genetic diversity, and increased vulnerability to environmental changes. To the extent that global warming scenarios prove to be correct, long-term climate change may become a serious problem for amphibians, and the taxa may be restricted to montane habitats that already are essentially insular relicts.

As specialists in herpetology, we want to emphasize that the taxa discussed here are the subjects of recent and ongoing phylogeographic studies using the most advanced techniques of phyletic and genetic analysis. Consequently, their taxonomy is in a state of flux. More importantly, however, they are of continuing interest to biologists studying the evolutionary processes that shape modern species of terrestrial vertebrates.

To prevent further declines and losses in the herpetofauna of the southern California mountains, additional research must be conducted to increase our knowledge of the distribution, habitat needs, life history, and phylogenetic relationships of the taxa occurring there. Collaboration between the scientific community, the private sector, and public agencies at the Federal, State and local levels will be essential to obtaining the necessary data and incorporating them into sound management programs. These programs must be monitored regularly to ensure that desired objectives are being met. Only then can we expect that the montane components of southern California's rich biodiversity will be maintained for continuing scientific study and public enjoyment.

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The Spotted Owl in Southern California: Ecology and Special Concerns for Maintaining a Forest-Dwelling Species in a Human-Dominated Desert Landscape¹

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Abstract

The California spotted owl is an uncommon forest-dwelling resident of southern California, found in most of the major mountain ranges in the region. We studied this species from 1987 to 1998 in the San Bernardino Mountains and collected empirical and demographic evidence that the population declined during this period. Numerous factors may affect the long-term viability of spotted owls in this region. Key factors include a naturally fragmented distribution, loss and degradation of nesting habitat, loss and degradation of dispersal habitat, severe drought, and (potentially) air pollution. Our insight into the persistence of this owl is limited because we do not know the cause of the population decline we observed in the San Bernardino Mountains. However, it is likely that the decline has resulted from a complex interaction among weather, habitat changes, prey dynamics, and other factors. We provide a regional update on this owl and discuss the problems that may be affecting the species in southern California.

Key words: California spotted owl, habitat degradation, population decline, *Strix occidentalis occidentalis*

Introduction

The spotted owl (*Strix occidentalis*) ranges from southwestern British Columbia into Baja California Norte along the Pacific Coast. In addition, its distribution includes the southern Rocky Mountains from Utah and Colorado into the mountains of Mexico, where it reaches its southernmost occurrence near Mexico City (Gutiérrez and others 1995). It primarily occurs in mountainous terrain where it typically occupies closed-canopied forests (Gutiérrez and others 1995). However, the spotted owl also occupies steep, narrow canyons with relatively few trees in some portions of the southwestern United States (Rinkevich and Gutiérrez 1996).

The American Ornithologists' Union (1957) recognizes three subspecies: The northern spotted owl (*S. o. caurina*) is found in the Pacific Northwest and northwestern California, the California spotted owl (*S. o. occidentalis*) occurs in most California mountains other than those occupied by the northern subspecies, and the Mexican spotted owl (*S. o. lucida*) ranges from southern Utah and Colorado into

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Mexico (Gutiérrez and others 1995). The northern and Mexican subspecies are listed as “threatened” under the Endangered Species Act (U.S. Fish and Wildlife Service 1990, 1993) because of habitat loss and failure of existing regulatory mechanisms to protect the owl.

In southern California, forested habitat is restricted to the upper elevations of the higher mountain ranges and in canyon bottoms along streams and rivers. Thus, suitable spotted owl habitat is discontinuous and results in a series of semi-isolated owl populations within the region (*table 1*; LaHaye and others 1994, Noon and McKelvey 1992). The largest of these populations, located in the San Bernardino Mountains, declined between 1987 and 1998 (*table 2*; LaHaye and others 1999).

Table 1—*The estimated number of territories within each subpopulation of the southern California spotted owl metapopulation. Data from LaHaye and others (1994).*

Subpopulation	Estimated number of territories
Northern Monterey	50
Southern Monterey	30
Cerro Alto	3
Southern Santa Lucia	16
Sierra Madre	12
San Rafael	40
Santa Ynez	18
Mt. Pinos	15
Tecuya	10
Cobblestone	10
Tehachapi Mountains	12
Pelano	20
San Gabriel Mountains	95
San Bernardino Mountains	133
Santa Ana Mountains	12
San Jacinto Mountains	20
Thomas Mountain	10
Palomar Mountain	30
Black Mountain	5
Volcan Mountain	16
Cuyamaca Mountain	10
Laguna Mountain	15

The California Spotted Owl Technical Assessment Team (CASPO) evaluated the California spotted owl and presented “Areas of Concern” and “Recommendations” for maintenance of this subspecies in southern California (see Verner and others 1992: 7, 16). The purpose of this paper is to review these issues in the context of new information and to qualitatively evaluate the progress toward maintenance of this subspecies in southern California since CASPO.

Spotted Owl Ecology

Spotted owls are found in riparian/hardwood forest, live oak (*Quercus chrysolepis*)/bigcone Douglas-fir (*Pseudotsuga macrocarpa*) forest, and mixed conifer forest in southern California (Gutiérrez and others 1992). About one third of the known spotted owl sites are located in each forest type (Gutiérrez and others 1992). Spotted owl reproduction was found to be higher in live oak/bigcone Douglas-fir forest than in mixed conifer forest (LaHaye and others 1997); however, reproduction in riparian/hardwood sites was not considered. We speculate that owl reproduction in riparian/hardwood sites is similar to live oak/bigcone Douglas-fir sites because these forest types are similar in elevation and vegetation association (that is, they are typically surrounded by chaparral).

Table 2—*Spotted owl survey effort and banding activity between 1987 and 1998 in the San Bernardino Mountains of southern California. Table from LaHaye and others (2001).*

Year	Territories		Territorial owls		Juvenile owls	
	Number surveyed	Pct occupied	Number pairs	Number singles	Pct banded ¹	Number banded
1987	42	95	32	8	0	15
1988	78	95	56	18	42	16
1989	115	90	81	23	42	52
1990	127	86	90	19	72	47
1991	132	76	86	12	79	44
1992	136	65	78	11	91	49
1993	141	63	78	11	90	52
1994	143	68	84	13	86	70
1995	145	70	86	15	93	38
1996	146	67	89	9	93	54
1997	147	62	80	11	96	41
1998	148	59	76	11	95	23

¹ Percent of the territorial population banded prior to each field season, including newly recruited territorial owls.

Spotted owls prey on a variety of insects, birds, and mammals (Smith and others 1999). The dusky-footed woodrat is their primary prey and appears to be important to reproductive success in this owl (Smith and others 1999). Spotted owls in southern California rarely occur above approximately 2,400 m elevation (Gutiérrez and others 1995). This is most likely due to the decline in woodrat density at higher elevations (Grinnell 1908).

Little information has been collected on home-range sizes of spotted owls in southern California. However, reported home ranges in mixed-conifer habitat varied in size from approximately 400 hectares to 3,300 hectares (Zimmerman and others 2001). We suspect that these values are near the extremes for this species in this habitat type. Some lower elevation owl sites may be smaller than 400 hectares because suitable habitat is restricted to narrow strips of riparian vegetation.

Areas of Concern

CASPO identified a set of potential threats (see Areas of Concern, Verner and others 1992: 7) that we used as the outline for our qualitative assessment.

Natural Isolation of Habitat and the Regionally Restricted Distribution of Spotted Owls

Areas capable of supporting the forested habitat used by this species are uncommon in southern California because forest is restricted to higher elevations. Thus, opportunities to expand the amount of spotted owl habitat are limited (Verner and others 1992). In addition, the continued urbanization of the southern California lowlands may exacerbate the difficulties of owl movement between mountain ranges by creating additional barriers to dispersal (see below).

Dispersal Habitat

Spotted owl dispersal habitat includes the forest types mentioned above, as well as a variety of other forested and nonforested habitats (Gutiérrez and others 1985). Dispersal may be necessary to maintain populations of spotted owls within the region, and it is potentially critical to the continued existence of several of the smallest populations (LaHaye and others 1994, Noon and McKelvey 1992). However, no inter-mountain movements were recorded between 1987 and 1998 (LaHaye and others 1994, 2001). We do not know whether movements between mountain ranges have always been low or if this is a recent phenomenon reflecting reduced opportunities for successful dispersal caused by modifications to inter-mountain vegetation by humans.

Numerous riparian areas, which once existed at lower elevations and were potential dispersal corridors, have been degraded by water extraction or lost to channelization during the last century. In addition, numerous small coast live oak (*Q. agrifolia*) stands have been eliminated or modified by urbanization and are no longer usable by spotted owls. Some of these live oak stands were known to occasionally support nesting pairs (Heller 1893, Lillie 1891, WFVZ #21,133, WFVZ #69,985, WFVZ #84,150, WFVZ #121,717) and may have served as stepping-stones for dispersal among the region's mountain ranges.

Habitat Trends

Most montane forests in southern California are administered by the USDA Forest Service. However, substantial acreage of forest also exists on private lands. CASPO was unsure of the trend in the amount of montane forest in this region, and we retain that uncertainty today. Similar concerns were expressed about the integrity of owl habitat (for example, quality and fragmentation, Verner and others 1992).

Historic logging, which occurred during the 19th century and from 1950 to 1980 (Johanneck 1975, Robinson 1989), undoubtedly reduced the amount and quality of owl habitat in several mountain ranges in the region. Recent (to 2001) logging activity has been limited to infrequent commercial timber sales and localized fuelwood extraction. Although, spotted owls have reoccupied some logged sites, the current suitability of previously logged forest and the extent of reoccupation of these

forests by spotted owls are unknown. No analysis has been conducted on the effect of fragmentation on spotted owls in southern California (Franklin and Gutiérrez 2002).

Urbanization in the form of primary and vacation homes has degraded or consumed some forest in most mountain ranges. The results of spotted owl surveys conducted between 1987 and 1998 in the San Bernardino Mountains indicated that a large area of potentially-suitable spotted owl habitat, enough to support 10-15 pairs, existed between Running Springs and Crestline (LaHaye and others 1999). However, only four pairs have been found in this area, and owls were found only in undeveloped sites. Thus, residential development within montane forests may preclude spotted owl occupancy, even when closed-canopy forest remains on developed sites.

Forests in southern California have been subjected to major changes in disturbance regime during the past 150 years. Logging, urbanization, water diversions, wildfire, and mining have produced dramatic local impacts. Intensive grazing during the late 1800s (Minnich 1988), fire suppression since 1900 (McBride and Laven 1976), and air pollution since the 1930s (Miller and McBride 1998) have affected most forests in the region. These impacts have altered the growth and regeneration of forest vegetation (Minnich and others 1995) within owl habitat and could be influencing the dynamics of spotted owl prey. While we are unsure how these changes have affected this owl, if they negatively affect prey abundance or availability, maintaining a regional population of spotted owls will require thoughtful planning and management.

Water Diversion and Stream Channelization

Spotted owl habitat associated with riparian areas is subject to direct effects such as removal of riparian forests due to channelization and other land-clearing activities and indirect effects such as vegetation degradation caused by water extraction and human recreation. Both may ultimately result in loss of suitable habitat. Riparian forests and other woodlands at low elevations have been modified at a faster rate than montane forests because they occur in areas targeted for development, flood control, or domestic water production. However, the extent of this habitat decline and the proportion of the southern California spotted owl population that historically resided in these forests are unknown.

Wildfire

Wildfire is a constant threat in southern California (Keeley and others 1999, Minnich 1983), and the effects of wildfires are becoming more severe (that is, fires are larger and hotter, Minnich 1983). In addition, Minnich (1980) suggested that the total area of live oak/bigcone Douglas-fir forest has declined during the last century due to changes in fire regime. Stand-replacing fires may become more commonplace. Most resource agencies recognize this problem, but public concerns about air quality, safety, and liability often prevent application of large-scale prescribed fire programs (Biswell 1989). Thus, managers recognize the threat of fire to wildlife habitat and humans, but little progress has been made toward implementing effective fuels reduction programs through controlled burning and other methods.

Recreational Activities

Human recreation may be a contributing factor to spotted owl habitat degradation. With approximately 15 million people in the southern California area, the demand for recreational opportunities is constantly increasing. Much of the focus for this demand is on public lands in the mountains and riparian areas. Direct impacts, such as killing owls, are probably uncommon. However, indirect impacts such as trampling vegetation and habitat lost to development of new parks, campgrounds, trails, and roads may have significant cumulative effects on spotted owl habitat. We are unaware of a region-wide assessment of these impacts.

Drought

To the areas of concern listed by CASPO, we add the negative effects of drought and air pollution (see below). It is well known that weather can affect demographic processes in spotted owls (for example, Franklin and others 2000, North and others 2000). We hypothesize that drought can also have negative long-term effects on their habitat.

The majority of the demographic data for the San Bernardino Mountains spotted owl population were collected when annual precipitation was below average. The results of demographic analyses showed that reproduction was strongly dependent on precipitation patterns (LaHaye and others unpublished data³). However, survival was not related to weather. In addition to the direct effect of weather on reproduction, the current extended drought is degrading montane forest in many areas (that is, increased tree mortality in forests occupied by owls) due to water stress, which will likely alter the quality and distribution of spotted owl habitat in the region.

Air Pollution

Air pollution affects large areas of southern California, especially on the cismontane sides of the major mountain ranges (Miller and McBride 1998). Pollutants such as ozone and nitrogen oxides may affect vegetation growth and subsequent densities of spotted owl prey. In addition, there may be direct effects on the portion of the owl populations that receive the highest concentrations of air contaminants, because birds lack a DNA repair mechanism for lung tissue (Rombout and others 1991).

Recommendations

Below, we review CASPO's recommendations for the spotted owl in southern California (Verner and others 1992: 16) and provide additional evaluation and comment when appropriate.

Spotted Owl Inventories

CASPO's first recommendation was to inventory all potential habitats in southern California to provide an accurate estimate of the size of each population. These

³ Unpublished data on file at the Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN

estimates are essential and have considerable influence on the results of modeling subpopulation and metapopulation persistence (LaHaye and others 1994, Noon and McKelvey 1992). Although thorough inventories have not been completed, Stephenson (1991) estimated the amount of suitable habitat available within all of the major mountain ranges and provided estimates of the potential number of owls that each mountain range could support. Given the recently acquired information on demographic variability associated with this species (Franklin and others 2000, Seamans and others 2002), we suspect that some of the smaller owl populations may not currently exist (see *table 1*). Indeed, the San Bernardino Mountains and San Jacinto Mountains spotted owl populations seem to have declined substantially during the past decade based on recent surveys (LaHaye and others 1999, Gutiérrez and others unpublished data⁴, respectively).

Monitoring Demography

CASPO also felt it was essential to monitor the demography of the owl throughout the region. When their evaluation was released there were two spotted owl demography projects in progress (Gutiérrez and Pritchard 1990, LaHaye and others 1992). CASPO recommended that two additional demographic projects be initiated to estimate correlation of population dynamics and to provide estimates of movement rates among subpopulations. These new projects were not initiated. Thus, estimates of these parameters are still unavailable.

In addition, CASPO recommended continued funding for the existing demography studies. However, funding was discontinued in 1994 for the San Jacinto Mountains' population study and in 1999 for the San Bernardino Mountains' owl study, despite evidence that both populations were declining.

Maintain Habitat for all Known Pairs

CASPO argued that the overall numbers of spotted owls in southern California and the small sizes of many of the known populations required maintenance of habitat for all known pairs. This recommendation was generally accepted and implemented by the USDA Forest Service (USDA Forest Service 1993). However, due to incomplete surveys and private ownership of some areas containing spotted owl habitat, it is not clear how effective this policy has been. A small number of spotted owls were known or suspected to exist on private lands in several of these mountain ranges. We could not determine the degree of protection afforded these owls. To the best of our knowledge, the San Bernardino National Forest was the only national forest in southern California to develop a formalized plan for protecting spotted owl habitat (USDA Forest Service 1989). This plan described the criteria by which a site qualified as a designated owl territory, the amount of protected forest to be included within a designated territory, the desired characteristics of forest to be protected, the potential disturbance factors, and seasonal closures designed to minimize disturbance to nesting owls.

⁴ Unpublished data on file at the Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN

Formulating Regional Guidelines

CASPO believed that it was necessary to develop southern California regional guidelines for effective protection of this species. They recommended assembling a team of specialists to formulate these guidelines. This recommendation has not been accomplished as of 2002. (Editor's note: the four southern California national forests completed a California spotted owl management strategy in 2004.)

Conclusions

Since CASPO (Verner and others 1992), considerably more has been learned about the ecology of the spotted owl in southern California (Carlson and others 1998, LaHaye 1997, LaHaye and others 1992, 1994, 1997, 2001; Smith and others 1999, 2002). However, the status of the overall population of this species in the region is still unclear. Demographic estimates continue to indicate the largest spotted owl population in southern California is declining (LaHaye and others unpublished data⁵). Policy and management of this species do not appear to be clear or consistently implemented. Further, little effort is devoted towards monitoring the species and its habitat.

As the human population in southern California continues to expand, the need for additional space and resources is likely to increase pressure on the remaining habitat supporting the spotted owl. Continued habitat degradation, in conjunction with the unknown cause(s) of the species' regional decline, leads to an uncertain future for the spotted owl in southern California, particularly for the small, isolated populations.

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⁵ Unpublished data on file at the Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN

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Bats in the South Coast Ecoregion: Status, Conservation Issues, and Research Needs¹

Karen L. Miner² and Drew C. Stokes³

Abstract

California's bat fauna is one of the most diverse in the United States. Of the 25 species of bats in the state, 24 have been detected in the south coast ecoregion. Many of these species appear to have experienced population declines in the ecoregion, and 16 are officially recognized as sensitive (including one endangered) by wildlife regulatory agencies. Data from recent field survey work conducted by bat researchers were compiled in order to provide a tentative assessment of the current status of bats within the south coast ecoregion. These data suggest that the pallid bat (*Antrozous pallidus*), Townsend's big-eared bat (*Corynorhinus townsendii*), and California leaf-nosed bat (*Macrotus californicus*) have experienced population declines and could be seriously threatened, particularly at lower elevations. This may also be true for some of the region's other bat species, such as the western red bat (*Lasiurus blossevillii*), but additional research is needed. The Yuma myotis (*Myotis yumanensis*), Mexican free-tailed bat (*Tadarida brasiliensis*), and big brown bat (*Eptesicus fuscus*) were frequently encountered in both Krutzsch's (1948) and recent field inventories, so they appear to remain relatively common at this time. The major threat to bats in the ecoregion is the loss of habitat (especially riparian and oak woodland habitats) due to urban expansion as well as extermination or disturbance of bat colonies. Characterization of species-specific distribution and seasonal habitat use patterns is needed so that land managers can address both foraging and roosting habitat requirements from a landscape perspective. Research is also needed regarding the effects of urbanization, insect control, tree/snag management, bat exclusions, mine closures, and recreational activities, specifically rock-climbing, on bat populations.

Key words: bat conservation, Chiroptera, habitat loss, population status, species diversity

Introduction

California has the fourth highest diversity of bat species in the United States, following Arizona, New Mexico, and Texas, with 25 species representing three families. Twenty-four of these species occur in the south coast ecoregion of the state, indicating the importance of the region to bat diversity. Over two-thirds of the region's bat species are officially recognized as sensitive by the California Department of Fish and Game, U.S. Fish and Wildlife Service, and/or Federal land management agencies at this time (*table 1*). The California Department of Fish and Game (B. Bolster pers. comm.) reports that four additional species have been proposed to become *California Species of Special Concern* in the latest draft of "Mammal Species of Special Concern in California" (CSC* in *table 1*).

¹ An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

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Table 1—Bats of California and their legal status. All except *Myotis occultus* have been previously documented in the south coast ecoregion.

Family/ Scientific name ¹	Common name	Legal status ²
Phyllostomatidae	American leaf-nosed bats	
<i>Macrotus californicus</i>	California leaf-nosed bat	CSC, FSS, BLM
<i>Choeronycteris mexicana</i>	Mexican long-tongued bat	CSC
<i>Leptonycteris curasoae yerbabuenae</i>	Lesser long-nosed bat	FE ³
Vespertilionidae	Mouse-eared bats	
<i>Myotis lucifugus</i>	Little brown bat	none
<i>Myotis occultus</i>	Arizona myotis	CSC, BLM
<i>Myotis yumanensis</i>	Yuma myotis	FSC, BLM
<i>Myotis velifer</i>	Cave myotis	CSC, BLM ³
<i>Myotis evotis</i>	Long-eared myotis	FSC, BLM
<i>Myotis thysanodes</i>	Fringed myotis	FSC, CSC*, BLM
<i>Myotis volans</i>	Long-legged myotis	FSC, CSC*, BLM
<i>Myotis californicus</i>	California myotis	none
<i>Myotis ciliolabrum</i>	Small-footed myotis	FSC, BLM
<i>Lasionycteris noctivagans</i>	Silver-haired bat	none
<i>Pipistrellus hesperus</i>	Western pipistrelle	none
<i>Eptesicus fuscus</i>	Big brown bat	none
<i>Lasiurus blossevillii</i>	Red bat	CSC*, FSS
<i>Lasiurus xanthinus</i>	Western yellow bat	CSC*
<i>Lasiurus cinereus</i>	Hoary bat	none
<i>Euderma maculatum</i>	Spotted bat	CSC, FSC, BLM
<i>Corynorhinus townsendii</i>	Townsend's big-eared bat	CSC, FSC, FSS, BLM
<i>Antrozous pallidus</i>	Pallid bat	CSC, FSS, BLM
Molossidae	Free-tailed bats	
<i>Tadarida brasiliensis</i>	Mexican free-tailed bat	none
<i>Nyctinomops femorosaccus</i>	Pocketed free-tailed bat	CSC
<i>Nyctinomops macrotis</i>	Big free-tailed bat	CSC
<i>Eumops perotis californicus</i>	Western mastiff bat	CSC, FSC, BLM

¹ Scientific names after Koopman (1993), with the exception of *Corynorhinus townsendii* (Frost and Timm 1992, Tumlison and Douglas 1992), *Lasiurus blossevillii*, and *L. xanthinus* (Baker and others 1988, Morales and Bickham 1995).

² Legal status categories include Federal Endangered (FE), Federal Species of Concern (FSC), California Species of Special Concern (CSC), Forest Service Sensitive (FSS), and Bureau of Land Management Sensitive (BLM). Source: Calif. Dept. of Fish and Game, Special Animals List of July 2002 and species proposed to become California Species of Special Concern (CSC*, DFG—B. Bolster pers. comm.)

³ Currently known in the state from only two or three recent public health records from urban areas in the ecoregion (Constantine 1998).

Despite the high diversity and sensitivity of bats in the south coast ecoregion, this group of mammals has been largely ignored during environmental review of proposed projects and in recent multi-species planning efforts. This is primarily due to the lack of information on the distribution, seasonal habitat associations, and population status of bat fauna. The purpose of this paper is to bring together recent bat inventories, in order to attempt a preliminary assessment of population status and research needs for this ecologically important group of mammals in the south coast ecoregion of California.

Historic and Recent Field Studies

Early studies of bats covering portions of the south coast ecoregion of California include Grinnell (1918), *A Synopsis of the Bats of California*; Krutzsch (1948), *Ecological Study of the Bats of San Diego County, California*; and Vaughan (1954), *Mammals of the San Gabriel Mountains of California*. While all three studies presented species records for the region, only Krutzsch (1948) attempted to assign estimates of relative abundance of species with respect to environmental factors, such as gross climatic zones, topography, life zones, and plant associations (table 2). In addition, 18 of the 24 species in the ecoregion are represented in Krutzsch's study. This allows us some measure by which to compare and contrast historic and current information regarding bat species richness and diversity within the ecoregion.

Table 2—Relative abundance of bats in San Diego County (A-abundant, C-common, R-rare) by topographic areas during the 1930s and '40s, after Krutzsch (1948). Scientific names as in table 1.

Species	Coastal plain	Inland valley	Western foothills	Mountains	Eastern foothills	Desert
<i>Ma. californicus</i>		R	R			C
<i>C. mexicana</i>	R	R				
<i>M. yumanensis</i>	C	A	A	C		
<i>M. evotis</i>			C	C		
<i>M. thysanodes</i>			C	C	R	
<i>M. volans</i>			R	R		
<i>My. californicus</i>	C	C	A	A	C	C
<i>M. ciliolabrum</i>		R	C	C	C	C
<i>P. hesperus</i>		C	C		A	A
<i>E. fuscus</i>	C	A	A	A	C	
<i>L. blossevillii</i>	C	C	C			
<i>L. cinereus</i>	C	C	C			
<i>C. townsendii</i>	C	A	A	A	C	C
<i>A. pallidus</i>	A	A	A	R	C	C
<i>T. brasiliensis</i>	A	A	A	C	C	
<i>N. femorosaccus</i>			R		R	
<i>N. macrotis</i>	R					
<i>E. perotis</i>	R	R	C		R	

The only recent published literature on bat distribution in the region is a review of public health records by Constantine (1998), in which he focused on range extensions of ten rare or uncommon species. However, government agencies and private individuals have conducted inventories of bat fauna at various locations throughout the ecoregion in recent years. Written reports or data for some of these efforts have been obtained to develop a picture of the current status of bats in the ecoregion. These studies vary in duration, intensity, and area covered, but all used at least two of the three primary detection methods for bats: mist-net capture, acoustic detection, and roost searches. The most extensive of the studies is the 3-year study by the USDA Forest Service on bat habitat associations within the four southern California national forests (Simons and others 2000), conducted for the Southern California Mountains and Foothills Assessment (Stephenson and Calcarone 1999). Results from this study have been divided according to national forest boundaries to provide a more geographic representation of the data. The most intensive of the studies presented are those for Orange County (Remington 2000) and Marine Corp Air Station at Miramar

(MCAS Miramar) in San Diego County (Hunsaker 2001), for which the total nights of effort were 68 and 73, respectively, with multiple visits to most, if not all, of the sites sampled. Data from the collection of unpublished studies have been summarized and grouped into two general topographic categories: studies conducted in the coastal plain or inland valley areas, with the majority of sampling sites located under 300 meters elevation, and studies conducted in the foothills or mountain areas with the majority of sampling sites above 300 meters (*table 3*). This division roughly corresponds to the topographic divisions in *table 2* (after Krutzsch 1948), as well as the current location of the expanding edge of urbanization. The general study areas are mapped in *figure 1*.

There are several caveats to keep in mind when comparing results of these studies. Selection of sample sites among studies was subjective, and the distributions of the sites are not likely representative of habitats present within the study area. Bat researchers typically select sites near water or suspected roosts where the probability of detecting and capturing bats is higher. The seasonal distribution of sampling effort also varied among studies with most, if not all, of the effort focused on the summer season. Within the region, some species are more commonly detected during migration (for example, silver-haired bat, *Lasionycteris noctivagans*) or in winter months (Mexican long-tongued bat, *Choeronycteris mexicana*, and hoary bat, *Lasiurus cinereus*). The studies also differ in the relative emphasis of the survey methods employed. Some species are not readily detected acoustically due to either low call amplitude or inconsistent use of echolocation (Townsend's big-eared bat, *Corynorhinus townsendii*, and Mexican long-tongued bat), while others are not readily captured in mist nets (western mastiff bat, *Eumops perotis*). In addition, species identification based solely on limited acoustic data can be problematic, as with *Myotis* species. In consideration of the above, we recognize that the lack of species detection within any one study does not necessarily mean that a species is absent from the study area. However, together these studies do provide some indication of the frequency at which species are detected during field investigations across the ecoregion.

Both Krutzsch (1948) and recent field studies (*table 3*) detected 18 species. However, Krutzsch's list included the Mexican long-tongued bat, while recent studies include the spotted bat (*Euderma maculatum*). In general, both historic and recent studies indicate that species diversity is higher in the foothills and mountains than the coastal plain and inland valleys in terms of the relative frequency of detection, particularly for the genus *Myotis*.

Other Records

Five other species occurring in the ecoregion, unaccounted for in the above studies, include the little brown bat (*Myotis lucifugus*), cave myotis (*Myotis velifer*), western yellow bat (*Lasiurus xanthinus*), silver-haired bat, and the federally-listed endangered lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*). These species are reported in the ecoregion based on a few individual specimens and/or public encounters in urban settings only (Bond 1977, Constantine 1998). Additional information on bat distributions can be obtained through investigation of encounters reported by the public (Remington 2000, KLM and DCS pers. obs.) These records compliment recent field studies by providing information for the coastal plain/inland valley

Table 3—Summary of recent bat inventory studies in the south coast ecoregion showing the number and percent (shown in *italics*) of sites at which each bat species was detected. The studies are grouped into two general topographic categories: coastal plain and inland valleys (A-F) and foothill and mountains (G-N).

Species	Study ¹													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
	Effort (nights/sites)													
<i>Ma. californicus</i>	68	30	12	73	16	36	33	3	11	14	21	26	33	35
<i>M. yumanensis</i>	6	26	9	23	7	24	21	7	8	12	17	14	21	19
<i>M. evotis</i>						1								
<i>M. thysanodes</i>						4								
<i>M. volans</i>						15	7	5	5	3	3	7	4	
<i>My. californicus</i>	6	19		15	6	13	15	7	5	5	3	3	7	4
<i>M. cililabrum</i>	100	73		65	86	54	71	100	63	42	18	21	33	21
<i>P. hesperus</i>						3			1	7	2	3	7	3
<i>E. fuscus</i>						13			13	58	12	21	33	16
<i>L. blossevillii</i>										1	2	2	1	5
<i>L. cinereus</i>										8	12	14	5	26
<i>C. townsendii</i>											2	3	3	4
<i>E. maculatum</i>											12	21	14	21
<i>A. pallidus</i>	3				2	7	8		6	7	9	7	9	12
<i>T. brasiliensis</i>	50				29	29	38		75	58	53	50	43	63
<i>N. femorosaccus</i>					4	10	12	4	6	10	4	4	6	10
<i>N. macrotis</i>					57	42	57	57	75	83	24	29	29	53
<i>E. perotis</i>		2		1	7	9	8	3	3	10	9	8	3	3
		8		4	100	38	38	43	38	83	53	57	14	16
	4	17		3	6	12	17	4	7	10	9	9	18	14
	67	65		13	86	50	81	57	88	83	53	64	86	74
	1		1	2	4	2	1		4	1	1		1	5
	17		11	9	57	8	5		50	8	6		5	26
				1	2	4			4	1		1	2	3
				4	29	17			50	8		7	10	16
					1	3		1	2	4			1	5
					14	13		14	25	33			5	26
											1			1
											6			5
	3	7				3	1	2	2		4	3		
	50	27				13	5	29	25		24	21		
	6	18	1	11	7	16	11	2	6	8	3		3	5
	100	69	11	48	100	67	52	29	75	67	18		14	26
	2	5		9	7	13	10		6	9			2	7
	33	19		39	100	54	48		75	75			10	37
			1		1	3			2	1				
			11		14	13			25	8				
	6	12		10	7	12	13	2	8	10	6	1	7	11
	100	46		43	100	52	62	29	100	83	35	7	33	58

¹ A) Orange County, Remington 2000; B) Camp Pendleton Marine Corp Base, Brown and Berry 1999; C) Pt Loma, USGS 2002 unpublished data D) Marine Corp Air Station, Miramar, Hunsaker 2001; E) San Diego National Wildlife Refuge, Stokes unpublished data; F) San Diego County MSCP area, USGS 2002 unpublished data; G) Southern Santa Ana Mountains, Fisher & Crooks 2000; H) Potrero Creek, Riverside County, Stokes unpublished data; I) Ysabel Ranch Preserve, USGS 2002 unpublished data; J) Cleveland National Forest, Descanso District, USGS 2002 unpublished data; K) Los Padres National Forest, L) Angeles National Forest, M) San Bernardino National Forest, and N) Cleveland National Forest, Simons and others 2000.

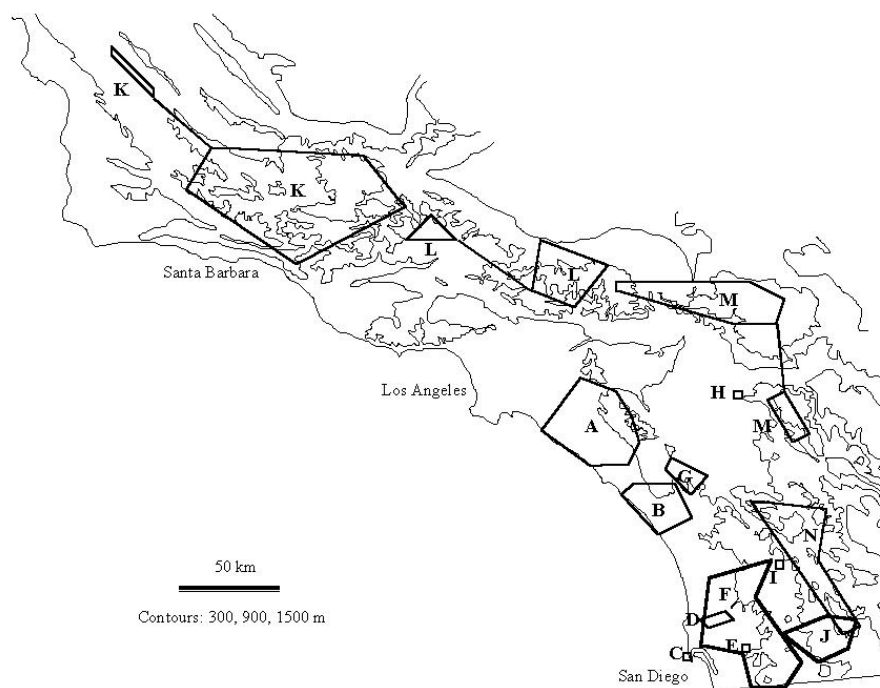


Figure 1—Locations and general area covered by recent bat inventories conducted within the south coast ecoregion. Letters correspond to studies as in *table 3*.

topographic regions, which are more urbanized now than during Krutzsch’s study and, therefore, under-represented in recent fieldwork conducted in wildlands.

Current Population Status

Declining Populations

Inferences regarding the population status of bats in the south coast ecoregion can be made from the information presented above. There is reasonably strong evidence of population declines within the ecoregion for three species: the pallid bat (*Antrozous pallidus*), Townsend’s big-eared bat, and California leaf-nosed bat (*Macrotus californicus*).

The pallid bat is a large-bodied species that typically roosts in a variety of crevice-like situations and feeds primarily on large arthropods, including several terrestrial species (Barbour and Davis 1969). It appears to have undergone a serious decline within the ecoregion, particularly in the low-lying areas. Krutzsch (1948) described the coastal race as being abundant from sea level through the western foothills, occurring in riparian, chaparral, oak savannah, and cultivated areas. All of the roosts located by Krutzsch were in man-made structures, often in association with other common species such as the Yuma myotis (*Myotis yumanensis*), big brown bat (*Eptesicus fuscus*), and Mexican free-tailed bat (*Tadarida brasiliensis*). Vaughan (1954) referred to this species as “probably the most common and characteristic bat of the citrus belt” at the Pacific base of the San Gabriel Mountains. However, by the 1970s only one of twelve roosts previously described by Krutzsch as having been

consistently occupied for a decade in San Diego County was still extant (P. Brown pers. comm.). In recent years, the pallid bat has been detected in the Transverse Range (Simons and others 2000), sycamore-oak riparian areas in and around the Santa Ana Mountains (Brown and Berry 1999, Fisher and Crooks 2000, Remington 2000), and a few inland valley sites in southern San Diego County (USGS 2002⁴). During the last decade in San Diego County we have observed numerous colonies occupied by the three common bat species listed by Krutzsch as pallid bat associates; however, very few pallid bat colonies have been documented. Although this species can be found in rural settings, it appears to be intolerant of urban development (E. Pierson pers. comm., Remington 2000). Populations will likely continue to decline as urban expansion encroaches into the foothills of the region.

The Townsend's big-eared bat occurs in a variety of habitats, including desert scrub, sagebrush, chaparral, and deciduous and coniferous forests, where it feeds primarily on moths (Barbour and Davis 1969). However, its distribution is strongly correlated with the availability of roosting habitat such as caves or cave-like structures including mines, tunnels, abandoned buildings, and bridges (Pierson and Rainey 1998a). According to Krutzsch (1948), the Townsend's big-eared bat was "widely and commonly distributed from the seacoast to the desert." He described it as common on the coastal plain and abundant in the inland valleys, foothills, and mountains (*table 2*). Now it appears that within the south coast ecoregion the species is relatively rare and limited primarily to the foothill and mountain areas (*table 3*). Pierson and Rainey (1998a) reported that the cismontane maternity colonies described by Krutzsch in San Diego County were no longer extant. This species was often encountered during recent mine surveys conducted above 850 m within the ecoregion, but few maternity colonies were confirmed (Miner and others 2000, Simons and others 2000). The Townsend's big-eared bat is not readily detected in mist net or acoustic surveys; roost searches are the most efficient survey method for this species. However, roost surveys must be undertaken with caution because disturbance at the roost can result in abandonment by this species. The loss of or disturbance to both maternity and hibernation roost sites has been recognized as the primary threat to the Townsend's big-eared bat throughout the western United States (Pierson and others 1999). There are few known extant maternity colonies within the ecoregion, and none can be considered adequately protected. Due to the species' vulnerability to human disturbance at roost sites, further declines might be expected as the human population increases within the region.

The California leaf-nosed bat is a tropical, insectivorous species that ranges north into the lower Sonoran life zone of southern California, Arizona, and New Mexico. It is an obligate cave or mine roosting species and requires roost temperatures in excess of 26°C year-round to survive because it lacks the ability to hibernate (Bradshaw 1962 in Anderson 1969). Historically, the California leaf-nosed bat was known from a few caves, tunnels, or mines in the inland valleys of the south coast ecoregion (Bond 1977, P. Brown pers. comm., Constantine 1998, Grinnell 1918, Krutzsch 1948). Live individuals of this species have not been observed at the Los Angeles/Ventura County sites since the late 1940s or early 1950s (Constantine 1998), nor have they been seen at the northern San Diego County sites since the early 1900s (P. Brown pers. comm.). However, one extant small colony (less than a dozen bats) continues to persist in a tunnel at an inland valley site in southern San Diego

⁴ Unpublished data on file, U.S. Geological Survey, Western Ecological Research Center, San Diego, CA.

County (P. Brown pers. comm., USGS 2002⁵). While the California leaf-nosed bat can still be found in the California deserts, this species appears to have been all but extirpated from the south coast ecoregion.

Stable Common Populations

Based on the information provided by the various bat inventories (*table 3*) and the authors' experience investigating calls received by San Diego Bat Conservation (SDBC), it is clear that three species—Yuma myotis, Mexican free-tailed bat, and big brown bat—are relatively common within the south coast ecoregion and appear to be relatively urban-adapted. All three readily roost in man-made structures. The Yuma myotis forages primarily over open water, although it will forage in other habitats, and often roosts near available water sources. The Mexican free-tailed bat covers large areas while foraging over a variety of habitats. This, along with its generalized roosting requirements (caves, rock crevices, buildings, and bridges), makes it probably the most adaptable species in urban landscapes. The big brown bat is typically found in association with wooded areas, whether natural or planted. Although fairly common in both field studies and SDBC public contacts, evidence suggests that this species might not persist in small isolated habitat fragments or highly urbanized areas (Remington 2000.)

Stable Uncommon and Rare Populations

There are several uncommon-to-rare species that appear to have relatively stable populations within the ecoregion. These include the western pipistrelle (*Pipistrellus hesperus*), small-footed myotis (*Myotis ciliolabrum*), long-eared myotis (*Myotis evotis*), fringed myotis (*Myotis thysanodes*), long-legged myotis (*Myotis volans*), and Mexican long-tongued bat. While the desert population of western pipistrelle is abundant in rocky areas, the coastal population apparently always has been less abundant (Kruttsch 1948). This species appears to still be present in rocky canyon habitat of the inland valleys, foothills, and mountains. The small-footed myotis occupies the same topographic regions as the western pipistrelle but seems to be associated more with riparian and wooded habitats. While still regularly encountered, both of these species may be experiencing habitat loss in the lower elevations of their range within the ecoregion.

The long-eared myotis, fringed myotis, and long-legged myotis occur primarily in forested habitat in the mid- to upper elevations of the region. Based on limited historic collections, they likely have never been particularly common, especially the latter two species (Grinnell 1918, Kruttsch 1948, Vaughan 1954). Recent field studies in the upper elevations of the ecoregion detected these species at a few sites within each study area, indicating that they are patchily distributed throughout the forests. These species have been documented roosting in snags or trees in other portions of their range (Barclay and Brigham 1996). However, during the USDA Forest Service's southern California forest bat study, individual bats of these species were radio-tracked to rock crevices and building roosts (Miner and Brown 1996). The only maternity colony documented during the study was a building roost of long-eared myotis (~ 30 individuals). Timber harvest is the major threat to these species in other portions of their range (Barclay and Brigham 1996). While currently this is not a serious threat within the ecoregion, there is concern that the removal of snags or

⁵ Unpublished data on file, U.S. Geological Survey, Western Ecological Research Center, San Diego, CA.

trees, such as is done for hazard abatement, fire suppression, and forest pest management, may seriously impact *Myotis* species. Of particular concern is the lack of known extant maternity colonies for the fringed myotis and long-legged myotis (B. Bolster pers. comm.).

The Mexican long-tongued bat feeds on pollen and nectar, specializing in the flowers of agaves and columnar cactus. It will also visit hummingbird feeders and other nectar-rich plants (Arroyo-Cabrales and others 1987, W. Peachey pers. comm.), possibly even farmed avocado plants in the ecoregion (public contact investigations). The southern part of the ecoregion represents the northwestern extreme margin of the otherwise subtropical distribution of the Mexican-long-tongued bat. It roosts in shallow caves and mines throughout most of its range. However, in California the species has yet to be documented in the wildlands and instead is found in residential areas, roosting in garages, sheds, porches, and under houses built on stilts. The Mexican long-tongued bat was first recorded in San Diego County in the late 1940s in developed areas along the coast and inland valleys (Olson 1947). Since then, individuals have been turned in to public health departments in Los Angeles, Orange, and Ventura counties (Constantine 1998). While the Mexican long-tongued bat is regularly seen during fall and winter in San Diego residential areas, it is as yet undocumented that it remains during the maternity season, and it is presumed not to breed in California.

Increasing Populations

The western yellow bat is another primarily subtropical species. It is known to roost among the fronds of palm trees and was first recorded in palm habitat of the California desert in the 1940s (Constantine 1946). Now it is regularly encountered year-round in urban areas throughout the region, primarily in association with planted palm trees (Constantine 1998, D. Simons pers. comm., KLM and DCS pers. obs.), and it is assumed to breed within the ecoregion (P. Brown, pers. comm.). This apparent expansion into the ecoregion may be in response to exotic landscape plantings and possibly to global warming (Constantine 1998).

Status Unknown

It is not possible to determine the population status for the 11 remaining species within the ecoregion based on available information. This is due to either the seasonal or elevational bias of the field studies or the lack of comparable historical data. The survey effort for most of the field studies presented above (*table 3*) was concentrated during the summer months. Therefore, tree-roosting species such as the silver-haired bat and hoary bat that occur in the ecoregion primarily during migration or winter are less frequently encountered. Most hoary bat records within the ecoregion are between late September and May (Vaughan and Krutzsch 1954, authors' public contact investigations). However, some individuals remain all summer in the higher elevations of the mountains (KLM and DCS pers. obs., Simons and others 2000, Vaughan and Krutzsch 1954). The higher detection frequency of hoary bats in the most recent field studies in San Diego County (studies E and F in *table 3*) is due to spring survey effort, when hoary bats are migrating. The silver-haired bat is a migratory species associated primarily with coniferous forests and is not known to breed in southern California (Barbour and Davis 1969). It is only represented within

the ecoregion from public contact records (Constantine 1998), presumably encountered during migration.

Urbanization in the south coast ecoregion has removed habitat primarily at lower elevations. For bat species that rely on the impacted habitat types, population status would be predicted to decline. Such appears to be the case for the western red bat and California myotis (*Myotis californicus*). However, surveys focused on these habitat types, as well as urban landscaped areas, are needed before conclusions can be drawn. The western red bat (*Lasiurus blossevillii*) is a solitary, migratory species that roosts in the foliage of trees and shrubs (Shump and Shump 1982). It has a strong association with riparian woodlands, especially in the lowlands of the Central Valley and southern California (Pierson and others 2000). It has also been observed to roost in orchards (Constantine 1959, Grinnell 1918, Kruttsch 1948, Vaughan 1954). According to Grinnell (1918), the sexes segregate during late spring and summer, with females remaining in the lowlands and males moving to higher elevations. However, Kruttsch (1948) found both sexes of this species to be common year-round from the coast up into the western foothills. After reviewing location records for the species, E. Pierson (pers. comm.) postulated that coastal southern California could provide very important wintering as well as summering habitat for the western red bat. Additional studies are needed at lower elevations during both winter and summer to determine whether this species, like riparian birds, has indeed suffered critical habitat loss from agricultural conversion, reservoir construction, and urban expansion. The California myotis has generally been considered to be common to abundant throughout all topographic regions of the ecoregion (Kruttsch 1948), particularly in oak woodland canyons (DCS pers. obs., Vaughan 1954). However, current data suggest that local declines may be occurring in the more developed portions of the coastal plains and inland valleys.

Bat surveys in urban settings in coastal plain and inland valley areas could help determine the status of other bat species in the ecoregion as well. Constantine (1998) documented the first and only two specimens of the federally listed, endangered lesser long-nosed bat for the state from southern California public health records. This species is similar in habit to the Mexican long-tongued bat in that it is migratory, forages on pollen and nectar, and roosts openly in cave-like situations. Like the Mexican long-tongued bat, it appears to be found within the ecoregion during the fall and winter in association with exotic landscaping in urbanized areas. Another species that is only known in the ecoregion from a few public health records is the cave myotis, which previously was only known in the state along the Colorado River (Constantine 1998). While these records may represent vagrants or inadvertently transported individuals, it is possible that these species, like the Mexican long-tongued bat and western yellow bat, may be expanding their range into the ecoregion.

It is difficult to determine current population status relative to historic occurrence information for several species of bats, including the western mastiff bat, big free-tailed bat (*Nyctinomops macrotis*), pocketed free-tailed bat (*Nyctinomops femorosaccus*), and spotted bat. This is due primarily to the fact that acoustic detection is now used more frequently as a survey method, greatly increasing the detectability of these species. Historically, the greatest concentration of western mastiff bat roosts documented in the state was in southern California (Pierson and Rainey 1998b). Many of these roosts were located near the base of the Transverse Range in the Los Angeles basin, often in buildings. Natural roosts for this species are located primarily in rock crevices on cliffs and large rock outcrops. The western mastiff bat

was detected in all but the USGS Point Loma study represented in *table 3*, and it was previously detected at Point Loma as well (P. Brown pers. comm.). This does not necessarily mean that it is abundant within the ecoregion. The detection rate of the mastiff bat is greater relative to other species because it has an echolocation call falling within the human range of hearing that can be heard at distances up to 300 meters. Because of this, its relative abundance can be overestimated. Of particular concern is the apparent decline of this species in the northern portion of the Los Angeles basin. In their statewide review of the western mastiff bat, Pierson and Rainey (1998b) were unable to detect this species in areas that had provided numerous historic records. The western mastiff bat was also recorded only from one site in the Angeles National Forest (*table 3*), providing further evidence for a possible decline in that area. This species typically forages over wide-open spaces of various habitats (Pierson and Rainey 1998b). It is likely that urban development of the coastal plain has greatly reduced foraging habitat for this species in the ecoregion.

As with the western mastiff bat, pocketed and big free-tailed bats appear to be more frequently detected now than historically, both in field studies (*table 3*) and public health records (Constantine 1998). This could be due to increases in their populations within the region or to improved survey methods and increased public contact with these species. Both of these species roost in rock crevices on cliff faces and have been found to use abandoned rock quarries in San Diego County (KLM and DCS pers. obs.). The pocketed free-tailed bat is detected throughout the southern portion of the south coast ecoregion and east through the deserts. The big free-tailed bat is much rarer and found further north along the coast than the pocketed free-tailed bat (Constantine 1998).

The spotted bat always has been represented in the region by few records and is probably so rare as to be easily missed without committing to focused searches. Likewise, the Transverse Ranges forming the northern border of the ecoregion may represent the most southern limit of the little brown bat in the state, explaining the rarity of records for this species.

Conservation Issues

Although specific information from the south coast ecoregion is lacking, the basic ecology of bats and information from focused studies conducted elsewhere provide indications of relevant conservation issues. Bats have specific seasonal roosting requirements that may or may not be met within a given roost, area, or region. Most bats will change roosts several times over their annual cycle, through longitudinal or altitudinal migration or local movements (Barbour and Davis 1969). Recent research has shown that many tree roosting species will switch roosts every few days (Barclay and Brigham 1996). This means that multiple roosts of varying temperature regimes need to be available within appropriate habitat and flight distance of the species for a population to remain viable. Bats also need adequate foraging habitat within the nightly commute distance from a given roost. Commute distances vary among species (Pierson 1998) and seasonally within a given species (Brown and others 1995). Therefore, spatial distribution of roosts and foraging habitat may be critical for sustainable bat populations. This necessitates that a landscape-level approach be taken when considering bat conservation, especially in a region experiencing large-scale urban development and increased habitat fragmentation such as the south coast ecoregion.

Another important conservation issue with respect to bats is the wanton destruction of or disturbance to bat colonies. Many species of bats aggregate into colonies during at least a portion of their annual cycle, making them vulnerable to catastrophic events. This is particularly true for colonies that find the microclimatic conditions of man-made structures favorable, placing them in close proximity to humans. Irrational fears and misconceptions regarding health risks have led to the needless destruction of numerous bat colonies. In addition, several species of bats, most notably the Townsend's big-eared bat (Pierson and others 1999), will abandon roosts if frequently disturbed. Due to low fecundity (typically one pup per year, Barbour and Davis 1969), longevity (individuals may live for over a decade, Hill and Smith 1984), and the fact that colonial bats typically exhibit high site fidelity from year to year (Lewis 1995), recovery or recolonization is slow if it occurs at all. While public education can help dispel myths about bats, and humane exclusions can spare the lives of bats, physical protection of occupied roosts is crucial for bat conservation, particularly for the rarer species.

Even though there is a wide range of threats to bats (Pierson 1998), the greatest threat in the south coast ecoregion is urban/suburban expansion and its associated impacts to roosts and foraging habitat. Loss or conversion of habitat at the lower elevations, particularly of riparian and oak woodlands, has likely had significant impacts on regional bat fauna. Moreover, once bats take up residence in suitable anthropogenic roosts and are discovered, they are often driven out or exterminated. Even tree trimming activities (for example, palm skinning) can impact bats that attempt to roost in landscape plantings. The effects of urbanization reach beyond the immediate developed areas. These edge effects include recreational activities, which increase disturbance to nearby natural roosts and mines, and increased predation from human commensal animals, particularly domestic cats. Thus, the urban-wildland interface may act as a sort of population "sink," where bats appear to be common at first (possibly even attracted to man-made structures) but then decrease in abundance or richness with time and further development of the area (Remington 2000). As the urban landscape continues to encroach into the foothills, the number and relative abundance of bats in the ecoregion is likely to decline.

Other relevant threats to bats in the south coast ecoregion include water projects or the development of transportation routes, in which riparian habitat is reduced or geomorphic roosting habitat (cliffs and mines) is blasted or inundated. Several historic roosts appear to have been lost in this fashion (Pierson pers. comm.). However, dams and highway bridges do provide roosting habitat for some species of bats. Many of the dams and bridges within the region currently house bat colonies, primarily of Yuma myotis and Mexican free-tailed bats. Bridge replacement or alteration has the potential to eliminate resident colonies, but California Department of Transportation and other jurisdictions are now considering impacts to bats by their bridge projects and ways to avoid them.

Closure of mines for hazard abatement or renewed mining activities can greatly impact many species of bats, including several threatened species, such as the Townsend's big-eared bat (Brown 1995, Riddle 1995, Tuttle and Taylor 1994). The USDA Forest Service and Bureau of Land Management are making an effort to conduct bat surveys for such projects and address potential impacts.

Recreational activities such as cave or mine exploration and rock climbing can disturb bats, potentially affecting reproductive success and survival or causing roost abandonment. While impacts from cave and mine entry are well documented (Hill

and Smith 1984, McCracken 1989, Tuttle 1979), impacts to bats from rock climbing need to be investigated. Once important mine roosts are discovered, protection measures (for example, gating) should be implemented following established guidelines for the species involved.

Prescribed burns and wildfires can create snags and cavities favored by several species of bats for roosting (Barclay and Brigham 1996), but these snags also may be destroyed in a fire or even selectively removed afterwards to reduce perceived hazards. Another concern stems from the observation that some lasiurine bats will roost under leaf litter during winter (Moorman and others 1999, Saugey and others 1998) and, thus, could be killed when fires (for example, prescribed burns) occur during winter months. Smoke inhalation also can kill roosting bats if the fire or smoke enters the mines or caves.

Because most of our bats are insectivorous, the application of pesticides is a threat to bats. Not only is there a potential for reduction of the prey base, but bats also may be directly poisoned, either through consumption of tainted prey or by being sprayed while roosting in trees or orchards. Although chlorinated hydrocarbons, which were documented to impact bats (Clark 1981), are now banned in the United States, the effects of the now popular organophosphates on bats and other wildlife have not been fully investigated. Even application of Bt (*Bacillus thuringiensis*) may significantly reduce the prey base, especially moths, which form the majority of the diet for many species of bats (Ross 1967). For further discussion of conservation issues and threats to bats, see Pierson (1998).

Research Needs

Bats need to be recognized as ecologically important members of natural communities that warrant greater research effort within the ecoregion. Due to the lack of current information, until now bats have been excluded from regional habitat conservation planning efforts. General bat inventories need to be conducted across the ecoregion during all seasons. Priority should be given to the coastal plains and inland valleys where habitat loss is proceeding rapidly and species appear to be on the decline. These areas also appear to be important to wintering bats and as foraging areas for far-ranging species that roost in the foothills, such as the free-tailed bats.

Focused, systematic surveys need to be conducted to determine the status and distributions of species that appear to have suffered population declines and are vulnerable to extirpation. These species include the California leaf-nosed bat, Townsend's big-eared bat, pallid bat, and western red bat, followed by the western mastiff bat, hoary bat, and possibly the California myotis. The availability of suitable roost sites is a major limiting factor for many species, and roosting aggregations are extremely vulnerable to disturbance or destruction by humans. Therefore, roost sites, particularly for the rarer species, need to be located and given the highest level of protection. However, it is also important to determine and protect the foraging habitat associated with those roosts if the colony is to remain viable. To this end, research into species-specific home-range size and attributes, including juxtaposition of roosting and foraging habitat, would be valuable. This is particularly true with respect to preserve design and management. Land managers also would benefit from information on the effects of recreational activities, such as rock-climbing, and the effects of prescribed fire.

Given that the bats of the region are almost exclusively insectivorous, research also is needed on factors affecting insect distribution and abundance, including the effects of pesticides, exotic vegetation, and artificial lights.

The south coast ecoregion, with its rapidly increasing human population and associated urban expansion, provides an ideal opportunity to study patterns of urban landscape use by bats and the effects of habitat loss and fragmentation on bat species diversity and reproductive success (Remington 2000).

Other potential research topics relevant to the ecoregion include the response of bats to riparian habitat restoration, the effectiveness of artificial roosts used as mitigation, the effects of climatic change on bat distribution, and the value of bats as indicators of healthy ecosystems.

While in the past bat research has been logistically difficult, recent technological advancements provide valuable tools to aid ecological investigations. We hope that current and future efforts will greatly expand our knowledge of this fascinating and ecologically important group of animals and provide the information necessary for their conservation within the ecoregion and elsewhere.

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The Santa Margarita River *Arundo donax* Control Project: Development of Methods and Plant Community Response¹

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Abstract

A large-scale effort to control the aggressively invasive exotic species *Arundo donax* in the Santa Margarita River watershed in California's south coast ecoregion was initiated in 1997. The project was prompted by the need for Marine Corps Base Camp Pendleton to address impacts to habitat for federally-listed endangered species and wetlands regulated by the Army Corps of Engineers. As of 2000, 27 km of the main stem of the Santa Margarita River had been treated. The methods employed were tested in preliminary trials before widespread implementation; additional techniques emerged during the course of the project. Although the primary target is *A. donax*, 14 other invasive exotic species that also threaten riparian ecosystem functions were treated when encountered. Vegetation-monitoring transects were established in *A. donax* removal areas to document the effectiveness of the different treatments and recovery of plant communities. *A. donax* was reduced by over 90 percent after the first treatment and accounted for less than 2 percent absolute cover after three follow-up annual treatments. An experiment testing low-cost methods for establishing woody species after *A. donax* control was also conducted. Cuttings were installed with no follow-up maintenance. Approximately 30 percent of *Baccharis salicifolia* and large (3-6 m) willow cuttings survived 2 years.

Key words: *Arundo donax* control, invasive species, riparian restoration, Santa Margarita River

Introduction

Arundo donax is an invasive, non-native plant seriously impacting much of the riparian habitat throughout coastal California including Marine Corps Base Camp Pendleton. It is estimated to have infested 68 percent of the riparian vegetation in the central portion of the Santa Ana River (Douthit 1993) and is thought to be the most serious exotic pest plant problem in southern California coastal rivers (Bell 1998). It grows up to 10 m tall and can be found in small clumps to monocultures of hundreds of hectares (Cummins and Zedler 1998, Dudley 2000). It is not known to produce viable seed in the western United States, and so it spreads only vegetatively through rhizomes or stem fragments (Dudley 2000). Establishment from vegetative parts requires either burial in deep, moist layers of soil or near-saturated conditions at the surface for prolonged periods. Therefore, establishment of new patches occurs primarily in conjunction with flooding. Between flood events, spread occurs outward from existing patches (Else 1996). Prior to initiation of control on the Santa

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Margarita River on Camp Pendleton, *A. donax* occupied approximately 26 percent of the riparian system, including 13 percent of the 2-year floodplain (bankfull channel geomorphic surface), 39 percent of the 2-10-year floodplain (active floodplain geomorphic surface) and 23 percent of the riparian system outside of the 10-year floodplain (terrace geomorphic surface) (Cummins and Zedler 1998, Smith and Lichvar 1999). The total area infested (greater than 80 percent *A. donax* cover) in the watershed prior to treatment was estimated at 300 ha (260 ha on Camp Pendleton and 40 ha upstream) on over 40 km of the main stem and tributaries (Giessow, unpubl. data).

Need for Control

Large stands of *A. donax* displace native vegetation and associated wildlife species and increase flood and fire hazard (Bell 1998, Dudley 2000). On the Santa Margarita River, three endangered species have suffered habitat loss resulting from invasion of *A. donax*: *Vireo bellii pusillus* (least Bell's vireo), *Empidonax traillii eximius* (southwestern willow flycatcher), and *Bufo californicus* (arroyo toad). On the Base, habitat loss resulting from *A. donax* invasion is considered to pose the greatest threat to arroyo toads (ACS/ES Camp Pendleton, 1994), which likely are unable to move through dense stands (Lovich and others 2001). In San Diego County, however, most riparian restoration has been done to mitigate impacts to the least Bell's vireo (Kus 1998).

Because riparian communities are adapted to high levels of natural disturbance, one strategy proposed for recovery of these systems is to remove *A. donax* and other invasive exotics and rely on natural flood dynamics for the recovery of native communities. Because of the high cost of restoration of woody riparian habitats, *A. donax* removal followed by natural re-colonization by native species achieves a cost savings that allows much larger areas to be restored (Bell 1998). On Camp Pendleton, *A. donax* control, with or without replanting of native vegetation, serves to mitigate temporary and permanent impacts to endangered riparian species. This is based on the premises that natural processes will result in the recovery of native habitats that support the listed species and that control will prevent future habitat losses from anticipated *A. donax* spread (ACS/ES Camp Pendleton 1994, Babbitt and others 1995).

Strategies for Control

Control efforts need to be coordinated and sustained due to the sheer size of the effort required to eradicate *A. donax* (Bell 1998). At the current cost of \$49,000 per ha for eradication (initial control and 19 years of follow-up), the total cost to eradicate *A. donax* from the Santa Margarita River watershed is estimated at \$15,000,000 (J. Giessow unpubl. data⁴). It is unlikely that such a sum is available from a single source, even in smaller amounts spread over time, and consequently, it is likely that there will be discontinuities in control efforts between the beginning and the end of eradication.

Throughout southern California, restoration of riparian habitat is compromised by *A. donax* invasions of restored sites (Stein 1998). Because *A. donax* establishes readily from vegetative fragments, but not from seed, it was evident that control at

⁴ Unpublished data on file at Dendra Inc. 1003 Hygeia Ave. Encinitas, CA 92024

the Santa Margarita River should proceed from the upstream portions of the watershed downstream. Without this approach, removal in the lower reaches would be only temporary, because dispersal of vegetative parts downstream would reestablish populations. The lack of seed production means that once *A. donax* is removed from a drainage in this manner, it can remain free of *A. donax* indefinitely. Reintroduction by human activities (for example, illegal dumping of yard trimmings) can occur, but it is rare enough that periodic checks should be sufficient to prevent its reestablishment. The likelihood of discontinuities in the overall control effort heightens the need to begin upstream.

Site-specific control methods needed to be developed where *A. donax* was intermixed or adjacent to habitat for federally listed species, to avoid direct and indirect impacts to those species as required under the Federal Endangered Species Act. This was achieved through limits on control activities during the breeding season for southwestern willow flycatchers and least Bell's vireos (March 15 to August 31) and the use of methods that minimize damage to native woody species during control activities. To avoid damaging egg masses of arroyo toads, *A. donax* control is limited during the toad breeding season, generally from February 1 to July 15. In addition, activities are minimized near damp sandy areas during September to avoid impacts to juvenile arroyo toads.

The most effective time to begin control using foliar spray treatments is August, when the plant begins to move photosynthate into the rhizomes after flowering but before the onset of winter dormancy, when leaves turn yellow, usually beginning in November (Bell 1998). Because of the need to avoid impacts to endangered species, the actual time available for foliar herbicide application is approximately 8 to 10 weeks per year, from mid-September to the onset of winter dormancy. Mechanical control theoretically can occur at any time, but it is restricted during the spring breeding season. Occasional exceptions have been made in informal consultation with the U.S. Fish and Wildlife Service, allowing control during the breeding season in large, solid stands of *A. donax* and toward the end of the breeding season in August if it could be documented that all nesting endangered species had left the area.

In 1994, the U.S. Army Corps of Engineers issued permits for three actions under the Clean Water Act that required on-site *A. donax* control one to four times. In 1995, at the request of the Marine Corps, the Corps of Engineers modified the permits to consolidate the control efforts, move them upstream, and extend the length of control to 5 years. To accomplish this, the Marine Corps partnered with The Nature Conservancy, the Mission Resource Conservation District, and private land owners to move mitigation commitments as far as possible upstream in the watershed. This consolidated project was conducted as an experiment to test control methods for watershed-wide eradication. Our objectives were to document treatment effectiveness on *A. donax* removal, improve methods as we learned more, document and minimize costs of treatment, and monitor plant community recovery. Our expectation was that *A. donax* could be removed on a large scale and that within 5 years the cover would be at a maintenance level of less than 5 percent. Plant community recovery objectives were defined by numerical targets for areas of riparian habitat throughout the Base. When it became clear that watershed-wide eradication of *A. donax* was feasible and the recovery of woody species was proceeding slowly, we added a restoration component to evaluate inexpensive methods of woody-species establishment. Because least Bell's vireos are one of the

primary target species intended to benefit from ecosystem recovery following *A. donax* control, we focused our attention on the recovery of native woody species. As of fall 2000, *A. donax* treatments had been initiated and were in various stages of completion on 43 km of the river. All of the control projects were initially funded for 5 years of treatment.

Methods

Treatment of A. donax

Based on our initial evaluation of methods, we selected foliar application of a 6 percent glyphosate solution as the primary method of control (Giessow and Giessow 1998). We used a second approach, the cut stem method, where there was a risk of overspray onto native species from foliar application. With the cut stem method, *A. donax* stalks are cut close to the ground and herbicide (100 percent solution) applied within two minutes of cutting. In solid stands of *A. donax* with only isolated small willows (less than 5-cm diameter stems), the willows were cut back to 1 m in height, and plastic bags were placed over them prior to foliar herbicide application in an effort to foster post-treatment site recovery. A concerted effort was made with both methods to preserve as much native woody vegetation as possible within and adjacent to treatment areas to enhance site recovery. These individuals provide seed and propagules for vegetative reproduction.

Approximately 8 km of river supporting 25 ha of *A. donax* was treated with foliar application of herbicide between September and November 1997. Crews used 4-wheeled all terrain vehicles (ATV) with a 190-liter (50-gallon) power sprayer and 30-50 m of hose to access sites. Typically, one ATV was used to haul the pesticide and spray equipment, with crew members following on foot. When sites were over about 1.5 km from the access point, filtered creek water was used to mix with the herbicide. Use of the filtered creek water led to increased maintenance costs for the sprayers, so the cost of travel was balanced against the maintenance costs. Because the *A. donax* clumps were too dense to penetrate, coverage of central stems within large clumps was obtained by spraying from a 7-m aluminum extension ladder. To ensure that all stems were sprayed, patches larger than 10-15 m across were accessed from 1-m wide trails cut through them.

Because of access and cost considerations, the foliar treatment was not followed by cutting and/or mowing of dead stems. Three primary concerns developed regarding leaving dead standing biomass: 1) the dead stems would be more likely than live *A. donax* to wash downstream and become lodged behind bridges, 2) dead standing material is a fire hazard, and 3) the addition of so much dead material to the river system would alter habitat for sensitive estuarine species such as tidewater gobies (*Eucyclogobius newberryi*). The concern for bridges was high because of past problems at Camp Pendleton caused by vegetation, including *A. donax*, during flood events. We subsequently addressed the fire hazard in part by manually knocking down strips of dead *A. donax* (leaving the stalks on the ground) to act as fire breaks.

Removing and processing *A. donax* biomass can be difficult and costly. Huge volumes of material are generated (up to 45 kg m⁻²) when the biomass is removed (A.H.B.M. Wijte pers. comm.). In addition, removal of biomass is not always possible in remote sections of the river with little access or in areas where damage to habitats supporting federally listed endangered species would result. These concerns

led to the initiation in 1997 of experimentation with mechanical removal of the entire plant. Approximately 3 ha were treated in an initial mechanical control project in the fall of 1997. Both stems and rhizomes were removed with a clamshell bucket on a trackhoe or excavator and processed through a tub grinder to minimize potential for resprouting and make the material re-usable as mulch. To avoid impacts to native species, this method was used only in solid stands where access without damage to native woody species was feasible. Starting in 1999, we were required by Air Pollution Control District regulations to spray water for dust control as the biomass was being ground. After extraction of the stalks and rhizomes with the track hoe, laborers walked over the site and removed remaining pieces of rhizomes. Scattered resprouting from missed pieces of rhizome were either pulled by hand or treated with herbicide.

Resprouts from both the mechanical and cut stem methods were often retreated with foliar spraying the following spring. This was done to prevent the *A. donax* stalks from growing so tall that the less effective cut stem method was again required in the fall to avoid overspray onto native species. Native woody vegetation 3 m or taller can be avoided using mechanical removal, although *A. donax* left near those plants must be treated using cut stem or foliar herbicide application.

Vegetation Monitoring

Twenty-one transects were established in 1997 to monitor the effectiveness of the foliar *A. donax* treatment. The locations of all transects were recorded at sub-meter accuracy using a Trimble Pro XR GPS (global positioning system) unit. The transects varied in length from 12 m to 39 m and extended 2-5 m beyond the *A. donax* patch measured. Due to the small size of the mechanically treated area, only two transects were established, both 50 m in length.

Initial sampling was carried out from October to November 1997 after the first *A. donax* control treatments had been applied. Re-sampling was conducted in October 1998, 1999 and 2000. Fall, rather than spring, sampling was done to minimize activities in least Bell's vireo habitat during the breeding season.

Aerial vegetation and ground cover were recorded every meter along the transect line using the point intercept method (Bonham 1989). At each point, a height pole was held vertically and the composition of the canopy cover described by recording the species of every plant that intersected the pole. Height of each plant contacting the pole was recorded to the nearest 0.1 m. The number and type of *A. donax* resprouts (rhizome or branch) were recorded within a 1-m belt along the length of the transect. Surface soil texture was measured for all transects using a sedimentation test in which soil aggregates were dissolved; and the proportions of sand, silt and clay were determined based on the quantity of soil settling during specified time periods.

The percentage of absolute foliar cover was calculated by summing all of the interceptions for each species along a transect and dividing by the number of points on the transect. Species were grouped for analysis by life form (herb, tree, or shrub) and origin (native or exotic) into the categories *A. donax*, exotic herbs, native herbs, native shrubs, native trees, and no vegetation. The herbaceous categories included all non-woody species except *A. donax*. The dominant species within the exotic and native herb communities were determined from a tally of herb-species interceptions

within each treatment. Native trees included *Salix lasiolepis*, *S. laevigata*, *S. gooddingii*, and *Populus fremontii*, while native shrubs included *Baccharis salicifolia*, *S. exigua*, *Vitis girdiana*, *Toxicodendron diversiloba*, *Malacothamnus fasciculatus*, and *Sambucus mexicana*. The “no vegetation” category included all points with no live aerial cover.

The initial vegetation composition (pre-treatment) at each site was estimated from the immediate post-treatment data with the aid of aerial photographs taken at a scale of 1:3000 in October 1997. Pre-treatment shrub and tree cover was assumed to be equal to post-treatment cover. Pre-treatment *A. donax* cover was based on the physical presence of stalks on the transect.

A linear regression model was used to evaluate the effects of treatment, floodplain position (active floodplain or terrace), and soil texture (expressed as percent sand) over time on absolute vegetation cover by life form. *A. donax* resprouting (resprout density) over 2 years following foliar herbicide treatment was analyzed using linear regression. Annual changes in percent absolute foliar cover within treatments were evaluated using Student's t-tests.

Site Restoration

A. donax was mechanically removed from a 25-ha site 11 km from the river mouth during fall 1999/winter 2000. A small-scale restoration experiment was carried out in January 2001 within 30 5x5-m plots to test the effect of mulching on survival of cuttings planted to revegetate the site. Fifteen plots were covered with a 25 cm thick layer of mulch consisting of chipped *A. donax* ranging from 1-15 cm in length. Because stem and root fragments of *A. donax* rarely sprout when spread at this depth (Lawson and Smead 2001), we chose it as the mulch material.

All 30 plots were planted with three pole cuttings and five whip cuttings. The pole cuttings were willows (*S. exigua*, *S. lasiolepis*, or *S. gooddingii*); whip cuttings consisted of two *B. salicifolia* and three willows. All plant material was collected locally. Pole cuttings 3-6 m in length were planted 2.5-3 m deep in holes that were drilled with a 3-m auger. Whip cuttings 50-125 cm long were planted 25-50 cm deep. The whip cuttings were scarified at the base to encourage root formation and planted using rooting hormone. Typically, the surface soils were moist from 20-30 cm but dry until the upper fringe of the groundwater was encountered 0.5-2 m deep. The bottom 30 cm of most holes was moist or saturated. A few locations were completely dry below the moist surface. Most holes were silty sand for the entire profile, although some were coarse sand. Poles were watered before and after cuttings were planted with approximately 20 liters of water.

Survival and canopy dimensions were measured after 2 years, in January 2003. Canopy volume was calculated from the canopy dimensions using volume formulas based on the shape of the plant (Ludwig and others 1975 in Bonham 1989). Surface soil texture was measured and expressed as percent sand for each plot using the sedimentation test described above.

The effect of treatment (mulch, no mulch) on survival and canopy volume of *B. salicifolia* and of willows after 2 years was analyzed using linear regression with percent sand and distance from the active river channel as covariates.

Results

Response of A. donax to Treatment

A wildfire burned 7 of the 21 foliar transects in September 1998 prior to the 1998 sampling. To control for the effect of fire on our results, the burned and unburned transects were analyzed separately in all years.

Live *A. donax* foliar cover was reduced by more than 90 percent after 1 year and by almost 100 percent after 3 years with both the foliar spray and mechanical removal (table 1). While it is difficult to provide an exact measure of kill because there is no practical way to measure the amount of live rhizomes underground, both methods effectively killed the plants, including rhizomes, with very little resprouting in subsequent years.

In 1998 and 1999, all live *A. donax* cover on the burned transects was the result of rhizome resprouting. In the unburned stands, *A. donax* stem density averaged 0.04 m⁻² in 1998 and 0.02 m⁻² in 1999, while in the burned stands it averaged 0.06 m⁻² in 1998 and 0.19 m⁻² in 1999. Rhizome sprouting appears to have been stimulated by the burns; however, the difference in resprouting between the burned and unburned stands was not statistically significant ($F = 1.56$, $df = 41$; $p = 0.21$).

Table 1—Mean percent absolute cover by life form following foliar spray ($n=14$ transects), foliar spray/burn ($n=7$ transects), and mechanical removal ($n=2$ transects).

	1997	1998	1999	2000
Foliar Treatment ($df=3$)				
<i>A. donax</i>	68.0 ¹ (20.0) ² a	1.5 (4.1) b	0.0 (0.0) b	1.4 (4.3) b
Exotic Herb	22.5 (18.6)	30.4 (22.0)	47.6 (31.6)	52.4 (47.8)
Native Herb	28.1 (32.3)	44.3 (30.5)	27.7 (37.9)	26.9 (20.9)
Native Shrub	15.4 (23.1)	6.4 (9.3)	9.6 (14.4)	11.3 (20.4)
Native Tree	23.9 (20.7)	11.7 (11.1)	15.8 (20.1)	22.2 (24.4)
No Vegetation	8.3 (17.4)	37.1 (22.1)	29.3 (23.4)	25.4 (14.1)
Foliar Treatment-Burned ($df=3$)				
<i>A. donax</i>	92.2 (6.1) a	1.6 * ³ (2.8) b	1.4 (2.5) b	0.0 (0.0) b
Exotic Herb	9.3 (11.2)	1.8* (2.5)	63.1 (22.4)	88.0 (29.8)
Native Herb	5.7 (6.7)	3.3* (2.4)	35.4 (13.3)	33.5 (13.6)
Native Shrub	6.3 (14.9)	0.0* (0.0)	3.5 (7.5)	12.4 (23.5)
Native Tree	22.5 (23.5)	0.0* (0.0)	7.2 (6.9)	11.4 (9.9)
No vegetation	0.9 (2.3)	93.8* (6.1)	25.1 (15.9)	6.9 (6.0)
Mechanical Treatment ($df=3$)				
<i>A. donax</i>	100.0 (0.0) a	7.9 (11.1) b	0.0 (0.0) b	0.0 (0.0) b
Exotic Herb	0.0 (0.0) a	147.1 (22.1) b	100.0 (13.9) c	93.2 (15.2) c
Native Herb	0.0 (0.0)	52.9 (13.9)	23.5 (27.7)	53.0 (44.3)
Native Shrub	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.0 (2.8)
Native Tree	0.0 (0.0)	0.0 (0.0)	1.0 (1.4)	0.0 (0.0)
No Vegetation	0.0 (0.0)	3.0 (4.2)	2.0 (2.8)	3.9 (5.5)

¹ Mean separation using Student's t-tests. Means within a row followed by the same letter are not significantly different at $p = 0.05$.

² Values in parentheses are one standard deviation.

³ Means followed by an * were from plots sampled 1 month after a wildfire.

If *A. donax* is not killed completely by the herbicide, sprouting may occur at the leaf and branch nodes on the stems. In an earlier study, plants that by their above-ground appearance were thought to be dead resprouted over a year after treatment (Giessow and Giessow 1998); we saw this occasionally during this study as well. These resprouts were easy to kill with one foliar herbicide application. Although we did not monitor individual plants, where leaf and branch node sprouts were detected on transects none were found the year following re-treatment. In 1998, eight sprouts were counted on two transects; they were treated, and none were detected in those transects in 1999. Likewise, five sprouts were detected on two different transects in 1999; by 2000 there were none.

Plant Community Development

The influence of floodplain position and soil texture on absolute vegetation cover by life form was analyzed separately for the burned and unburned foliar-treated sites using linear regression. In the unburned foliar-treated transects, the only significant response to treatment other than the decrease in *A. donax* was an increase in native herb cover. Native herbs increased in cover as a function of two two-way interactions between year and floodplain position ($F = 2.72$; $p = 0.06$) and floodplain position and percent sand, which ranged from 63 to 98 percent ($F=7.19$; $p=0.01$), revealing that floodplain position influenced native herb growth in certain soil types, but in a manner inconsistent across years. In 2000, but not in other years, the percent cover of native herbs decreased in coarser soils in the terrace but not in the active floodplain. No significant changes in vegetation cover occurred on the burned transects other than the decline in *A. donax* cover.

The post-treatment exotic herb community was dominated by *Hirschfeldia incana* in all years, followed by *Conium maculatum*, *Melilotus alba*, and *Chenopodium album*. *Artemisia douglasiana* was the most frequently encountered native herb in all years except 1998, when it was the second most frequent. *Phacelia cicutaria* was the next most frequently encountered native herb, followed by *Ambrosia acanthicarpa*. While absolute cover of herbs varied by treatment and year, the same species dominated.

Cover of native trees and shrubs was initially low on all treated areas, and none of the changes over the course of the study were significant. However, while not statistically significant, absolute cover of both trees and shrubs on the unburned transects showed the same pattern, dropping from 1997 to 1998 and then increasing each year thereafter (*table 1*). We also noted interesting though not statistically significant differences in cover on different geomorphic surfaces. In each year, the cover of native shrubs was higher (by 4-25 percent) on the active floodplain than on the terrace, while for native trees it was lower (by 6-15 percent) on the active floodplain than on the terrace.

With the mechanical treatment, in addition to the response by *A. donax* there was significant inter-annual variation in exotic herb cover but not in native herb cover (*table 1*). Exotic herbs increased rapidly in cover the first year after treatment, followed by a significant fluctuation between the second and third years. Native herb cover increased post-treatment, but the change was not statistically significant.

Site Restoration – Survival and Growth

Distance from the active river channel to the restoration plots ranged from 30 to 320 m. Percent sand on the plots ranged from 23 to 84 percent. Survival of willow pole cuttings averaged 31 percent per plot ($n=28$ plots, $s.d.=36$), while for willow whip cuttings survival averaged only 1 percent per plot ($n=28$ plots, $s.d.=6$). Per plot survival of the *B. salicifolia* whip cuttings averaged 28 percent ($n=29$ plots, $s.d.=34$).

Linear regression modeling of the effects of mulching and covariates distance to river and soil texture (percent sand) on survival significantly predicted willow pole survival ($r^2=0.28$; $p=0.05$). Survival was nearly twice as high (37 percent) on unmulched plots as it was on mulched plots (20 percent). Mulch treatment interacted with soil texture, such that within mulched plots willow survival decreased as percent sand increased, while in plots without mulch there was no pattern between survival and soil texture ($F = 3.27$; $p = 0.08$). A significant model was also produced describing *B. salicifolia* survival ($r^2=0.50$; $p=0.05$). *B. salicifolia* survival, however, was unrelated to mulching and was a function of an interaction between distance to river and percent sand ($F=6.45$; $p=0.02$). Survival was highest on finer textured soils farthest from the floodplain.

The average canopy volume on the restoration plots was 1.4 m^3 ($s.d.=1.2$) for *B. salicifolia* and 1.5 m^3 ($s.d.=2.2$) for the willows. Canopy volume was unrelated to mulch treatment, distance to river, and soil texture.

Costs

A. donax Treatment

The costs for *A. donax* control are highly variable depending primarily on accessibility of the site and density of the *A. donax*. The costs reported below exclude program management and reporting. For the foliar spray method supplemented with the cut stem method, our average annual costs per ha dropped by over 85 percent after the initial treatment and did not change significantly after that for retreatments (table 2). These costs did not include any manipulation or removal of the biomass. The cost to create several firebreaks by knocking down dead standing biomass was almost \$5,000 per ha of firebreak. This work had to be done by hand because the sites could not be accessed by mechanized equipment without damaging riparian woodland habitat.

Because of the problems with biomass management, the mechanical treatment was never fully implemented as originally planned. The cost for mechanically removing and grinding about 14 ha of *A. donax* in 1998/1999 was approximately \$19,800 per ha. This includes estimated costs of treating the *A. donax* with herbicide using cut stem and foliar application around native vegetation within and around the margins of the site and treating resprouts in the first spring, but does not include costs for biomass management. Treatment costs for the follow-up annual treatments are

Table 2—Labor, herbicide and cost per ha for foliar treatment of *A. donax*.

	Labor (man hours/ha)	Herbicide (liters/ha)	Total Treatment (cost/ha)
Year 1 (initial treatment)	150	130	\$9,900
Year 2 (1st re-treatment)	15	7	\$1,350
Year 3 (2nd re-treatment)	12	2	\$1,100
Year 4 (3rd re-treatment)	15	2	\$1,200

estimated to be the same as for the foliar spray method, because with so little live *A. donax* left, the primary costs are associated with getting to the site and searching for the few live stems present.

Site Restoration

The average labor cost per whip cutting was 0.32 hours and per pole planting was 1.07 hours. The mulching of the plots required 26 hours of labor plus the cost of the equipment. The planting of 180 whip cuttings required a total of 58.25 hours: 10 hours for collecting cuttings and 48.25 hours for planting the cuttings. The planting of 115 pole cuttings required 123.5 hours: 30 hours for collecting the pole cuttings and 93.5 hours for planting. The time required for mulching is not included in either the pole or whip cutting calculations. Planning, report writing, and monitoring are not included in these estimates.

Discussion

Efficacy of Control

While mid-November is often cited as the date of onset of winter dormancy in *A. donax* (Bell 1998), our experience, based on evaluation of plants in the field, is that it is often later, particularly near the coast. In addition, we have found that the plants are still susceptible to the herbicide after leaf yellowing begins when there is still green tissue present. A site-by-site evaluation of dormancy can extend the limited time available for foliar herbicide application.

Both foliar herbicide application and mechanical removal that includes removal of the rhizomes are effective methods of *A. donax* control and allowed us to meet our objective of less than 5 percent cover in 5 years. With both methods we were able to minimize damage to existing native trees and shrubs. We found that foliar treatment was less costly than mechanical and easier to accomplish in areas with poor access. On the other hand, mechanical treatment resulted in the use of less herbicide, consistent with general Navy policy directing the minimization of pesticide use (U.S. Department of the Navy 2002). Our initial conclusions were that both methods were useful in specific situations; however, difficulties and costs associated with grinding and using the biomass caused us to discontinue the mechanical removal method in 2001. Problems included spontaneous combustion of the piled, chipped biomass, presumably caused by increased decomposition of wetted material resulting from water sprayed to control dust. Insufficient need for the mulch for landscaping or other uses on the Base led to a lack of use and build-up of the stockpiles. While resprouting is low when the material is spread thin (Lawson and Smead 2001), it can be high in large stockpiles, creating a need for further treatment.

The two treatment methods affect *A. donax* plants differently. With foliar spray treatments, very high kill of the aboveground biomass is achieved with little subsequent resprouting. After the foliar spray treatment, the *A. donax* plant tissue dies gradually over several months. We hypothesize that this gradual death is not accompanied by rhizome resprouting because the hormones that suppress resprouting are still present in the stems and are only gradually declining. Based on elevated stem counts on transects where the stems were removed by wildfire compared to unburned transects, such an effect may last for a year. However, some resprouting can occur on

foliar-sprayed plants with intact stems that have had no live aboveground biomass for over a year, so follow-up surveys and treatment are needed.

The low degree of resprouting following foliar spray contrasts with the rapid resprouting response to other methods where the stems or rhizomes are cut. There are also differences between the cut stem and mechanical treatments with respect to resprouting. When plants are pulled out of the ground during mechanical removal, many of the rhizome fragments resprout quickly. These resprouts are easily killed with herbicide application, as evidenced by the reduction in cover from 7.9 percent to 0 percent between 1998 and 1999 (*table 1*). Resprouting from entire rhizome masses left after the cut stem method requires repeated treatments over several years to kill. In an earlier study, after 2 years of annual treatment over 1.3 stems m⁻² of live *A. donax* remained (Giessow and Giessow 1998). At that time, the stand was foliar sprayed to meet regulatory requirements.

Regardless of the method used in the initial treatment of *A. donax*, retreatments require approximately 12-15 hours of labor per ha of initially treated material. This effort includes both searching for resprouts and treatment time. It is important to note that the area searched during retreatments may be an order of magnitude larger than the initially treated area because retreatments cover all suitable habitat within the reach of the river in which the initial treatment occurred. Although this is a coarse estimate, it is sufficient for developing cost estimates for the entire treatment cycle and making management decisions. Once the first 4 consecutive years of retreatment have occurred, it is advisable to revisit the site less frequently to allow *A. donax* to grow to a noticeable size and optimize retreatment expenditures.

The importance of understanding riparian zone physical and ecological processes to produce consistent, successful riparian restoration has been noted (Goodwin and others 1997). This is also true of exotic plant eradication. To achieve watershed scale eradication of *A. donax*, all sites with the target exotic must be treated, not just the sites most likely to support a desired plant community within a specified time frame. Otherwise, *A. donax* will reinvade downstream sites after flooding, compromising natural and restored habitats (Stein 1998). The beneficial effects of *A. donax* removal on a site with low flood return interval may be indirect and take the form of removing the potential for reinfestation at another site.

Plant Community Recovery

While not statistically significant, we detected trends in the response of native shrubs and trees to removal of *A. donax*. We believe that the decline from 1997 to 1998 was a result of flooding. Rainfall at the Lake O'Neill weather station (approximately 2 km from the study site) in the winter of 1997/1998 measured 802 mm, more than double the 125-year average of 351 mm (Office of Water Resources, Camp Pendleton unpubl.⁵ data). Flood damage to native trees and shrubs was seen on a number of plots (J. Giessow pers. obs), and similar floods in the local vicinity had been reported to destroy up to 40 percent of standing vegetation (Hawkins and others 1997). After the initial decline, rainfall measured 218 mm in 1998/1999 and 225 mm in 1999/2000 (Office of Water Resources, Camp Pendleton unpubl. data), and native trees and shrubs showed a steady increase in cover, although the time frame was insufficient

⁵ Unpublished data on file at the Office of Water Resources, Marine Corps Base, Camp Pendleton, CA 92055

for cover to equal or exceed the initial cover. The decline and subsequent increase in shrub and tree cover probably reflect an interaction of flood damage and increased moisture availability for plant growth resulting from the *A. donax* control (Dudley 2000) and flooding (Kus 1998). As would be expected, previously existing trees and shrubs often showed an increase in canopy cover in areas that had supported dense *A. donax* stands. Plants adjacent to sites, notably *Vitis girdiana* (wild grape), spread into treated areas and can produce significant amounts of cover (Giessow and Giessow 1998).

New herbaceous cover developed much more rapidly on the mechanically cleared sites than on the foliar sprayed sites, and exotic herbs generally accounted for much of the difference in cover between the treatments. After mechanical removal, the sites were characterized by bare, loose soil—good conditions for weedy species establishment (Hoshovsky and Randall 2000). The foliar-treated *A. donax* stands developed cover much more slowly. The *A. donax* litter cover provided few sites where seedlings could germinate and survive. However, the herbs that did establish tended to be large individuals, presumably because they had less competition from neighboring plants.

Understanding site potential is key to predicting and evaluating recovery. While woody species occur on all three geomorphic surfaces, their presence and ability to establish is controlled by the potential for flood damage as flood return interval becomes shorter and by lack of establishment events as flood return interval gets longer (Harris 1987, Hawkins and others 1997). As a result, not all sites occupied by *A. donax* have the same potential natural community. Soil and hydrologic variation in riparian areas results in mosaics of plant communities (Platts and others 1987). Expectations for system recovery after *A. donax* eradication must take into account that events that provide bare saturated soil suitable for willow recruitment are uncommon on the terraces, and even on the active floodplain they may occur with a frequency of only once in 10 years. While the active floodplain is the most suitable place for woody riparian species recruitment (Else 1996), the terraces support both riparian woodland and riparian scrub habitats (Smith and Lichvar 1999). If woody habitats are desired in the terraces after *A. donax* control, active restoration may be needed to achieve this goal within a short time frame.

Active Restoration

Our experiments evaluating methods to improve the survival of cuttings showed that mulching was counterproductive for establishing willows, whose survival was nearly twice as high on plots with no mulch. Mulching had no apparent effect on the survival of *B. salicifolia* or on the ultimate canopy volume of either this species or willows. Soil texture influenced survival of both willows and *B. salicifolia*. For willows, the effect was a simple one of lower survival on coarser soils. For *B. salicifolia*, however, survival was highest on finer textured soils farthest from the floodplain. Finer textured soils have higher available soil moisture (Brady 1974), which could explain higher survival in these soils. It is possible that unrecorded variation in other factors, such as microtopography at the study site, had an effect on factors important for survival, such as water availability.

Where natural processes are not expected to lead to a desired plant community within a specified time frame, our results show the use of cuttings to be an option to speed recovery, without the expense of planting and irrigating container stock.

Planning the installation of cuttings when high rainfall is predicted may be a feasible way of increasing survival and thereby decreasing unit costs. Because the plant material takes relatively little time to collect and is done at the time of planting, less advance planning is necessary, providing more flexibility in scheduling this activity. Considering the episodic nature of establishment and growth of woody riparian species and its link to flooding (Else 1996, Kus 1998), such a strategy may result in more canopy development over a specified time frame.

Identifying and Tracking New Invasions

The most neglected part of managing new invasions is the identification of new problem species at the earliest possible time. Identifying, tracking, and treating new invasions so that one problem exotic species is not replaced by another is extremely important (Hoshovsky and Randall 2000). While this study focused on *A. donax* control, Camp Pendleton's program has, in fact, identified 14 species to be controlled. Ecosystem managers need to know when new invasive species appear and then quickly develop and implement strategies to treat them. Watershed-wide coordination is critical. Having a large-scale program in operation makes it much faster and easier to tackle new exotic species that threaten sites where *A. donax* has been removed. This was demonstrated with two new invasive exotic species found on the Santa Margarita River: German ivy (*Delairea odorata*) was identified on approximately 1.5 ha of land on a tributary to the Santa Margarita River, and perennial pepperweed (*Lepidium latifolium*) was found over a larger area in the watershed in 2000. Because of existing funding and close coordination between the Marine Corps, Mission Resource Conservation District, and private landowners, treatment of both species was initiated within a month of discovery.

In the midst of a complicated large-scale task such as the *A. donax* program, the subsidiary task of looking for new species can be overlooked. In addition, the resources used to survey can be hard to justify when no new infestations are found, even though the increase in control costs from delayed detection can be substantial and exceed the cost of surveys (Hoshovsky and Randall 2000). While detection of new exotic species should draw on existing monitoring work, it needs to be an independent task with multiple visits every year initially and every few years in the long term. It should include vouchering and review of status. The review could be as simple as comparison with the California Exotic Pest Plant list (CalEPPC 1999). Exotic species that are not on the list should be evaluated to determine if they are recent escapes and a decision made as to whether to carry out localized control, no treatment, or full eradication.

The potential for new exotic species to invade and the detection and control of all upstream occurrences of *A. donax* must be addressed. A watershed-based organization that encompasses both public and private landowners is needed to coordinate watershed-based control over the long term and develop a program to detect new invasions before they spread. A Weed Management Area has been established for the Santa Margarita River watershed that addresses these issues (California Department of Food and Agriculture, Santa Margarita Watershed WMA: <http://smslrwma.org>).

Conclusions

The impetus for *A. donax* eradication in the Santa Margarita River is based on the premise that its removal will result in an increase in riparian cover and functional values for endangered species, as well as an avoidance of future habitat losses if *A. donax* were to spread throughout drainages (ACS/ES, Camp Pendleton 1994, Babbitt and others 1995). *A. donax* eradication is feasible, and although much has been accomplished, substantial funding is needed to complete the job. Strategically timed and placed restoration and long term exotic species management, including detection and control, can insure that the ecosystem-recovery benefits of *A. donax* eradication efforts are realized in a cost-effective manner.

The temporal and spatial scales selected to evaluate recovery and to plan and execute post control restoration will determine to a large extent whether *A. donax* control is judged successful in improving riparian habitat for endangered species. Short-term expectations for succession at *A. donax* control sites must be balanced with the restoration of the natural functioning of the entire system.

Recovery objectives should be defined for specific management units. To effectively allocate resources, feasible objectives, including a time frame and measurable criteria, must be stated as clearly as possible from the beginning (Briggs 1996).

Management units should be based on geomorphic surfaces. Sites within units should be prioritized according to their potential for unassisted recovery. Sites with high potential may be a lower priority for scarce restoration funds than sites with lower potential. A site on a terrace that has the hydrology to support woody riparian species but a low occurrence of suitable natural establishment events could be a target for planting of cuttings.

The time frame to judge success should be tied to flood events of specific magnitudes. The criteria to evaluate restoration success should take patch size into consideration and reflect the natural mosaics of plant communities in the management unit.

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Diptera Community Composition and Succession Following Habitat Disturbance by Wildfire¹

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Key words: coastal sage scrub, diversity, flies, postfire, richness

Extended Abstract

Introduction

Both biogeographic (for example, latitude) and local (for example, soil) processes determine composition and succession of biotic communities. Postfire succession of vegetation has been studied intensively in chaparral and coastal sage scrub. Fewer studies have examined postfire succession of animals, even though fires can drastically alter their abundance and diversity (Ahlgren and Ahlgren 1960, DeBano and others 1998). Work on response to fire has focused on vertebrates, with few studies on insects, several yielding conflicting results. Little is known about community ecology of Diptera. Flies exhibit high alpha-diversity, show remarkable variation in foods and habitats (occupying every trophic level), and are highly vagile (recolonization is likely to occur quickly). Studies of arthropod succession are important for understanding mechanisms that determine community structure, which can be critical to land management, conservation, and reserve design (Kremen and others 1993).

We examined Diptera community differences between burned and unburned sites at family and guild levels. We focused on a mid-successional period (2.5 to 4 yr after a burn). Full recovery of burned sage scrub requires 5–10 yr and may never equal the preburn state (Westman 1981). We hypothesized that (1) Diptera communities differ qualitatively between burned and unburned plots; (2) recolonization occurs in a predictable order of scavengers, animal feeders (predators, parasitoids, and hematavores), plant feeders (pollinators and herbivores), and detritivores; (3) local-scale processes drive short-term vegetation recovery because many sage scrub shrubs reestablish from rootstock and seeds that survive fire; and (4) geographic-scale processes drive Diptera community reestablishment because flies recolonize from surrounding intact areas, not from the disturbed site itself.

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Methods

We sampled 12 burned and 12 unburned plots (50-m diameter) in coastal sage scrub at the Southwestern Riverside County Multispecies Reserve at Lake Skinner, California, following a 1993 fire. We quantified vegetation using standard point-intercept and line-transect methods. We sampled arthropods at 3-month intervals from March 1996 to December 1997 using malaise traps (1 trap/plot/sampling period), vacuums (5 transects/plot/period), and pitfalls (7 traps/plot/period). Specimens were identified to family and classified into foraging guilds.

Fluctuations in family richness over time did not differ between unburned and burned plots (profile analysis; $P > 0.15$, $n = 8$ samples), so data were pooled by site across sampling periods. Differences between unburned and burned plots in vegetation and Diptera were tested with MANOVA (multiple analysis of variance). The association between vegetation and Diptera abundance was determined with Mantel tests. The pattern of Diptera recolonization was inferred using isotonic regression of mean percent correct classification from discriminant function analyses (DFA) for each family ($n = 36$). Means and SEs were calculated by guild ($n = 7$). Our H_0 was *discrimination of plots is equal across guilds*; our ordered expectation H_A was *detritivores \geq pollinators \approx herbivores \geq predators \approx parasitoids \approx hematophages \geq scavengers, with at least one strict inequality*.

Results

A total of 12,437 individual flies in 46 families were collected, with Chironomidae by far the most abundant family collected. Because of potential swamping, malaise-collected Chironomidae were excluded from analyses. The next best represented families were Cecidomyiidae, Anthomyiidae, Tipulidae, Empididae, Chloropidae, and Phoridae.

Burned and unburned plots differed significantly in vegetation structure and composition (MANOVA, Wilks' $\Lambda = 0.12$, $P < 0.01$), but community composition of Diptera did not differ between plots at the level of family (Wilks' $\Lambda = 0.07$, $P > 0.5$) or guild (Wilks' $\Lambda = 0.48$, $P > 0.05$). Nevertheless, there was a strong association between vegetation and Diptera families (Mantel standardized $r = 0.28$, $P < 0.02$) and guilds ($r = 0.22$, $P < 0.05$). Scavengers occupied burned sites with roughly equal frequency as unburned, so their abundance was a poor discriminator of plot type; detritivores were much more abundant on unburned sites and were better discriminators of plot type (*table 1*). Our data supported the recolonization sequence we predicted for Diptera guilds ($S = 6.38$, $P < 0.05$), underscoring the unequal (but predictable) recovery rates.

Discussion

Dipteran communities recovered quickly from impacts of fire, consistent with previous studies of overall insect abundance (Force 1981, Moya-Raygoza 1995) and Diptera in particular (Delettre 1994). Burned sites were indistinguishable from unburned sites in overall community, with common generalist feeders and scavengers equally represented; Lomonaco and Almeida (1995) reported the same pattern. Similarity across plots resulted from similarity in abundance of dominant fly

families; presence/absence data may yield different interpretations of community equality (Patten and Rotenberry 1998) but an ordination with such data produced comparable results in our case.

We detected a distinct, predictable pattern of guild recolonization following a successional sequence from scavengers to animal-feeders to plant-feeders to detritivores. Our results support the hypothesis that the key to community structure is extrinsic biogeography rather than intrinsic local processes (Cornell and Lawton 1992). Local processes play an important role (abundances of some families differed markedly). These processes probably include microhabitat (Tolbert 1975) and relative amounts of shrubs and herbs (Bährmann 1984), which affect guilds (and thus families) differently.

Table 1—Percent correct classification of burned and unburned plots using discriminant function analysis. Means were calculated across families within each guild (thus the different sample sizes for each guild). The ordered expectation of isotonic decrease is significant ($0.01 < P < 0.05$).

Diptera guild Sample size	Mean % (\pm SE) correctly classified	per guild (n_i)
detritivore	60.1% \pm 2.6	14
pollinator + herbivore	54.2% \pm 3.0	9
predator + parasitoid + hematavore	50.4% \pm 4.7	12
scavenger	45.1% \pm 6.8	11

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Patterns and Processes of Arthropod Community Succession after a Fire¹

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Key words: coastal sage scrub, detritivores, diversity, herbivores, predators

Extended Abstract

Introduction

At present little is known about arthropod recolonization and community succession after disturbance. Arthropods are critical in ecosystems as members of food webs and accelerators of nutrient cycling. The degree to and speed with which they return to disturbed habitat is thus of great interest to researchers and land managers alike.

We compared abundance and diversity of arthropods in mid-successional (after a 1993 wildfire) and mature California coastal sage scrub (CSS), a vanishing ecosystem in southern California (Westman 1981) that is threatened primarily by urban development (Davis and others 1994), associated increases in wildfire intensity (Minnich 1983), and invasion by non-native grasses (Alberts and others 1993).

Our general purpose was to determine whether arthropod communities in mid-successional habitat are qualitatively different from those in mature habitat. Specifically, we investigated whether foraging guild structure, abundance, and diversity differ in relation to fire history and whether there is evidence of failure in community recovery after a fire. Lastly, we compared our results for the entire arthropod community to those for just the Diptera, a highly volant insect order within which all guilds are represented.

Methods

We collected arthropods from 12 burned and 12 unburned 50-m-diameter plots at the Southwestern Riverside County Multispecies Reserve by Lake Skinner, California. Arthropods were sampled with pitfall (7 traps/plot/sampling period) and vacuum (5 transects/plot/sampling period) at 3-month intervals from March 1996 to December 1997. Vegetation structure and percent cover were sampled using standard point-transect and line-intercept methods. All arthropods were identified to morphospecies within family with the exception of the Apterygota, Acari, Collembola, Isopoda,

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Psocoptera, Thysanoptera, Aphididoidea, and Coccoidea, which were counted. Each arthropod taxon was assigned to a foraging guild (detritivore, flower visitor, hematavore [blood feeder], herbivore, parasitoid, predator, or scavenger).

Abundance and richness were compared between burned and unburned plots using *t*-tests with Dunn-Šidak corrections for multiple comparisons. Detrended correspondence analysis (DCA) was performed on abundance per site of all arthropods identified to morphospecies. Axis identity was determined by correlating plot scores on each axis (DC I and DC II) with vegetation variables. Families occurring only once were omitted from analysis.

Results

A total of 52,926 arthropods were collected with vacuum and pitfall samples. The distribution of arthropod guilds was more even in unburned than burned CSS. Proportionally more detritivores and herbivores were found in burned areas, and more flower visitors occurred in unburned sites. Overall, more arthropods were collected from burned sites, including significantly more detritivores and marginally more herbivores and predators. Abundance of arthropod orders followed a similar pattern to that of guilds, with orders associated with detritivore and herbivore feeding guilds tending to be more abundant in burned sites, but only Psocoptera (detritivores) were significantly more abundant in burned sites.

Species richness per site of the six dominant arthropod orders (Hymenoptera, Araneae, Homoptera, Diptera, Coleoptera, Hemiptera) was remarkably similar across burned and unburned sites. Assemblages of families appeared to be qualitatively different among burned and unburned sites. Detrended correspondence analysis of family abundances produced a relatively short gradient (length = 1.14; 4.0 represents complete turnover). However, sites were separated according to fire history along DC I and along a grass cover gradient on DC II (*fig. 1*). Families positively associated with mature, unburned sites were Saturniidae (Lepidoptera), Corinnidae (Araneae), and Ptinidae (Coleoptera). Families associated with low grass cover were Kinnaridae (Homoptera), Cucujidae (Coleoptera), and Dermestidae (Coleoptera). All orders strongly associated with DCA axes I and II were relatively uncommon in our samples. Therefore, their associations independent of other orders are tenuous.

Conclusions

Results suggest that arthropod guilds are more evenly distributed in mature vs. mid-successional coastal sage scrub. Mid-successional sites supported a higher abundance, but not a higher richness, of arthropods. Much of this difference in abundance was a result of higher numbers of detritivores in burned areas. Arthropod assemblages at the family level were associated with fire history and correlated with degree of grass cover, primarily as a result of the distribution pattern of relatively rare families (*fig. 1*). Grass invasion appeared to be affecting arthropod community composition in coastal sage.

The guild structure of all arthropods in burned sites differed from that of just the Diptera (see Patten and others, this volume). Taxa that are less mobile than Diptera may be subject to vastly different conditions affecting recolonization. These include

purely local processes, such as the ability to survive and reestablish after a fire from populations on site or nearby rather than recolonizing solely via immigration.

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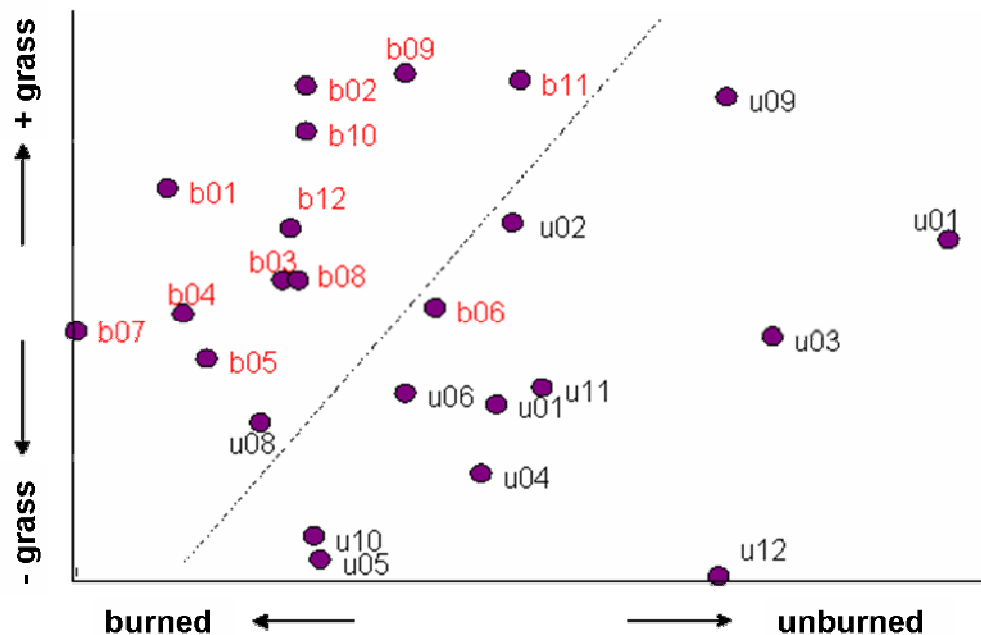


Figure 1—Detrended correspondence analysis of arthropod assemblages on burned and unburned sites. The dashed line is a heuristic to show the near complete simple separation of burned and unburned plots based on arthropod community composition.

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Monitoring the Effects of Natural and Anthropogenic Habitat Disturbance on the Ecology and Behavior of the San Diego Coast Horned Lizard (*Phrynosoma coronatum blainvillei*)¹

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Key words: body size, foraging preference, habitat disturbance, home range size, sage scrub

Extended Abstract

The sage scrub communities in which San Diego coast horned lizards (*Phrynosoma coronatum blainvillei*) typically occur are now restricted to only 10 to 15 percent of their former range and are currently subject to rapidly accelerating rates of loss. As a result of urban and agricultural development, pesticide use, collecting for the pet trade, off-road vehicle activity, and other human disturbance, San Diego horned lizards have undergone serious population declines in the last decade. In some areas, introduced exotic ant species have displaced the native harvester ants on which horned lizards depend. Because relatively little is known of the biology of coast horned lizards, basic information on their habitat and resource requirements, as well as their behavior and reproductive physiology, is critical to developing effective management plans for their survival.

Although San Diego coast horned lizards appear able to persist in semi-disturbed habitats, the extent to which these areas can support viable populations over the long term is unknown. To address this information gap, we compared several aspects of the behavioral ecology of the San Diego coast horned lizard between undisturbed Riversidian sage scrub and habitat disturbed by either fire or historic grazing on the Southwestern Riverside County Multi-Species Reserve during 1995 and 1996.

In 1996, we radio-tracked 11 male and 9 female horned lizards. Once located, each lizard's position was recorded to ± 1 m using a GPS (global positioning system) equipped to receive real-time differential corrections. For the 10 males and 4 females for which enough data points were available to measure home range size reliably, home range size was estimated using two methods: the convex polygon method and a grid cell technique that produces a two-dimensional frequency distribution describing

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spatial utilization of the home range. While there was no significant difference in the home range size of adult males and females, there was a tendency for convex polygon home ranges in disturbed habitat to be larger than those in undisturbed habitat ($U=10$, $df=12$, $P=0.15$). Using a grid size of 10 m^2 , differences in the spatial utilization of home ranges in disturbed and undisturbed habitat were significant ($U=5.5$, $df=12$, $P=0.04$). In addition, lizards in disturbed habitat overlapped more conspecifics on average than those in undisturbed habitat ($U=6$, $df=12$, $P=0.04$).

To document foraging preferences of horned lizards, we dissected scat from disturbed and undisturbed habitats on the reserve and identified the species consumed based on head morphology. In both the number of ant species consumed ($T=2.49$, $df=32$, $P=0.02$) and total number of prey types ($T=2.18$, $df=32$, $P=0.04$), horned lizards in undisturbed habitat exhibited richer diets than those in disturbed habitats (fig. 1).

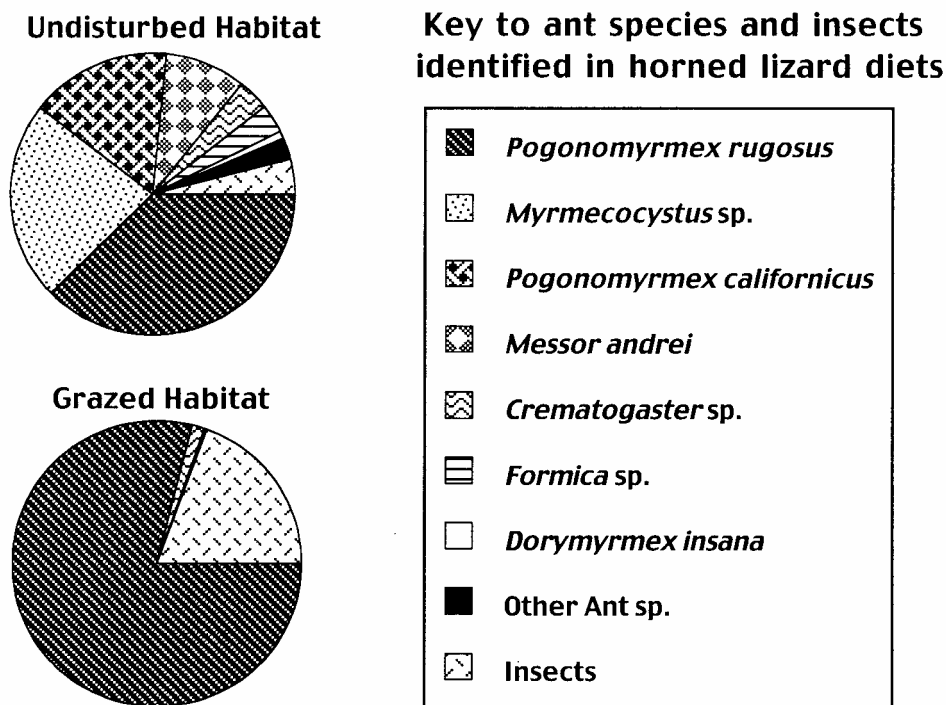


Figure 1.

We measured snout-vent length (SVL) and body mass of 27 adult males, 25 adult females, and 206 juveniles in order to compare morphology of horned lizards in disturbed and undisturbed habitats. Using a two-factor analysis of variance with sex and disturbance level as independent variables, we found that individuals of both sexes from undisturbed habitat were larger in SVL ($F = 13.68$, $df = 1, 48$, $P = 0.0006$) and body mass ($F = 14.03$, $df = 1, 48$, $P = 0.0005$) than those from disturbed habitat. In contrast, analysis of covariance indicated that there were no differences in growth of hatchlings in SVL ($F = 1.40$, $df = 1, 184$, $P = 0.24$) or body mass ($F = 1.59$, $df = 1, 184$, $P = 0.21$) between disturbed and undisturbed habitats.

In summary, horned lizards in disturbed habitats utilize larger home ranges with lower plant diversity and greater overlap among individuals. Increased home range size may represent a compensatory response to the lower species richness of insects, particularly ants, found in disturbed habitats. Horned lizards in disturbed habitats exhibit smaller adult body size than those in undisturbed habitats. That growth rates of hatchlings during their first season are similar across habitats suggests that differences in adult size are not the result of differences in early growth of hatchlings. Rather, these differences may be due to differential growth later in the maturation period or to differences in predation pressure. The initial response of horned lizards to habitat disturbance appears to be behavioral rather than physiological. The greater spatial requirements of horned lizards in disturbed habitats should be considered in determining the area needed to support a viable population over the long term.

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Fire Management in Some California Ecosystems: A Cautionary Note¹

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Key words: Bishop pine, chaparral, closed-cone conifer, mixed-conifer forest, regeneration, stand renewal

Extended Abstract

Introduction

Fire has been recognized as a natural and important physical factor in many ecoregions of North America. We wish to point out that our understanding of the biocomplexity of our natural ecosystems is far from complete; in particular, the role of fire in vegetation succession and ecosystem health deserves more scrutiny where biodiversity conservation is a primary or major goal of management. We present four case studies from southern California that are evidence of species and community persistence and renewal in the absence of wildfire or in the presence of low frequency fire events. A simplistic application of the “fire is good and necessary” paradigm may put certain taxa and habitats at risk.

Study Areas and Methodology

1. Santa Cruz Island off Santa Barbara contains three distinct stands of Bishop pine (*Pinus muricata remorata*). This pine species has long been considered to belong to the group of closed-cone and obligate fire conifers (Vogl and others 1977). The present study searched for evidence of spontaneous cone opening, germination, and stand renewal in the absence and presence of fire. Field observations were made on live and dead trees regarding pine cone status. Cones were also collected and monitored for opening and seed release. Seeds were planted in commercial soil and mulch in the open air. Study plots on the island were monitored as to the number of seedlings per hectare. The opportunity to assess the pine’s response to a hot fire arose when a prescribed fire event went out of control in 1994 (Walter and Taha 2000). The research hypothesis was defined as *Bishop pines of Santa Cruz Island do not require periodic fire events for seed germination and stand regeneration*.

2. The North San Diego region in the Carmel Valley near Del Mar is unusually rich in endemic plant and animal taxa. Monitoring and conservation evaluation of

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several undisturbed chaparral parcels at and near Carmel Mountain was carried out in 1995-96. Dozens of vegetation transects were made, comparing burned and unburned chaparral patches (Walter 1996). The research hypothesis was worded as *The unusual arborescence, composition, and structure of this chaparral ecosystem are a result of a long absence of fire.*

3. The James San Jacinto Mountains Reserve near Idyllwild (Riverside County) is the site of a long-term post-fire succession study (Walter, in preparation) at the chaparral-mixed forest ecotone. A 5x80-m transect was established on completely burned ground at an elevation of 5,800 feet after a major wildfire in August 1974. Vegetation succession has been monitored for 25 years. The initial research hypothesis tested was *Post-fire succession includes a short-term chaparral stage of circa 15-20 years duration followed by mixed forest regeneration and dominance.*

4. The James Reserve is surrounded by a complex, unburned forest community near Hall Canyon. This mixed conifer-oak forest is species-rich and appears to contain a number of different age cohorts. For this study, we censused three slope transects of 1x100-m at 5,500 feet elevation for species abundance and tree height. The research hypothesis for this forest surrounding the James Reserve was *This species-rich and mature forest does not require fire for stand renewal.*

Results

Bishop Pine on Santa Cruz Island

After the drought years of the early 1990s a significant portion of the island's Bishop pines died. Subsequently, aided by sheep removal, seedling and sapling pines began to replace the dead trees and expand from the remnant forest stands into surrounding grassland. In 1998 and 1999, detailed studies and experiments on cones of island Bishop pine (Walter and Taha 2000) revealed that (1) some cones open while still on the tree under a normal temperature regime, (2) all cones may release their seeds when exposed to normal summer temperatures and solar radiation, and (3) seeds germinate easily and grow well in normal soil.

In 1994, study plots near pine snags contained hundreds of healthy pine seedlings; their density reached more than 1,400 seedlings per hectare. The December 1994 hot wildfire event, however, killed most remaining pine trees as well as thousands of seedlings in the affected area. Five years later (1999), only a small number of seedlings (about 10/ha) were detected on the burn site.

North San Diego Chaparral Ecosystem

Carmel Mountain and a few adjacent chaparral patches constitute rarely seen mature and over-aged chaparral with dominant shrubs such as *Ceanothus verrucosus*, *Xylococcus bicolor*, *Comarostaphylis diversifolia*, *Cercocarpus minutiflorus*, and *Adenostoma fasciculatum*. In canyon bottoms, this community forms dense arboreal thickets because one or more recent fire events jumped across slopes without burning these habitats.

On the high mesa of Carmel Mountain there is a shallow valley with open habitat dominated by shrubs, bunch grasses, rocky ground, and several small trees of mission manzanita (*Xylococcus bicolor*) attaining record heights of 5 to 7 m. Nearby, an

old California sagebrush (*Artemisia californica*) has become woody, with a diameter of about 15 cm. The vegetation must not have burned for ages, that is, over several historic fire cycles or generations. This ecosystem differs from frequently burned chaparral. It is likely quite stable and not senescent.

Chaparral-Mixed Forest Ecotone Succession (San Jacinto Mountains)

After 25 years of succession, the chaparral community (*Ceanothus leucodermis* *Arctostaphylos glauca*) is still a dominant matrix and shows no sign of senescence. Resprouting oaks (*Quercus chrysolepis* and *Q. wislezinii*) and sapling pines (*Pinus coulteri*) are a minor part of the chaparral vegetation in and around the transect. It may take more than 100 years to bring back a mixed forest stand resembling the pre-fire vegetation at this ecotone location.

Hall Canyon Forest Ecosystem (San Jacinto Mountains)

The mixed conifer-oak forest of Hall Canyon, located on the east slope of the San Jacinto Mountains, has been subjected to several natural mortality factors (drought, insects, and wind throw) over the past 25 years. However, it has not experienced a stand-burning fire in more than 200 years. An analysis of woody vegetation data (seedlings included) from three 1x100-m transects shows a mixed forest dominated by canyon live oak, black oak, incense cedar, and sugar pine. The stand structure of Hall Canyon is complex, with dominant species having average heights of 0.099 m, 0.24 m, 1.05 m, and 0.53 m respectively. The low average height values obtained are representative of the large number of seedlings and saplings observed and are also indicative of the varied age structure within the forest. Preliminary research results for the mature conifer-oak forest of Hall Canyon show significant regeneration of dominant tree species after episodes of severe drought, insect infestation, wind throw, and in the absence of fire.

Discussion

The continental distribution of the Bishop pine is peculiarly coastal and insular, suggesting that this species is actually persisting as a fire evader, although it cannot persist in more interior regions where the occurrence of hot fires is more likely. We conclude, therefore, that fire is not a necessary agent for regeneration of the island Bishop pine populations, of the species as a whole, and possibly of other closed-cone conifers as well. The Santa Cruz Island Bishop pine can be categorized as a “pyrofugal” taxon (Walter and Taha 2000).

Some North San Diego chaparral patches represent a unique biodiversity asset. We conclude that old and mature chaparral remains viable and species-rich in this coastal study region; there is a low incidence of natural fire events. Mature and fire-free chaparral constitutes a unique habitat due to the quality of its structure as well as its species composition (lichen richness, and so forth). In light of the generally short successional cycles seen in California’s chaparral ecosystems, this habitat qualifies as old growth or ancient chaparral in analogy to the old growth forests of the Pacific Northwest. Any control burn of this habitat would eliminate a unique plant and probably also a corresponding animal community. Patches of ancient chaparral deserve priority conservation management.

Our research hypothesis was not validated at our ecotone succession transect in the San Jacinto Mountains. This surprising result provides evidence that long-term fire cycles have in the historic past included between-fire intervals of 100 years or more resulting in an open conifer-oak forest with a minor understory of tall chaparral shrubs. Cultural fire suppression should be ruled out as a contributing factor to extended fire-free intervals in this part of California. The Hall Canyon forest history of the last 25 years offers further support for forest regeneration and rejuvenation in the absence of fire. Catastrophic wind throws and a severe and prolonged drought episode followed by insect infestations have opened up the forest canopy, created excellent breeding opportunities for cavity-requiring vertebrates and sunlight for tree seedlings.

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Spatial and Temporal Variation in Ephemeral Pool Crustacean Communities¹

Janette Holtz², Marie A. Simovich, and Thomas Philippi

Key words: habitat loss, rainfall pattern, species diversity, vernal pools

Extended Abstract

Vernal pool habitat losses in San Diego County, California, are estimated at 95 percent and will increase as development continues. The majority of San Diego's remaining pools are located at the Marine Corps Air Station, Miramar. Crustacean communities in eight vernal pools in San Diego County were sampled over 3 years that differed in rainfall amount and pattern. In 1994, rains occurred late but were moderate in quantity, and species richness ranged from 1 to 22 species; 1998 was a high rainfall El Niño year, and pools varied from 0 to 15 species; 1999 was a low rainfall La Niña year, and pools contained 4 to 7 species. No spatial pattern was seen among neighboring pools. Longer-lived pools had more species, including the more rare species; smaller pools included the more common taxa (*table 1*). Diversity within pools varied between years, although the highest rainfall year did not result in the highest diversity (*fig. 1*). These data indicate the necessity of surveying multiple pools over a period of several years to establish baseline data for these complex communities. Therefore, adequate monitoring of restored or created pools must extend over several pools and several years. Certain species present within a cyst bank may not hatch every year due to weather conditions or other factors. Some species hatch repeatedly after a filling but may not breed and replenish the bank.

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Table 1—Number of species of vernal pool crustaceans in 4 different pools sampled in 3 different years (A = 1994, B = 1998, and C = 1999). Pools 1 and 2 persisted much longer than pools 6 and 7. Pool 7 was not sampled in 1999.

Pool number: Year	<u>Long-lived Pools</u>						<u>Short-lived Pools</u>					
	<u>1</u>			<u>2</u>			<u>6</u>			<u>7</u>		
	A	B	C	A	B	C	A	B	C	A	B	C
Anostraca												
<i>Branchinecta sandiegoensis</i>	x	x		x	x		x	x		x	x	
<i>Branchinecta</i> juveniles	x	x	x	x	x	x	x	x	x	x	x	
Total # of species	1	1	(1)	1	1	(1)	1	1	(1)	1	1	-
Cladocera												
<i>Macrothrix hirsuticornis</i>	x	x	x	x	x	x	x	x	x			
<i>Ceriodaphnia dubia</i>	x	x		x	x	x	x				x	
<i>Moina micrura</i>	x			x			x					
<i>Alona cf diaphana</i>	x	x		x	x			x				
<i>Simocephalus</i> sp.	x	x		x								
Total # of species	5	4	1	5	3	2	3	2	1	0	1	-
Ostracoda												
<i>Cypris pubera</i>	x	x	x	x	x	x	x	x		x	x	
<i>Cypris</i> sp. 1	x	x	x	x	x	x	x	x				
<i>Cypris</i> sp. 2	x	x		x	x		x					
<i>Cypris pustulosa</i>	x	x	x		x	x						
<i>Limnocythere glypta</i>	x	x		x	x						x	
<i>Potamocypris</i> sp.	x	x		x	x							
<i>Prionocypris</i> sp.	x											
<i>Cypris virens</i>		x		x	x							
<i>Cypridopsis vidua</i>				x								
<i>Herpetocypris</i> sp.												
Ostracod N												
Unknown				x								
Total # of species	7	7	3	7	8	3	3	2	0	1	2	-
Copepoda												
<i>Acanthocyclops vernalis</i>	x	x	x	x	x	x	x	x	x	x	x	
<i>Acanthocyclops robustus</i>	x	x	x		x		x	x	x	x	x	
<i>Hesperodiaptomus franciscanus</i>	x	x		x	x		x					
Total # of species	3	3	2	2	3	1	3	2	2	2	2	-
TOTAL # OF SPECIES	16	15	7	15	15	7	10	7	4	4	6	-

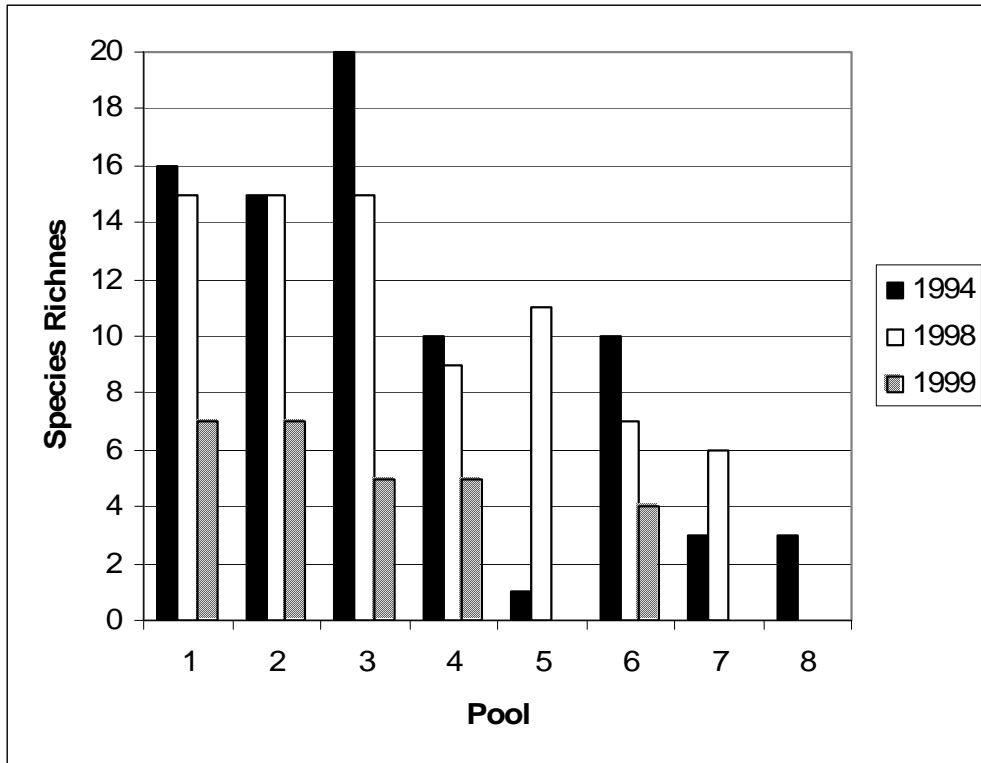


Figure 1—Comparison of species richness in 1994, 1998, and 1999 in eight vernal pools in San Diego County.

Habitat Ephemerality and Hatching Fractions of a Diapausing Anostracan (Crustacea: Branchiopoda)¹

Marie A Simovich², Thomas E. Philippi³, Ellen T. Bauder⁴, and Jacob A. Moorad⁵

Key words: *Branchinecta sandiegonensis*, diapause, fairy shrimp, San Diego County, vernal pool

Extended Abstract

Diapause allows aquatic organisms to survive periods of drydown in intermittent pools. However, often not all of the individuals hatch in response to a filling event. This prolonged diapause can be a bet-hedging adaptation to unpredictability in the duration of filling events. Under the simplest bet-hedging model of selection on prolonged diapause, the fraction of eggs hatching in any filling event should approximate the fraction of filling events lasting long enough for successful reproduction. We quantified filling durations in seven vernal pools in San Diego County inhabited by the endemic fairy shrimp *Branchinecta sandiegonensis* (Branchiopoda: Anostraca) for all winter and spring events from 1983 to 1996. For any given rainfall event, larger, deeper pools held water longer than smaller, shallower pools. However, the distributions of filling durations did not differ significantly among these pools, so selection should be similar across pools. Approximately 28 percent of the filling events lasted 17 days or longer, the developmental time to first reproduction (under field conditions) in *B. sandiegonensis*. Laboratory hatching experiments determined a maximum hatching rate of 28 percent at 10°C, with lower hatching percentages at higher and lower temperatures. The close fit between the probability of adequate filling duration and the hatching fraction, and the similar distributions of filling durations among these pools, suggests that creating pools with hydrology suitable for *B. sandiegonensis* may require care to match the filling durations to which this species appears adapted.

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An expanded version of this report was published as Philippi, T.E.; Simovich, M.A.; Bauder, E.T.; Moorad, J.A.; Moorad, J.A. 2001. **Habitat ephemerality and hatching fractions of a diapausing anostracan (Crustacea: Branchiopoda)**. Israel Journal of Zoology 47(4): 387-396.

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Bee Diversity Associated with *Limnanthes* Floral Patches in California Vernal Pool Habitats¹

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Key words: *Andrena limnanthis*, Andrenidae, Jepson Prairie, solitary bees, species richness, wetlands

Extended Abstract

As with other kinds of wetland habitats in California, approximately 90 percent of vernal pool habitat (estimated) has been lost in California. In southern California, losses are estimated to be even greater. The flora of these endangered habitats is reasonably well known, especially the spring flowering annuals that are found in or at the margins of vernal pools (for example, *Blennosperma*, *Limnanthes*, *Lasthenia*, and *Downingia* species). However, the insect visitor fauna associated with these floral species is much less well known, and what work has been done has been limited primarily to the northern Central Valley region. The insect visitors associated with vernal pool plants are of ecological importance because many vernal pool plant species are self-incompatible and require outcrossing to reproduce. Previous studies indicate that species of solitary bees are especially dominant members of the insect visitor fauna associated with vernal pool plants. One of our recent studies examined the bee fauna associated with floral patches of *Limnanthes douglasii* ssp. *rosea* using a new sampling or monitoring method. We used colored pan traps or water traps to assess the species richness and abundance of the bee fauna associated with seven *L. douglasii* ssp. *rosea* populations or patches. These *Limnanthes* populations were located at Jepson Prairie Preserve near Sacramento. Prior to this study, basic quantitative information on bee species richness and abundance in these endangered wetland habitats had been lacking.

We found remarkably high levels of bee species richness and abundance associated with the *Limnanthes* patches sampled at Jepson Prairie Preserve. A total of 1,970 bees were trapped over four sampling dates. Of the 1,970 bees caught, 1,598 were individuals of a native solitary bee, *Andrena limnanthis*. *Andrena* (*Hesperandrena*) *limnanthis* is a specialist on the pollen of *L. douglasii* ssp. *rosea* and a few closely related *Limnanthes* species. Our study revealed that 32 bee species were foraging in these *L. douglasii* ssp. *rosea* patches over a 3-week period. Approximately two-thirds of the bee species belong to the family Andrenidae, many

¹ A poster version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

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of which are thought to be endemic to vernal pool habitats. The mean number of bees caught per sampling unit, averaged over patches and dates, was 118.8 ± 20 SE (standard error), range 32-283. The mean number of bee species caught per sampling unit, averaged over patches and dates, was 9.3 ± 0.8 SE, range 5-18. The number of *A. limnanthis* individuals and the number of bee species with intermediate levels of abundance was higher than expected. The shape of the bee species abundance curve was most similar to the log series or lognormal theoretical species abundance models.

These results suggest that the diversity of vernal pool plant visitors may be underrated by most wetland ecologists and professionals. Many of the same vernal pool plants that host a variety of oligolectic or specialist bees and non-oligolectic bees in central and northern areas are also found in southern California vernal pool habitats. Thus, we propose that a similar level of bee diversity may occur in southern California vernal pool habitats. Because surprisingly little is known from these southern areas, we recommend that similar studies of the bee fauna of southern California vernal pool habitats be undertaken. Our results here will provide baseline data for future monitoring efforts. Such information is critical to biologically informed decisions involving the conservation and restoration of biodiversity in the remaining vernal pool habitats in California.

Atmospheric Nitrogen Deposition and Habitat Alteration in Terrestrial and Aquatic Ecosystems in Southern California: Implications for Threatened and Endangered Species¹

Mark Fenn, Mark Poth, and Thomas Meixner²

Key words: air pollution, amphibians, montane forests, N-enrichment, nitrate, runoff

Extended Abstract

Recent studies in the transverse ranges (including Class I Wilderness areas) of southern California have emphasized the strong linkage between levels of air pollution-related atmospheric nitrogen (N) inputs into montane watersheds and levels of nitrate in surface and subsurface drainage waters (*fig. 1*). Nitrate concentrations in streamwater in southern California are the highest in North America for wildland watersheds. High nitrate concentrations in runoff are a result of excessive ecosystem enrichment with N from atmospheric deposition. When N enrichment results in the removal of biological N limitation and the N retention capacity of the system is exceeded, the ecosystem is described as “N saturated.” Nitrogen-saturated forests are analogous to over-fertilized agricultural fields with high nitrate runoff. The primary symptom of an N-saturated ecosystem is high nitrate concentrations in the soil solution, in soil leachate, and in groundwater and streamwater (Fenn and others 1998). Vegetation in N-saturated ecosystems contains high levels of N, and excess N also builds up in litter and soil organic matter, especially under fire suppression regimes. Stand densification is likely to be exacerbated by N deposition.

Due to the interaction of N deposition with land management activities, it is possible that past, present, and future land management practices (including fire suppression, introduction of invasive species, and forestry practices) could minimize or exacerbate the adverse effects of N deposition on terrestrial and aquatic ecosystems. Hydrologic flowpaths in a watershed also influence the impact of atmospheric N deposition on aquatic ecosystems. In summary, chronic N deposition results in excess N in terrestrial, riparian, and aquatic habitats. This dramatic change in the chemical environment of these habitats has high potential to upset the normal communities of vegetation, microbes, and micro- and macro-flora and fauna either

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via direct effects on sensitive organisms or via cascading effects on the food chain. As an example, evidence suggests that elevated nitrate levels in pond water may be toxic to larvae of several western frog species that are in decline (Marco and others 1999). Because of the excessively high N enrichment of many southern California ecosystems, the effect on key species is a neglected area of research that should be addressed.

Average nitrate concentrations in streams in Devil Canyon in the western San Bernardino Mountains fall within the low end of the range of concentrations that cause developmental, physical, and behavioral abnormalities in sensitive amphibian species (Rouse and others 1999). However, peak concentrations in streams in the western San Bernardino Mountains are more than twice as high as average values and may have acute effects on sensitive amphibian species. Tadpole and larval stages appear to be the most sensitive life stages. Amphibian prey and predators also can be affected by elevated nitrate, a fact that may alter predation pressure and ecological balance. However, studies on the effects of elevated streamwater nitrate on aquatic biota have not yet been done in the San Bernardino Mountains.

Recent studies suggest that chronic N deposition may be a factor in the shift from native shrub species in coastal sage scrub ecosystems to exotic annual grasses – a widespread phenomenon in the remaining coastal sage habitats in southern California (Padgett and others 1999). Changes in vegetative communities may also be occurring in the forest understory in N-saturated forests, but this has not been investigated sufficiently. In high N deposition sites in the San Bernardino Mountains,

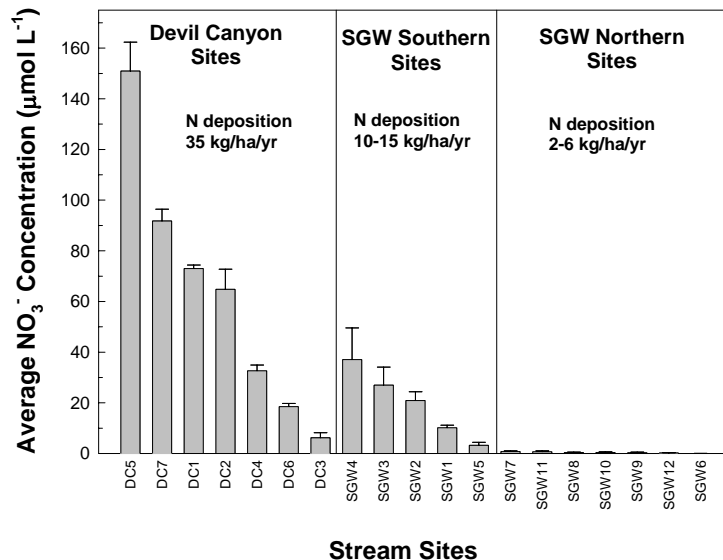


Figure 1—Average streamwater nitrate concentrations in Devil Canyon (high N deposition area in the western San Bernardino Mountains), along the southern side of the San Gorgonio Wilderness (SGW) (moderate N deposition), and on the northern side of the SGW (low N deposition; Fenn and Poth 1999).

the ecosystem is highly N enriched as evidenced by high N concentrations in foliage (of understory and overstory species), litter, mineral soil, soil solution, soil leachate, and trace gas emissions from soil (Fenn and others 1996). Forested sites further away from N pollution sources (motor vehicle emissions and dairy farms) receive atmospheric N deposition loads which are at least 5-10 fold lower, and plant growth is highly N limited – which is the normal condition for these forests. Thus, the long-term ecological and environmental impacts of decades of elevated atmospheric N inputs into wildland ecosystems in southern California remains an important and sometimes under-appreciated issue for natural resource managers, especially in the face of ever-increasing human populations.

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Surveys for California Red-Legged Frog and Arroyo Toad on the Los Padres National Forest¹

Valerie K. Hubbart and Thomas G. Murphey²

Key words: amphibians, monitoring, range expansion, stream channels, suitable habitat

Extended Abstract

Starting in the spring of 1999 through the fall of 2000, USDA Forest Service biologists have conducted surveys throughout the Los Padres National Forest for the federally-listed California red-legged frog (*Rana aurora draytonii*) and arroyo toad (*Bufo californicus*). Sites known to have frogs or toads present were monitored for breeding and possible impacts of Forest Service activities. Potential impacts to frogs and toads include roads, trails, campgrounds, off-highway vehicles, grazing allotments, and introduced species.

Historical locations and areas having suitable habitat for both species were visited to confirm occupancy. Day surveys were conducted to confirm presence of eggs and tadpoles, in the breeding season, and to determine areas that had potentially suitable habitat for adults. Night surveys were performed to establish presence or absence of adult frogs and toads. When adults were present, the locations of individuals were recorded and mapped, and pertinent habitat information was collected. Habitat information included land use, dominant vegetation, air and water temperatures, pool depth and location, and general hydrological information about the site.

Approximately 267 kilometers of stream channel have been surveyed. Survey results are summarized as the maximum number of adults seen within sub-watersheds (*table 1*). These numbers should not be interpreted as exact counts of current populations. Surveys through August 2000 have resulted in 11 new locations on the Los Padres National Forest for red-legged frogs and an expanded range for arroyo toad on upper Piru Creek near Castaic Mine and Goldhill Campground in Ventura County, based on past surveys (Stephenson and Calcarone 1999). Arroyo toad breeding was confirmed in these drainages: Piru Creek, Aqua Blanca Creek, Sespe Creek, Indian Creek, Mono Creek, and the Santa Ynez River. Arroyo toad breeding occurred from April to the end of May, and toads were still calling as late as the end of June, 2000. Breeding for California red-legged frog occurred from February to the end of March and at all sites that contained more than one frog.

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Table 1—Results of May 1999 to August 2000 amphibian surveys on the Los Padres National Forest.

Sub-watershed	Maximum # of Adults Observed		Total Area Surveyed (km.)	Creeks/Rivers Surveyed
	California Red-legged Frog	Arroyo Toad		
Arroyo Seco	0	0	8.7	Arroyo Seco, Santa Lucia and Tassajara
Carmel	50	0	18.0	Carmel River and Miller fork of Carmel*.
San Antonio	0	0	3.6	North Fork San Antonio
Monterey Coastal Streams	14	9	17.0	Little Sur, Sycamore Cyn.*, Laffler Cyn.*, Hare Cyn., Limekiln, Kirk, Mill, Wild Cattle, Prewitt, Plasket, Willow, Salmon, Alder, Villa, Redwood Gulch, Dutra and San Carpofo
Salinas	6	0	21.7	Salinas* and Navajo
San Luis Obispo Coastal Streams	18	0	5.9	Morro, East. fork Morro* and Chorro
Hausna	0	0	1.6	Trout
Arroyo Grande	5	0	5.7	Big Falls*, Little Falls* and Lopez Cyn.
Cuyama	23	0	21.4	Branch*, Alamo*, Cuyama, Stephens Cyn., Pine Cyn., Aliso Cyn., Bates Cyn. and Rancho Nuevo
La Brea	78	0	20.0	North fork La Brea*, South fork La Brea* and Main fork La Brea*
Sisquoc	34	1	12.6	Sisquoc* [#] and Horse Cyn.
Manzana	35	0	7.2	Manzana* and Davey Brown
Santa Ynez	242	70	50.0	Santa Ynez* [#] , Oso, Cachuma*, Mono* [#] , Indian* [#] , Blue Cyn.* [#] , Agua Caliente* [#] , Fox* and Alder*
Matilija	0	0	0.8	N. Fork Matilija
Sespe	0	54	26.2	Sespe [#] , Middle Lion, Rock and Rose Valley
Piru	0	44	47.0	Piru [#] , Agua Blanca [#] , Canton Cyn., Reasoner Cyn., Dominquez Cyn. and Lime Cyn.

* Drainages with California red-legged frogs present.

Drainages with arroyo toads present.

Future surveys will be conducted to further identify areas of potentially suitable habitat and to locate new breeding areas. Inventorying and monitoring will continue where Forest Service activities may result in adverse impacts on the listed species.

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