

UNIVERSITY OF CALIFORNIA

Los Angeles

Terrestrial Arthropods as Indicators of Restoration Success in Coastal Sage Scrub

A dissertation submitted in partial satisfaction of the  
requirements for the degree Doctor of Philosophy  
in Geography

by

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*For my parents, Joyce and Jerry Longcore*

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## **ABSTRACT OF THE DISSERTATION**

Terrestrial Arthropods as Indicators of Restoration Success in Coastal Sage Scrub

by

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Ecological restoration increasingly is relied upon for regional conservation planning, especially in southern California, where development is consuming natural habitats at a rapid pace. However, restoration attempts vary widely and there is seldom any attempt to measure the success of efforts beyond plant survival. Arthropods increasingly are recognized as efficient bioindicators because they respond quickly to environmental changes, have large population sizes, and are easily sampled. I sampled terrestrial arthropod communities with pitfall traps at

three differently aged coastal sage scrub restoration sites and 15 comparison sites to quantify the terrestrial arthropod fauna of coastal sage scrub and to develop a measure of restoration success in recreating native arthropod diversity. Five years of collections at comparison sites were used to quantify the year-to-year and seasonal variation of arthropod species and these parameters were correlated with climatic conditions. Arthropod diversity and evenness were significantly lower at restoration sites than undisturbed native sites although vegetation parameters were similar. Both detrended correspondence analysis (DCA) and Ward's method of agglomerative clustering separated restoration from comparison sites based on arthropod incidence and abundance. These differences could not be explained by vegetation characteristics. Invasive arthropods, *e.g.*, Argentine Ant (*Linepithema humile*), European Earwig (*Forficula auricularia*), and Dooryard Sowbug (*Armadillidium vulgare*), were found at all sites but were significantly more common at restoration sites. I conclude that arthropods should be included in restoration monitoring protocols and performance criteria and that greater attention should be paid to preserving habitat continuity for native arthropod communities during the revegetation process.

# Chapter 1. Ecological Restoration Assessment and Biodiversity

## Introduction

Ecological restoration is the attempt to return degraded lands to a natural state (Ewel 1987). Ecological restoration is often undertaken as compensatory mitigation for habitat destruction caused by development projects. These restorations usually take place under the auspices of public agencies such as the U.S. Army Corps of Engineers, the U.S. Fish and Wildlife Service, or state and local agencies, yet their long-term success in replicating destroyed habitat types is not often adequately assessed. Most restoration projects have success criteria that focus on reestablishment of plant species with little attention to vertebrate or invertebrate animal species — with the exception of species with special regulatory protections (*e.g.*, Kus 1998). Functional attributes, such as sediment stabilization or water quality, are sometimes used to assess wetland restoration projects (Bartoldus 1994; Brinson and Rheinhardt 1996; Rheinhardt *et al.* 1997). Few projects, however, have as their goal the reestablishment of biological diversity at many taxonomic levels, nor do they contain mechanisms to monitor post-restoration diversity. One promising avenue to develop more comprehensive assessments of ecological restoration projects has been the use of arthropod community structure as an indicator of the success of restoration in recreating a functioning natural community.

Arthropods increasingly have been recognized as efficient indicators of ecosystem function and recommended for use in conservation planning (Rosenberg *et al.* 1986; Kremen *et al.* 1993; Finnamore 1996). Recently, many researchers have



assessed habitat quality and measured habitat differences using arthropods (*e.g.*, Niemelä *et al.* 1993; Pollet and Grootaert 1996; Rykken *et al.* 1997). Further, arthropod groups have been used to track restoration success in a variety of contexts. Garono *et al.* (1996) described caddisfly community structure in wetland mitigation projects. Arthropod communities have been described in the appraisal of strip mine reclamation for over 20 years (Parmenter and MacMahon 1990; Holl 1995; Holl 1996; Andersen 1997; Andersen and Sparling 1997). Peters (1997) investigated the recovery of soil microarthropods to assess a prairie restoration and Jansen (1997) looked at orders and sizes of forest litter invertebrates to track tropical forest restoration. Williams (1993) investigated arthropod communities in restored riparian woodlands. Rosenberg *et al.* (1986) discussed the importance of a consideration of insect populations in environmental assessment and cited numerous studies from the 1970s and 1980s that use insects to monitor toxicity, bioaccumulation, and response to pollution and contamination.

Monitoring restoration projects with arthropods has many advantages (Kremen *et al.* 1993; Finnamore 1996). The short generation times of most arthropods make them ideal to track year-to-year change in a site, while their small size makes them efficient monitors of subtle yet important variations that may influence the quality of a habitat. Arthropods occupy the widest diversity of microhabitats and niches, and play more ecological roles, than any other group of animals. They have diverse body sizes, vagilities, and growth rates. Their large population sizes, reproductive potential, and short generation times allow the collection of statistically significant sample sizes using relatively passive methods with little potential for depleting populations. They also respond quickly to

environmental change, tracking habitat disturbance much faster than other taxa. Arthropod collections can be maintained virtually indefinitely. Among the disadvantages of using arthropods as bioindicators — especially for evaluating restoration success — is a paucity of baseline data with which to compare restored sites, limited taxonomic expertise to identify arthropods, a lack of natural history information for many species, limited research linking arthropod communities to vertebrate communities, and difficulties in evaluating large databases.

In southern California, where restoration projects have become commonplace practice to offset the impacts of rapid urbanization, there is a critical need to measure restoration success. If restoration is to be used as part of local and regional biodiversity conservation strategies, land managers and regulatory agencies must have metrics available to evaluate disparate and unreplicated restoration attempts and to understand the development of the entire biotic community on restored sites. In the chapters that follow, I compare the terrestrial arthropod communities of different-aged coastal sage scrub restoration sites in southern California with nearby reference sites to:

- define arthropod community composition and variation for natural coastal sage scrub in southern California;
- develop a common metric for measuring restoration success; and
- describe arthropod community development on restored sites.

To address these three objectives, I compared the results of a five-year arthropod pitfall trap monitoring effort of undisturbed and disturbed natural coastal sage scrub with results from one year of monitoring three completed restoration projects. To address the first objective, I identified and enumerated the arthropod

species sampled by a standard method over a five-year period and described their phenologies through monthly averages of abundance. I then investigated the role of climate in structuring these communities by asking to what degree arthropod abundances were correlated with temperature and precipitation. The second objective was addressed by comparing arthropod communities from restored and reference sites in terms of composition, abundance, richness, nativity, and their relationship to vegetation parameters. These comparisons are based on specific expectations prompted by completed studies of succession in old-field systems. The final objective of describing arthropod community development on restoration community development was investigated by using differently aged restorations as a surrogate for a longitudinal study. Here I asked whether restorations exhibit the same pattern of guild composition of early succession sites.

### **Restoration Evaluation**

The implementation of ecological restoration projects is plagued by three interrelated problems. First, because restoration projects are implemented in different ways, with varying planting regimes and approaches, there are scant established methods to evaluate success of one relative to another. Each is its own unreplicated experiment, leaving the challenge to regulatory agencies to evaluate restorations on relatively superficial criteria, for example, percent plant survival. Second, there are few data on the recovery of natural communities in restored areas, leading to difficulties with evaluating restoration success, and with incorporating restoration into regional conservation planning. Third, many regions, even well-studied regions such as southern California, lack detailed, quantitative data

describing natural communities under normal disturbance regimes to use as reference data by which to judge restoration attempts.

What constitutes “success” for a restoration project is problematic. A National Research Council committee proposed the definition: “the return of an ecosystem to a close approximation of its condition prior to disturbance” (National Research Council 1992). Unfortunately, restoration of terrestrial communities for compensatory mitigation almost never has recreation of a complete natural community its goal. Rather, success criteria for terrestrial projects are most often expressed in terms of native plant cover (Society for Ecological Restoration 1997). Assessment of terrestrial mitigation lags behind that developed for wetlands (*e.g.*, Rheinhardt *et al.* 1997).

Although integrated yet into research on restoration, biological assessment measures have been developed in other contexts that are useful in discussing restoration success beyond plant cover. Water resource managers have long used biological indicators to evaluate water quality, especially toxicity. To address the wider variety of human impacts on water quality, Karr and Dudley (1981) developed a measure of “biological integrity,” which is “the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region.” By extension, restoration is the act of reestablishing the “biological integrity” of a site. For example, Karr’s Index of Biological Integrity measures fish communities in three major categories: 1) species richness, 2) trophic composition, and 3) abundance and condition. Arthropod communities offer the opportunity to evaluate similar parameters for a terrestrial community. As important

components of all natural systems — “the little things that run the world” (Wilson 1987) — an appropriate native invertebrate community is certainly necessary to consider a restoration successful.

Understanding the differences between arthropod communities from restored sites and reference sites is deepened by knowledge of the process of community development on restored sites. This process can be grounded in ecological theory, specifically as it pertains to: 1) old field succession, 2) invasion ecology, and 3) disturbance ecology. Research in each of these areas can lead to specific hypotheses about what might be expected in arthropod communities from restoration sites.

### **Succession**

The response of insect communities to old field succession is an established topic of ecological research (*e.g.*, Murdoch *et al.* 1972; Southwood *et al.* 1979; Brown and Southwood 1983; Hendrix *et al.* 1988; Brown 1991). However, we have only begun to apply knowledge of succession to the process of community recovery in restoration projects (Parmenter and MacMahon 1990; Williams 1993; Jansen 1997). Research on succession and insect communities focuses on two topics: 1) plant taxonomic and structural diversity and its relationship to insect diversity, and 2) guild structure of insect communities during succession.

Little is known about the determinants of arthropod species richness or diversity (Samways 1990a). However, many of the general features of other ecological communities are seen in arthropod communities, such as species-area relationships, density compensation, and response to habitat complexity (Lawton and Strong 1981; Denno and Roderick 1991). Succession studies have made some

progress correlating habitat complexity and diversity to arthropod species richness (Murdoch *et al.* 1972; Southwood *et al.* 1979; Moran and Southwood 1982; Brown and Southwood 1983; Hendrix *et al.* 1988).

Research on old field succession and on restorations suggests a close relationship between plant diversity and arthropod species richness (Murdoch *et al.* 1972; Southwood *et al.* 1979; Hawkins and Cross 1982; Stinson and Brown 1983; Parmenter and MacMahon 1987; Parmenter and MacMahon 1990). For example, Murdoch *et al.* (1972) showed a positive relationship in species richness, evenness, and diversity between plants and insects in old fields. They also found that foliage height diversity (structural diversity) was positively correlated with species richness. Other research has shown that for groups that strictly eat plants, plant species diversity is a better predictor of insect abundance than structural attributes (Brown and Hyman 1986). In relation to restoration projects, Majer *et al.* (1984) and Greenslade and Majer (1993) have shown increased richness of collemboloids and ants with increased age and diversity of species planted; others have found a significant correlation between number of plant species and both the number of Coleoptera species and Orthoptera species (Parmenter and MacMahon 1987; Parmenter *et al.* 1991).

Arthropod guild structure has similarly been investigated in old field studies (Root 1967). Although arthropods were important in the development of the concept of guilds (Root 1973), few studies have been completed that investigate arthropod guilds for stable natural habitats or in succession. Moran & Southwood (1982) found that most guilds showed a “striking uniformity” in their proportions across plant species and biogeographic realms, while Teraguchi *et al.* (1977) observed a

constant trophic structure in old fields under different environmental stresses. Hendrix *et al.* (1988) found that all guilds colonized rapidly during the earliest stages of succession, with phytophages dominant. Moran and Southwood (1982) also found phytophages dominant in trees. However, Hendrix *et al.* (1988) noted that exotic plant species have a lower species richness and diversity of arthropods, especially phytophages. They also failed to find the constancy between sites in guild proportions described by Moran and Southwood (1982). Although not explicitly addressing the issue of arthropod guild structure, Peters (1997) found that higher diversity in soil microarthropods in native versus restored prairie was due to the abundance of rare, predatory arthropods. This research provides an ample basis to predict development of arthropod guild structure at restorations and to compare restorations with the unaided succession of old fields.

### **Invasion Ecology**

The success of biological invasions has been the topic of considerable investigation. Elton suggested that areas with more native species would exhibit “biotic resistance,” reducing invasion effects through competition, predation, parasitism, and disease (Elton 1958). Disturbed habitats are therefore easier to invade because disturbance decreases this “biotic resistance” (Elton 1958) or increases the availability of a limiting resource (Hobbs 1989). Elton’s identification of the importance of disturbance has been upheld by subsequent research (Orians 1986). Biological disturbance can transform ecosystem structure and function (Vitousek 1986). Examples abound where non-indigenous plants and animals alter

resource utilization, trophic structure, and disturbance frequencies in native ecosystems (Vitousek 1990).

Because restoration sites by definition are highly disturbed, invasion ecology suggests that they will be highly susceptible to invasions and will be invaded by species that are associated with human disturbance. Furthermore, just as intact native communities resist invasion, invasive species, once established, are probably resistant to recolonization by native species. The characteristics that make a species a successful invader — low intraspecific competition, interspecies aggression, high fecundity (Holway *et al.* 1998) — also often make it able to hold its ground. One would therefore predict that despite reestablishment of a native plant community, sites that have been restored from a highly disturbed condition would be dominated by exotic invertebrates. Would-be restoration sites also become dominated by exotic plant species, but current restoration practice involves active management of exotic plant species in the attempt to reestablish native vegetation.

A number of exotic arthropods have invaded habitats in southern California (*e.g.*, European earwig, *Forficula auricularia*, the isopods *Armadillidium vulgare* and *Porcellio laevis*, the spider *Dysdera crocata*, and the Argentine ant, *Linepithema humile*). The best example is that of the Argentine ant, which has been shown to displace native ants in direct competition (Human and Gordon 1996), and to expand its range into native habitats under conditions of increased water from residential development (Suarez and Case 1996; Purdum 1997). Wherever it has been introduced, the Argentine ant has transformed native arthropod communities (Erickson 1971; Ward 1987; Cole *et al.* 1992; Human and Gordon 1997; Way *et al.* 1997; Holway 1998a; Suarez *et al.* 1998). Information about *Forficula* is limited to



documentation of the use by *Forficula* of native bee nesting cavities inhibiting usage by the megachilid bees (Barthell *et al.* 1998) and a conjectural identification of *Forficula* and *Armadillidium* as predators of the larvae of the endangered Quino checkerspot butterfly (Ballmer and Hawks, unpublished ms). Little research has been completed on the influence of exotic species on arthropod communities at restored sites.

### **Disturbance Ecology and the Role of History**

A third area of ecological thought provides insight on the outcome of restoration attempts and their arthropod communities, that of research on ecological disturbance. Ecologists are prone to stressing the importance of local, deterministic processes, such as competition and predator-prey interactions, in determining community structure. Less appreciated is a robust consideration of historical processes — even historical accident — as important in structuring communities (May 1986; Ricklefs 1987). Elton (1955) specifically argued that the observable order in natural communities could not result from chance events. Elton's invasion ecology does acknowledge the role of chance events — disturbance — as important, but only for its function in reducing competition and “biotic resistance” or changing nutrient availability. However, the literature on ecological disturbance has appreciated the role of history and random events in shaping ecosystems (Sousa 1984; Pickett and White 1985; Savage *et al.* 1996).

Disturbance ecologists attempt to elucidate the role of natural disturbance in ecosystem structure and species distribution, as well as the comparative role of anthropogenic disturbance. In doing so, they recognize that whole landscapes can be

transformed by combinations of historical accidents and recognize that ecological communities are not the coherent inflexible entities suggested by traditional population-genetic models. Further, traditional ecological theory assumes an equilibrium environment, deviations from which are counteracted by demographic or genetic variation (Hengeveld 1997). Both disturbance ecology and Quaternary paleoecology have provided a recognition of a non-equilibrium environment, leading to the conclusion that species do not rapidly adapt to new surroundings but rather move to track their optimum environmental conditions (Huntley and Birks 1993; Hengeveld 1997). The concept of the cohesive assemblage has given way to the recognition of the individualistic nature of species (Gleason 1926), an old idea given new weight. At the scale of terrestrial arthropods and restoration projects, disturbance ecology suggests that site history is important and that following intense disturbance — which all restoration sites have by definition experienced — the community that reestablishes itself may bear little resemblance to that which was there previously or even in surrounding areas.

### **Outline of the Dissertation**

In the following three chapters I address the opportunity for and problems of assessing ecological restoration projects by measuring and comparing terrestrial arthropod communities of restoration sites and comparable undisturbed and disturbed native habitats. Chapter 2 is concerned with the composition, abundance, and variation of arthropods in coastal sage scrub. It presents the results of this five-year study, with a concentration on the natural characteristics of the arthropod community without extensive attention paid to the restoration sites. The chapter provides

quantification of the degree to which arthropod abundance varies during the course of the year (seasonal variation) and the variation in the amplitude of those cycles from year to year (yearly variation). The relationship of yearly cycles in abundance to climatic variables are compared and discussed. The results presented in this chapter provide guidance for the choice of data with which to compare arthropods at restoration sites in the following chapter.

Chapter 3 presents and discusses the analysis of arthropod community abundance, diversity, and structure on restored and nonrestored sites. This effort involves only one year of contemporaneously sampled data, because of the high degree of yearly variation evident in the five-year dataset. Vegetation characteristics of the sites are compared and the relationship between vegetation and arthropod communities is explored. The importance of exotic species as disruptive invaders is analyzed and discussed.

Chapter 4 discusses five themes that emerge from the results presented in Chapter 2 and Chapter 3. First, the research indicates that sites that are revegetated with native species do not develop native arthropod communities. Arthropods at restoration sites in virtually all studies are of lower diversity or altered community structure than reference communities. Second, exotic species play an important role in structuring the arthropod communities at restoration sites. Some ecological explanations for this function are discussed. Third, some arthropod species are good indicators of habitat quality, specifically a subset of the predator guild. The utility of these species as indicators and their ecological importance is discussed. Fourth, the importance of climate and the yearly and seasonal variation of arthropods are discussed with implications for monitoring techniques and invasion biology. Fifth,

the observed disconnection between vegetation and arthropod communities at restoration sites is discussed. Recommendations for restoration implementation and monitoring are proposed in response to each major finding.

## Chapter 2. Composition and Variation of Terrestrial Arthropod Communities in Coastal Sage Scrub

### Introduction

Coastal sage scrub is a highly endangered plant community found in coastal regions of southern California (O'Leary 1990). An estimated 70–90% of all coastal sage scrub has been lost to agricultural and urban land uses (Noss *et al.* 1995). Currently extensive multi-species planning efforts are underway for coastal sage scrub, many of which rely on restoration as a management tool (California Department of Fish and Game 1999). Research into the effectiveness of restoration in this habitat is therefore of high value to conservation planning.

Coastal sage scrub is found “scattered along the coast” from the Oregon border of California south to the San Francisco Bay region, through the lower elevations of the outer and inner Coast Ranges, the Transverse and Peninsular ranges of southern California, and southward into Baja California (Axelrod 1978). This distribution has been divided into six subassociations, Franciscan, Diablan, Lucian, Venturan, Riversidian, and Diegan (Axelrod 1950). The vegetation height ranges from 0.5 to 1.5 m with shrubs the dominant life form. In contrast with chaparral, most shrubs have soft leaves and survive the characteristic hot, dry summers of the Mediterranean climate by dropping them. In the Venturan coastal sage scrub that is the subject of this study, the dominant taxa are *Artemisia*, *Baccharis*, *Encelia*, *Eriogonum*, *Haplopappus*, *Salvia*, and *Rhus/Malosma*. Coastal sage scrub is found exclusively in the Mediterranean climate zone, with precipitation highly variable

from year to year, but usually receiving 250–450 mm between November and April (Kirkpatrick and Hutchinson 1980). Fire constitutes an integral part of coastal sage scrub ecology. The community is fire adapted and characterized by a pulse of fugitive fire-following plant species after burns at intervals of 10 to 50 years (O’Leary 1988). An extensive bibliography of coastal sage scrub research is available (O’Leary *et al.* 1994).

Little is known about the quantitative composition of most insect communities. Species lists have been compiled for specific regions and areas, but often the numerical composition and structure of those communities has not been quantified. While seasonal and yearly variation in arthropod species abundance has been investigated for some geographic regions and taxonomic groups (*e.g.*, Baker 1986; Wolda *et al.* 1992; Wolda and Marek 1994; Stewart 1995; Bultman and Mathews 1996; Wolda and Chandler 1996; Broza and Izhaki 1997; Stapp 1997; Leps *et al.* 1998; Novotny and Basset 1998; Souty-Grosset *et al.* 1998), these parameters are largely unresearched for arthropods in coastal sage scrub. The relative abundance of insect species and their yearly variation in seemingly static habitats is important to describe community structure, and to define reference conditions for ecological restoration.

Comprehensive research on the arthropods of coastal sage scrub is in its infancy. Arthropod community studies in southern California in general are limited. Examples include Force’s study of post-fire insect communities in chaparral (Force 1981), a survey of the spiders of coastal sage scrub (Prentice *et al.* 1998), and a forthcoming article on the arthropods of urban coastal sage scrub fragments (Bolger *et al.*, in press). Other details of community structure and ecology must be gleaned

from studies of species or families (see references in Hogue 1993). Other community studies are ongoing, but not yet published. A taxonomically broad description of coastal sage scrub arthropods would therefore constitute a valuable contribution to current knowledge.

The development of invertebrate populations has been used to assess the performance of restorations (Andersen and Sparling 1997; Greenslade and Majer 1993; Jansen 1997; Parmenter and MacMahon 1990; Peters 1997; Williams 1993). Such attempts, however, depend on the ability to compare the site to reference conditions that represent the desired goal. These comparisons vary either in space (same time, comparable habitats), in time (historical data, same place), or both (historical data, comparable habitats) (White & Walker 1997). Our ability to compare communities that vary in space and time depends on knowledge of the natural degree of variation of the community's numerical variation. Such knowledge is also necessary to detect secular changes in community composition. Without knowing the normal level of seasonal or yearly variation in arthropod abundance, one cannot discern between changes in abundance that are within the range of normal cyclical variation or that are part of a secular change in the community.

The high degree of interannual and seasonal variation in arthropod communities is well established (Borror *et al.* 1989) and this variation is long known to be influenced by climatic factors (Uvarov 1931). The coastal sage scrub of California has a Mediterranean climate that exhibits high interannual variation, requiring a long-term study for a full description of its invertebrate fauna. Yearly and seasonal variations of the fauna are important to ecological restoration for at least three reasons:

- 1) the potentially different reactions by native and exotic species populations and their implication for exotic invasions,
- 2) the need to define normal variation for purposes of defining reference conditions for restoration attempts, and
- 3) the use of yearly population variation estimates in designing statistically robust long-term monitoring programs.

Several southern California invasive exotic species (*Linepithema humile*, *Forficula auricularia*, *Armadillidium vulgare*, *Porcellio laevis*, and *Dysdera crocata*) have received attention as ecological invaders, with considerable study of *Linepithema* but less of the other invertebrates (Mooney *et al.* 1986). A number of explanations have been provided for the success of Argentine ants as invaders and their subsequent displacement of native arthropod fauna. They include abiotic conditions — increased moisture (Holway 1998b; Human *et al.* 1998) and disturbance as measured by distance to edges (Human *et al.* 1998) — and behavioral characteristics — the lack of intraspecific aggression (Holway *et al.* 1998), and aggressive exploitation and interference competition (Human and Gordon 1996; Holway 1999). The effect on native ants and ecosystems is similarly well documented (Holway 1998a; Kennedy 1998; Suarez *et al.* 1998).

*Forficula auricularia*, European earwig, has been recorded in southern California (Los Angeles County) since 1931 (Langston and Powell 1975). Despite their potential to disrupt native arthropod communities — they feed on foliage and both living and dead insects — there has been little documentation of the species' spread from urban centers of introduction into native habitats. Similarly, *Armadillidium vulgare*, Dooryard Sowbug, has invaded California landscapes with



startling rapidity. It was established in San Francisco in 1926 and in less than fifty years became one of the most common animals in California grasslands (Paris 1963). It too has the potential to usurp significant ecological space because it scavenges widely, feeding on dead leaves, fungi, dead animals, and other organic matter (Paris 1963).

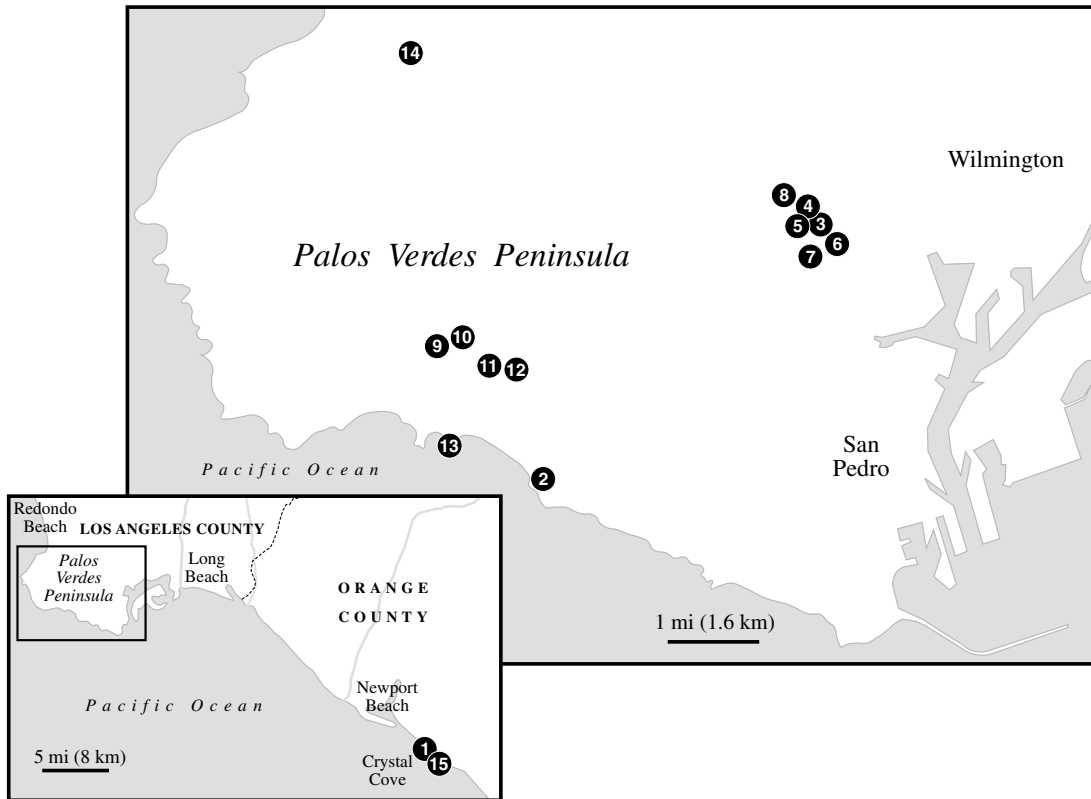
However, little research has been completed to evaluate and assess the differential effect of yearly and seasonal variation in precipitation and temperature on native and exotic arthropods. Bolger (pers. comm.) reports that Argentine ants were in greater abundance in southern California during the 1998–1999 winter season because of increased precipitation from the El Niño/Southern Oscillation (ENSO) event. Yearly and seasonal variation in terrestrial arthropod abundance is important to define reference conditions for the evaluation of restoration projects, especially in Mediterranean and other highly variable climates (White and Walker 1997). To date, the differences in population size between years for terrestrial arthropod species in southern California have not been described. There may be species whose abundance is relatively stable from year to year while others are highly variable, depending on their autecological needs. Documenting these potential differences would provide valuable information to design focused monitoring and assessment techniques. For example, larger, longer-lived species and large predators may be better indicators of habitat quality than shorter-lived species. In coastal sage scrub, such species might be scorpions (Vejovidae), which may live up to 25 years (Polis and Sissom 1990).

The ability to design experiments to detect long-term change in terrestrial arthropod communities depends on estimates of yearly variation. Power analysis

allows calculation of sampling intensity necessary to provide sufficient statistical power to detect a specified change in a population for assessing restoration attempts or detecting responses to climate change (Gibbs *et al.* 1998). However, power analysis requires an estimate of the yearly coefficient of variation of a species to provide such guidance. Currently, the estimates for variation in arthropod groups are derived from few studies in limited habitats. Gibbs *et al.* (1998) report estimates from boreal forest for spiders (Renault and Miller 1972) and temperate fallow agricultural land for beetles (Jones 1976). It is likely that the yearly coefficient of variation of these groups varies among habitat types, and between species within the groups. Estimates of population variability are therefore needed for arthropods in general, for Mediterranean climates, and with some detail within taxonomic groups.

The objectives of this chapter include:

- 1) a description of the incidence and abundance of terrestrial arthropods in coastal sage scrub,
- 2) a description of yearly and seasonal variation exhibited by native and exotic arthropods in coastal sage scrub,
- 3) establishment of the relationship of this variation to precipitation and temperature, and
- 4) a comparison of the degree of variability within and between taxonomic groups and between native and exotic species.



**Figure 1. Location of Study Sites.** 1) Crystal Cove State Park-Pelican Point, 2) Ocean Trails, 3) DFSP-Restoration, 4) DFSP-Office, 5) DFSP-Disaster Shelter, 6) DFSP-Locoweed, 7) DFSP-South End, 8) DFSP-Hill, 9) Kelvin Canyon, 10) Fennel Hill, 11) Portuguese Canyon, 12) Klondike Canyon, 13) Inspiration Point, 14) Malaga Canyon, 15) Crystal Cove State Park-Crystal Cove.

## Methods

### *Study Localities*

The study localities are in 1) undisturbed, 2) disturbed, and 3) restored coastal sage scrub. The disturbed, undisturbed, and two of the restoration localities are on the Palos Verdes Peninsula, Los Angeles County, and the third restoration locality is 60 km south at Crystal Cove State Park in Orange County (Figure 1). All

sites are within 5 km of the Pacific Ocean. Qualitative descriptions of the study sites follow. Quantification of the vegetation structure and composition is provided in Chapter 3.

**Defense Fuel Support Point (DFSP).** The Defense Logistics Agency operates this Navy-owned facility, which is the only currently known locality for the federally endangered Palos Verdes blue butterfly. While much of the 120-ha installation was disturbed during the 1940s to construct underground fuel tanks, a contiguous area of approximately 11 ha of coastal sage scrub was left undisturbed. The integrity of these areas is indicated by the presence of mature *Opuntia prolifera* and intact cryptobiotic crusts. Six localities were sampled within the facility. **DFSP-Office** (*undisturbed*). This area is undisturbed with high native cover of mature coastal sage scrub. **DFSP-Disaster Shelter** (*undisturbed*). This area has high native cover, but is not diverse. **DFSP-Locoweed** (*undisturbed*). This area has high native cover, some invading pepper trees. **DFSP-South End** (*disturbed*). This area is in early succession following disturbance for the construction of a drainage channel and subsequent mowing. Mowing stopped in the early 1990s and recolonization of native shrubs was allowed. **DFSP-Hill** (*disturbed*). This is an area in early succession on fill left from a construction project in 1987. **DFSP-Restoration** (*restoration*). This area was disturbed by the construction of a drainage channel. It was cleared of exotic species, mostly grasses, by hand and planted in 1997 with native shrubs grown from cuttings taken on site. It was irrigated during planting in late 1997 but not during the study period.

**Landslide Area.** Geologically unstable soils have prevented the development of a large area on the southern slope of the Palos Verdes Peninsula.

Consequently, significant tracts of coastal sage scrub remain and are currently the subject of a comprehensive conservation planning process (California Department of Fish and Game 1999). Several localities with mature coastal sage scrub were sampled along the public right of way through this area: **Kelvin Canyon** (*undisturbed*), **Portuguese Canyon** (*undisturbed*), and **Klondike Canyon** (*undisturbed*). **Fennel Hill** (*disturbed*) is a highly disturbed locality in the landslide area, dominated by exotic species. The disturbance was likely some combination of grazing or dry farming during the early part of the century through at least the 1950s. It has been left fallow — perhaps occasionally disked — and has been colonized by exotic fennel (*Foeniculum vulgare*).

**Inspiration Point** (*undisturbed*). This locality has high native shrub cover on a coastal bluff. It was farmed in the 1920s but is now part of a public park. Because of the long time since disturbance and high native cover, this locality was considered an undisturbed site.

**Malaga Canyon** (*disturbed*). This locality is adjacent to a golf course and a predominantly riparian area, but with significant coastal sage scrub components. It was disturbed by a public engineering project in 1996.

The restoration sites (DFSP-Restoration, Ocean Trails, and Crystal Cove/Pelican Point) are included for comparison, but because they were only sampled for one year, they do not contribute to the analysis of yearly variation.

### ***Arthropod Data***

Terrestrial arthropod communities were sampled at each locality with pitfall traps. Such traps provide a quantitative measure of the ground-dwelling arthropod community composition, but have limitations. Pitfall trapping has been criticized for

measuring activity rather than abundance, under representing small species, and being overly sensitive to immediate surroundings (Greenslade 1964; Baars 1979; Spence and Niemalä 1994). However, as long as only pitfall trapping results are compared with each other and not taken to indicate absolute abundance, the method is accepted to provide useful comparative data (Topping and Sunderland 1992). Therefore, none of the abundances and relationships reported in this dissertation should be interpreted as actual abundance or actual percentages, but comparable only to other data collected by pitfall trapping. No perfect trapping methodology exists; results from all methods must be compared against similarly collected data.

**Table 1. Successful collections by locality, 1994–1998. Collections that had two or fewer species were omitted, as were collections where the trap was physically disturbed or washed out.**

<b>Locality (Number of Sites)</b>	<b>1994</b>	<b>1995</b>	<b>1996</b>	<b>1997</b>	<b>1998</b>	<b>Total</b>
<b>Reference</b>						
DFSP-Office (2)	2	18	22	22	13	<b>77</b>
DFSP-Locoweed (2)	16	16	22	21	21	<b>96</b>
DFSP-Disaster Shelter (2)	13	19	23	19	12	<b>86</b>
Kelvin Canyon (3)	21	24	23	26	29	<b>123</b>
Klondike Canyon (3)	24	26	29	37	34	<b>150</b>
Portuguese Canyon (3)	27	30	33	27	35	<b>152</b>
Inspiration Point (2)	16	11	19	15	21	<b>82</b>
<b>Disturbed</b>						
Fennel Hill (3)	24	28	26	33	34	<b>145</b>
Malaga Canyon (2/3)	26	28	29	21	22	<b>126</b>
DFSP-Hill (2)	10	18	20	24	24	<b>96</b>
DFSP-South End (2)			6	14	22	<b>42</b>
<b>Restoration</b>						
Crystal Cove (3)					25	<b>25</b>
Pelican Point (3)					24	<b>24</b>
Ocean Trails (3)					34	<b>34</b>
DFSP-Restoration (3)					35	<b>35</b>
<b>Total</b>	<b>179</b>	<b>218</b>	<b>252</b>	<b>259</b>	<b>385</b>	<b>1293</b>

Trapping was begun in 1994, with replicate traps added through 1997 (Table 1). The restoration sites were added in January 1998 (DFSP and Ocean Trails) and March 1998 (Crystal Cove). Traps were collected monthly through December 1998. Each locality is sampled at two or three sites approximately 20 m apart as topographic and vegetative features allowed. These trapping locations are referred to as “sites”; “localities” contain clusters of 2–3 “sites.” More intensive trapping at each locality was shown redundant in earlier research from the El Segundo sand dunes (Mattoni *et al.*, in press). In that study, we showed that for nine localities with between three and eight traps each, cluster analysis produced exclusive clusters for seven of the localities. This result means that additional traps at localities do not provide significant additional information that distinguishes their arthropod communities from other localities.

Pitfall traps consist of two one-quart plastic containers each 10 cm across and 13 cm deep, nested together and buried so that the rim of the inner container is flush with the soil. Each was covered with a 20-cm square thin plywood lid supported about 2 cm above the rim by wooden legs. Traps are filled to a depth of 2 cm with ethylene glycol (commercial antifreeze) as preservative, and the contents are collected monthly into 200-ml snap top plastic vials and returned to the laboratory for sorting.

The trapping network was expanded slightly 1995–1997 with the addition of replicate traps at some localities (Table 1). In 1998, the restoration localities were added to the trapping network. Each collection represented one trap at one site during one month. A locality with three trap sites yielded three collections per month. Collections that yielded fewer than two species and five individuals were

deleted from further analysis because the low specimen numbers resulted from external disturbance (*e.g.*, animals, humans, and excessive rain runoff). Differences in trapping effort per locality are accounted for by the number of sites sampled at each locality, the duration the locality was sampled, and the rate of trap failure through human or animal disturbance or flooding. For this portion of the study, the differences in sampling number are controlled for by expressing all results as abundance per trapping effort.

An experienced field entomologist — employed by the UCLA Department of Geography — sorted all specimens to family using standard keys. Those easily identified are assigned to species, while unidentified taxa are grouped into morphospecies or “recognizable taxonomic units” (*e.g.*, *Nebrites* sp. 1) based on visible characteristics. This method has been shown to correlate well with species as determined by taxonomic experts and to be cost effective (Kremen *et al.* 1993; Oliver and Beattie 1993; Oliver and Beattie 1996b; Oliver and Beattie 1996a). It has been used successfully (Ingham and Samways 1996; Didham *et al.* 1998; Bolger *et al.* in press), although it should not be used uncritically (Goldstein 1997). Goldstein’s (1997) criticism of the method concerned the use of morphospecies in conservation assessment, and questioned conservation priorities based on simple morphospecies richness. In contrast to the caricature of a morphospecies study as a simplistic management tool, this study addresses many aspects of incidence, abundance, community structure, and ecological function of species. Because of the overall scarcity of taxonomic expertise in most insect groups, morphospecies are a practical necessity. The number of specialists to make specific determinations is not sufficient to meet the needs of researchers conducting taxonomically broad studies.



Throughout the dissertation, the term “species” is used to mean both “species” and “morphospecies.”

The use of all arthropods sorted to morphospecies is a departure from most other work using arthropods as measures of restoration success, which generalize to order or concentrate on a single family or order. Jansen (1997), Peters (1997), and Williams (1993) keyed their specimens to order or family, while Garono and Kooser (1994), Anderson (1997), and Holl (1995; 1996) keyed to species, but limited their analyses to a single family or order. I argue that the determination of taxonomic identity below order is important because families, genera, and species react differently to environmental conditions and order-level aggregation obscures variation that may prove important to habitat assessment. Single-family studies may detect variation in habitat characteristics (Niemelä *et al.* 1993; Rykken *et al.* 1997) but are limited. In a study of diverse taxa in tropical forest (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, and soil nematodes) no one taxonomic group served as a sufficient indicator for diversity in others (Lawton *et al.* 1998). A broad taxonomic approach with significant taxonomic detail is necessary ensure detection of important variation among sampled sites and to identify important species in community composition.

### ***Climate Data***

The climate record for the nearest instrumental station — Daugherty Field in Long Beach, California, located approximately 15 km east of the Palos Verdes Peninsula — was obtained from the National Climatic Data Center for the period available, 1949–1998. Data included total daily precipitation and daily high temperature for all years except 1957–1959. Annual precipitation for a reference

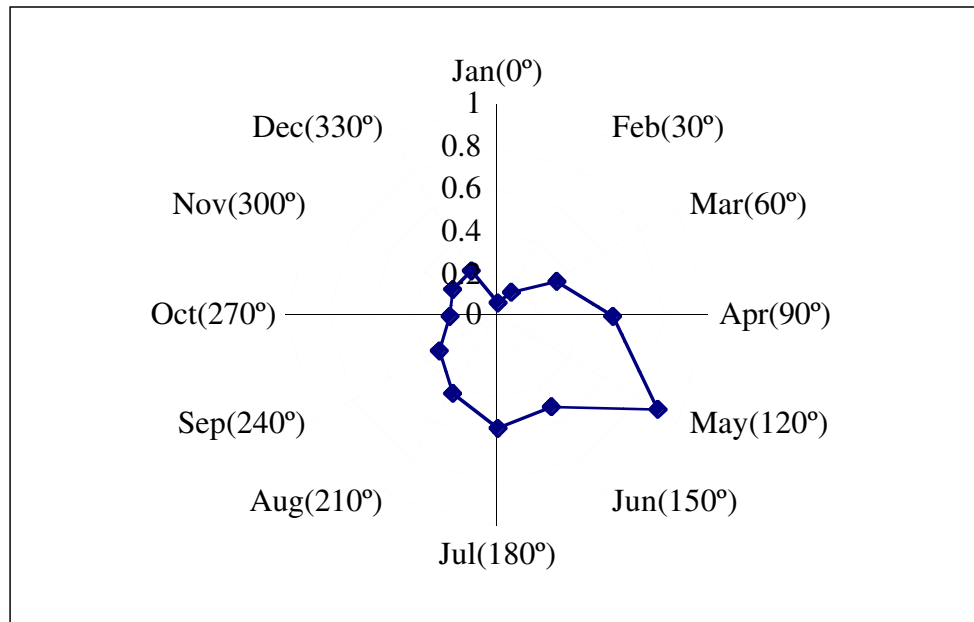
period (1949–1993) was compared with the study period (1994–1998) using a five-year trailing mean.

### ***Analysis of Arthropod and Climate Data***

**Yearly Variation in Arthropod Abundance.** For purposes of this analysis, the study localities were divided into seven undisturbed (reference) localities: (Portuguese Canyon, Klondike Canyon, Kelvin Canyon, Inspiration Point, DFSP-Office, DFSP-Disaster, DFSP-Locoweed), four disturbed localities (DFSP-Hill, DFSP-South End, Fennel Hill, and Malaga Canyon), and four restoration localities (DFSP-Restoration, Ocean Trails, Pelican Point, Crystal Cove). The mean abundance of each morphospecies collected was calculated for each of the five years of the study. For each species, these five yearly values represent the mean number of each morphospecies collected per trap-month during each year. The mean and standard deviation of those five data points was then calculated to provide a measure of the abundance of each species in the community over the entire study period (mean) and the degree to which the abundance of each species varies from year to year (expressed as coefficient of variation).

**Seasonal Variation in Arthropod Abundance.** Seasonal variation in arthropod abundance was expressed by calculating mean, standard deviation, and coefficient of variation of the number of each morphospecies in the collections ending in each month throughout the five-year sample period. For example, I calculated the mean number of *Eleodes gracilis* collected for each of the five collections (1994–1998) ending in January, February, March, etc. This calculation included all undisturbed and disturbed sites, but not restorations. The numbers represent the average number of each morphospecies collected in a trap during each

month. The coefficient of variation of monthly abundance (“seasonal coefficient of variation”) provides one measure of seasonality.



**Figure 2. Circular depiction of mean monthly abundance for Jerusalem crickets (*Stenoplematus* sp.). The mean angle of this distribution is 147° (late May) while its seasonality ( $r$ ) is 0.33.**

Seasonality was quantified a second way using circular statistics. Monthly arthropod abundance values were expressed as an angle (months converted to 0°–330° in 30° increments) and radius (abundance). The mean vector represented by the mean radius and angle of each set of monthly values was calculated as follows (Zar 1996):

Let  $a_i$  equal the angle corresponding to each month  $i$ , and  $\bar{a}$  equal the mean angle,

Let  $f_i$  equal arthropod abundance in each month  $i$ ,

$$X = \frac{\sum f_i \cos a_i}{\sum f_i} \text{ and } Y = \frac{\sum f_i \sin a_i}{\sum f_i}$$

$$r = \sqrt{X^2 + Y^2}$$

$$\tan \bar{a} = \frac{Y}{X}$$

The value  $r$  is the radius of the mean vector standardized for abundance and varies from 0 to 1. It provides a measure of the dispersion of the distribution, which can be interpreted as low (0) to high (1) seasonality. The mean angle represents the month of maximum abundance. Figure 2 provides an example of this method. Species with fewer than 0.1 mean individuals per trap per month were excluded from the analysis.

**Cross-Correlation of Climate with Arthropod Abundance.** Cross-correlation is used to describe the relationship between two time series. It provides a measure of the degree to which two series vary in concert with each other. In addition to contemporaneous variation, one series is lagged behind the other to measure a delayed response. The cross-correlation between arthropod abundance and precipitation and maximum daily temperature for 1994–1998 was calculated separately for each species. Precipitation and temperature were chosen as the two environmental cross-correlation variables because they have been identified as the two most important determinants of insect phenology (Uvarov 1931).

Cross-correlation was used to allow for the exploration of a lagged response between climate variables and arthropod abundance. If values were summed by year, relationships between fall precipitation and population size the following spring would be lost. Cross-correlation allows for the investigation of the complete monthly time series and many potential lagged response times to environmental variables. Results of the cross-correlation do require interpretation based on reasonable ecological explanations. Both precipitation and temperature show regular seasonal variation. Significant cross-correlation of arthropod abundance with these factors may be based on inherent seasonality rather than indicating a response to the

correlated variable. However, because precipitation varies greatly from year to year, a significant cross-correlation of arthropod abundance with precipitation is more indicative of an actual response to it. A lag between precipitation and arthropod abundance is consistent with precipitation causing increased plant productivity that in turn allows greater consumer and predator abundance later in the season. A significant lagged cross-correlation with average maximum daily temperature, which shows much less interannual variation, is more likely to show the inherent seasonal phenology in the species.

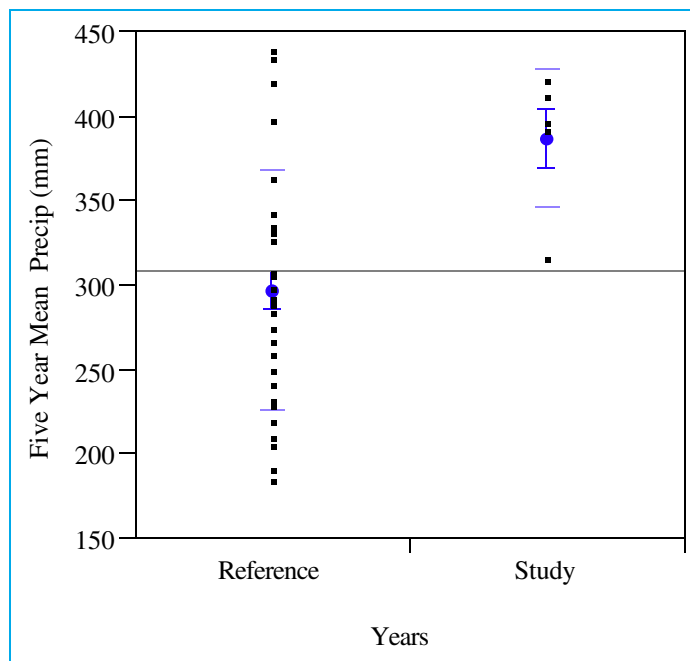
The precipitation time series was prepared by summing the precipitation during the period between each collection, usually 30 days, while the mean maximum daily temperature was calculated for the same period. A correlation coefficient ( $r$ ) for each species lagged from zero to six periods (months) after the climate variable and confidence intervals were calculated using the program Cross-Correlation (Holland 1999). The calculation assumes time series  $y_t^{(i)}$  and  $y_t^{(j)}$  represent arthropod species  $i$  and weather parameter  $j$ . The sample lag- $k$  cross-correlation coefficient is (Salas 1993):

$$r_k^{ij} = \frac{c_k^{ij}}{(c_0^i c_0^j)^{1/2}}, \text{ where}$$

$$c_k^{ij} = \left( \frac{1}{N} \right) \sum_{t=1}^{N-k} (y_{t+k}^{(i)} - \bar{y}^{(i)}) (y_t^{(j)} - \bar{y}^{(j)}) \text{ and } k \geq 0.$$

Confidence levels for  $r$  values were calculated in Cross-Correlation using a Monte Carlo method with  $10^6$  permutations. A logistic model regression was used to evaluate the effect of species abundance on the presence of a significant cross-correlation.

This method has an inherent difficulty in that it assumes that sample periods are equal. Although trapping was scheduled for monthly intervals, weather conditions and other unforeseen factors throughout the study period resulted in an average collection interval of  $32.37 \pm 12.32$  S.D. days. The large standard deviation results from one lapse in collecting from late October 1994 to February 1995. However, because traps continue to be operational during periods of non-collection the data were kept for analysis. This lapse does complicate the monthly averages because all specimens collected during this period were reported as February collections. However, given that these results were then averaged to yield monthly incidence, the resulting effect is small.

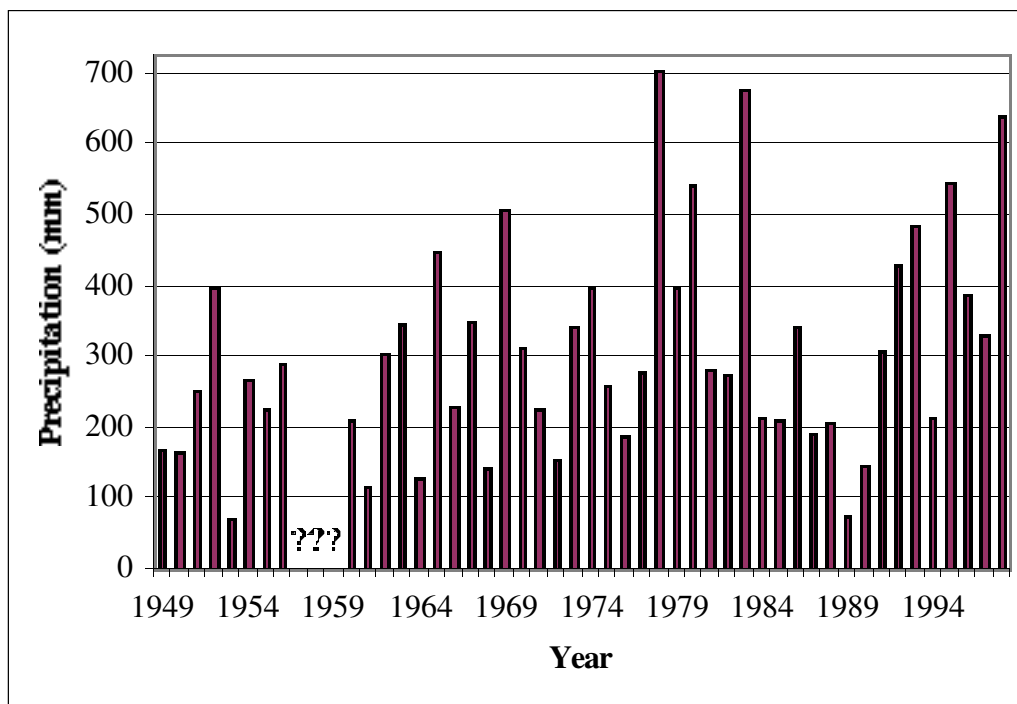


**Figure 3. Mean trailing five-year precipitation during reference period, 1949–1993, and study period, 1994–1998. Squares indicate the mean precipitation for the five years ending in each year of the study and reference periods. Dots indicate mean for each period with vertical standard error bars. Outer bars indicate standard deviation. The light horizontal line is mean trailing five-year precipitation for all years.**

## Results

### *Climate*

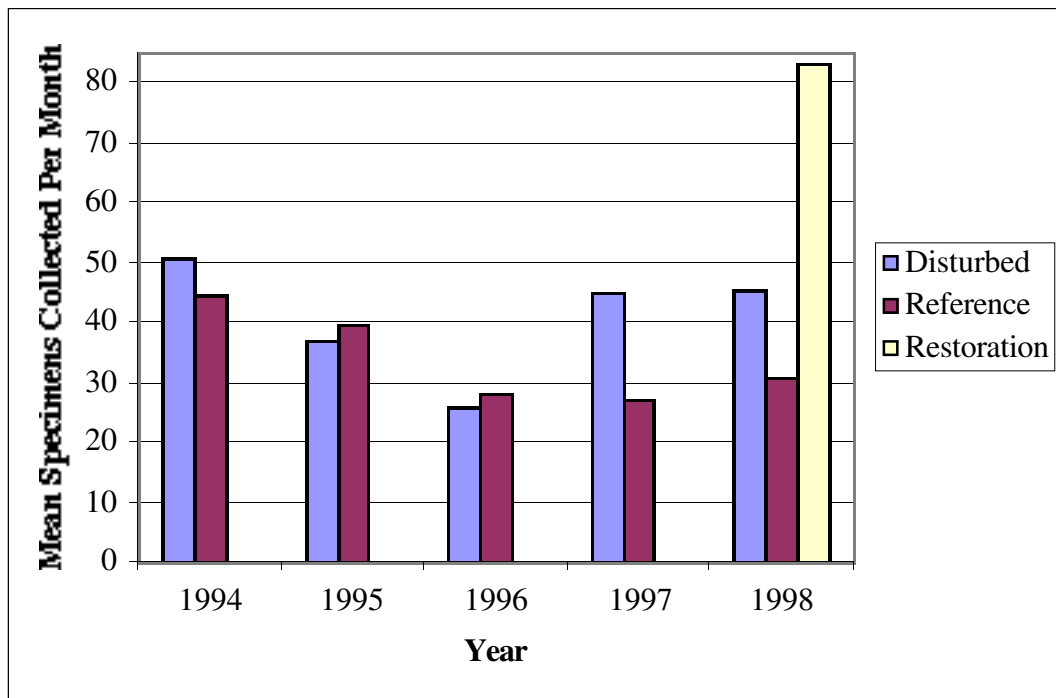
Mean trailing five-year precipitation for the five years of the study period was wetter than 34 previous five-year periods (Student's  $t$ ;  $p < 0.01$ ,  $387.95 \pm 41.82$  s.d. vs.  $297.75 \pm 71.45$  s.d. mm) (Figure 3). Indeed, the trailing five-year mean for the entire study period was greater than the mean of the entire recorded period. However, the study period was within the range of conditions in the reference period (185.72–440.44 mm) (Figure 4). The study period included the 1997–1998 El Niño/Southern Oscillation event.



**Figure 4. Yearly precipitation (mm) for Long Beach, 1949–1998. Data missing for 1957–1959.**

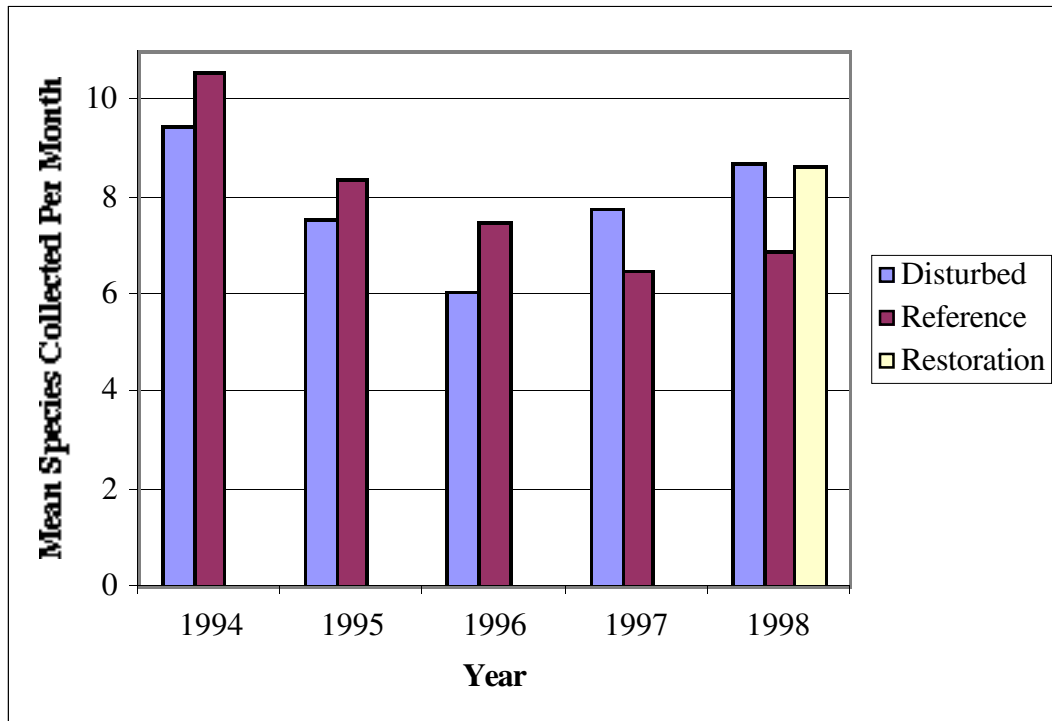
### *Arthropod Composition and Variability*

During the period 1994–1998, 1,293 successful trap collections were made (Table 1; page 23). The collections included 58,879 specimens of 206 morphospecies in 92 families representing 27 orders (Table 3; page 54). The mean number of specimens per month varied between years according to several factors (Figure 5). The increase in mean specimens per month in 1997 for disturbed sites resulted from the addition of DFSP-South End, which yielded many ants, to the trapping network. The high number of specimens per month at restoration sites resulted from abundant exotic species. Changes in the number of species per month similarly changed from year to year (Figure 6).



**Figure 5. Mean specimens collected per month at reference, disturbed, and restoration sites.**

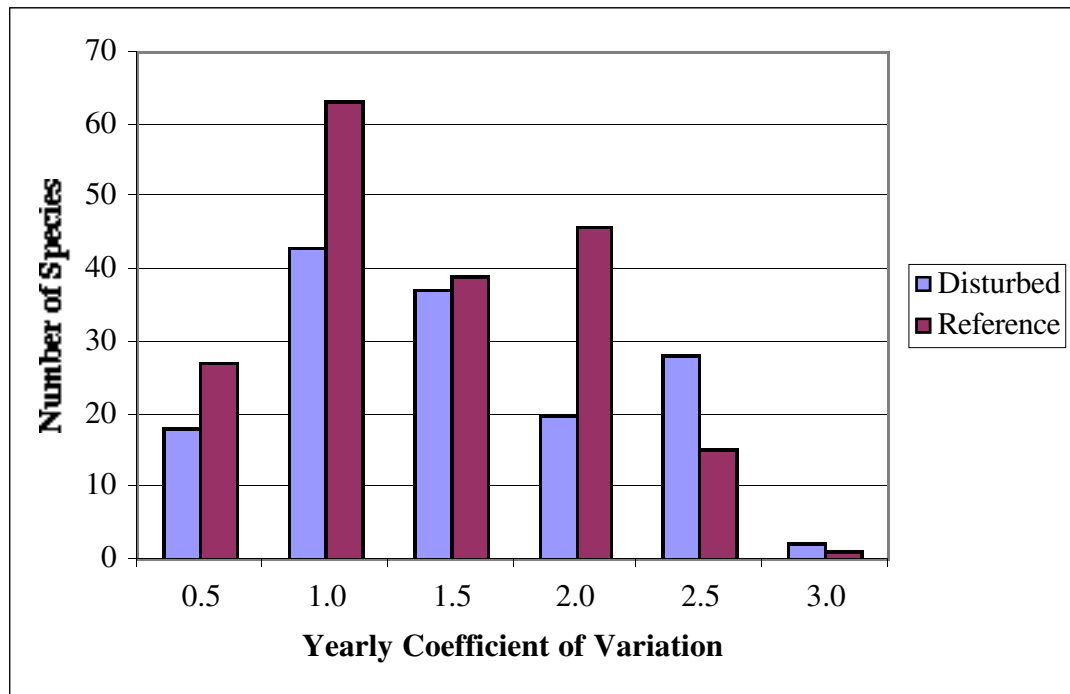




**Figure 6. Mean species collected per month at reference, disturbed, and restoration sites.**

### ***Yearly Variation in Arthropod Abundance and Richness***

Mean yearly catch and coefficient of variation for arthropod morphospecies and families are reported in Table 3 (page 54). The coefficient of variation for yearly population size at reference sites ranges from 0.18 to over 3.00 (mean= $1.24 \pm 0.63$ ) (Figure 7). Coefficients of variation for species at disturbed sites were slightly higher (mean= $1.31 \pm 0.68$ ) but not significantly different. While results are provided for all species recorded, estimates for yearly variation for species with fewer than 0.1 individuals per trap per month should be treated with caution. The two lowest coefficients of variation at reference localities were exotic species, *Forficula auricularia* (CV=0.19, N=3,158) and *Linepithema humile* (CV=0.24, N=11,759).



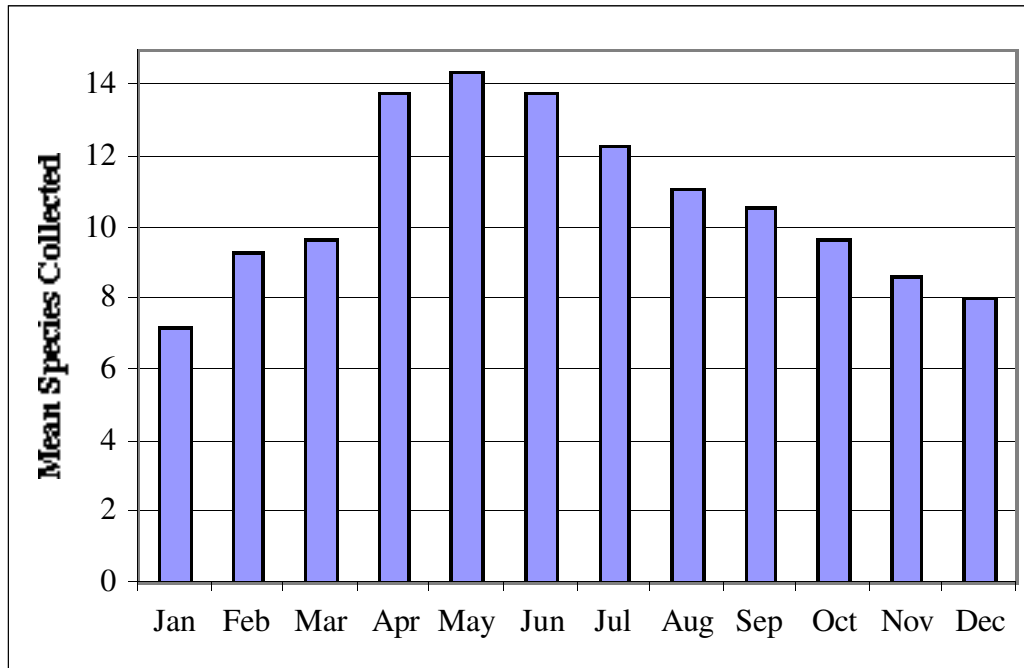
**Figure 7. Histogram of yearly coefficient of variation of arthropod species at reference sites (top) and disturbed sites (bottom).**

Several species and families had significantly different abundances between reference and disturbed sites over all five years combined (Table 2). These species and families may be good indicators of native habitats. For example, even given yearly variations, reference sites have significantly more scorpions, mostly *Paruroctonus sylvestrii* ( $p < 0.01$ ), and significantly fewer Solpugids, *Eremobates* sp. ( $p < 0.01$ ). *Eremobates* are a recorded prey species of *Paruroctonus* (Polis and Sissom 1990). Other indicator species and groups that are significantly ( $p < 0.01$ ) different between disturbed and undisturbed sites include staphylinid beetles, the tenebrionid beetle *Nyctoporis carinata*, the exotic earwig *Forficula auricularia*, and sand roaches (*Arenivaga* sp.) (Table 2). For these species and families, the differences between reference and disturbed sites are sufficient to outweigh yearly variation. By contrast, other species consistently have greater numbers in one habitat

type each year but the large yearly variation obscures the difference when considering the average over the five-year period.

**Table 2. Species and families with significant differences between reference and disturbed sites for all years. Values are mean yearly abundance  $\pm$  standard deviation, coefficient of variation. Probability values indicated as \*\*= $p < 0.05$ , \*\*\*= $p < 0.01$ , and \*\*\*\*= $p < 0.001$ .**

Taxon	N	Reference	<i>p</i>	Disturbed	Restored
<b>Ctenizidae</b>					
(Ctenizidae) sp. 1	62	0.063 $\pm$ 0.042, 0.67	**	0.002 $\pm$ 0.006, 3.00	0
<b>Pholcidae</b>					
(Pholcidae) sp. 1**	95	0.016 $\pm$ 0.008, 2.00	**	0.152 $\pm$ 0.091, 0.60	0.037
<b>Vejovidae</b>	<b>264</b>	<b>0.281<math>\pm</math>0.134, 0.48</b>	<b>***</b>	<b>0.052<math>\pm</math>0.054, 1.04</b>	<b>0.044</b>
<i>Paruroctonus silvestrii</i>	240	0.256 $\pm$ 0.124, 0.48	***	0.049 $\pm$ 0.048, 0.97	0.044
<b>Solfugae</b>					
<i>Eremobates</i> sp. 1	227	0.090 $\pm$ 0.035, 0.39	***	0.232 $\pm$ 0.074, 0.32	0.205
<b>Scolopendridae</b>					
<i>Scolopendra</i> sp. 1	45	0.012 $\pm$ 0.007, 0.58	***	0.047 $\pm$ 0.032, 0.68	0.066
<b>Entomobryidae</b>					
(Entomobryidae) sp. 1	1580	0.341 $\pm$ 0.247, 0.72	**	1.919 $\pm$ 1.407, 0.73	2.176
<b>Curculionidae</b>					
<i>Trigonoscuta</i> sp. 1	43	0.040 $\pm$ 0.023, 0.58	**	0.007 $\pm$ 0.011, 1.57	0
<b>Ptinidae</b>					
<i>Ptinus fur</i>	129	0.100 $\pm$ 0.082, 0.82	**	0.013 $\pm$ 0.016, 1.23	0.176
<b>Staphylinidae</b>	<b>1114</b>	<b>1.165<math>\pm</math>0.472, 0.41</b>	<b>***</b>	<b>0.202<math>\pm</math>0.040, 0.20</b>	<b>0.110</b>
<b>Tenebrionidae</b>					
<i>Coniontis</i> sp. 1	191	0.041 $\pm$ 0.015, 0.37	**	0.322 $\pm$ 0.228, 0.71	0.066
<i>Cratidus osculans</i>	1635	0.676 $\pm$ 0.390, 0.58	**	2.136 $\pm$ 0.934, 0.44	0.728
<i>Nyctoporis carinata</i>	1594	1.585 $\pm$ 0.508, 0.32	***	0.096 $\pm$ 0.030, 0.31	0.904
<b>Forficulidae</b>					
<i>Forficula auricularia</i>	3158	1.102 $\pm$ 0.208, 0.19	***	3.169 $\pm$ 0.639, 0.20	5.154
<b>Polyphagidae</b>					
<i>Arenivaga</i> sp. 1	391	0.367 $\pm$ 0.066, 0.18	***	0.096 $\pm$ 0.039, 0.40	0.044
<b>Anthomyiidae</b>					
(Anthomyiidae) sp. 1	148	0.014 $\pm$ 0.010, 0.71	**	0.265 $\pm$ 0.216, 0.82	0
<b>Tachinidae</b>					
<i>Archytas</i> sp. 1	7	0	**	0.017 $\pm$ 0.013, 0.76	0
<b>Reduviidae</b>					
(Reduviidae) sp. 2	43	0.044 $\pm$ 0.028, 0.64	**	0.011 $\pm$ 0.011, 1.00	0
<b>Formicidae</b>					
<i>Pheidole</i> sp. 1	170	0.009 $\pm$ 0.009, 1.00	***	0.195 $\pm$ 0.169, 0.87	0.485
<b>Gryllacrididae</b>					
<i>Stenopelmatus</i> sp. 1	569	0.489 $\pm$ 0.146, 0.30	**	0.256 $\pm$ 0.103, 0.40	0.154
<b>Gryllidae</b>	<b>201</b>	<b>0.190<math>\pm</math>0.062, 0.32</b>	<b>****</b>	<b>0.034<math>\pm</math>0.018, 0.53</b>	<b>0.063</b>
<i>Hoplosphyrum boreale</i>	179	0.177 $\pm$ 0.064, 0.36	****	0.019 $\pm$ 0.019, 1.00	0.051



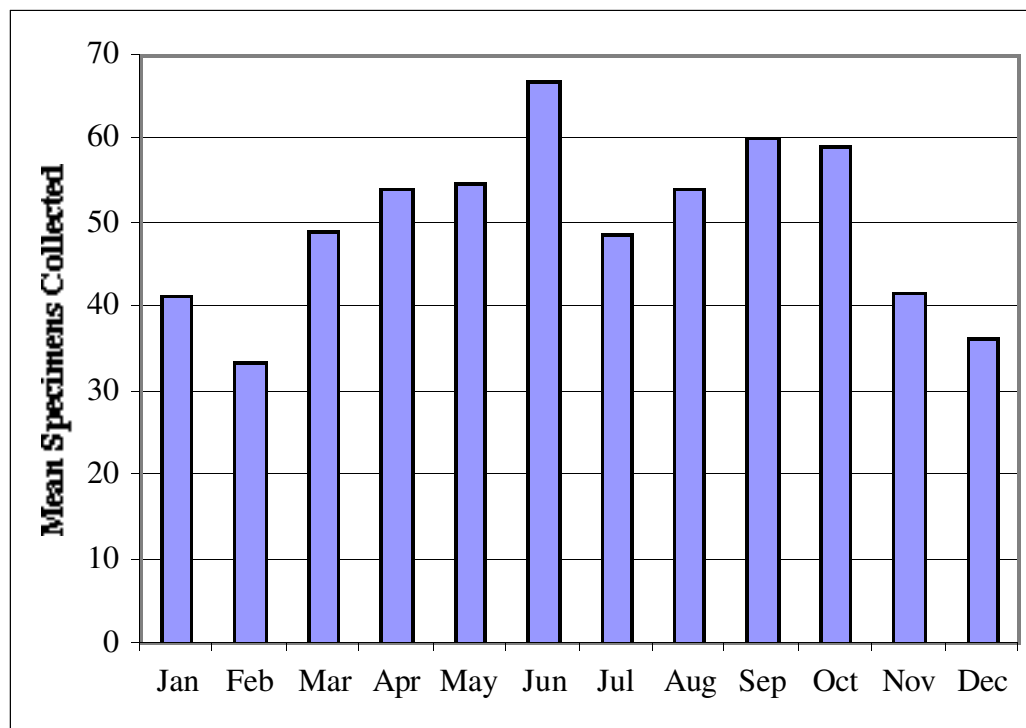
**Figure 8. Mean species captured per month, 1994–1998 at Portuguese Canyon.**

### ***Seasonal Variation of Arthropod Abundance and Richness***

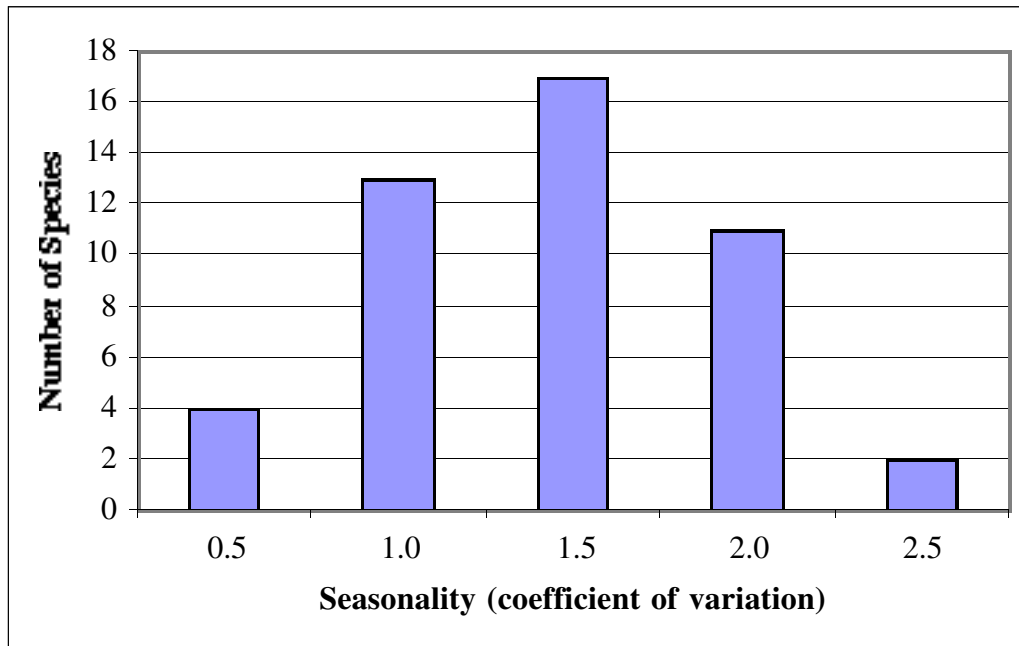
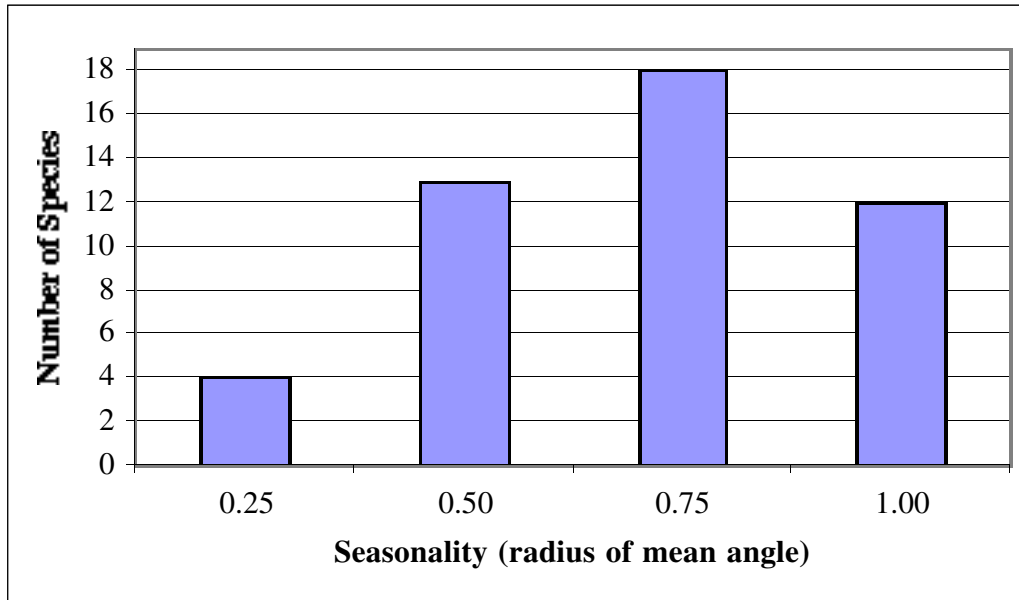
Species richness of monthly collections was highest during the spring (April, May, and June), decreasing through the summer and falling to a minimum in January, after which diversity increased during February and March before a significant jump to spring levels (Figure 8). Specimens per month showed a similar pattern, but with an additional peak in the late summer (Figure 9).

The monthly mean number of each morphospecies is given in Table 4. The monthly mean abundance simultaneously illustrates seasonality and relative commonness of each species across the study area. Seasonality, as quantified by the coefficient of variation of monthly abundance, was high (greater than one) for most species (155 of 183) (Figure 10). Rare species (monthly mean abundance less than 0.01) have high coefficients of variation because of their rarity.

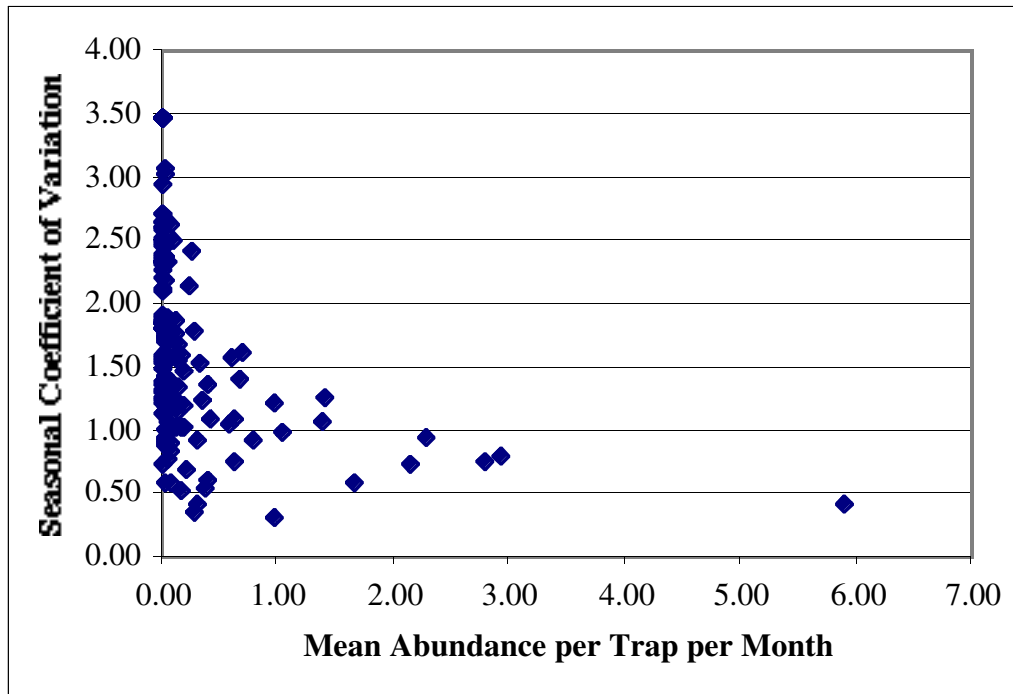
However, no significant relationship was detected between abundance and seasonality (Figure 11). When rare species are excluded, native species had a mean seasonal coefficient of variation twice as large as exotic species ( $p < 0.004$ ;  $1.23 \pm 0.46$  vs.  $0.64 \pm 0.28$ ). The significant difference remains with rare species included ( $p < 0.05$ ;  $1.36 \pm 0.42$  vs.  $0.92 \pm 0.79$ ). These patterns are similar for seasonality as measured as the radius of the mean angle using circular statistics (Figure 10).



**Figure 9. Mean specimens collected per month, 1994–1998 at Portuguese Canyon.**



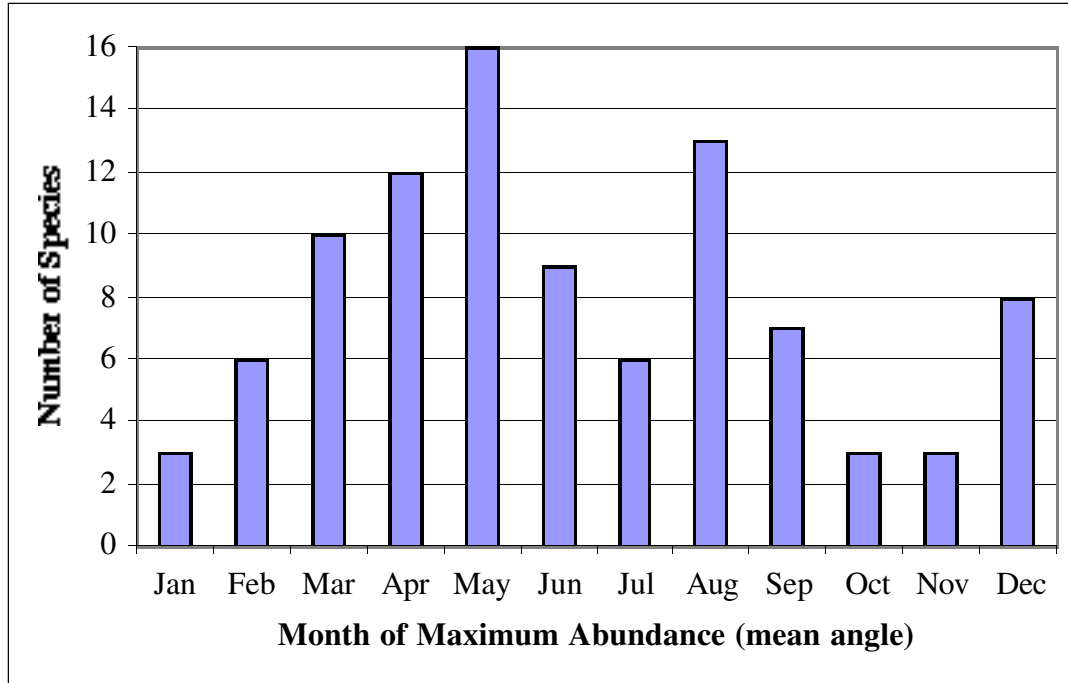
**Figure 10. Histogram of two measures of seasonality (radius of mean angle and coefficient of variation). Includes only species with mean monthly abundance greater than 0.1 (N=47).**



**Figure 11. Relationship between abundance and seasonal coefficient of variation.**

Species showed seasonal maxima in abundance throughout the year as indicated by the mean angle (Figure 12). The month with the most species maxima was May, followed by August, then April, March, and June. The six most common species illustrate typical seasonal patterns (Figure 13). The three most common exotic species (*Forficula auricularia*, *Armadillidium vulgare*, and *Linepithema humile*) have mean maximum abundances in March (radius=0.45), May (radius =0.48), and August (radius = 0.25), respectively. The native beetle *Calathus ruficollis* has a mean maximum abundance in December ( $r=0.45$ ) while another beetle *Eleodes laticollis* has its mean maximum abundance in August ( $r=0.32$ ) Bristletails (Machilidae) have a mean maximum abundance in August with higher seasonality ( $r=0.62$ ). The late summer maxima of such abundant species as

bristletails, *Linepithema humile* and *Eleodes laticollis* explain the increase in specimens during this season (Figure 5).

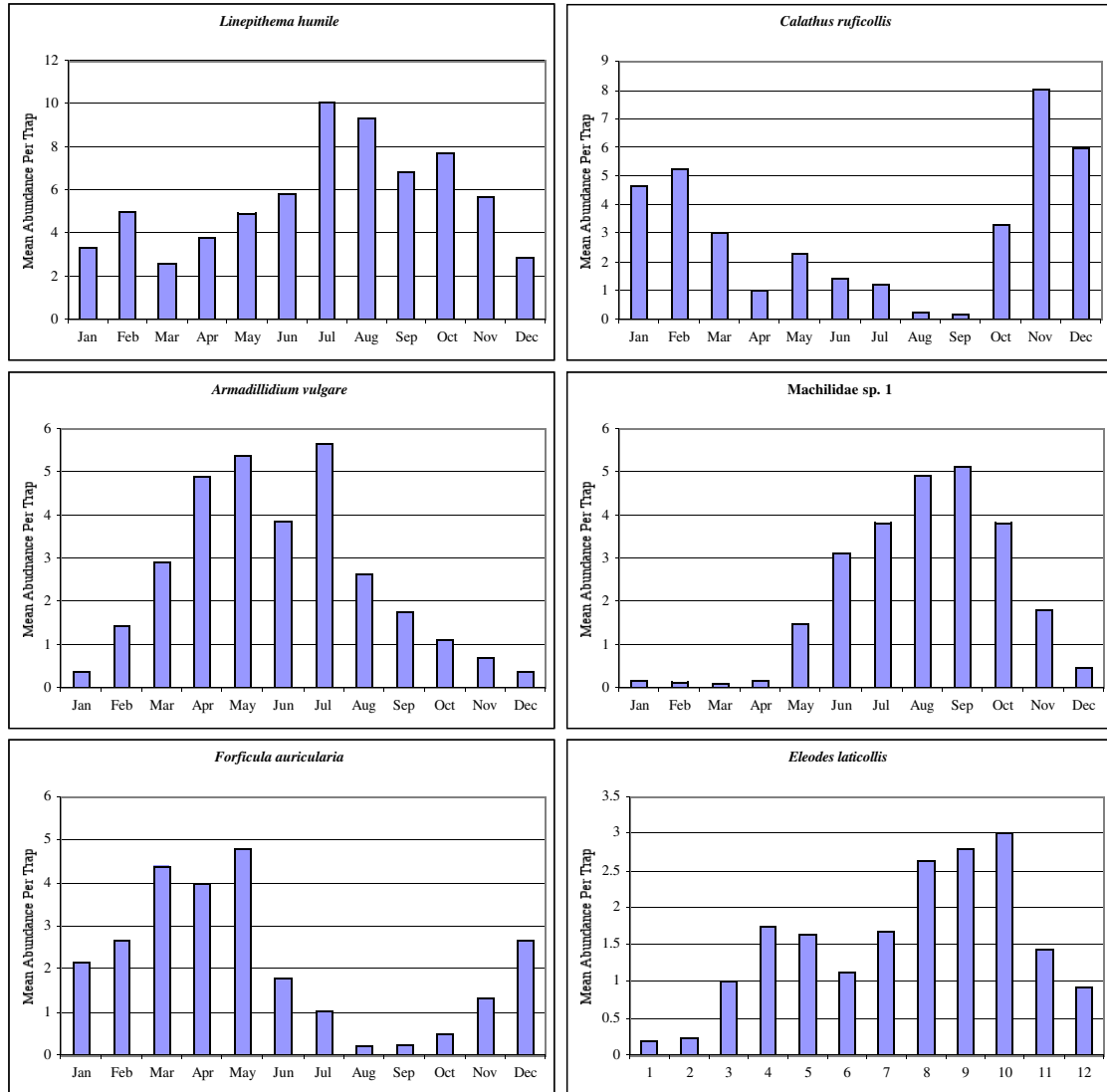


**Figure 12. Histogram of month of maximum abundance of arthropod species.**

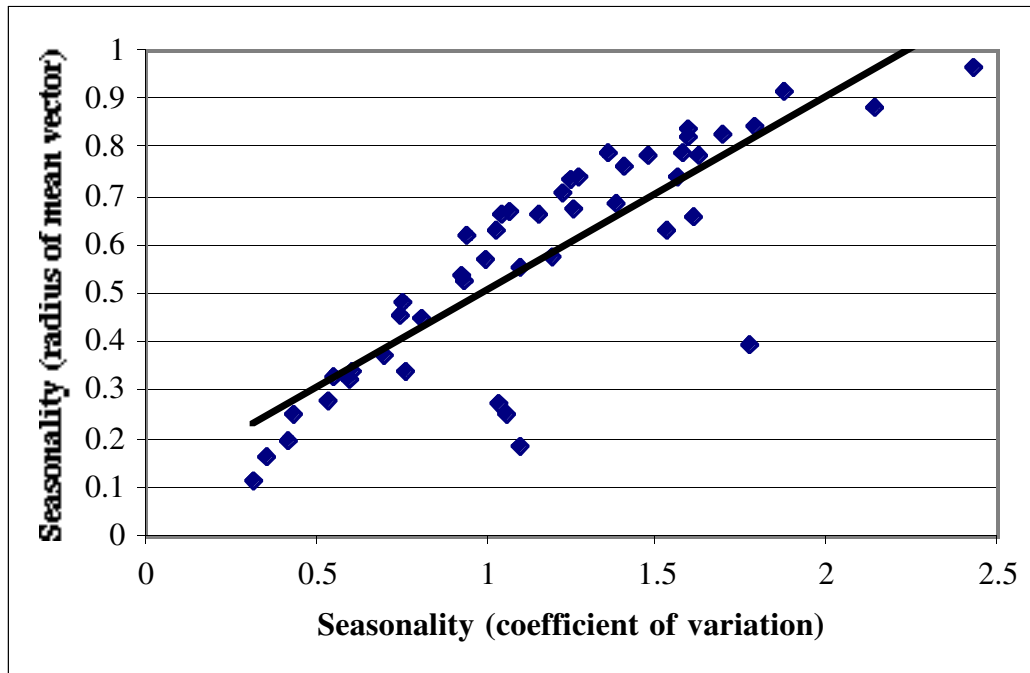
Species with a bimodal seasonal distribution were detected by correlating the seasonal coefficient of variation with seasonality measured using circular statistics ( $r$ ). Overall, the correlation was high, with both measures showing similar seasonality. However, a high seasonal coefficient of variation but a relatively low  $r$  indicated a bimodal or seasonal abundance pattern. Using the 47 species with mean monthly abundance greater than 0.1, only four showed this difference between the two measures of seasonality: two tenebrionid beetles *Eleodes gracilis* and *Eleodes* sp. 2, the native ant *Camponotus* sp., and a wolf spider Lycosidae sp. 1 (Figure 14). Difficulties distinguishing among tenebrionid beetles likely accounted for the seasonal distribution of the *Eleodes* species (see below and Figure 17). None of



these bimodal distributions exhibits a smooth rise to each peak, suggesting that a factor other than a natural population increase accounts for the patterns.



**Figure 13. Monthly abundance of the six most common arthropod species in the study.**

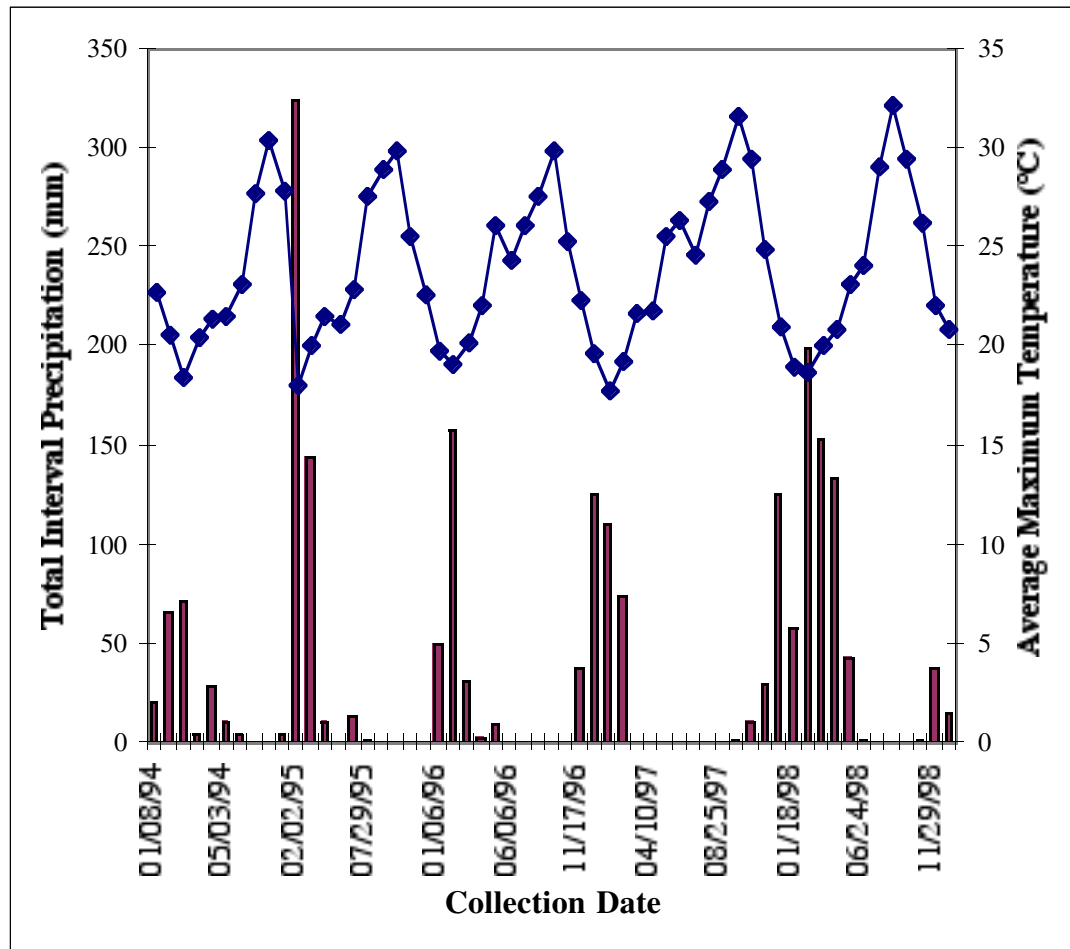


**Figure 14. Relationship between seasonal coefficient of variation and  $r$ . Includes 47 species with mean monthly abundance greater than 0.1.**

### ***Cross-Correlation of Arthropod Abundance with Climate***

Abundances of 50 out of 172 morphospecies at reference sites had significant cross-correlation with precipitation and maximum daily temperature (Figure 15; Table 3). Whether or not a species showed significant cross-correlation was closely related to the number of individuals collected. Abundance predicted the presence of a significant relationship in a simple logistic regression ( $p < 0.0001$ ,  $r^2 = 0.55$ ). No species with mean monthly per trap abundance less than 0.014 had a significant correlation and all species with abundance greater than 0.208 showed a significant correlation. However, for species with a significant correlation, abundance had no significant relationship with the strength of the correlation.

Cross-correlation values with precipitation was largely positive (38 positive vs. 12 negative), while cross-correlation with temperature was evenly split (26 negative vs. 24 positive) (Figure 16). The mean lag of the maximum cross-correlation from precipitation ( $2.8 \pm 2.1$  months) was slightly greater than for temperature ( $3.2 \pm 1.8$  months) ( $p < 0.07$ ).



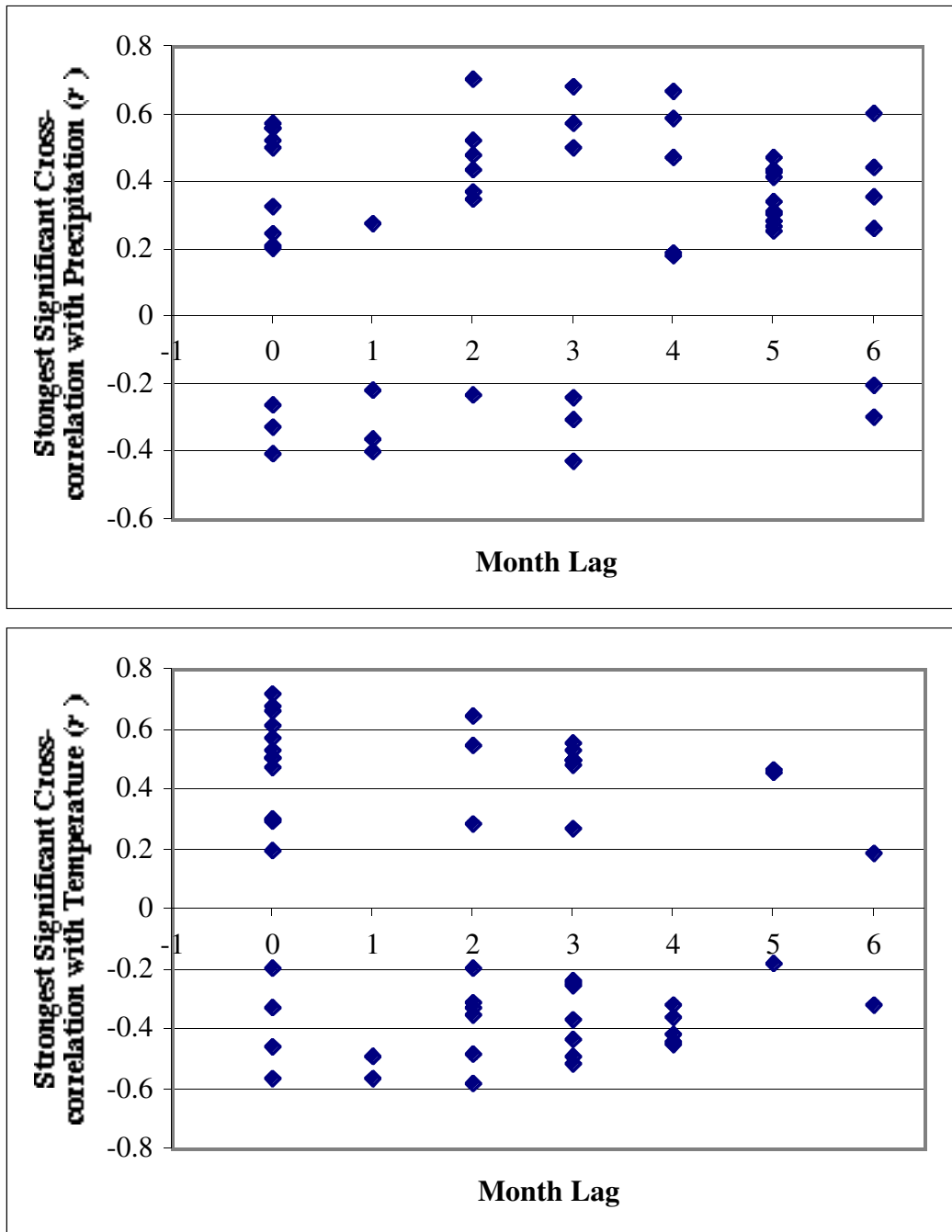
**Figure 15. Precipitation (bars) and maximum temperature (connected points) for the study period, 1994–1998. For each collection date, the total precipitation and average maximum temperature since the previous collection is given. The mean time between collections was 32 days. These two time series are used in the cross-correlation analysis.**

Cross-correlation between temperature and precipitation records was -0.617 with no lag ( $p < 0.001$ ). Because precipitation varies inversely with mean daily maximum temperature, many species correlated significantly with both precipitation and temperature records, either with opposite signs at the same lag or with the same sign with a six-month difference in lag. Many species showed a significant cross-correlation at more than one lag. In such instances, the highest correlation value is reported.

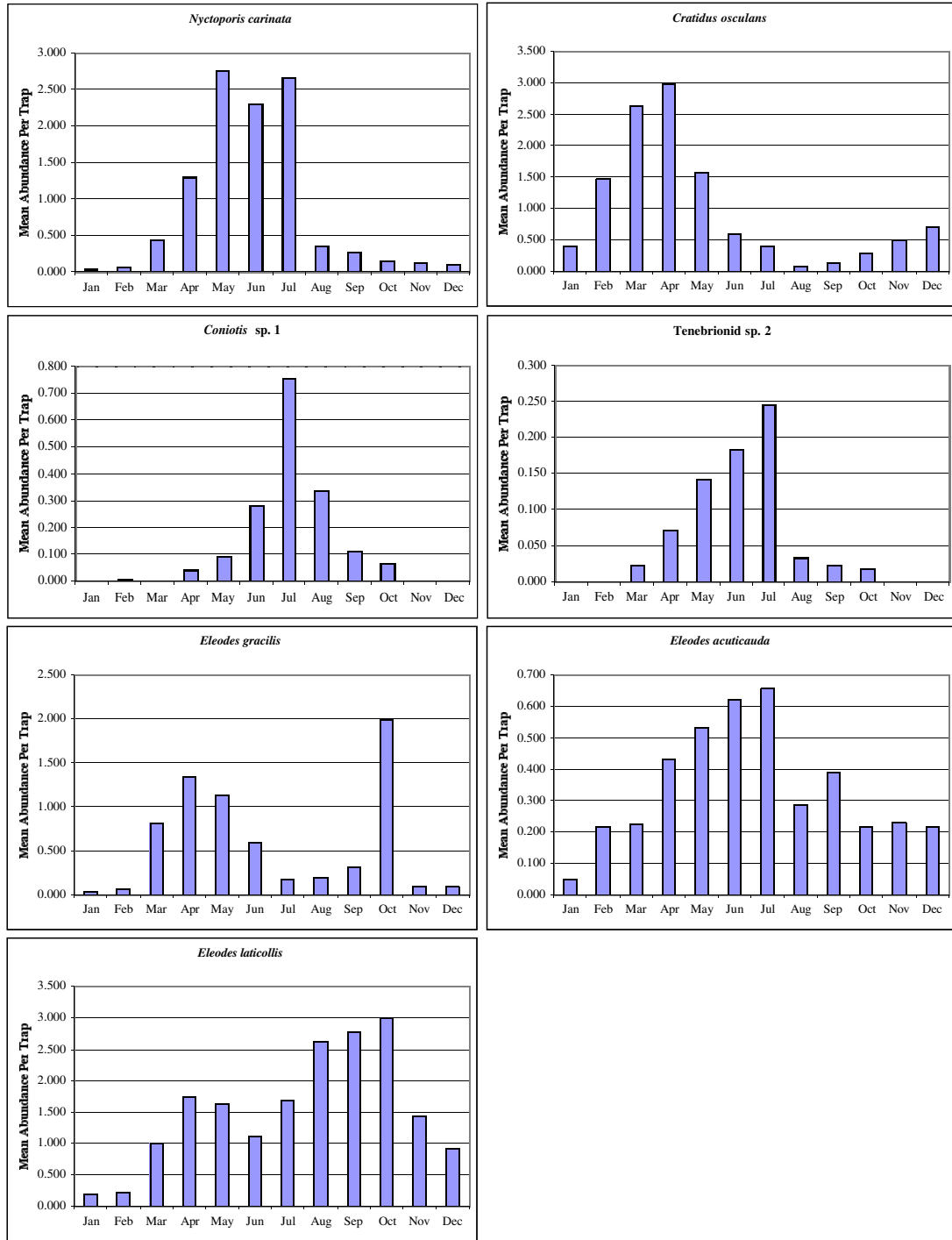
Most species that had significant cross-correlations were correlated with both climate parameters. The highest cross-correlation  $r$ -values were 0.717 for bristletails with temperature (no lag) and 0.703 for the tenebrionid beetle *Cratidus osculans* with precipitation (2-month lag).

Within families, there was little constancy among species and their relationship with climate variables. For example, the seven tenebrionid beetles with significant seasonal variation show maximum relationships with precipitation at 0, 2, 4, 5, and 6 month lags and with temperature at 0, 1, 3, and 4 month lags (see Figure 17).

The double maxima shown in *Eleodes gracilis* and *Eleodes laticollis* illustrate the difficulties of sorting thousands of specimens. The October spike in *Eleodes gracilis* numbers are likely misclassified *Eleodes laticollis*, while the March-May increase in *Eleodes laticollis* numbers is likely due to misclassification as well. These two species are extremely similar, varying only in width of the pronotum and slightly in the shape of the elytra. It is possible that other pairs of species were misclassified, but few other species in the study are as similar as these two.



**Figure 16. Lag and strength of strongest significant cross-correlations of arthropod abundance with climate.**



**Figure 17. Monthly mean catch of individuals per trap for seven tenebrionid beetle species.**

## Discussion

This chapter documents the composition and variation of terrestrial arthropods in coastal sage scrub as sampled by pitfall trapping. The data illustrate the close relationship between weather and arthropod abundance and show the year-round character of arthropod phenology in a Mediterranean climate. The ability to define a complete season is much more difficult for a Mediterranean climate than for climates with freezing winter temperatures or warm climates with constant precipitation.

The overlapping temporal distribution of arthropod species throughout the year present a much more complicated situation than do studies of arthropod seasonality that are limited to a short active season (Stapp 1997). Several characteristics of seasonality can be observed from the data. First, seasonality can differ considerably within families, perhaps indicating a seasonal partitioning of resources resulting from competition. These differences can serve to reinforce identifications of morphospecies. For example, the first two anthomiid fly morphospecies have different phenologies, one having maximum abundance during winter months, the other during the summer.

Second, yearly variation in morphospecies abundance as expressed by coefficient of variation was more variable and generally higher than those values expressed elsewhere in the literature. Gibbs *et al.* (1998) report a coefficient of variation for beetles of 0.58 with a minimum of 0.03 and a maximum of 1.48. The most reliable estimates from the present study are those with significant cross-correlation with environmental parameters. These species are sufficiently common to allow confidence in description of seasonal patterns of their abundance and a

considerable portion of the between-year variation can be explained. For these 15 beetle species, coefficients of variation for reference sites range from 0.32 to 1.97 with a mean of  $0.80 \pm 0.44$  s.d. This level of variation within a taxonomic unit is common in the results, suggesting that combined estimates of population variability where many species are lumped together are not appropriate and could lead to significant misapplication of resources if applied in power analysis for experimental design.

The large yearly variation in arthropod abundance reinforces the need to compare the same year's data when evaluating arthropod community structure, guild composition, or other measurements that involve comparison of abundances. As discussed above, only a few species transcend yearly variation to be consistent indicators of disturbed and reference conditions. However, within a given year, many more species show significant differences between reference and disturbed sites. Because of the close correlation of many species with weather, and the high variability of weather in a Mediterranean climate, all between-site arthropod comparisons must be made with data from the same year. In addition, multiple comparison sites are advisable, given the high within-year spatial variability in weather.

The strong relationship exhibited between weather and arthropod abundance does have difficulties. It is possible that, rather than seasonal variation in abundance, the results reflect either seasonal changes in species activity or changes in the trapping efficiency resulting from seasonal conditions. Certain features of the data argue against such an interpretation. Several species show a delayed reaction to precipitation, their numbers increasing in the summer proportionally to precipitation



the previous winter (*e.g.*, *Cratidus osculans*). If the number trapped resulted from changes in species activity responding to current conditions, there would be no explanation for the strong ( $r=0.703$ ) relationship with previous precipitation conditions. Another feature is that ecologically similar species (*e.g.*, tenebrionid beetles) exhibit distinctly different seasonal variation. While the possibility of differential trapping rates based on behavior or seasonal trap efficiency remains, the clear difference in patterns among such similar species seems unlikely to be an artifact of trapping methodology.

The randomness of sampling and correlation to absolute densities of specific taxa obtained by pitfall trapping has been questioned (Southwood 1966; Baars 1979; Spence and Niemalä 1994). However, Baars (1979) presented evidence that pitfall trapping provided an accurate estimate of population size for carabid beetles and the method enjoys widespread usage (Greenslade 1964; Baars 1979; Niemelä *et al.* 1993; Margules *et al.* 1994; Spence and Niemalä 1994; Rykken *et al.* 1997; Stapp 1997; Holway 1998a; Kennedy 1998).

Patterns of seasonal and yearly variation can be compared with abiotic conditions for those species for which they are known. I consider here several species because of their importance as ecologically disruptive invaders. Argentine ants, *Linepithema humile*, have been subject to considerable study to establish the abiotic conditions that promote its invasion. Human *et al.* (1998) report that Argentine ants are significantly positively correlated with high soil and air temperature and remain active up to 45°C. The result of the present study, that Argentine ant abundance on a seasonal scale is significantly correlated with maximum daily temperature ( $r=0.509$ ,  $p<0.001$ ), is consistent with this finding.

However, Argentine ants are not tolerant of high temperatures and are restricted to habitats with relatively cool and moist conditions (Holway 1998b). Therefore, the rate of invasion of Argentine ants has been found to be significantly related to high soil moisture, which Holway (1998b) modeled using stream flow as a surrogate variable. While the present study does not dispute these results — all of the sites were occupied by Argentine ants and thus the basic abiotic conditions must have been met — the presumed corollary that increased rainfall results in even more Argentine ants in previously occupied areas was not shown. At least for the localities in this study, yearly precipitation was not positively correlated with Argentine ant abundance.

Other abundant exotic species besides Argentine ants were more strongly related to temperature than to precipitation (*Dysdera crocata*, no lag,  $r=-0.460$ ,  $p<0.001$ ; *Forficula auricularia*, 1 month lag,  $r=-0.562$ ,  $p<0.001$ ; *Armadillidium vulgare*, 3 month lag,  $r=-0.488$ ,  $p<0.001$ ). Weather is an important mechanism in regulating *Armadillidium vulgare*; isopods are susceptible to death by both desiccation and drowning (Paris and Pitelka 1962; Paris 1963). In addition, their breeding period is determined by day length (Souty-Grosset *et al.* 1994), extending from March through June in California (Paris and Pitelka 1962). The observed seasonal pattern of abundance with a minimum during the winter months, and increasing through May, June, and July is consistent with both the species' known phenology and physical tolerances. Behavior may also influence seasonal patterns in trapped abundance as the species moves farther into the ground in response to dryness in the summer (Paris 1963), making it less likely to be captured in surface traps. Depressed numbers during the winter months is also consistent with Hassall

and Dangerfield's (1997) finding that density was negatively correlated with rainfall. The species' Mediterranean origin made it well adapted to invasion into California (Souty-Grosset *et al.* 1998).

The presence of *Armadillidium* and *Porcellio* in such abundance in California grasslands is a matter of some import. Paris speculated that the rapid colonization of California was evidence of ample food available and the exploitation of a niche (consumer of dead, decaying herbaceous vegetation) "less efficiently used by previous occupants" (Paris 1963). By the time the species invaded in 1926, California landscapes already had been transformed thoroughly by introduced grasses and widespread ranching and agriculture (Huenneke and Mooney 1989). It is therefore difficult to conclude whether the success of *Armadillidium* resulted from a naturally occurring "empty niche" or whether that niche was created through human action by the increase in yearly decaying biomass from Mediterranean grasses (Jackson *et al.* 1988).

*Forficula auricularia* populations fluctuate diurnally in an inverse relationship with maximum temperature (Chant and McLeod 1952). The results here confirm this pattern on a seasonal scale, with a negative correlation with maximum daily temperature, lagged one month. The species mates frequently and at any time of the year (Fulton 1924; Langston and Powell 1975). Earwigs are at their maximum abundance during the early spring, coinciding with the period of maximum overall species richness. Because their diet includes plants and living and dead insects (Langston and Powell 1975), it is possible that earwigs are responsible for decreases in native arthropod abundance through exploitation and interference competition as

well as predation. The role of this species and other exotic species in affecting native arthropod abundance will be discussed further in the following chapter.

## **Summary**

Arthropod communities in coastal sage scrub exhibit significant year-to-year and seasonal (within year) variation. Weather conditions are significantly correlated with seasonal patterns in arthropod incidence and abundance, with many species responding positively with a lag to precipitation. Abundance of native arthropods is highly variable between years, while exotic species in general exhibit lower annual variation. Yearly and seasonal abundance reveal the physiological preferences of species. Overall species abundance is greatest during the spring, but individual species may show maximum abundance during any season. Phenology and yearly variation are not consistent within families or orders.

For purposes of restoration assessment, arthropod communities must be compared between sites during the same year because of the large variation in abundance between years. Historical data are also useful to establish species incidence, but all comparisons that depend upon abundance should involve data from the same year. Furthermore, assessment should identify morphospecies, because species within the same taxonomic unit can respond differently to environmental parameters. Power analysis to design studies to detect long-term change in arthropod communities must take into account the differences in variability within orders and families or risk drastically over- or underestimated the power of an experimental design.