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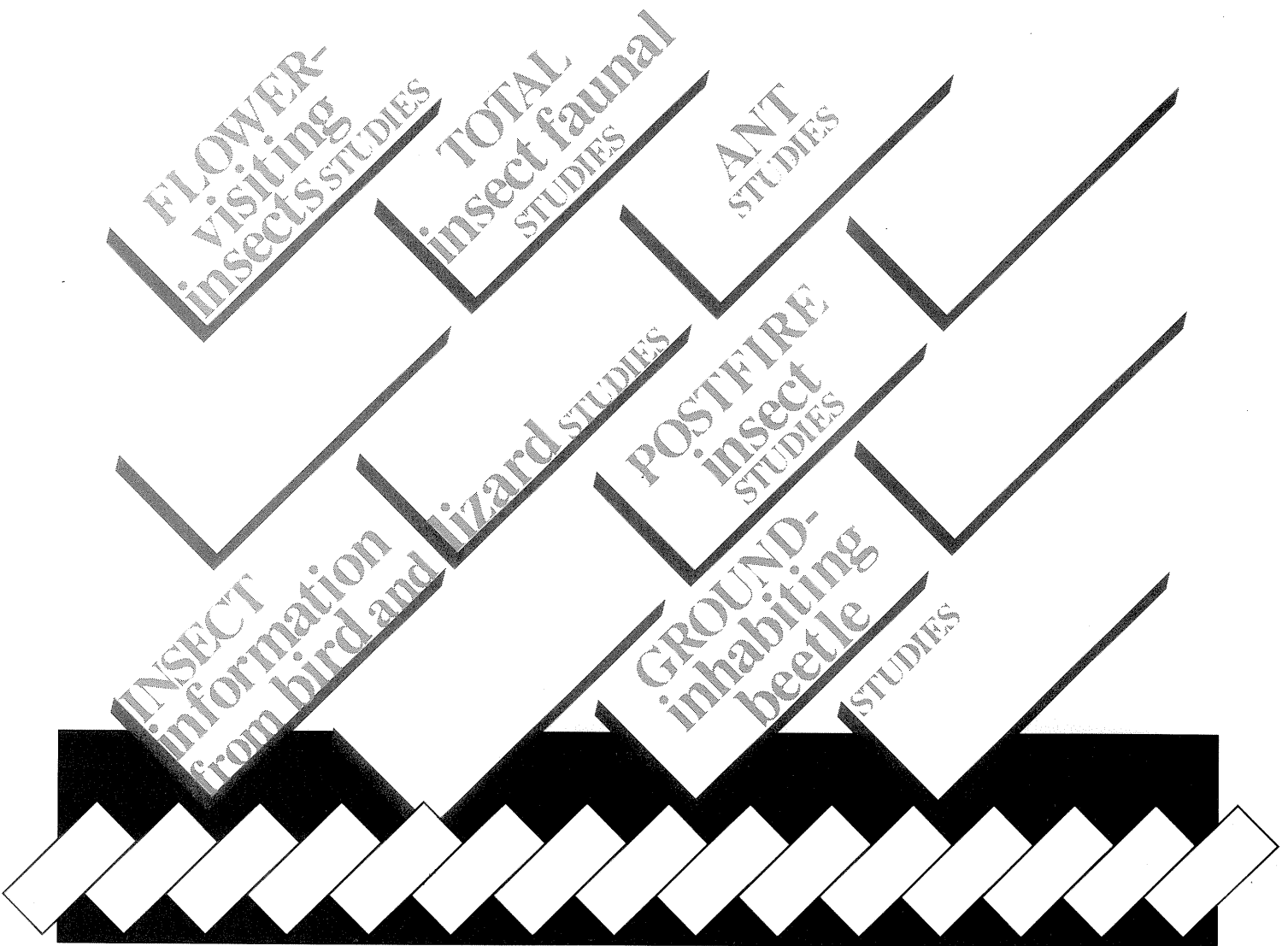
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Ecology of Insects in California Chaparral

Don C. Force



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Studies stimulated by the International Biological Program showed total insect faunal biomass and diversity to be greatest in the spring of the year, which matches increased plant growth and flowering at this time. Ground-inhabiting beetle studies indicated the family Tenebrionidae to be overwhelmingly dominant in biomass, but the family Staphylinidae to be richest in species numbers. Ant studies showed the chaparral community to be rich in ant species; seed gatherers were particularly important. Flower-visiting insects are more abundant and more species-rich in chaparral than in any other type of California vegetation. Bees especially are abundant and diversified and are responsible for most pollination. Postfire succession studies of insects indicate that the abundance of predators and flower visitors sharply increases following fire; parasitic and phytophagous insects (other than flower-visitors) increase more slowly. Insect herbivory appears to affect succession minimally.

Retrieval Terms: biomass, chaparral, diversity, ecology, insects, California

THE AUTHOR

DON C. FORCE is a professor of biological sciences at California State Polytechnic University, Pomona, California, and a Station cooperator. This paper was presented at the Symposium on the Classification and Distribution of California Chaparral Ecosystems, held in conjunction with the 60th Annual Meeting, Western Society of Naturalists, December 28, 1979, Pomona. It has since then been revised and updated.

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INTRODUCTION

Information on the interrelationships or dynamics among insects in the chaparral community is scant. Equally limited is published information on the biology of the chaparral insects. Hunt (1977) described the distribution of ants in Mediterranean scrub habitats in California and Chile, and reported a close resemblance between these insect communities. Information on insects associated with certain chaparral species is found in works by Essig (1958) and by Furniss and Barr (1975). By and large, however, entomologists have been preoccupied with describing and studying insects that enjoy a more economically important status. I know of no complete species list of insects found in the chaparral ecosystems of California.

Interest in chaparral insects from the standpoint of community ecology was stimulated by the International Biological Program (IBP) that was active from 1967 to 1974. In 1970, the U.S. National Science Foundation funded a Mediterranean Scrub Project that provided a comparative analysis of Chilean and California scrub vegetation and insects in these two communities (Mooney 1977, Thrower and Bradbury 1977).

This paper describes a small portion of the ecology of insects in chaparral ecosystems of California, and includes a review of earlier studies.

TOTAL INSECT FAUNAL STUDIES

Atkins (1977), Cody and others (1977) reported seasonal changes in biomass and diversity of chaparral insects in southern California (Echo Valley, San Diego County). Sampling of flying insects was accomplished with Malaise traps operating for 2- or 3-day periods every second week in representative chaparral vegetation, and with wet traps of fluid-filled plastic dishes placed in selected shrubs. None of the insects caught was identified beyond the family or subfamily level. For biomass data, the insects were oven-dried and the weights converted to 24-hour catch equivalents. As might be expected from plant seasonal and productivity data (Mooney and others 1977), the biomass of chaparral insects (for 1973) was greatest in the spring. The highest peak occurred at the end of March, after a very rapid increase from the lowest point in January. A secondary peak, much lower than the first, occurred in May, with an overall gradual decrease to the end of the year. This pattern was undoubtedly influenced greatly by the temperature and rainfall

pattern and the vegetational response to these factors. Naturally this productivity sequence of insects has a tremendous effect on vertebrate insectivores (e.g., Cody and others 1977).

Atkins (1977) also measured patterns of diversity using the Shannon-Wiener Index (Shannon and Weaver 1949) calculated from wet trap collections. This measure of diversity takes into account both the number of taxa and the relative abundance of each. Diversity for the total insect fauna (excluding bees, ants, and the parasitic Chalcidoidea wasps) in chaparral peaked in May (in 1973); its lowest point was in October. The diversities of three different trophic groups—herbivores (excluding flower visitors), predators and parasites (excluding Chalcidoidea), and scavengers—showed a bimodal tendency. Diversities tended to be greatest in April and May, with a second peak in August. The second peak was lower than the first in the herbivore and predator-parasite group, but higher in the scavenger group. Atkins then divided the herbivores into sap feeders and foliage feeders. Foliage feeders were more diverse for the first 6 months of the year, and sap feeders more diverse the remaining 6 months. His finding of greatest diversity occurring in April and May is certainly not unexpected. This is the season when most plant growth occurs along with a preponderance of flowering. Certainly these events would attract a great variety of plant feeders and pollinators. Predators and perhaps parasites would also be expected to take advantage of the increase in prey and hosts at this time. The secondary diversity peak of midsummer is more difficult to explain. Of course, these data are from a single year (1973) and could perhaps reflect some phenological occurrence of that particular year. The preceding winter (1972-73) was wet, but there was apparently no substantial midsummer rainfall that could have stimulated the activity of both plants and insects (Miller and others 1977).

Another possibility is that the elevated diversity index was caused not so much by a greater taxonomic richness (numbers of insect families), but instead by greater equality in numbers of individuals between each group. Atkins' finding of highest diversity in foliage feeders the first half of the year and sap feeders the second half correlates with resource availability. Foliage would naturally be more abundant and succulent during and immediately after the rainy season. Sap might be somewhat less available in the dry season than in the wet, but it would provide nutrition in addition to being a source of moisture when free water is scarce.

GROUND-INHABITING BEETLE STUDIES

Saiz (1977) made a 2-year study (1972-74) of the ground-inhabiting beetles of southern California chaparral (Echo Valley). His method of collecting was pit-fall trapping. He found the family Tenebrionidae was overwhelmingly dominant in biomass. About 90 percent of the biomass consisted of tenebrionid beetles whereas about 5 percent consisted of the family Carabidae. Other families comprised 1 percent each or less of the total biomass. Seasonally, the tenebrionids were most active from May to October, peaking in September. The carabid beetles in contrast, were most active from December to February. The taxonomic distribution of ground-inhabiting beetles differs strikingly from the biomass analysis. The Tenebrionidae represent only 13 species and the Carabidae only 2 species out of a total of 118. The family Staphylinidae dominates the species list with 29, but comprises only 1 percent of the total biomass. Thirty percent of the individuals trapped were Staphylinidae, 7 percent were Tenebrionidae, and 5 percent were Carabidae. This study of ground-inhabiting beetles in chaparral indicates considerable predation of small arthropods and other organisms by both Carabidae and Staphylinidae. The Tenebrionidae are probably mostly scavengers.

ANT STUDIES

Both Hunt (1977) and Cody and others (1977) studied the ant fauna in southern California chaparral (Echo Valley), as well as in other vegetation types during 1971-72. Details of collecting methods were not reported but see Hunt (1973). Using a 2000 m elevational gradient, he found a far richer ant fauna (45 species) at the 1000 m (chaparral) level than at the coastal site (15 species) or the 2000 m (montane) site (21 species). But the 1000 m figure is somewhat misleading since collecting at this site included open areas and wooded patches as well as chaparral covered areas. Hunt found that the ground-nesting ants in chaparral were distributed evenly throughout the habitat. Ant colonies in preformed cavities of limbs of shrubs were abundant. Seed-gathering ants were an important component of the total chaparral ant fauna.

FLOWER-VISITING INSECT STUDIES

Moldenke (1975, 1976, 1977, 1979a, b) made an extensive study of the insects that use floral resources as a source of food, not only in California chaparral and similar scrub type communities, but in several other vegetation types within the state as well. He collected more than 800,000 insects on 2200 plants (Moldenke 1976). Moldenke made a particularly close study of bees as pollinators. He emphasizes the point that, as a result of fire cycles, there are two separate and very distinct plant associations that can occur on the same land area in chaparral: the fire-germinated annual plants that occupy an area for 1 to several years following fire and the perennial plants that replace them in successional sequence. His principal study areas in southern California were Echo Valley for mature chaparral, and nearby Japatul Valley (San Diego County) for burned chaparral. Secondary study sites for other kinds of scrub vegetation in southern California were Torrey Pines (San Diego County) for coastal scrub and Ocotillo (Imperial County) for desert scrub. Study sites for chaparral in northern California were Jasper Ridge Biological Preserve (San Mateo County) and Camp Mather (Tuolumne and Mariposa Counties). Sampling was done by net collecting all insects that were observed visiting flowers throughout the study sites.

Plant species richness is greater after a burn than in later years as chaparral succession proceeds to maturity (Force 1981). The reasons for this difference are the three groups of plants that occur after fire. First, a large number of "fire annuals," or annual plants that grow from seeds which have been lying dormant in the ground until stimulated to germinate by fire. These seeds are derived from plants that grew following the previous fire. These annuals form a thick ground cover for perhaps 2 years following fire, and then are replaced rapidly by perennial shrubs. There is no understory of annual plants in older chaparral. Another group of plants present after fire is the suffrutescents that live for 3 to 7 years, and a third is longer living shrub seedlings and sprouts. Because the variety and abundance of flower-visiting insects might reasonably be expected to relate directly to floral variety and abundance, Moldenke (1977) reported plant species numbers and individual numbers as well as the same data for insects. Moldenke counted 44 species of plants in mature chaparral at Echo Valley compared to 85 species after a burn in Japatul Valley. As a means of further comparison with other southern California scrub vegetation types, he found 83 plant species in coastal scrub and 39 in desert scrub. Reasonably, then, one might expect nearly twice as many flower-visiting insect species in burned chaparral and coastal scrub as in mature chaparral and desert scrub.

The numbers of flower-visiting species Moldenke (1977) actually found in southern California counts were as follows: mature chaparral, 309; postfire chaparral, 254; coastal scrub, 119; and desert scrub, 182. The northern California chaparral counts were even higher: 316 species at Mather and 484 at Jasper Ridge. It appears from his data that the species richness of flower-visiting insects in scrub vegetation has relatively little to do with plant species richness. In fact, flower-visiting insect species counts were higher in mature chaparral than in any other vegetation type sampled. Moldenke (1976) reported insect species richness to be 25 to 33 percent lower in grasslands, at least 50 percent lower in northern California coastal scrub, coastal sage and dune scrub, and decidedly more than 50 percent lower in alpine tundra and mixed evergreen forest than in mature chaparral. In terms of the abundance (numbers of individuals) of these same insects, again chaparral leads the list of all vegetation types, although southern California sites are much lower in numbers overall than northern California sites.

Not all of these flower visitors are necessarily good pollinators. The most important native insect pollinators (excluding domesticated honey bees) in California are probably some of the larger bees like bumble bees and *Anthophora* spp. (Anthophoridae), the semisocial halictine bees, the larger bee flies (Bombyliidae), and the butterflies (Moldenke 1976). Some of the smaller, specialist, solitary bees are important in certain circumstances. Nearly all vegetation types have been invaded by the introduced honey bee (*Apis mellifera*), which has undoubtedly accounted for the competitive extinction of many native bee populations. California has some 1200 species of native bees which make up a large part of the flower-visiting insect fauna in chaparral and other vegetation types; bees pollinate 95 percent of the insect-pollinated plants in California. Moldenke (1979b) suggests that pollinator richness is greatest in warm, nonwindy situations where some bare ground is available for bee nesting (typical of many chaparral situations). Other flower-visiting insects which may be important pollinators under special conditions are certain beetles, muscoid flies, syrphid flies, wasps, and moths.

Since the variety and abundance of insect pollinators are so high in chaparral, Moldenke (1976) suggests that there must have been stringent competition by pollinators for plant species. He reported that many of the dominant chaparral plants are associated with specialist pollinating insects, a device for reducing competition among pollinators, and at the same time producing more effective pollination. Many chaparral plants exhibit mutually exclusive blooming times, still another way to make pollination more effective. Nearly all chaparral shrubs are self-sterile since pollinators of all kinds are abundant. The genus *Aesculus* is pollinated solely by butterflies and sphingid moths. The nectar is apparently poisonous to bee larvae (Benseler 1968).

Bees are extraordinarily abundant in chaparral. Moldenke (1976) attributes this to the virtual absence of low ground cover in mature chaparral, which leaves ample room for nesting sites of ground-nesting bees, and because of the frequent fires which provide dead branches for wood-nesting types. The very few annual plants found in mature chaparral are heavily outcrossed

by the abundance of bees and bee parasites (especially bombyliid flies) searching for bee nests. Many of the annual plants that are abundant after fire are self-compatible and are therefore not exclusively dependent upon pollinators for reproduction. However, Moldenke mentions two apparently specialist bee pollinators of the plant, *Emmenanthe penduliflora*, which usually is found blooming only the first year after fire. It is not known how the bees exist during those time periods between blooming of their only known host plants.

In terms of number of species and individuals of the various flower-visiting insect groups in chaparral, bees are by far the richest (number of species) and most abundant (number of individuals) in southern California, both in mature and burned chaparral (Moldenke 1976). In northern California, bees are the richest insect fauna, but beetles are much more abundant. Bee flies (Bombyliidae) are both rich and abundant chaparral residents all over California; wasps are species rich but relatively low in abundance. Butterflies, muscoid flies, syrphid flies, and moths are all relatively low in richness and abundance. In terms of importance as pollinators, bees are unquestionably dominant among the insects. A great variety and abundance of halictine bees are common in chaparral; these halictines are often generalist and opportunistic feeders and rather effective pollinators of the sequential series of flowering plants that occur in mature chaparral from early spring far into the summer (Moldenke 1977). The larger social bees (e.g., bumble bees) may be important in cool or even cold weather such as during early spring, especially in northern California. Moldenke has observed queen bumble bees foraging on *Arctostaphylos* during a full moon at midnight with 15 cm of snow still on the ground at the Mather site in northern California. Bee flies probably pollinate 10 to 20 percent of the flora in chaparral; wasps pollinate perhaps 5 percent. Sphecid wasps may be common pollinators of chaparral in the Sierra Nevada mountains. Beetle pollination is apparently poorly studied, but Moldenke observed that most flowers pollinated by beetles are visited by other pollen vectors as well. He reports that the tumbling flower beetles (Mordellidae), long-horned beetles (Cerambycidae), and metallic woodborers (Buprestidae) are important pollinators; but other beetles often do more damage by feeding on flower parts than benefit by pollinating. Butterfly pollination is rather frequent in chaparral, as is moth pollination. In fact, chaparral is apparently unusual among many vegetation types in having a number of plants that are pollinated by nocturnal moths.

The chaparral insect community structure was compared with that of other scrub vegetation types. The hot, desert scrub vegetation (Ocotillo site) sampled by Moldenke (1976, 1979b) also shows high numbers of solitary bee species, many of which are specialist feeders associated with both annual and perennial plants. Bee flies and wasps also are important pollinators. One of the characteristic phenomena associated with desert ecosystems is the annual variability of rainfall and therefore vegetation growth and blooming. It appears that wet years, producing abundant annual plant growth and blooming, produce few pollinators; and that dry years with few plants produce abundant pollinators. One would naturally expect just the reverse situation; to my knowledge, this enigma has not been explained

satisfactorily. Because of this condition, outcrossing of certain plants apparently takes place mostly in dry years of pollinator abundance. In areas of bimodal rainfall (early spring, summer), different pollinators tend to be present at the different times. Spring pollinators are often descendants of the Nearctic fauna, whereas summer pollinators are derived from Neotropical ancestors (Linsley 1958). Another characteristic of desert scrub is crepuscular pollination (Moldenke 1976). A number of these plants are pollinated in the evening or early morning by large, thermoregulatory insects such as large bees and sphynx moths. Of course, this is a time of relatively little wind in locations where high winds are often characteristic; windy conditions pose a very difficult problem for pollinating insects.

Southern California coastal scrub provides another good comparison with chaparral. Here too, windy conditions are often prevalent along with fog for a good portion of the time. These conditions are less than ideal for most insects. The insect pollinators in these areas decrease in species richness, individual abundance, and biomass (Moldenke 1979b). Small bodied insects become rather rare; large thermoregulatory species become the main pollinators since they can function during periods of fog and cold. Here generalist flower feeders are prevalent, and plants compete for these pollinators since they are not abundant.

POSTFIRE INSECT STUDIES

Force (1981, 1982) studied early (first 4 years) postfire succession of insects, in relation to that of plants, in the San Gabriel Mountains of southern California (San Dimas). Richness and diversity changes were reported for both insects and plants, whereas abundance changes were reported for insects only. A declining trend was found in most of these statistics the first 3 years following fire, but this trend was dramatically broken the fourth year when all the statistics abruptly rose. The insect data tend to parallel the plant data in magnitude throughout the study, but it is not known whether this correlation was cause-and-effect or mere coincidence. We still do not understand such things as the amount and importance of insect migration into a burn area immediately following fire, whether the size of a burn area influences the abundance and richness of the insects therein, and the influence that various kinds of weather has on postburn insects.

Force (1982) also studied the early succession of insect trophic groups and changes in total insect biomass at San Dimas. He found that parasitic forms were scarce immediately following fire except for bombyliid flies, which appeared to be primarily interested in nectar gathering. Parasitic hymenopterans were extremely scarce at first, but became more numerous by the fourth year. Biting flies were very scarce. Predatory insects were much more abundant and active than parasitic forms; they appeared to be preying mostly on flower visitors. Flower-

visiting insects were extremely abundant when sampling was first begun during the spring of the first year after the burn. They occurred in numbers that matched the profuseness of blooming, and many probably migrated into the burn area to take advantage of the annual plant bloom. The nonflower-visiting phytophagous insects established more slowly, and weather seemed to affect their richness and abundance greatly. More data are needed to verify all of these observations.

Insect biomass tended to peak annually in June and July; there was no obvious correlation between biomass and yearly rainfall. A comparison of insect biomass found by Atkins (1977) in San Diego County (Echo Valley) with that at San Dimas indicates certain differences. Of course, the sites were quite different in character, and sampling methods were also different. The Echo Valley biomass peaked earlier than that at San Dimas, and the September to October biomass was much lower at Echo Valley than the average at San Dimas during these months.

Mills (1983) has tested the effect of herbivory on seedling establishment in postfire southern California chaparral. This study was done in a 2.5 hectare prescribed burn in northern San Diego county (Sky Oaks Field Station). He found that insect herbivory had little, if any, effect on the first year survival of two species of shrub seedlings, *Ceanothus greggii* and *Adenostoma fasciculatum*. In the same study, Mills (1986) found that a significant impact occurred on *Ceanothus* during the second and third postfire years, but only when mammal herbivory was included. When only insect herbivory was allowed, *Ceanothus* held a competitive edge over *Adenostoma*. When both insect and mammal herbivory was allowed, the advantage switched to *Adenostoma*, indicating that mammal feeding reversed the competitive situation.

INSECT INFORMATION FROM BIRD AND LIZARD STUDIES

A scattering of information about chaparral insects is available from bird and lizard studies. Cody (1974) reported flying insect catches from both north and south slope chaparral in the Santa Monica Mountains of southern California in a 1968-69 census. The biomass (dry weight) from the north slope tended to peak later in the season and was greater overall than that from the south slope. He found a corresponding higher percentage of insectivorous birds on the north slope than on the south. Cody (Cody and Mooney 1978) also described a chaparral vertical density profile along with corresponding profiles for insect density and bird utilization. The insects were sampled using 10 cm x 10 cm "Tanglefoot" plaques placed at various elevations in the vegetation. Insect density appeared to be greatest at about 1.5 m above ground, which is also the level where vegetation density and bird insectivore activity (and, in fact, all bird

activity) were greatest. Fuentes (1976) mentioned in passing that the abundance of non-ant arthropods as potential lizard food decreases as the season gets hotter and drier in chaparral, but that the ant supply remains about the same all season (Fuentes 1974).

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