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Comparative Ecology of Ant Communities
in Mediterranean Regions of California and Chile

By

James Howell Hunt

B.S. (North Carolina State University) 1966
M.S. (Louisiana State University) 1969

DISSERTATION

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Approved: R K Colwell
Evert I. Schlinger
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Comparative Ecology of Ant Communities
in Mediterranean Regions of California and Chile

## ABSTRACT

by James Howell Hunt

The ecology of ant communities has been studied in Mediterranean regions of Chile and California. Field work was focused on faunal survey and the analysis of patterns of coexistence. A simple ecological classification for ants is presented that is based on the field work done. Such ecological features as temporal activity pattern, foraging site selection, and degree of foraging cooperation among the ants studied seem to represent an integrated pattern of resistance to or avoidance of predation by vertebrates. Experimental data are presented in support of this suggested pattern of relationship. Ant faunal survey collections were made at four sites spanning a 2,000 m elevational range in California and at four analagous sites in Chile. The Chilean survey was broadened to include ants of the entire country. Resource division patterns were detailed at a 1,000 m site in each country, with data being gathered from baits, mapped quadrats, nest observations, and direct field observations. Major components of resource division among ants at these sites are habitat selection, foraging strategy, and temperature or time-of-day preferenda. Most species apparently overlap broadly in food taken. Resource exploitation patterns at the two sites were noted to be similar, but a large component of the similarity is a result of taxonomic similarity of ants at the two sites, notably in species of common, widespread



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genera. Taxonomic differences between the sites are attributable to the biogeographic settings of the sites and to the isolation of Chile. Patterns of ant - habitat association along a 2,000 m elevational gradient are similar in the two regions. A major difference between ant communities in the two regions is the three-fold greater number of species in the California sites. The low number of species in Chile probably reflects both the influence of biogeographic isolation and low species packing. Low species packing in Chile may be attributable to low between-year predictability of rainfall. California species may be more closely packed than those of Chile in association with greater amplitude of daily and within-year temperature fluctuation (with a predictable pattern) than in Chile. Consequences of high species packing are greater difference among similar habitats in both number of species and species composition of the community. This study indicates that both consequences are expressed in California but not in Chile.

Approved

R K Colwell

August 28, 1973



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The research reported here was done during a program of graduate studies. As in any research of this nature, and particularly in a field study of this geographic breadth and of more than two years' duration, I have relied heavily upon the encouragement, assistance and advice of my academic mentors, my fellow students, and on many other friends. The list of friends who merit my thanks is very long indeed. The following persons, though, are a few among the many to whom I owe a special measure of gratitude.

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# INTRODUCTION

Robert MacArthur, shortly before his death, was asked to predict the future of ecology. His paper "Coexistence of Species" (MacArthur, 1972) presents his brief prediction that "there will be erected a two- or three-way classification of organisms and their geometrical and temporal environments... The principles of the ecology of coexistence will then be of the form 'for organisms of type A, in environments of type B, such and such relations will hold.'" MacArthur also observed that "our empirical knowledge [of species coexistence] comes mostly from birds," and that "students [of ecology tend to] tackle completely new and unexpected problems rather than tidy up those left by their teachers." He finally suggested that "competition and coexistence must be studied under a very wide spectrum of conditions before we can make the classification." These thoughts, taken together, adequately describe the spirit in which the research reported here was undertaken and is being pursued. With academic training in ornithology (Hunt, 1969a) and a deep interest in the ecology of species coexistence (Hunt, 1969b), I have sought the roots of a classification such as MacArthur describes. I have tried to go beyond the bird studies that have been and are being done and to explore the generality of the phenomena of coexistence in nature. Step one in the study was to select animals other than birds as a focus of research.

Ants (Hymenoptera: Formicidae) were selected for study. The selection was prompted by a variety of considerations, among them being that ants share with birds several features that engender



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success in comparative ecological studies. Ants are found in most terrestrial habitats throughout the world, with many species being both conspicuous and abundant. Ants are known to include both ecological generalists and ecological specialists. As consumer organisms ants are in the higher trophic levels of their communities and so, by their abundance and diversity, may be sensitive indicators of phenomena at lower trophic levels. It seems probable that ecological studies of ants in one area can successfully be generalized in reference to ant communities in other areas. An additional key feature of ant biology that prompted their selection was eusociality (Wilson, 1971). The importance of this feature is emphasized by Wilson (1963), who said, "If a capsule statement were required defining the prime significance of ants as research objects, it could be the following: the ants are a world-dominant taxon... which have achieved their radiation by means of social modifications. They are unique in the magnitude of this achievement... With the ants... we are allowed to witness the employment of social design to solve the most diverse ecological problems ordinarily dealt with by single organisms."

Following the selection of animals came the selection of sites for comparative community studies. A rare opportunity was suggested by D. H. Janzen and made possible by H. A. Mooney: the comparison of ant communities at analagous Mediterranean zone study sites in California and in Chile. The studies to be done would contribute to the aims and interests of the Mediterranean Scrub Project, Origin and Structure of Ecosystems Integrated Research Program, International Biological Program. The nature of



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the integrated program has made possible a careful focus on the ants themselves, with the results of other research, notably on climate and the plant community, being made available by other researchers.

The original proposal for this research was prepared in January, 1971. In it I listed four important questions to be answered: They were "1) what are the specific biological roles played by ant species at the study sites; 2) how do specific physical and biotic parameters of the different sites determine similar or different niche characteristics of the ant species present; 3) what are recognizable convergences in niche characteristics that typify ant species in similar sites and differentiate ant species in dissimilar sites; and 4) how successfully may quantitative observational data on ants be brought to bear on current niche-theory hypotheses of theoretical community ecology?" An attempt to answer these questions can now be made, though I feel that my studies have uncovered more questions than answers.



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## PREVIOUS STUDIES

Brief mention should be made of previous ant ecological studies. The most recent and valuable synthesis on ant biology is *The Insect Societies* by E. O. Wilson (1971). Ant ecological studies are reviewed in portions of Chapters 4 and 21, though the coverage is not exhaustive. To remedy this shortcoming a new work (C. R. Carroll and D. H. Janzen, in preparation) is being prepared reviewing the available ant ecological literature. Several outstanding ant community studies have recently been done (cf. Bernstein, 1971; C. R. Carroll, in preparation), though most such studies emphasize community description but little more (cf. Brian, 1952 et seq.; Room, 1971; Wilson, 1959; Yasuno, 1964 et seq.). The study of ants as keys to understanding community-level interactive phenomena is a rather recent development (cf. Culver, 1972; Levins, Pressick, and Heatwole, 1973). Ten years ago E. O. Wilson (1963), in discussing ants, said: "the study of their social biology must still be considered in an early stage, notwithstanding an already large literature." Perhaps the same could be said at this time concerning ant community ecology. In the ensuing presentation, therefore, when a conclusion is offered as tentative or a point is designated as in need of further research no excuse is given nor is any felt necessary. New ground has been broken; the research will continue.



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## FIELD PROCEDURES

Field studies of ants are best begun by simple observation. Much can be learned by seeing where and how an ant forages, how it interacts with its nestmates and with ants of other colonies and other species, and under what weather conditions it is most active. Information gathered this way can be quantified if obtained in a disciplined program of observation. In simple communities such observations may yield sufficient information that an investigator can adequately describe coexistence patterns of the species studied. In more complex communities, however, particular programs of non-random sampling plus manipulative experimentation may be required to elucidate the coexistence patterns. In this study I have relied heavily on observation with supplemental sampling and experimentation focused at particular problems.

First emphasis was placed on collecting, sorting, and identifying all ant species present at particular study areas. Most ants were located by simple searching of foraging and nesting sites at all times of day and night. The nesting sites included under stones and within hollow twigs and branches. I searched such sites periodically throughout my studies, even after I felt that the habitats present had been thoroughly sampled. In California I also examined samples taken from pitfall traps, extracted samples from litter using Tullgren and Burlese funnels, and swept vegetation with a sweeping net. The pitfall and Burlese samples included several species not otherwise seen; the sweeping method proved particularly useful at night.



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At two sites, one in California and one in Chile, I attempted a detailed mapping of ant nests in an area of chaparral habitat. Each area was marked into 10 $m^2$ quadrats using stakes and string; base maps were prepared. Nests were located by offering baits attractive to ants (tuna and honey) and then following ants with food to nest openings. The nest openings were numbered, flagged, and mapped using transparent overlays with the base maps.

Quantification of habitat selection and other parameters was also greatly facilitated by use of baits attractive to ants. The baits used were canned tuna (cat food was used in California), peanut butter, and honey. Extensive use has been made of such baits (especially tuna) by other investigators (Levins and co-workers) examining competitive interactions and measuring niche breadth, but this has not been my purpose. When two species are found together on a bait the most conservative inference to be drawn is that the species coexist in the same habitat and are attracted to the same bait. The mechanism of their coexistence remains unexplained. Undue emphasis on competition among workers for an unnaturally rich introduced food item ignores the findings of several studies (cf. Brian, 1952; Wilson and Hunt, 1966). These studies indicate that important determinants of ant community structure and development may be selection of and competition for nest sites among founding queens plus predation by workers of existing colonies upon founding queens. Baiting data can be extremely useful, however, if conservatively used. Quantification can be made of such parameters as selection of foraging site (baits on leaf litter vs. bare soil, for example) and recruitment of



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workers to a concentrated food source. Differential responses to the three different baits I used have also indicated possible difference in food preference among several species. Some species were not strongly attracted to the baits I offered, but harvester ants, for example, responded strongly to rolled oats offered as bait for rodents. Several ant species known to be present at the study sites were not found on any of the introduced baits.

Most of my bait data were gathered under the following format. A transect was run from woodland habitat across an open or disturbed habitat and into chaparral habitat. This was done at one site each in California and Chile. The transects were marked into 10 m segments using flagged stakes. Baits were then placed on the ground on or near the transect line. Three baits (one tuna, one honey, one peanut butter) were placed within 15 cm of one another. These baits were then checked periodically for several hours and the following data were recorded: position along the transect line, substrate on which the baits were placed, time of observation, ant species present on each bait, numbers of each ant species (estimated if more than 10), and whether the bait was in sun, shade, twilight, or darkness. At most baits in California the temperature was also recorded using a mercury thermometer with the unshaded bulb touching the substrate near one of the baits. Coverage of the transect was more thorough in California (>1,000 observations) than in Chile (360 observations).

Several other studies were also done. Diurnal activity patterns of three Chilean species were documented by counting foragers entering and leaving nest openings during a two-minute count



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period each half hour throughout the day. Hand counters and a stopwatch were used; temperature of the ground by the nest opening was recorded using an unshaded mercury thermometer. On several days these nests were shaded to alter their microclimate. The shade used was a highly reflective Thermos brand Space Blanket suspended horizontally, aluminum side up, about 1 m above the nest opening. In California a simple test was made of the use of stones for nest sites. I placed 30 concrete slabs 25 $cm^2$ and 4 cm thick on the ground, 25 in the mapped plot of chaparral and 5 in an oak grove. The slabs were put in place on 3 February 1972, and I searched for ants beneath them on 24 April 1973, Other studies will be described at appropriate places in the following pages.

The studies reported here concentrate on ants found at specific study areas. In Chile, however, a general survey of the entire ant fauna has been attempted, and the results of this survey are to be published separately (Snelling and Hunt, in preparation). This publication will summarize, both from the literature and my own observations, the known information on range, habitats, and habits of all Chilean species. This information is presented here in Appendix B. Corresponding information for species encountered at the California study sites is presented in Appendix D.

Throughout these studies I have taken voucher specimens (placed in alcohol) from nests, baits, and other samples for taxonomic determination by a specialist. Roy R. Snelling of the Natural History Museum of Los Angeles County has determined the identity of more than 600 such vouchers. Without his competent assistance the work reported here would have been inestimably more difficult.



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# FORAGING STRATEGIES

During my field studies it has become obvious that a major feature of resource division by ants is variation in foraging strategy among the species. Though particular food specializations are known for many ant species (Wilson, 1971), it is also believed that most ant species are food generalists and opportunistically exploit a large variety of food types (Wheeler, 1910). It is among these latter species in particular that different foraging strategies may be a major component of resource division. In the following paragraphs, therefore, I shall attempt first to construct a classification for the foraging strategies of ants and second to demonstrate why such a classification is of interest and importance. Though my own field experience is largely with generalist species in chaparral habitats, I feel that the classification is sufficiently general to have broad applicability.

The key feature of ant biology is eusociality. In studies of ant foraging ecology, particularly in attempts to characterize and classify the foraging styles or patterns of various species, I feel that components of the eusocial system are most important. The classification, then, involves a reduction of foraging pattern through an analysis of its component parts. I shall begin with the features I feel are most important.

1. Foraging cooperation. Given that the workers of a species are active simultaneously according to a temperature preferendum or diel activity rhythm, one may ask to what extent the efforts of these workers are coordinated. That is, do the workers forage solitarily or do they forage in groups?

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2. Recruitment. Recruitment is defined by Wilson (1971: 247) as "communication that brings nestmates to some point in space where work is required." Among ant species that forage solitarily one can distinguish three general levels of recruitment to food sources: none, where no nestmates are recruited; poor, where only a few nestmates are recruited; and good, where many nestmates typically are recruited.

3. Resource mobility. Recruitment in the same sense as for solitary foragers is unimportant among ant species that forage in groups. What seems important instead is a feature of the resource sought: is it stationary, such as seeds, leaves, or detritus; or is it mobile, such as living arthropods?

4. Polymorphism. Size polymorphism among worker ants can be important in the development of a foraging strategy. Wilson (1971, Chap. 8) presents a detailed discussion of ant polymorphism. He discusses five levels of worker caste polymorphism. Three levels are sufficient for the purposes of this classification. These are monomorphism, monophasic allometry, and distinct polymorphism. The first two of these are as defined by Wilson (1971), whereas the third includes three of Wilson's levels: diphasic allometry, triphasic allometry, and complete dimorphism. The three steps I am using reflect recognizable features that can be seen in the field. In the case of monomorphism, all workers are essentially identical with only slight size differences, if any. In the case of monophasic allometry, workers span a range of sizes but are of essentially the same body plan and proportions. In the case of distinct polymorphism, the workers both span a range of sizes and

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also show recognizably different body proportions when large and small workers are compared, even though distinctly different types may be connected by intermediate body form types.

These criteria, then, can be used to construct the diagrammatic classification shown in Figure 1. It can be seen that five major groups are recognized with three possible subdivisions within each. Genera with which I am familiar are given as examples. Certainly not all fifteen possibilities in this artificial construct are represented in nature; there are no known species without recruitment but having distinct worker polymorphism, for example. Moreover, it must be said that not all ant species can be neatly assigned to a group; certainly there would be arbitrary or questionable assignments. In general, however, the groupings seem valid for the majority of ant species under study.

Assignment of species in a local fauna to the groups shown in Figure 1 is a good beginning for studies of resource division. The major groups are analagous to guilds (sensu Root, 1967). Within a group, then, resource division by time and space is the next important step. Beyond time and space other criteria must be employed. Two are given here as examples.

1. Size. The size of ants varies greatly among and sometimes within species. Though size is often the most visible difference among ant species, it seems to me to be less important than the features already mentioned. One cannot say a priori that small ants take small food items and large ants large items. Many small ants working simultaneously, for example, may more effectively occupy a large food item than can one or a few large ants. A

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Figure 1. An ecological classification for ants. See text for explanation. 1 = monomorphism; 2 = monophasic allometry; 3 = distinct polymorphism; ? = I have not encountered ants during my studies that fall in these categories; X = no species are believed to exist that fall in this category.

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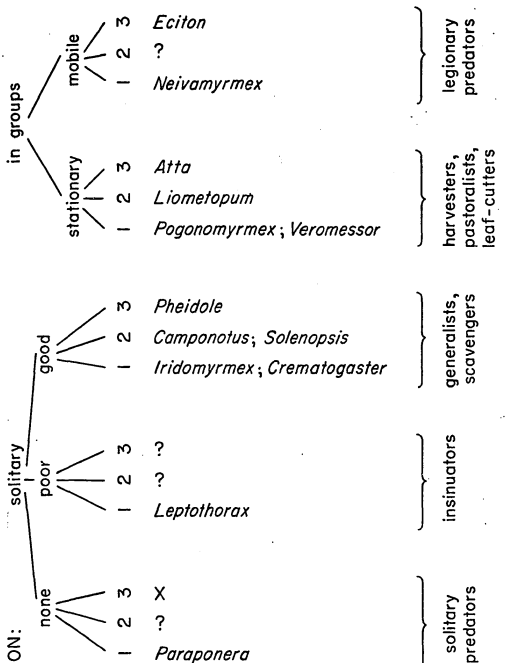


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large ant that searches more area per unit time than a small one is perhaps more likely to find and exploit small food items. Within a guild, however, among species exploiting a common food source in a similar way, different sizes could correlate well with exploitation of different portions of a resource spectrum.

2. Individual species behavior. Different behaviors associated with the use of different food sources among species seem almost trivial as a departure point for studies of foraging differences. Certainly an individual predatory ant behaves differently than an individual aphid pastoralist. Behavioral differences might be important, however, among species that exploit a common resource in a similar way. For example, several species of ants in Echo Valley, California were observed foraging on shrubs. Individuals of *Pseudomyrmex apache*, *Camponotus anthrax*, and *Formica occidua* all search leaves in a similar pattern. A forager ran out a twig until it encountered leaves. It then moved on to a leaf, circled the leaf perimeter, and then moved to the next leaf and again circled the perimeter. The species seemed to do this at different rates in the order *Pseudomyrmex>Camponotus>Formica*, with the slower species seemingly performing a more thorough coverage of the leaves. These different rates of searching might confer differential success on the species.

The preceding discussion has presented a hierarchical ordering of criteria that can be used in the ecological study of a local ant fauna. Two examples using Mediterranean-climate ant faunas are given later in this paper. For the moment, however, let us return to the classification shown in Figure 1.

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The main groups of the classification in Figure 1 correspond in general to established taxonomic groupings. This is not a surprising result: evolution would be expected to have proceeded within major adaptive groups. Neither is this result trivial: it directs us to look at selective forces that might have been operative in directing the evolution of these groups.

Here, perhaps, we need to consider further some morphological and behavioral attributes of the different taxonomic groups that are not usually considered, and the involvement of these attributes with the foraging strategies. These attributes are features that have forced themselves upon my attention as I have observed the ants in the field. They are criteria best studied in living animals. I wish to consider the following: aggressiveness, palatability, and cryptiveness. The point to be made is straightforward: not all ants are alike, and the patterns of difference vary in a coherent way.

AGGRESSIVENESS. Ants may show aggressiveness among themselves and toward other animals. Our interest here is in aggressiveness of ants toward vertebrates. Most people have encountered aggressive ants unwillingly but memorably by being bitten, stung, or annoyed. The curious who pass beyond such an encounter can easily note for themselves that many ant species are innocuous, from our human point of view, whereas others are only mildly irritating, and some, at the extreme, can inflict severely painful stings. One inquisitive biologist has done comparative sampling of sting potency with himself as the experimental subject (Janzen, 1972). My personal experience has included fire ants, harvesters, and

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ponerines. Though my tolerance of hymenopteran stings is good, my academic curiosity was not sufficient for me to sample the sting of *Paraponera clavata*, encountered in the lowlands of Ecuador. These ants, by their large size and aggressive demeanor, seemed to deserve the respect accorded them by biologists and residents in tropical areas.

PALATABILITY. In recent years perhaps the most dramatic progress in research with ants has concerned their behavioral chemistry and the unravelling of pheromone systems. In the process of this research by a variety of investigators, a rather remarkable variety of gland-produced substances has been identified from a wide variety of ants (Wilson, 1971). Many of these chemicals are species-specific (Sudd, 1967); some are even caste-specific within species (R. Duffield, personal communication). Many have odors sufficiently distinctive that one myrmecologist of my acquaintance even claims to identify ants by smell. It is not surprising, then, that different ant species not only smell different but taste different.

My technique for tasting ants is simple. I capture an ant by hand, remove its sting if it has one, and crush the head if it is large enough to bite. I then immediately place the ant on the upper anterior one-third of my tongue and taste it with my mouth closed, rolling it against the roof of my mouth. After a moment I crush the ant two or three times between my incisors, taste it again as before, then spit it out.

The results of this admittedly crude sampling can be briefly summarized. Most *Camponotus* spp. and *Myrmecocystus* spp. I have

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tried have a distinct citrus-like flavor, some even tasting like lemon candy. R. R. Snelling (personal communication) reports that repletes of *Myrmecocystus* spp., with their abdomens swollen with honeydew, make tasty snacks to relieve the tedium of excavating their deep nests. In many ant species (including, of course, most very small ones) I can detect very little flavor or none at all. Of particular interest here are the *Pogonomyrmex* spp. that, with their stings removed, have no distinctive flavor. Some species, however, notably *Liometopum occidentale* encountered in the present study, have a decidedly noxious flavor. One or two of these ants are sufficient to stiffle any academic curiosity that might involve large samples.

CRYPTIVENESS. This third feature is more difficult to accurately assess. The generous observer will grant, however, that not all ant species are equally conspicuous. Some ants are cryptic by virtue of small size or dark coloration; others are cryptic in behavior. In searching a site for ants, some species are quickly and easily seen, others are found only after rummaging through litter or searching nest sites, while still other species may be found only in Burlese samples of litter material. A night visit during favorable weather may reveal completely different species to be conspicuous and active at night than are conspicuous and active by day.

These features of aggressiveness, palatability, and cryptiveness did not strike me independently as being worthy of study. They came instead from a general synthetic observation: the ants that are most conspicuous are generally either aggressive and have

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a sting, or they are distasteful. Ants that are cryptic in habits or, in temperate zones, that are active by night are in general neither aggressive nor distasteful. To me this suggests a relationship to predation.

In temperate zones the principal predators of foraging ants are lizards. The relationship of lizard predation to ant foraging pattern can be examined under three hypotheses: 1) not all ants are equally susceptible to being eaten; 2) not all ants are equally suitable for being eaten; and 3) susceptibility and suitability have a negative correlation.

Susceptibility is a measure of the overlap in time and space of prey and their predators. At the study sites where I have worked the overlap of lizards and their prey is being examined in detail by another IBP investigator, Eduardo Fuentes. His data will cover habitat use and activity patterns of lizards and habitat preference of the prey. The only component of the system not adequately sampled by Fuentes' work is activity patterns of the prey. Activity patterns of ants are discussed by Sudd (1967), who notes that temperature, light, circadian rhythm, or combinations of these control ant activity patterns. Alterations in activity patterns can be caused by rain or clouds, or they can be induced by artificial manipulation of microclimate (Hodgson, 1955; my own studies). A common feature of ant activity patterns in hot, seasonal habitats is that many species typically active by day show lowered activity during extreme summer heat and extend their activities into the warm summer nights (Sudd, 1967). I noted this to be the case with many ant species in Echo Valley, California. Table 1 lists several

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Table 1. General activity pattern of common (abundant and conspicuous) ants in Echo Valley, California.

Exclusively or largely nocturnal

*Camponotus semitestaceous*

*Camponotus quercicola*

*Myrmecocystus testaceus*

Exclusively or largely diurnal

*Pogonomyrmex subnitidus*

*Veromessor andrei*

*Liometopum occidentale*

*Tapinoma sessile*

*Myrmecocystus flaviceps*

*Formica* spp.

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of the larger ant species commonly found in Echo Valley. They are grouped in the table according to two general classes of diurnal pattern. These are ant species that are easily noticed by even a casual observer. A generality can be made concerning their susceptibility to lizard predation: those exclusively or largely nocturnal are generally not susceptible; those exclusively or largely diurnal are susceptible.

The suitability of ants as prey items for lizards can be determined through only one test: is a particular ant species eaten by lizards or not? There are two approaches to the test: 1) analysis of lizard stomachs collected in the field, and 2) through data taken from laboratory feeding trials.

Most, if not all, lizard species found in Echo Valley include ants in their diet, though only *Phrynosoma coronatum* specializes on ants as prey (E. Fuentes, personal communication). In July, 1972, I captured two adult *Phrynosoma* for feeding experiments. The animals were maintained together in a glass-sided 10 gallon aquarium with 4 cm of fine sand in the bottom. A 60 watt light bulb over the aquarium provided light and warmth during the day. The animals did not eat in captivity for more than a week after capture. Thereafter, however, both took first ants and then mealworms. The animals were maintained largely on mealworms for another week before being released. During that week I offered several species of ants to the lizards in a series of feeding trials. Usually 8 or 10 ants of a single species were offered to the lizards at one time. Conditions of the trials were not controlled for temperature, time, or nutritional state of the lizards, so the data can

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be given confidence on only a nominal scale, as in Table 2. In every case, all ants offered at one time were either eaten or not.

There are two interesting results of this simple experiment: the three species not eaten are diurnal and susceptible to predation in field situations, and two of the species eaten (*Camponotus quericola* and *Myrmecocystus testaceus*) are exclusively nocturnal and not susceptible to predation by lizards in the field. The other species eaten are diurnal and so are susceptible.

The second analysis of suitability, that involving ants actually eaten in the field by lizards, yields data that are more precise but less easily interpreted than data from feeding trials. Table 3 presents data on the stomach contents of 24 lizards collected in Echo Valley by Eduardo Fuentes. I considered only ants in my analysis; Fuentes (in preparation) will present data on the total diets of these lizards. The ant data are based on ant heads found in the stomachs. Identifications were made to genus only (though specific determinations were made where I could do so with confidence). Size (maximum head width) was taken for *Camponotus* spp. heads only.

The abundance of individuals by genus in the lizard stomachs is not correlated with the frequency of occurrence of the genera on baits placed along a transect line (Table 4) crossing several habitats (Spearman Rank Correlation Coefficient, $r_s = .161$). That is, the lizards are probably not taking the ants in the frequency in which they occur. Ants represent a coarse-grained resource from the point of view of a lizard. Several important facets of this grain coarseness should be mentioned.

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Table 2. Feeding trials with two captive *Phrynosoma coronatum*.

| | Eaten | Not Eaten |
|---|---|---|
| *Camponotus dumetorum* | X | |
| *Camponotus quercicola* | X | |
| *Liometopum occidentale* | | X |
| *Tapinoma sessile* | | X |
| *Formica* sp. | | X |
| *Pogonomyrmex subnitidus* | X | |
| *Veromessor andrei* | X | |
| *Myrmecocystus testaceus* | X | |

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| | N | Camponotus | Pogonomyrmex | Crematogaster | Tapinoma | Formica | Myrmecocystus | Conomyrma | Pheidole | Leptothorax | Iridomyrmex | Liometopum |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sceloporus occidentalis* | 9 | 48,4, 2,1, 1,2 | 0 | 3,5,6 | 5,1 | 2,7, 1,4 | 7,7,1 | 1,4 | 1 | 1 | 0 | 1 |
| *Uta stansburiana* | 8 | 0 | 0 | 3,2,1 | 1,9, 2,1 | 0 | 1 | 3 | 5,4 | 1,7 | 1,1,2 | 0 |
| *Phrynosoma coronatum* | 2 | 2,19 | 49,1 | 1 | 1,1 | 8 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Sceloporus orcutti* | 2 | 2,1 | 0 | 27 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 |
| *Cnemidophorus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Eumeces* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 3. Numbers of ant heads in stomachs of lizards collected in Echo Valley, California. N = number of lizard stomachs sampled. Numbers in table are the numbers of heads per each stomach.

Table 4. Ranked abundances of ants as found in lizard stomachs (Table 3) and on baits (Table 8).

| | Ranks | |
|---|---|---|
| | Stomachs | Baits |
| *Camponotus* | 1 | 2 |
| *Pogonomyrmex* | 2 | 11 |
| *Crematogaster* | 3 | 7 |
| *Tapinoma* | 4 | 1 |
| *Formica* | 5 | 3 |
| *Myrmecocystus* | 6 | 10 |
| *Conomyrma* | 7 | 9 |
| *Pheidole* | 8 | 6 |
| *Leptothorax* | 9 | 8 |
| *Iridomyrmex* | 10 | 5 |
| *Liometopum* | 11 | 4 |

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Table 5 presents totals of ants in the lizard stomachs and records from the transect baits grouped according to subfamily. The important point to note is that the Dolichoderinae are most abundant on transect baits but least abundant in the stomach contents. The dolichoderines *Liometopum occidentale* and *Iridomyrmex pruinosum* are of particular interest, because these species typically forage in conspicuous columns with many ants active together, yet they are represented by the fewest number of individuals in any of the stomachs (Table 3). Note, too, that the two dolichoderine species offered to the captive *Phrynosoma* were not eaten (Table 2). These data, taken collectively, support the contention that dolichoderines are resistant to predation, presumably by virtue of the distasteful chemicals they contain. That small (but not large) samples of these ants are found in the lizards' stomachs supports the contention that lizards do encounter these ants but do not feed frequently on them.

As indicated in Table 3, several *Formica* heads were found in six stomach samples, but, as shown in Table 2, the *Formica* offered to the captive *Phrynosoma* were not eaten. The two *Formica* spp. found in Echo Valley are colored shades of dull grey and red in a pattern nearly identical to *Liometopum occidentale*. In my early work in the region I did not at first recognize *Liometopum* to be a dolichoderine; I thought it was a *Formica* species. Many *Formica* species are brown in color. It seems highly probable that the *Formica* offered to the *Phrynosoma* may not have been eaten due to their mimetic similarity to *Liometopum*. It is possible, then, that the *Formica* species in Echo Valley may enjoy lowered predation

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Table 5. Subfamilial representation of ants in lizard stomachs (Table 3) and on baits (Table 8). $n_b$ = number of bait observations; $r_b$ = rank on baits; $n_s$ = number of heads in lizard stomachs; $r_s$ = rank of stomach contents data.

| | $n_b$ | $r_b$ | $r_s$ | $n_s$ |
|---|---|---|---|---|
| Formicinae | 278 | 2 | 1 | 124 |
| Dolichoderinae | 399 | 1 | 3 | 46 |
| Myrmicinae | 150 | 3 | 2 | 115 |

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pressure due to mimetic similarity to *Liometopum*. Further research is clearly required on this point.

Note in Table 3 that *Pogonomyrmex* harvester ants are found only in stomachs of *Phrynosoma coronatum*, the horned lizard. As I mentioned above, *Phrynosoma* species are considered to be ant specialists. That *Pogonomyrmex* were not found in the stomachs of other lizard species may be explained by the following observations communicated by R. R. Snelling (personal communication). Snelling has kept *Phrynosoma* sp. as pets in his home. These lizards were usually fed workers of *Pogonomyrmex subnitidus*. On two separate occasions, however, several *P. californicus* were offered instead, and these ants swarmed the lizards, biting and stinging them. One lizard subsequently stopped eating altogether and died (presumably of starvation). The other lizard continued to eat *Formica* spp., *Myrmecocystus* spp., and other ants, but it retreated from all *Pogonomyrmex* and from majors (but not minors) of *Solenopsis xyloni*, which are similar in appearance to *Pogonomyrmex*. All *Pogonomyrmex* can sting. An encounter such as Snelling described that might occur between a young or small lizard (*Uta stansburiana*, for example) and one or a few *Pogonomyrmex* could well be sufficient to deter further attempts at predation by that lizard on harvesters. The continuing predation on *Pogonomyrmex* by *Phrynosoma* requires further investigation. Smith and Bragg (1949) have reported toads from Oklahoma whose stomachs bristled with ant stings in the stomach lining. Perhaps *Phrynosoma* spp. are the "toads" of the lizard world.

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Snelling's observation concerning the majors of *Solenopsis xyloni* further suggests that ants may enjoy lowered predation pressure through a mimetic similarity to a predation-resistant ant species. I suggest that this is the case with *Veromessor andrei*. This harvester species has no sting, but it forages in conspicuous columns and is very similar in appearance to *Pogonomyrmex* spp. The very compact foraging columns of *Veromessor* may, in fact, be a component of the mimetic system that maximizes the visual impact of a mass of harvesters and minimizes the exposure of isolated individuals.

*Veromessor* can be distinguished from *Pogonomyrmex* most easily in the field by the much longer spines on the dorsum of the thorax. Wilson (1959) commented on spinescence in the New Guinea ant fauna: "Worker spinescence is best developed in those species that nest in the ground and low arboreal zones *and forage a great deal above ground* [emphasis mine]. High-arboreal and subterranean species are notably non-spinescent, a trait presumably associated with the cramping conditions of their favored nest sites of trophophoric fields." I would suggest that Wilson's observation shows correlation of spinescence and exposure to vertebrate predators; non-spinescence in the subterranean and high-arboreal zones may reflect low predator exposure and lack of selective pressure to maintain spinescence. One could also conjecture that non-spinescent species would have to be superior competitors in subterranean and high-arboreal habitats in order to persist at all. As a final note on this subject I should add that spinescence is unquestionably best

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developed in Myrmecines, most of which can sting. Most formicines are notably non-spinescent.

Formicines are the ants that seem, as a group, least resistant to predation. These, then, are the ants that for predator avoidance must rely most heavily on such measures as behavioral crypticity and nocturnality. Note in Table 3, however, that *Camponotus* spp. were the ants most heavily preyed upon by the lizards sampled. What, then, is the situation with regard to these common formicines?

Of the *Camponotus* heads in the stomach samples, *C. anthrax*, *C. sp395*, and *C. dumetorum* could be identified to species. Most of these heads were of minor workers, and only a few were of media workers. No majors of *C. dumetorum* were found. Data from a Chilean species, *C. distinguendis*, will support the point to be made.

A single nest of *C. distinguendis* was monitored for two successive days. At the beginning of each hour from 08:00 to 17:00 a count was begun of foragers leaving the nest. Every third emerging forager was collected until a sample of 6 was taken or until ½ hour had passed. Weather conditions on the two days were similar (Table 6). The only difference between the two days was that on the second day I placed a tuna bait about .5 m north of the nest opening, whereas the first day was sampled without the bait, as a control. The sampling revealed no significant difference in the rates at which foragers left the nest on the two days (Wilcoxon matched-pairs signed-ranks test, T = 21, n.s.). Figure 2 illustrates that there was also no difference in the size of foragers

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Table 6. Hourly soil surface temperature (°C) and foraging rate (ants/min. leaving nest) of a colony of *Camponotus distinguendis* on two days. See text.

| Time | Soil temperature (°C) 1st day | 2nd day | Rate (ants/min.) 1st day | 2nd day |
|---|---|---|---|---|
| 08:00 | 30.0 | 33,5 | 1.44 | 2.67 |
| 09:00 | 38.5 | 42.0 | 1.36 | .72 |
| 10:00 | 44.0 | 44.5 | .33 | .50 |
| 11:00 | 47.5 | 47.0 | .30 | .16 |
| 12:00 | 50.5 | 47.0 | .06 | .00 |
| 13:00 | 48.0 | 46.0 | .16 | .10 |
| 14:00 | 46.5 | 44.0 | .40 | .76 |
| 15:00 | 40.0 | 40.0 | 1.12 | .88 |
| 16:00 | 35.0 | 34.0 | .69 | 2.11 |
| 17:00 | 24.5 | 24.0 | .13 | .23 |

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Figure 2. Frequency histogram of *Camponotus distinguendis* head widths for workers sampled from a nest on two successive days. First (control) day, without bait present, is above the line. Second (experimental) day, with bait present, is below the line.

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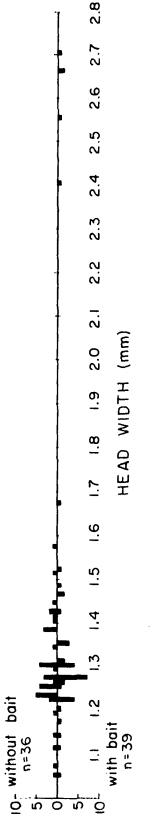


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leaving the nest, except that on the second day 5 major-size foragers were taken. It should be stressed that on the first (control) day no majors at all were seen leaving the nest. On the second (experimental) day several majors in addition to those sampled were seen leaving the nest. Many of the foragers, including majors, went to the tuna bait on the second day. The implication of the experiment is that major-size workers leave the nest only when a rich food supply has been located. These large workers are exposed to possible predation only when the possible foraging yield is high.

This result gains support from the work of King and Walters (1950) on *Formica obscuripes*, an only moderately polymorphic formicine. They found that larger workers usually remain in the nest while smaller workers do most of the foraging. Wilson (1971) cites similar findings on *Formica rufa* by Adlerz (1886) and *F. sanguinea* by Dobrzanska (1959). Wilson also reports that a reverse pattern is seen in *Solenopsis saevissima*, with larger workers the more frequent foragers. I would point out that *S. saevissima* is a stinging myrmecine whose larger workers would probably have more potent stings than the smaller workers. This reverse pattern would thus be expected under the general pattern of predator-prey relationships I have been presenting.

The experiment with *C. distinguendis* was not conclusive. More intensive sampling concentrated during the peak activity periods of early morning and late afternoon should show not only a worker size response to concentrated food sources but also a foraging rate response. Further investigation of this phenomenon is planned.

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At this point the information on foraging strategies can be summarized. The data presented are obviously preliminary yet sufficient to suggest the following conclusions:

1. The subfamilial relationships of an ant species, its size, and its pattern of worker polymorphism are all important correlates of its basic foraging strategy.

2. The observed relationships between different foraging strategies and different sets of morphological attributes strongly suggests that the different foraging strategies have been influenced by vertebrate predators, most probably by lizards. The well-established historical record, in which fossil species resemble modern ones (Wilson, 1971), suggests that this relationship has obtained since early in the evolution of ants. Predation pressure may well have been an important selective influence on the development of the various subfamily lineages of ants.

3. Conspicuous diurnally foraging ants, notably myrmicines and dolichoderines in this study, tend to be resistant to predation by lizards.

4. Conspicuous nocturnal foragers, notably formicines in this study, are not resistant to predation and avoid it by nocturnality. [This may not be the case in the lowland tropics where predators (especially dendrobatid frogs) may be active throughout the night.]

5. Diurnally foraging formicines minimize their loss to predators through behavioral crypticity and/or through exploitation of worker size polymorphism. In size polymorphic species small workers typically do most foraging; large workers typically leave the nest only at times of greatest probable food return.

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6. Worker spinescence seems positively correlated with susceptibility to predation.

7. Ants not resistant to predation may exploit mimetic similarity to species that are predator resistant. Such mimetic complexes may involve species of different subfamilies.

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## THE ANTS OF FUNDO SANTA LAURA, CHILE

Fundo Santa Laura is a privately owned parcel of land in Province Santiago, Chile, some 50 km NNW of Santiago and about 8 km W of TilTil. Elevation is about 1,000 m, on the east-facing slope of the low coastal mountains. Climate is of the Mediterranean pattern, and vegetation is typically of the shrub or chaparral type, known locally as *matorral*. The Fundo is the primary study site in Chile for the Mediterranean Scrub Project of the International Biological Program. Detailed analyses of climate, geography, vegetation structure and diversity, and other aspects of the site are in preparation by a number of authors (Miller, in preparation; Thrower and Bradbury, in preparation; Carter, 1973; Parsons, 1973).

Sixteen species of ants are known from the Fundo (Table 7). As a first step toward understanding the resource division patterns of these species I have made the following assortment of species into the five main groups introduced in Table 1 in the preceding section:

Group foragers, mobile prey: None

Group foragers, stationary prey: None

Solitary foragers, no recruitment: None

Solitary foragers, poor recruitment: *Pogonomyrmex bispinosus*, *Solenopsis latastei*, *Dorymyrmex antarcticus*, *Pseudomyrmex lynceus*, *Lasiophanes hoffmanni*, *Camponotus chilensis*, *Camponotus distinguendis*

Solitary foragers, good recruitment: *Solenopsis gayi*, *Tapinoma antarcticum*, *Lasiophanes picinus*, *Brachymyrmex giardii*

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Table 7. Bait transect data for ants at Fundo Santa Laura, Chile. N = total number of bait observations; Obs. = number of observations per bait type where H = honey, T = tuna, PB = peanut butter; Freq. = frequency (%) of observations per bait type when N > 15 and where H = honey, T = tuna, PB = peanut butter; $\overline{X}$ = average number of foragers found per bait observation plus or minus one standard deviation.

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| | Obs. | | | | Freq. | | | |
|---|---|---|---|---|---|---|---|---|
| MYRMICINAE | N | H | T | PB | H | T | PB | $\bar{X}$ |
| *Pogonomyrmex* (Ephebomyrmex) *angustus* Mayr | 0 | 0 | 0 | 0 | | - | | - |
| *Pogonomyrmex* (P.) *bispinosus* (Spinola) | 2 | 2 | 0 | 0 | | - | | - |
| *Nothidris bicolor* (Ettershank) | 0 | 0 | 0 | 0 | | - | | - |
| *Solenopsis gayi* (Spinola) | 85 | 8 | 35 | 42 | 09 | 41 | 49 | 53.7±51.7 |
| *Solenopsis latastei* Emery | 0 | 0 | 0 | 0 | | - | | - |
| DOLICHODERINAE | | | | | | | | |
| *Dorymyrmex chilensis* Forel | 0 | 0 | 0 | 0 | | - | | - |
| *Dorymyrmex antarcticus* Forel | 32 | 23 | 9 | 0 | 72 | 28 | 0 | 5.6± 6.0 |
| *Tapinoma antarcticum* Forel | 73 | 35 | 24 | 14 | 48 | 33 | 19 | 46.1±76.3 |
| PSUEDOMYRMICINAE | | | | | | | | |
| *Pseudomyrmex lynceus* (Spinola) | 0 | 0 | 0 | 0 | | - | | - |
| FORMICINAE | | | | | | | | |
| *Myrmelachista hoffmanni* Forel | 0 | 0 | 0 | 0 | | - | | - |
| *Lasiophanes hoffmanni* (Forel) | 2 | 0 | 2 | 0 | | - | | - |
| *Lasiophanes picinus* (Roger) | 25 | 2 | 23 | 0 | 08 | 92 | 0 | - |
| *Brachymyrmex giardii* Emery<br>*Brachymyrmex levis* Emery | 17 | 7 | 10 | 0 | 41 | 59 | 0 | 11.4±13.0 |
| *Camponotus* (Tanaemyrmex) *chilensis* (Spinola) | 35 | 19 | 14 | 2 | 54 | 40 | 05 | 2.7± 2.9 |
| *Camponotus* (Tanaemyrmex) *distinguendis* (Spinola) | 45 | 17 | 27 | 1 | 38 | 60 | 02 | 3.6± 4.0 |

Foraging habits unknown: *Dorymyrmex chilensis*, *Pogonomyrmex angustus*, *Nothidris latastei*, *Myrmelachista hoffmanni*, *Brachymyrmex levis*

The assignment of species to poor and good recruitment classes was arbitrarily set at an average of 10 ants per bait (Table 7). *Solenopsis latastei* was included among species with poor recruitment because, though it did not come to transect baits, I saw it frequently enough on baits in other areas to know that its recruitment is poor. The species having unknown foraging habits are three species that are rare at the site plus *Brachymyrmex levis*, which is uncommon at the site and indistinguishable from its more common congener, *B. giardii*.

A second, more traditional, approach to species assortment is by habitats. Figure 3 illustrates a 130 m line transect running from a small stream up a hillside and into the matorral. The array of points and bars above the drawing illustrates distribution of 15 of the species. Note that four species are found only along the first 20 meters of transect, which is that portion of the line that passes through the dense streamside vegetation. The other 11 species shown are encountered beyond the margin of this dense vegetation. This suggests that the ants are recognizing at least two distinct habitats, streamside woodland and matorral.

It is now possible to combine the strategy and habitat groups and, in addition, to consider the criterion of polymorphism discussed in the previous section. This produces the arrangement of species shown in Figure 4. The species clusters shown in the figure can be treated rather easily for a further analysis of species coexistence patterns.

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Figure 3. Habitat distributions for fourteen species of ants at Fundo Santa Laura, Chile. The array of spots and bars illustrates occurrence of the species in the habitats illustrated at the bottom of the figure.

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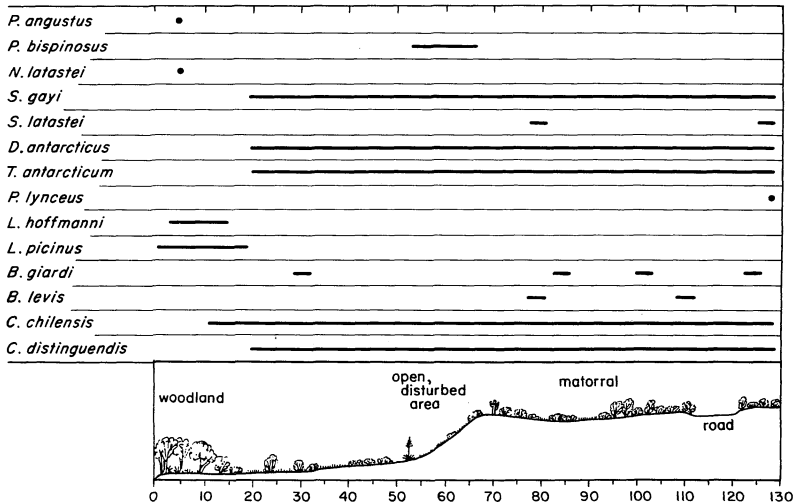

Figure 4. Ecological classification of common ant species at Fundo Santa Laura, Chile. See text for explanation.

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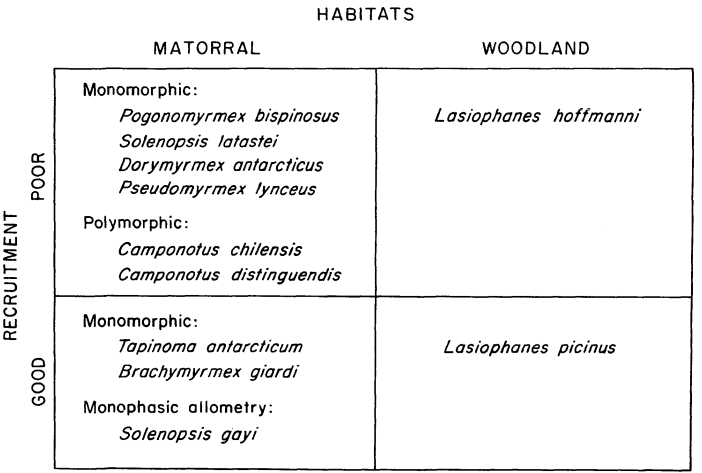




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The four species that are size monomorphic, have poor recruitment, and are found in matorral are completely dissimilar from one another. *Pogonomyrmex bispinosus* is congeneric with many North American harvester ants, though seeds do not seem a conspicuous part of this species' diet. This species is rather large, builds nests in soil exposed to sun, and is uncommon at the Fundo. *Solenopsis latastei* is a minute ant having small colonies. Roy Snelling (personal communication) considers it to be a thief ant (Wheeler, 1910). Thief ants typically live in or near the nests of other species and steal food therefrom. The foragers of *S. latastei* that I found on baits seem to function as "insinuators" in the sense of Wilson (1971). "Insinuators" are species that have elusive behavior when feeding among behaviorally more aggressive species. *Pseudomyrmex lynceus* is completely arboreal and is restricted to nesting in shrubs where hollow stems for nesting can be found. *Dorymyrmex antarcticus* is a small generalized scavenger, which I will discuss more fully below.

The two *Camponotus* species are about the same size. Both nest in soil, usually under a covering stone, and they seem very similar in food habits ($\chi^2$=3.36 for difference among the three baits types is not significant). The pattern of resource division between the two is clear, however. *C. distinguendis* is primarily a terrestrial forager found in open areas; *C. chilensis* is largely an arboreal forager found in dense aggregations of shrubs. The distinction was so clear-cut in the field that I have made no specific statistical test of the separation. No *C. chilensis* nests were found in the mapped plot of open matorral.

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*Tapinoma antarcticum* and *Brachymyrmex giardii* are dissimilar. *T. antarcticum* is an aggressive though small ant having large colonies. *B. giardii* is an inconspicuous small ant that seems, like *Solenopsis latastei*, to be an insinuator. *B. giardii* has "honeypot" repletes in its nest (I collected one nest of these) and so would emphasize honeydew in its feeding.

Other groups of species seem to be important potential competitors. For example, the two *Lasiophanes* species are the only common species restricted to woodland habitat. *Lasiophanes picinus* was encountered on 25 baits, *L. hoffmanni* on only 2. When numbers of individuals on the baits are considered, *L. picinus* is the more common by a factor of 120 to 1. I once observed about 100 *L. picinus* on a tuna bait but none at all on a honey bait less than 10 cm away. Three *L. hoffmanni* were on that honey bait, but none were on tuna. In addition, I have found *L. hoffmanni* on *Cryptocarya alba* foliage more than a meter above the ground; no *L. picinus* have been seen foraging the shrubs. *L. hoffmanni*, then, probably has somewhat different food and foraging site preferences than its more common congener.

*Solenopsis gayi* and *Camponotus distinguendis* overlap broadly in habitat. Their different foraging strategies have been mentioned. *C. distinguendis* is also considerably larger than *S. gayi*. *C. distinguendis* is a solitary foraging carpenter ant; *S. gayi* is a swarming fire ant. The species were found together on baits 9 times, *C. distinguendis* on the upper surface and *S. gayi* underneath. Possible different food preferenda are illustrated by different representations on the three bait types ($\chi^2=34.3$ $p<.001$). These two

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species, then, are somewhat different in food preference and distinctly different in foraging strategy.

*Dorymyrmex antarcticus* and *Tapinoma antarcticum* are both dolichoderines and were noted to compete strongly for honey baits. I found that baits placed out early in the morning were found first by *D. antarcticus*, which was later replaced by *T. antarcticum*. *T. antarcticum* continued on the baits through the day until the species retreated to its nests, at which time *D. antarcticus* reoccupied the baits. These observations represent the typical diurnal activity patterns of the species, illustrated in Figure 5. That figure illustrates a sunny, warm day, and Figure 6 shows activity patterns of the species on a cloudy, cool day. Observations associated with Figure 6 suggested that the two species might be regulating their activity patterns according to ground surface temperatures. This was tested experimentally using a highly reflective shade (Thermos brand Space Blanket) over a nest on a sunny, warm day. Such an experiment with two nests of *D. antarcticus* is illustrated in Figures 7 and 8. Figures 9 and 10 show a similar experiment with a colony of *T. antarcticum*. The *T. antarcticum* colony was typical for the species in having more than one entrance to its nest, and throughout the shading period (Figure 10) the colony shifted its major activity to whichever entrance appeared to be warmest at the time. At about 15:30 the colony took its larvae and began an apparent emigration to a new nest site under unshaded stones about 1 m away. The experimental evidence thus strongly indicates that these two species do regulate their foraging activities according to soil surface temperatures, and that coexistence of the two is achieved through differential temperature preference.

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Figure 5. Temporal activity patterns of *Dorymyrmex antarcticus* (triangles), *Tapinoma antarcticum* (circles), soil surface temperature (dotted line) and insolation (dashed line) at Fundo Santa Laura, Chile, on 4 October 1972. Foraging rates are ants per minute passing the entrance(s) of a single nest of each species counted for a two-minute period each ½ hour. Soil surface temperature was measured using an unshaded mercury bulb thermometer with the bulb touching the soil. Insolation values were recorded by a pyroheliometer (Belfort Instrument Company) located approximately 300 m from the nests studied.

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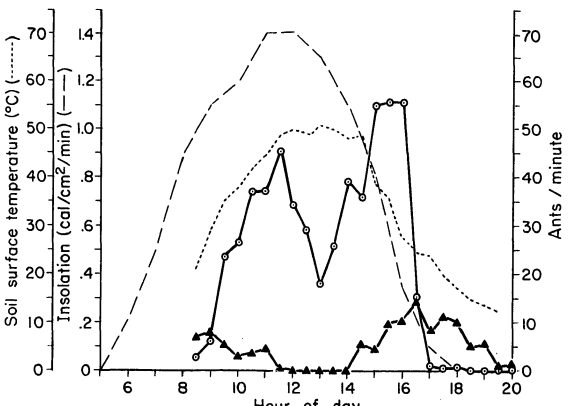


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Figure 6. Activity patterns on 5 October 1972 of the same nests as in Figure 5. Symbols and lines as in Figure 5.

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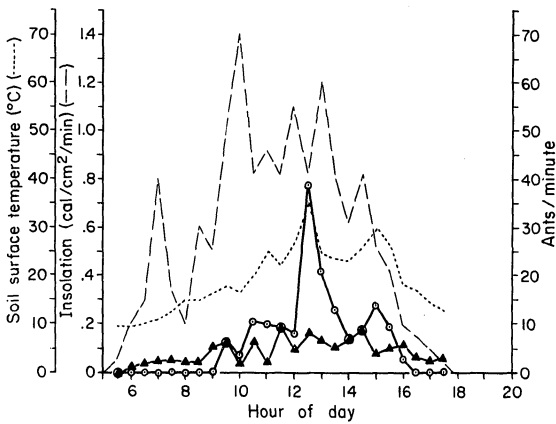


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Figure 7. Activity pattern on 19 October 1972 of the same *Dorymyrmex antarcticus* colony as in Figures 5 and 6. Artificial shade illustrated by crosshatching. Symbols and lines as in Figure 5.

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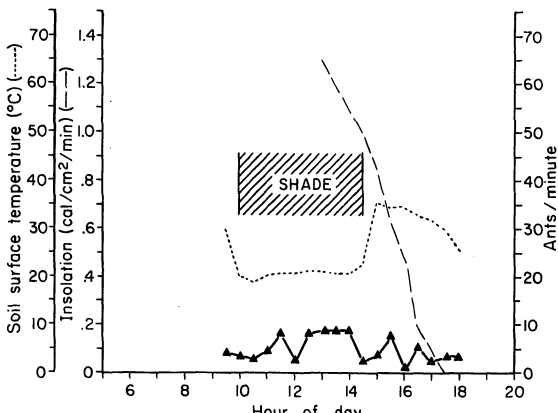


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Figure 8. Activity pattern on 19 October 1972 of a *Dorymyrmex antarcticus* colony approximately 10 m from that illustrated in Figure 7. Symbols and lines as in Figure 5.

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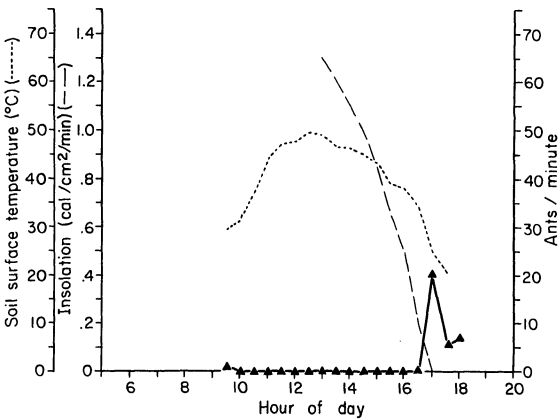


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Figure 9. Activity pattern on 1 November 1972 of the same *Tapinoma antarcticum* colony as illustrated in Figure 5. Symbols and lines as in Figure 5.

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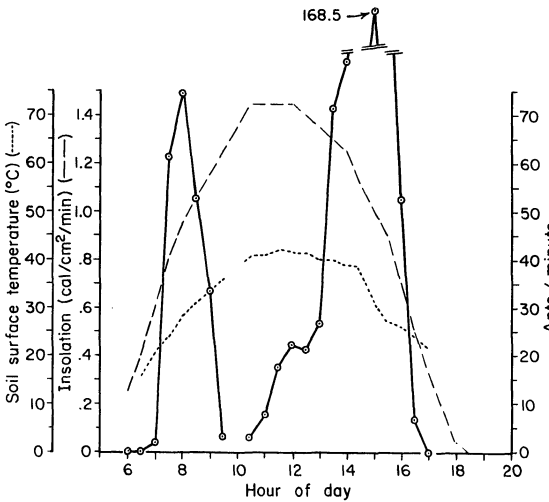


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Figure 10. Activity pattern on 2 November 1972 of the same *Tapinoma antarcticum* colony as illustrated in Figure 9. Artificial shade illustrated by crosshatching. Symbols and lines as in Figure 5.

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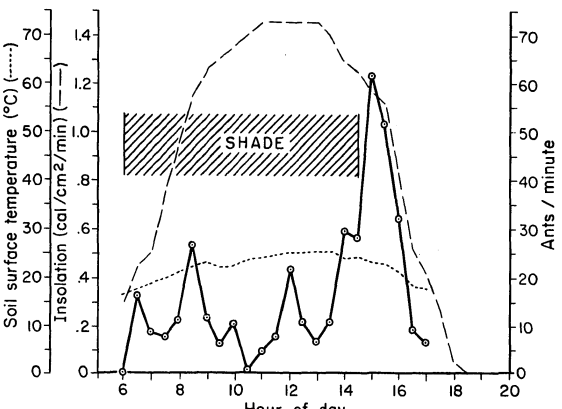


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Brief mention should be made of the four uncommonly encountered species. *Pogonomyrmex angustus* is known at the Fundo from a single forager found in woodland habitat. I found the species at other sites living in leaf litter and I believe it to be near the northern periphery of its range at the Fundo. *Nothidris latastei* is also known at the Fundo from a single forager that was found in woodland leaf litter. The habits and habitats of this species are not known. *Myrmelachista hoffmanni* is known at the Fundo from a few foragers found inside a house plus a few foragers taken by Jaime Hurtubia. The species is known to nest only in hollow cavities of large shrub stems. Its rarity in the region is almost certainly a result of charcoal production by local residents, which has left few large stems. *Dorymyrmex chilensis* is known at the Fundo from a single nest located in a site that was cultivated pasture approximately 10-15 years ago.

One other species, *Solenopsis* sp., has been collected nearby and is probably present at the Fundo. It seems to be a soil-dwelling thief ant and is perhaps the smallest ant species in Chile. It might be found by intensive Burlese sampling.

In summary, then, some coexistence patterns of the sixteen ant species at Fundo Santa Laura were not difficult to explain. However a most important question remains unanswered. That question, of course, concerns actual overlap in food taken by the species. I will discuss this point in a following section.

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## THE ANTS OF ECHO VALLEY, CALIFORNIA

The primary North American study site for the Mediterranean Scrub Project is in Echo Valley, San Diego County, California. The site is approximately 65 km east of San Diego and 7 km north of Descanso on the Boulder Creek Road. The leased parcel of land includes well-developed chaparral (last burned in 1950) and a grove of large oaks (unburned for many years), mostly *Quercus agrifolia*. Detailed studies of the local geography, plant associations, weather, and microclimate are in preparation by other authors (Thrower and Bradbury, in preparation; Parsons, 1973; Carter, 1973; Miller, in preparation).

Forty-five species of ants (Table 8) have been collected from an area approximately .5 $km^2$. This is a surprisingly rich fauna for the area and habitat type (Snelling, personal communication). These species can be assigned to the five major groups introduced in Figure 1 as follows:

Group foragers, mobile prey: *Neivamyrmex nigrescens*

Group foragers, stationary prey: *Veromessor andrei*, *Pheidole* spp. (3)

Solitary foragers, no recruitment: none

Solitary foragers, poor recruitment: *Pogonomyrmex* spp. (2), *Leptothorax* spp. (4), *Pseudomyrmex apache*, *Conomyrma* spp. (2), *Camponotus* spp. (11), *Prenolepis imparis*, *Myrmecocystus* spp. (2), *Formica* spp. (2)

Solitary foragers, good recruitment: *Crematogaster californica*, *Iridomyrmex pruinosum*, *Liometopum occidentale*, *Tapinoma sessile*, *Camponotus dumetorum*, *Monomorium minimum*

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Table 8. Bait transect data for ants at Echo Valley, California. N = total number of bait observations; Obs. = number of observations per bait type where H = honey, T = tuna, PB = peanut butter; Freq. = frequency (%) of observations per bait type when N > 15 and where H = honey, T = tuna, PB = peanut butter; $\overline{X}$ = average number of foragers found per bait observation plus or minus one standard deviation.

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| | Obs. | | | | Freq. | | | |
|---|---|---|---|---|---|---|---|---|
| DORYLINAE | N | H | T | PB | H | T | PB | $\bar{X}$ |
| *Neivamyrmex nigrescens* (Cresson) | 0 | 0 | 0 | 0 | | - | | - |
| MYRMICINAE | | | | | | | | |
| *Paramyrmica rugiventris* (M. Smith) | 0 | 0 | 0 | 0 | | - | | - |
| *Pogonomyrmex californicus* Mayr | 0 | 0 | 0 | 0 | | - | | - |
| *Pogonomyrmex subnitidus* Emery | 6 | 0 | 6 | 0 | | - | | 3.5(± 2.0) |
| *Stenamma californicum* Snelling | | | | | | | | |
| *Stenamma diecki* Emery | 3 | 0 | 0 | 3 | | - | | 1.0(± 0.0) |
| *Veromessor andrei* (Mayr) | 0 | 0 | 0 | 0 | | - | | - |
| *Veromessor stoddardi* Emery | 0 | 0 | 0 | 0 | | - | | - |
| *Pheidole californica* (Emery) | 32 | 14 | 8 | 10 | 43 | 25 | 31 | 20.1(±20.3) |
| *Pheidole hyatti* Emery | 27 | 10 | 9 | 8 | 37 | 33 | 30 | 21.3(±20.8) |
| *Pheidole pilifera pacifica* Wheeler | 0 | 0 | 0 | 0 | | - | | - |
| *Crematogaster californica* (Emery) | 46 | 6 | 34 | 6 | 13 | 73 | 13 | 26.4(±34.0) |
| *Crematogaster mormonum* Emery | 0 | 0 | 0 | 0 | | - | | - |
| *Crematogaster noctourna* Buren | 0 | 0 | 0 | 0 | | - | | - |
| *Monomorium minimum* (Buckley) | 16 | 1 | 3 | 12 | 06 | 18 | 75 | 12.3(±13.3) |
| *Solenopsis molesta* (Say) | 0 | 0 | 0 | 0 | | - | | - |
| *Leptothorax andrei* Emery | 29 | 6 | 1 | 22 | 20 | 03 | 76 | 1.3(± 0.8) |
| *Leptothorax gallae* M. Smith | 0 | 0 | 0 | 0 | | - | | - |
| *Leptothorax nevadensis* Wheeler | 8 | 0 | 0 | 8 | | - | | 2.2(± 1.0) |



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| | Obs. | | | | Freq. | | | |
|---|---|---|---|---|---|---|---|---|
| | N | H | T | PB | H | T | PB | $\overline{X}$ |
| *Leptothorax rugatulus* Emery | 3 | 3 | 0 | 0 | | - | | 1.3(± 0.5) |
| PSEUDOMYRMICINAE | | | | | | | | |
| *Pseudomyrmex apache* Creighton | 0 | 0 | 0 | 0 | | - | | - |
| DOLICHODERINAE | | | | | | | | |
| *Iridomyrmex pruinosum* (Roger) | 72 | 35 | 23 | 14 | 48 | 32 | 19 | 32.9(±38.1) |
| *Conomyrma bicolor* (Wheeler) | 0 | 0 | 0 | 0 | | - | | - |
| *Conomyrma insana* (Buckley, 1866) | 31 | 9 | 18 | 4 | 29 | 58 | 13 | 3.6(± 4.7) |
| *Liometopum occidentale* Emery | 106 | 43 | 57 | 6 | 40 | 54 | 05 | 16.2(±15.6) |
| *Tapinoma sessile* (Say) | 195 | 74 | 91 | 30 | 38 | 47 | 15 | 14.7(±19.8) |
| FORMICINAE | | | | | | | | |
| *Camponotus* (Camponotus) *quercicola* M. Smith | 0 | 0 | 0 | 0 | | - | | - |
| *Camponotus* (Camponotus?) *n.sp. 395* | 0 | 0 | 0 | 0 | | - | | - |
| *Camponotus* (Myrmaphaenus) *n.sp.* | 0 | 0 | 0 | 0 | | - | | - |
| *Camponotus* (Myrmentoma) *anthrax* Wheeler | 47 | 25 | 22 | 0 | 53 | 47 | 0 | 4.2(± 3.3) |
| *Camponotus* (Myrmentoma) *clarithorax* Emery | 0 | 0 | 0 | 0 | | - | | - |
| *Camponotus* (Myrmentoma) *n.sp.* | 0 | 0 | 0 | 0 | | - | | - |
| *Camponotus* (Myrmentoma) *hyatti* Emery | 1 | 0 | 1 | 0 | | - | | 2.0(± 0.0) |
| *Camponotus* (Myrmentoma) *nearcticus* Emery | 6 | 4 | 2 | 0 | | - | | 2.6(± 2.5) |
| *Camponotus* (Tanaemyrmex) *dumetorum* Wheeler | 56 | 7 | 48 | 1 | 12 | 86 | 01 | 12.9(±11.8) |
| *Camponotus* (Tanaemyrmex) *n.sp.*nr. *vicinus* Mayr | 0 | 0 | 0 | 0 | | - | | - |

| | Obs. | | | | Freq. | | | |
|---|---|---|---|---|---|---|---|---|
| | N | H | T | PB | H | T | PB | $\bar{X}$ |
| *Camponotus* (Tanaemyrmex) *semitestaceous* Emery | 47 | 10 | 35 | 2 | 21 | 74 | 04 | 1.8(± 1.6) |
| *Camponotus* (Tanaemyrmex) *vicinus* Mayr | 0 | 0 | 0 | 0 | | - | | - |
| *Prenolepis imparis* Say | 5 | 3 | 1 | 1 | | - | | 1.4(± 0.9) |
| *Acanthomyops californica* (Wheeler) | 0 | 0 | 0 | 0 | | - | | - |
| *Myrmecocystus flaviceps* Wheeler | 2 | 1 | 1 | 0 | | - | | 1.5(± 0.7) |
| *Myrmecocystus testaceus* Emery | 12 | 9 | 3 | 0 | | - | | 1.9(± 1.5) |
| *Formica occidua* Wheeler<br>*Formica pilicornis* Emery | 106 | 43 | 57 | 6 | 40 | 54 | 06 | 2.9(± 3.9) |
| *Polyergus breviceps* Emery | 0 | 0 | 0 | 0 | | - | | - |



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Foraging habits unknown: *Crematogaster* spp. (2), *Acanthomyops californicus*, *Polyergus breviceps*, *Veromessor stoddardi*, *Solenopsis molesta*, *Paramyrmica rugiventris*.

Assignment of species to poor and good recruitment classes was made at an average of 10 ants per bait observation for those species found on baits (Table 8). Other assignments to groups were based on direct observation or, in a few cases, on probable similarity to congeners whose habits are known. The species whose foraging habits are unknown are mostly uncommon or rare in Echo Valley.

A different analysis of species assortment is illustrated in Figure 11. The figure shows a 160 m transect running from an oak grove into the chaparral. Above the sketch are illustrated the collection records of ants that came to baits placed along the transect. As can be seen, the species can be grouped by habitat preference. There are species associated with the oak grove, with the area of bare soil and *Eriogonum*, and with the chaparral. Other species are distributed across two or more habitats. The following, then, is a grouping of the ant fauna according to habitat preference. All species collected at the site are included.

Oak woodland habitat: *Liometopum occidentale*, *Leptothorax rugatulus*, *Camponotus* n.sp., *C. quercicola*, *C. clarithorax*, *Prenolepis imparis*, *Paramyrmica rugiventris*, *Crematogaster mormonum*, *C. noctourna*

*Eriogonum* habitat: *Pogonomyrmex subnitidus*, *P. californicus*, *Veromessor andrei*, *V. stoddardi*, *Iridomyrmex pruinosum*, *Myrmecocystus testaceus*, *M. flaviceps*, *Camponotus semitestaceus*, *Pheidole hyatti*, *Monomorium minimum*

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Figure 11. Habitat distribution of 23 ant species in Echo Valley, California. The array of dots illustrates actual collection records for the species at baits placed along the transect illustrated.

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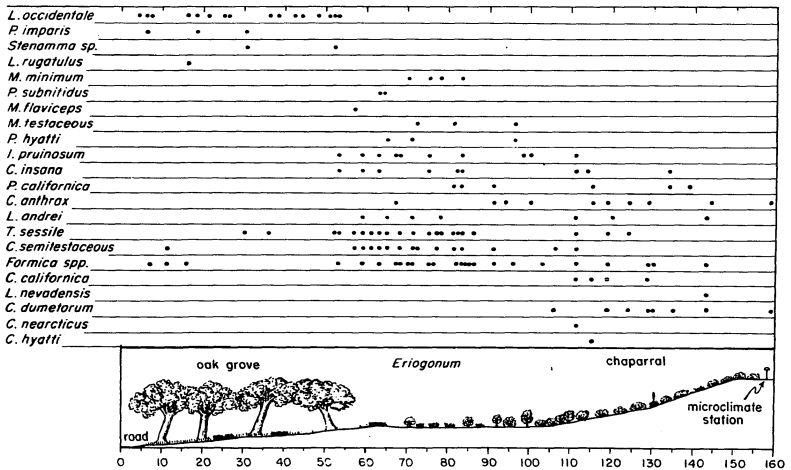


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Chaparral habitat: *Crematogaster californica*, *Camponotus dumetorum*, *Leptothorax nevadensis*, *Pseudomyrmex apache*, *Camponotus nearcticus*, *C. hyatti*

A group of species can be recognized that includes species found outside the oak grove that apparently do not distinguish between *Eriogonum* and Chaparral habitats. These include *Pheidole californica*, *Leptothorax andrei*, *Conomyrma insana*, *Camponotus anthrax*, *Camponotus n.sp. 395*.

Species distributed in all habitats are *Formica* spp. (2) and *Tapinoma sessile*.

Species for which too few records are available to determine habitat preference are *Pheidole pilifera pacifica*, *Leptothorax gallae*, *Polyergus breviceps*, *Camponotus n.sp.*, *C. vicinus*, *C. n.sp.* nr. *vicinus*, *Acanthomyops californica*, *Neivamyrmex nigrescens*, *Stenamma* spp. (2), *Conomyrma bicolor*, and *Solenopsis molesta*.

The two assortments (by strategy group and by habitat) can be considered simultaneously. They can be combined, along with criteria of polymorphism, to yield the groupings of species shown in Figure 12. These groups are considered in detail in the following paragraphs.

Oak woodland, poor recruitment, monophasic allometry: *Camponotus quercicola*, the largest species encountered in this study, is apparently a generalized forager that restricts its activities to sites on or very near the large oak trees. It forages only at night; no foragers have been seen even in twilight hours. *Camponotus n.sp.* and *C. clarithorax* are much smaller than *C. quercicola*. They, too, restrict their activities to sites on or near the large oaks, but foragers of both species have been seen

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Figure 12. Ecological classification of common ants in Echo Valley, California. See text for explanation.

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HABITATS

| RECRUITMENT | OAK WOODLAND | *Eriogonum* | CHAPARRAL |
|---|---|---|---|
| POOR | Monomorphic:<br>*Leptothorax rugatulus*<br>Monophasic allometry:<br>*Camponotus n. sp.*<br>*Camponotus quercicola*<br>*Camponotus clarithorax*<br>*Prenolepis imparis* | Monophasic allometry:<br>*Pogonomyrmex subnitidus*<br>*Pogonomyrmex californicus*<br>*Myrmecocystus testaceus*<br>*Myrmecocystus flaviceps*<br>Polymorphic:<br>*Camponotus semitestaceus* | Monomorphic:<br>*Leptothorax nevadensis*<br>*Pseudomyrmex apache*<br>Monophasic allometry:<br>*Camponotus nearcticus*<br>*Camponotus hyatti* |
| GOOD | Monophasic allometry:<br>*Liometopum occidentale* | Monomorphic:<br>*Iridomyrmex pruinosum*<br>*Monomorium minimum*<br>Monophasic allometry:<br>*Veromessor andrei* | Monomorphic:<br>*Crematogaster californica*<br>Polymorphic:<br>*Camponotus dumetorum* |

both by day and at night. I cannot discern a pattern of ecological separation for these two species. *Prenolepis imparis* has repletes in its soil nests (Talbot, 1943) and so certainly emphasizes honeydew in its diet.

*Eriogonum* habitat, poor recruitment, monophasic allometry: the *Myrmecocystus* species are honey ants (Wilson, 1972) having large repletes in their deep soil nests. *M. testaceous* is exclusively nocturnal in foraging habits; *M. flaviceps* forages only by day. The two *Pogonomyrmex* species are harvester ants (Cole, 1968) and emphasize seeds in their diets. Resource division between these two species is not clear, but *P. californicus* seems to prefer more disturbed sites than *P. subnitidus*. At the Echo Valley site *P. subnitidus* alone is found north of the main oak grove; its nests are found commonly in the untravelled fire roads through the chaparral. South of the main oak grove both species are found, with *P. californicus* nests being common in dirt roads that are travelled by vehicles almost daily. In a study in the Mojave Desert Bernstein (1971) found that *P. californicus* and *P. rugosus* do not differ in habitat preference, but that these two species show different preferred temperatures for foraging and have different elevations as centers of greatest abundance.

*Eriogonum* habitat, good recruitment, monomorphic: *Iridomyrmex pruinosum* is a small dolichoderine that swarms abundantly on baits. *Monomorium minimum* is a small myrmicine that does not form the distinct, active foraging columns characteristic of *Iridomyrmex*. Differential representation on the three bait types illustrates possible different food preferenda ($\chi^2=20.1$ $p<.001$).

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Chaparral habitat, poor recruitment, monomorphic: *Pseudomyrmex apache*, like all Pseudomyrmecines (D. H. Janzen, personal communication), is restricted to nesting in hollow stems of shrubs. It is almost exclusively arboreal in its foraging. *Leptothorax nevadensis* nests in soil and probably forages as an insinuator.

Chaparral habitat, poor recruitment, monophasic allometry: *Camponotus nearcticus* and *C. hyatti* are uncommon in Echo Valley. Resource separation between these two species is not clear at the study site. *C. nearcticus* was also found at a mountain study site; *C. hyatti* was also found at a coastal study site. Echo Valley may represent an area of range overlap in species that are typically separated by different altitudinal preference.

Field notes on all species are presented in Appendix D, and ecological segregation of congeneric species is discussed. The information presented in the preceding paragraphs and in Appendix D yields the same conclusion as for the ant species of Fundo Santa Laura, Chile. Ecological separation for most species is easily seen.

The analysis of ecological segregation as presented in the preceding paragraphs does not sufficiently cover ant ecology in Echo Valley. Habitat - oriented studies, as presented in the following paragraphs, yield a more complete picture.

Oak Grove Habitat

The most conspicuous and characteristic feature of ant ecology in the oak grove is the overwhelming numerical predominance of two species: *Liometopum occidentale*, a dolichoderine, and *Formica pilicornis*, a formicine. These diurnal species are abundant on the

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ground, climbing trunks of the oaks, and on the oak foliage. The two species seem to have little overlap in foraging territories. I censused 18 tree trunks, examining each for five minutes during morning hours from eye level to the ground, and noted all species found and their ranked abundance (Table 9). *Liometopum* was the most abundant species on seven trunks; *Formica* was the most abundant on ten; *Prenolepis imparis* was most abundant on one, with *Formica* second on that tree. One of the *Liometopum*-dominated trees had a few *Formica occidua* foragers. None of the *Formica*-dominated trees had any *Liometopum*. Six other species were found foraging in lesser abundances in the sampling. Their co-occurrence with the two abundant species did not appear haphazard and suggested that the two abundant species shared the trees they foraged with particular subsets of other species. A chi-square test for simple presence or absence of other species with the two dominants was highly significant ($\chi^2=7.61$; $p<.01$), indicating that *Formica* may actively be excluding subdominant species from the trees it controls. Further sampling was attempted in May, 1973, to validate this conclusion, but no subdominants were seen foraging on any of the trees. The trees at this date were responding to the very wet winter by dropping almost all their old leaves and producing an abundant crop of new foliage. No aphids were found in a visual survey of several branches of the trees. I expect another sampling attempt in mid- or late summer, 1973, to be more successful.

On 3 February 1972, I placed 5 concrete slabs, approximately .3 $m^2$ and 5 cm thick, on the ground in the oak grove to investigate the possibility that the absence of stones suitable for soil-dwelling species to nest beneath might limit the presence of such

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Table 9. Collection records of ant species on 16 oak trees in Echo Valley, California, See text.

| Most Abundant Species | Other Species, Ranked |
|---|---|
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | - |
| *F. pilicornis* | *L. rugatulus* |
| *F. pilicornis* | *C. essigi>C. mormonum=P. imparis>L. rugatulus* |
| *L. occidentale* | *Camponotus sp.* |
| *L. occidentale* | *L. rugatulus>F. occidua* |
| *L. occidentale* | *L. rugatulus>C. essigi* |
| *L. occidentale* | *L. rugatulus>C. essigi* |
| *L. occidentale* | *L. rugatulus=C. essigi=C. nocturna* |
| *P. imparis* | *F. pilicornis>L. rugatulus=V. andrei= I. pruinosum* |

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species. On 24 April 1973, none of the slabs showed any ant activity beneath them. This may also indicate that conditions underneath were not sufficiently "mature" for colonization.

Ant species other than the dominants in the oak grove are generally small and inconspicuous (excepting the large nocturnal species). These small species frequent the leaf litter and loose soil. In general the oak grove habitat seems the most complex for ants in the region. It certainly is the habitat I understand the least.

*Eriogonum* Habitat

Ant species abundant in and characteristic of this habitat are harvesters, honey ants, and small dolichoderines. These same species or their congeners are abundant in and characteristic of arid habitats, particularly deserts, throughout the southwestern United States. This habitat in Echo Valley offers less plant cover than the other two habitats. Such plant cover would presumably offer some amelioration of microclimatic extremes. Such plant cover would also, it seems, offer opportunity for cryptiveness and avoidance of predation by lizards. It is not surprising to me, therefore, that the species common in the *Eriogonum* habitat all seem obviously resistant to lizard predation through one strategy or another.

Chaparral Habitat

A plot of chaparral 50 m on a side was marked into 25 subplots of 10 $m^2$. Seven of these were chosen for mapping and study: three matched pairs covering a range of plant cover values and a seventh that included a small pole-facing gully slope. In these plots 101 nest openings were located and marked (Table 10). The only clear

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inference, other than species presence and abundance, to be drawn from the table is that *Camponotus dumetorum* is more abundant in the plots having more open space among the shrubs (Spearman Rank Correlation, $r_s$=.756; p<.05). Other possible inferences of the sampling are that *Crematogaster californica* tends not to be found in the plots with more open space, and *Tapinoma sessile* seems associated with the pole-facing gully slope from these data. Such inferences as these require much more extensive sampling, however. My impression from my survey work in the region is that the first suggestion concerning *Crematogaster* is true, whereas that concerning *Tapinoma* is not.

Throughout the chaparral many ant species are found nesting under large stones. It seemed possible that some species might possibly be limited by a lack of suitable stones for nesting. To test this I placed 25 concrete slabs, approximately .3 $m^2$ and 5 cm thick, on the ground in the mapped plot. Ten slabs were placed in one randomly chosen member of each pair of mapped plots, and five slabs were placed in one half of the gully plot. The slabs were put in place on 3 February 1972, and I checked for ants beneath them on 24 April 1973. The data (Table 11) strongly indicate that stones both are used for nesting and are more suitable for nesting in plots with higher percent plant cover. Of the species found (Table 12), *Camponotus dumetorum* takes best advantage of the slabs offered.

In general it can be said that *C. dumetorum* is the most abundant species in chaparral in Echo Valley. All species commonly found in chaparral (except *Pseudomyrmex* spp. and *Neivamyrmex* spp.) seem to be generalized scavengers.

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Table 10. Assortment of 101 ant nests censused in seven 10 $m^2$ study plots in chaparral, Echo Valley, California.

| Plot | B5 | B4 | E1 | F1 | B2 | C2 | F5 |
|---|---|---|---|---|---|---|---|
| % plant cover | 40 | 50 | 65 | 70 | 85 | 85 | 80 |
| *Camponotus dumetorum* | 16 | 19 | 10 | 2 | 6 | 6 | 8 |
| *Camponotus anthrax* | | 1 | 4 | 5 | | | |
| *Crematogaster californica* | | | 2 | 1 | 1 | 6 | |
| *Leptothorax nevadensis* | 1 | | 2 | 1 | | | 1 |
| *Iridomyrmex pruinosum* | | | | 1 | | | |
| *Tapinoma sessile* | | | | | | | 4 |
| *Conomyrma insana* | | | | | | | 1 |
| *Camponotus sp. 395* | | 1 | | | | | 2 |
| Total Nests | 17 | 21 | 18 | 10 | 7 | 12 | 16 |

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Table 11. Summary of data from slabs placed in chaparral as potential nest sites. Ants = ants present beneath slabs; Galleries = galleries present beneath slabs. See text.

| Plot | C2 | F1 | B5 | F5(gully) |
|---|---|---|---|---|
| % Cover | 85 | 70 | 40 | 75 |
| Ants | 7 | 3 | 0 | 1(per ½ plot) |
| Galleries | 9 | 4 | 3 | 2(per ½ plot) |

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Table 12. Summary of data from slabs placed in chaparral as potential nest sites. N = number of slabs under which each species listed was found.

| | N |
|---|---|
| *Camponotus dumetorum* | 6 |
| *Camponotus sp. 395* | 3 |
| *Crematogaster californica* | 1 |
| *Leptothorax nevadensis* | 1 |

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## COMPARISON OF CHILE AND CALIFORNIA

In the preceding two sections I have detailed the descriptive ecology of ants at two sites. A primary aim of these studies has been to compare these sites, presenting each as a representative sample of its biogeographic region. This work represents the first direct comparative study of two such widely separated ant faunas (E. O. Wilson, personal communication). A best departure point for the comparison, then, is an overview of the regional faunas from which the study site faunas are drawn.

Chile and California are the political geographic regions in which the two sites are situated. Faunal surveys of these regions are available and serve as a basis for comparison. Fifty-eight species of ants are known from Chile (Appendix A). Two hundred and four are known from California (Appendix C). This rather large difference parallels the study site results (16 species vs. 45 species) and requires further discussion. I shall examine several factors in turn.

AREA AND LATITUDE. The larger area (Chile=741,958 $km^2$; California=411,121 $km^2$) and greater latitudinal extent of Chile are factors that would favor a larger fauna, not a smaller one. Even if the northern one-third of Chile is dismissed as unsuitable for ants (a not too unreasonable assumption), the factors of area and latitude do not seem candidates for explanation of the difference.

COLLECTING BIAS. It might seem likely that Chile has been less intensively surveyed than California. Kempf's (1970) catalogue listed only 56 species for Chile, several of questionable status. After my own intensive field survey plus a careful museum

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survey by R. R. Snelling, the faunal list for Chile is 58 species. I feel that future survey work in Chile will reveal only a few additional species, and these will be sibling species or semi-species related to known forms, cryptobiotic species (species that nest and forage in concealed sites), or perhaps outliers of other South American species in poorly collected regions of the Andes. I should also point out that my survey work in southern California has been limited to only a few sites in a small geographic area, yet my studies there have involved three previously known but undescribed species, established range extensions of several other species, and revealed another new species previously unknown to myrmecologists (Snelling, in preparation). I feel, then, that collecting bias cannot be the explanation of the faunal differences.

ISLAND EFFECTS. Biogeography has been revitalized in recent years by the insular equilibrium theories of MacArthur and Wilson (1967). Their ideas have found application not only in reference to actual islands (Heatwole and Levins, 1972; MacArthur, Diamond, and Karr, 1972; Simberloff and Wilson, 1969, 1970) but also to such diverse "islands" as mountaintops (Brown, 1971; Vuilleumier, 1970) and plant species (Janzen, 1968). Considering Chile and California as islands, it becomes immediately apparent that, in terms of the island model, Chile is more "distant" from continental source areas than is California. The Atacama Desert and the Andes are stark, often lifeless barriers bounding much of Chile. The corresponding deserts and mountains that bound California certainly are not so barren. The degree of effectiveness of the barriers surrounding Chile, however, is open to speculation. Most ant species have winged reproductives that are highly motile. Some kinds of ants

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are frequent and abundant colonizers of true islands (Levins, Pressick, and Heatwole, 1973). Only army ants and some species of genera such as *Tapinoma* and *Iridomyrmex* do not have winged queens and would be unable to cross these barriers. There are 31 army ant species, for example, known from Argentina (Kusnezov, 1953) but none from Chile (Snelling and Hunt, in preparation). California has 8 army ant species, which comprise 3.9% of the total California fauna. It seems, then, that desert and mountain barriers may explain the absence of army ants in Chile. Such barriers may also have some isolating effect on the total Chilean ant fauna. For example, such widespread genera as *Pheidole* and *Crematogaster* are not represented in Chile. [There is a single record for *Pheidole* from Arica in the Atacama Desert.] The full extent of the isolation, however, is unknown. I do not feel that island isolation effects alone are sufficient to explain the magnitude of the difference between Chile and California.

FAUNAL DIFFERENCES. California and Chile are in different biogeographic realms. Faunal differences between the Nearctic and Neotropical realms might therefore contribute to the observed differences between the study regions. Table 13 presents the numbers of ant species per subfamily for Chile, California, Tucuman (Argentina), and Arizona (United States). Proportional representation of species per subfamily was tested both between and within biogeographic realms using the data of Table 13. Chi-square values and associated probabilities are presented in Table 14. The results of this testing are of interest. The strongest similarities are seen between the comparative areas within biogeographic realms. The strongest difference is between the summed faunas for the

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Table 13. Numbers of ant species assorted by subfamilies for four comparative geographic regions. Ca = California; Ch = Chile; Az = Arizona; Tu = Tucuman; ChCa = Chile + California; CaAz = California + Arizona; AzTu = Arizona + Tucuman; TuCh = Tucuman + Chile.

| | Ch | Ca | Az | Tu | ChCa | CaAz | AzTu | TuCh |
|---|---|---|---|---|---|---|---|---|
| Ponerinae | 7 | 6 | 6 | 20 | 12 | 11 | 26 | 26 |
| Dorylinae | 0 | 8 | 16 | 6 | 8 | 19 | 22 | 6 |
| Myrmicinae | 19 | 94 | 90 | 72 | 113 | 151 | 160 | 91 |
| Pseudomyrmicinae | 2 | 2 | 2 | 4 | 4 | 2 | 6 | 6 |
| Dolichoderinae | 13 | 8 | 9 | 19 | 20 | 9 | 26 | 31 |
| Formicinae | 17 | 86 | 53 | 16 | 103 | 110 | 69 | 33 |
| Total | 58 | 204 | 176 | 137 | 260 | 302 | 309 | 193 |

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Table 14. Chi-square values and associated probabilities for comparisons of geographic areas as given in Table 13. See text.

| | $X^2$ | p< |
|---|---|---|
| Ca/Az | 8.63 | .20 |
| Ch/Tu | 15.48 | .01 |
| ChCa/AzTu | 23.64 | .001 |
| Ch/Az | 29.58 | .001 |
| Ch/Ca | 34.67 | .001 |
| Ca/Tu | 52.80 | .001 |
| CaAz/TuCh | 62.29 | .001 |

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biogeographic realms. Biogeographic effects, therefore, may be considerable. It is noteworthy, however, that comparison of the summed climatic regions (Mediterranean=ChCa; Desertic=AzTu) yields a chi-square value less than half that of the biogeographic realms comparison. This is suggestive that faunal similarities may be associated with climatic regime and are not obscured by biogeographic setting.

A better comparison of taxonomic similarity can be obtained at the generic level. Table 15 shows a breakdown of the numbers of genera in the Chilean and Californian faunas. Note that more than one-fourth of the Chilean genera are not found in North American, and more than one-third of the California genera are not known from South America. Of the ten Chilean genera also found in North America, ten are represented by species in California. Of the twenty-one California genera also found in South America, eleven are not represented in Chile.

The ten shared genera have widespread distributions on the two continents, typically with numerous species in each genus. That these genera are shared between California and Chile is not surprising, then, but points out an important confounding factor in taxonomic comparisons: similarities between any two areas are frequently based on widespread genera typically represented by abundant species that are relatively important in their respective communities. Dissimilarities between any two areas are frequently based on less widely dispersed genera represented by species that are typically relatively unimportant in their respective communities. In summary, Chile and California show faunal similarities based on common, widespread genera and show faunal dissimilarities associated

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Table 15. Ant genera of California and Chile grouped according to biogeographic distribution. A = ant genera found in North or South America but not both; B = genera found in North America and northern South America; C = genera found in both North and South America; D = exotic genera of Old World origin. Assignment of genera to categories follows Brown (1973).

| | A | B | C | D | Total |
|---|---|---|---|---|---|
| California | 11 | 5 | 21 | 4 | 41 |
| Chile | 7 | 1 | 10 | 1 | 19 |

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with the biogeographic realms in which the study regions are located.

FUNCTIONAL DIFFERENCES. Comparison of the ants of Fundo Santa Laura and of Echo Valley has revealed many similarities. The species encountered most abundantly on baits in each area are *Tapinoma* species. The most visibly conspicuous diurnal terrestrial foragers in each area are *Camponotus* species of the subgenus Tanaemyrmex. *Conomyrma bicolor* of California and *Dorymyrmex antarcticus* of Chile could not be distinguished if seen together in the field. Each area has honeydew-gathering species with "honeypot" repletes. Neither area has solitary or specialist predators among the ant species. Neither area has fungus gardening ants. The abundance of generalist scavengers in each area yields a strong impression of similarity between the two areas. The strongest similarities, however, are noted to be among species of the common, widespread genera mentioned previously. The greatest differences between the areas are attributable to species in genera not shared between the two areas. Thus any comparisons of similarity are confounded by taxonomic constraints.

Another aspect of functional comparison between the two areas involves rates of species turnover or replacement from site to site in the two regions. For this purpose collections were made at a mountain (2000 m) site, a coastal sage site, and a coastal sage-with-succulents site in each region. Figures 13 and 14 show the locations of these study sites. Tables 16 and 17 list the species collected at those sites. (Species not named are grouped with congeneric ecological equivalents.) These data show that the intermediate elevation site in each region has the richest fauna. More

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Figure 13. Study site localities in Chile. Primary site = Fundo Santa Laura; mountain site = Cerro Robles; coastal sage site = Zapallar; coastal sage-with-succulents site = Los Molles.

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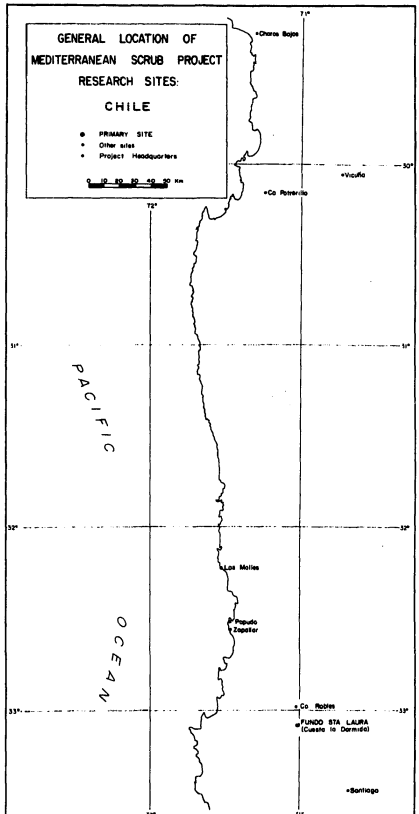


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Figure 14. Study site localities in California. Primary site = Echo Valley; mountain site = Mt. Laguna; coastal sage site = Camp Pendleton; coastal sage-with-succulents site = Punta Banda.

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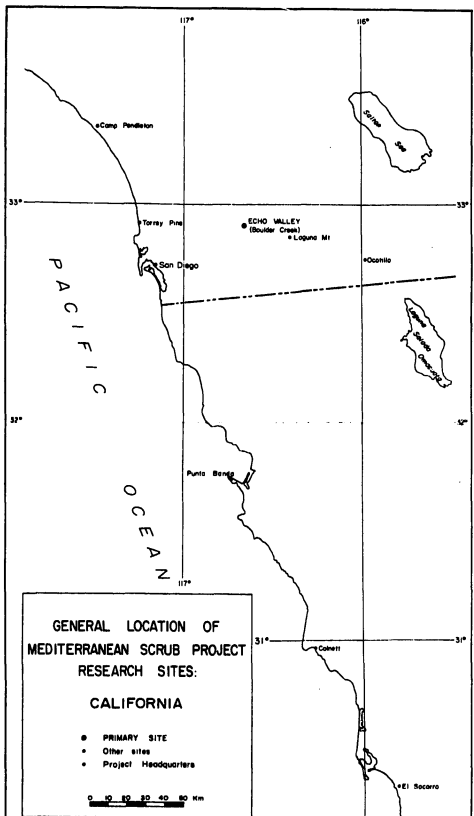


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Table 16. Elevational distribution and macrohabitat association of ant species collected at four sites in Chile. M = mountain site; P = primary site; Cs = coastal sage site; Cu = coastal sage-with-succulents site. See Text.

| | M | P | Cs | Cu | |
|---|---|---|---|---|---|
| *Lasiophanes hoffmanni* | | x | | | |
| *Lasiophanes picinus* | | x | | | woodland |
| *Pogonomyrmex angustus* | x | x | | | |
| *Nothidris bicolor* | x | x | | | |
| *Myrmelachista* spp. | x | x | | | |
| *Camponotus chilensis* | x | x | | | |
| *Solenopsis latastei* | x | x | x | | |
| *Solenopsis* sp. | x | | x | | |
| *Dorymyrmex* spp. | x | x | x | x | |
| *Tapinoma antarcticum* | x | x | x | x | matorral |
| *Brachymyrmex giardii* | | x | x | x | |
| *Pogonomyrmex bispinosus* | | x | x | x | |
| *Solenopsis gayi* | | x | x | x | |
| *Camponotus distinguendis* | | x | x | x | |
| *Pseudomyrmex lynceus* | | x | | x | |
| *Brachymyrmex levis* | | x | | | |

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Table 17. Elevational distribution and macrohabitat association of ant species collected at four sites in California. M = mountain site; P = primary site; Cs = coastal sage site; Cu = coastal sage-with-succulents site. See text.

| | M | P | Cs | Cu | |
|---|---|---|---|---|---|
| *Paxamyrmica rugiventris* | | x | | | |
| *Crematogaster noctourna* | | x | | | |
| *Camponotus clarithorax* | | x | | | |
| *Formica pilicornis* | | x | | | |
| *Polyergus breviceps* | x | x | | | woodland |
| *Crematogaster mormonum* | x | x | | | |
| *Leptothorax rugatulus* | x | x | | | |
| *Liometopum occidentale* | x | x | | | |
| *Camponotus quercicola* | x | x | | | |
| *Prenolepis imparis* | | x | x | | |
| *Camponotus n.sp.* | x | x | | | |
| *Pogonomyrmex submitidus* | x | x | | | |
| *Camponotus semitestaceous* | x | x | | | |
| *Camponotus vicinus* | x | x | | | |
| *Acanthomyops californicus* | x | x | | | |
| *Monomorium minimum* | x | x | x | | |
| *Solenopsis molesta* | x | x | x | | |
| *Neivamyrmex* spp. | x | x | x | | |
| *Conomyrma bicolor* | x | x | x | | |
| *Tapinoma sessile* | x | x | x | | |
| *Pheidole hyatti* | x | x | x | x | |
| *Crematogaster californica* | x | x | x | x | |
| *Conomyrma insana* | x | x | x | x | |
| *Formica occidua* | x | x | | x | |
| *Camponotus nearcticus/ C. hyatti* | x | x | | x | |
| *Leptothorax andrei* | | x | x | | chaparral |
| *Pseudomyrmex apache* | | x | x | | |
| *Pheidole californica/ P. clementensis* | | x | x | | |
| *Veromessor andrei* | | x | x | x | |
| *Camponotus n.sp.* | | x | x | x | |
| *Myrmecocystus* spp. | | x | x | x | |
| *Camponotus dumetorum/ C. festinatus* | | x | x | x | |
| *Solenopsis xyloni* | | | x | x | |
| *Veromessor stoddardi* | | x | | | |
| *Leptothorax nevadensis* | | x | | | |
| *Iridomyrmex pruinosum* | | x | | | |
| *Camponotus n.sp. 395* | | x | | | |
| *Camponotus anthrax* | | x | | | |
| *Stenamma californicum* | | x | | | |
| *Stenamma diecki* | | x | | | |
| *Pheidole pilifera pacifica* | | x | | | |
| *Camponotus n.sp.nr. vicinus* | | x | | | |
| *Pogonomyrmex californicus* | | x | | | |
| *Leptothorax gallae* | | x | | | Unknown |

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time and care were spent collecting at these two sites, but the lists for the secondary sites are felt to be nearly complete nevertheless.

Very few species were collected at secondary sites in either region that were not also collected at the primary site. In each region one species was collected at the mountain and coastal sage sites but not the primary site. Absence of these species at the primary site most probably reflects insufficient collecting rather than a real discontinuity. The other Chilean species collected at secondary sites but not the primary site are congeneric with a species that is at the primary site and appear to be ecological equivalents with their congeners. The same is true in California with only one exception: *Solenopsis xyloni* is abundant at the coastal sites but has no ecological equivalent at the primary site.

In tables 16 and 17 congeneric ecological equivalents are grouped, and species are listed according to collection locality. These tables illustrate several important points. A large component of the species richness at the primary sites is attributable to habitat diversity. Species shared with the mountain sites typically are woodland species. This would be expected, as woodland is the common habitat at the mountain sites. Species shared with the coastal sites are typical of matorral, chaparral, or open habitats. No woodland habitat is present at the coastal sites. The species that are found at all sites in either region are typically found in open or disturbed habitats.

The ant species in Tables 16 and 17 are clearly distributed in the same pattern as their preferred habitats. Elevation per se, at least over a 2,000 m span, has little effect. High species

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richness at intermediate elevations is largely a result of habitat variety and richness. Another component of the intermediate elevation species richness may be that these sites do not show the climatic extremes of the other sites: summer xeric extremes at the coastal sites and winter cold extremes at the mountain sites. None of the secondary sites, however, is faunistically distinct from its corresponding primary site. Only one species, *Solenopsis xyloni* in coastal California, represents an adaptive strategy not exploited at the primary site. With this exception, the patterns of species distribution across an elevational range are nearly identical in California and Chile.

At this point, then, the ants at study sites in Chile and California seem very similar in every aspect of ecological comparison except one: species richness. The greater abundance of ant species in California remains largely unexplained. Some theoretical development is necessary before dealing with this last point of comparison.

THE STRUCTURE OF FAUNAL ASSOCIATIONS. Imagine an association in which several consumers are harvesting resources, with each consumer harvesting in a unique way. That is, each consumer would represent a different guild. There are three ways in which more consumers might be added to such a community.

First, a species not previously a part of the association can appear and exploit a portion of the available resources in a manner similar to one of the species already present. One of the guilds would then contain two species. Second, a species can appear and exploit a portion of the resource base in a manner not represented by any of the species already present. That is, the invading species

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would define a new guild. Third, a species can appear and consume one or more of the consumer species already present as its resource. The new species would be a predator at the next higher trophic level and would also have defined a new guild.

If ants are now considered as a concrete example, it can be seen that the latter two patterns of species addition have been of minor importance in the communities I have studied. Ants that prey on ants (dorylines) are uncommon. Species that exploit a unique food resource in a distinctive manner are few in number. Most of the species studied are food generalists and apparently overlap broadly in resources consumed. For most of the species studied, food may represent a fine grained resource. The addition of species to an association by addition of species to an existing guild is therefore the most important pattern in the ant communities I have studied.

Theoretical exploration of the number of species within a guild that are supportable by a given resource spectrum falls in the subject area of species packing. Models of species packing have been formalized mathematically by Levins (1968), MacArthur (1969, 1970, 1972), MacArthur and Levins (1967), and others. In a graphical and mathematical analysis of patchy distributions and relative species abundances, MacArthur (1972: pp. 233-235) introduces four predictions that are of interest and possible significance in regard to the present study:

1. Where species are not closely packed, similar habitats will have similar species with only slight differences in abundance.

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2. Where species are very closely packed, similar habitats may be occupied by very different collections of species; that is, distributions are patchy.

3. Where species are very closely packed, similar habitats may be occupied by very different numbers of species.

4. A fluctuating environment sets a limit to the closeness of packing; the greater the fluctuations, the less close the packing can be.

SPECIES PACKING IN CHILE AND CALIFORNIA. Analysis of species packing should ideally be focused on interspecific distances and overlaps along some axis of niche space. Among ants, habitat overlap values are rendered nearly meaningless by differences in foraging strategy. Species of dissimilar foraging strategy frequently overlap broadly in habitat; species of similar foraging strategy frequently partition habitat in either time or space. The most realistic measure of interspecific distances and overlaps, then, would be an analysis of food actually taken by the species. Food habits of ants, however, particularly of generalist scavengers, are nearly impossible to determine in detail. E. O. Wilson (personal communication) concurs in my opinion that this is the most difficult (if not impossible) part of ant field studies. In lieu of food habit studies I hope in the future to be able to assess the contribution of foraging strategy to within-habitat segregation. Much field work remains to be done, though, before even rough estimates can be made. For the present, then, I must rely on qualitative assessment of MacArthur's four predictions.

The first two predictions concern the patchiness of distributions among similar habitats. One instance of such patchiness has

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been noted in this study. *Solenopsis xyloni* is a common soil-nesting generalized scavenger at the California coastal sites, but it is not found at the primary site. Five species of soil-nesting *Camponotus* are found at the primary site, but none of these are found at either coastal site. One soil-nesting *Camponotus* species is found at the coastal sage-with-succulents site, but this species is not found at any other study site. It seems possible to me that *Solenopsis xyloni* and the five soil-nesting *Camponotus* species are mutually exclusive in chaparral habitat.

One clear instance of patchy distribution within a habitat has been noted in this study, also in California. The phenomenon of the association of subdominant species with *Formica pilicornis* and *Liometopum occidentale* on oaks illustrates a pattern of within-habitat patchiness, although that pattern requires more careful documentation. A similar, clearly defined pattern of patchy distributions has been documented in the very rich ant fauna of Ghana (Room, 1971).

MacArthur's third prediction concerns numbers of species within a habitat. The data of Tables 16 and 17 are useful here. Numbers of woodland species can be compared between the mountain and primary sites. The totals for Chile are 4 vs. 6; the totals for California are 5 vs. 10 species. The woodland habitat values show somewhat greater difference among California sites. Chaparral or matorral habitats can be compared among the primary and the two coastal sites. The totals for Chile are 9:8:7; the totals for California are 28:14:10. The chaparral and matorral values illustrate clearly different species numbers among California sites but similar species numbers among sites in Chile.

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From these qualitative measures, then, one may reason conversely that ant species in California are more closely packed than are species at corresponding sites in Chile. This led me to speculate, in regard to MacArthur's fourth prediction, that Chile might have greater climatic (rainfall) fluctuations than does California. In fact, with reference to Colwell's (in press) analysis of periodic phenomena, the year to year predictability is lower in Chile, with low contingency being the key source of low predictability in these unconstant seasonal environments. V. C. LaMarche (personal communication) confirms this climatic difference based on his studies of tree rings in the two areas.

According to D. H. Janzen (personal communication), increased within-year climatic fluctuations could increase the potential for species richness. If species assort themselves according to temperature preferenda, then increased amplitude of daily and within-year temperature fluctuations could yield higher species richness if predictability, based on contingency, were sufficiently high. The studies of Miller (in preparation) and Miller, Roberts, and Hynum (in preparation) have confirmed that the California sites indeed have greater daily and within-year temperature amplitudes than do the Chilean sites. The contingency and predictability of these fluctuations has not yet been calculated.

The tentative conclusion, then, is that the greater ant species richness in California has several components. Biogeographic setting and the isolation of Chile contribute in part. This isolation would yield a lower species immigration curve that would result in a lower species equilibrium number [Ch(1) in Figure 15)] than for California (Ca in Figure 15). It is possible, however,

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that this is insufficient explanation for the very large threefold difference. I suggest, therefore, that species packing phenomena associated with the predictability and amplitude of climatic phenomena impose further constraints on Chilean species richness in the form of a higher extinction rate. This would yield an even lower species equilibrium [Ch(2) in Figure 15] that might more fully explain the observed difference.

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Figure 15. Island equilibrium model (after MacArthur and Wilson, 1967) for ant species numbers in Chile and California. See text for explanation.

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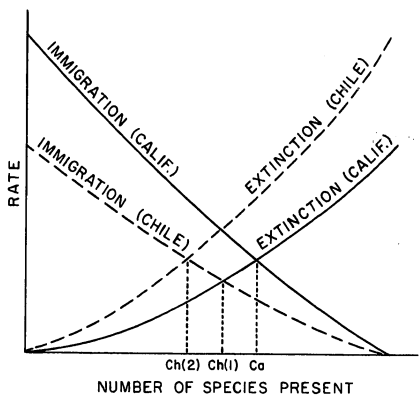


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## DISCUSSION

There are unquestionable parallels between the ant faunas of the study sites in California and Chile. The faunas are taxonomically similar. E. O. Wilson (personal communication) considers the similarities remarkably close. This suggests that the major climatic pattern (of the wet winter, dry summer Mediterranean type) defines an environment that has been exploited by similar faunistic stocks in the two areas. Patterns of behavior and resource exploitation by ants are similar in the two regions, but this primarily reflects the close association of taxonomy and ecology in ants. I do not feel that there is strong functional convergence between the two regions that is independent of taxonomic associations. The similar patterns of species turnover along altitudinal gradients reflects the very close association of ant species with their preferred habitats. It seems that habitat diversity may be the primary component of within-site ant species diversity in both Chile and California.

Habitat diversity determines ant species diversity, however, only to the extent that a mixture of several habitats brings different ant species associated with each habitat into proximity with one another. Ant diversity within a homogeneous habitat type is not well correlated with microhabitat diversity. Parsons (1973) has studied shrub species diversity and structural diversity at the study sites in the two regions. His findings show that Chilean shrub communities are more diverse in terms of both species and form than are comparative California communities. Ant species richness in these habitats is greater, however, in California.

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I feel that the proposed relationship of climatic fluctuation to the closeness of species packing is operative in these communities. The year-to-year predictability of rainfall could affect the basic feeding strategies of the species involved. The California fauna includes species that emphasize seed-gathering and homoptera-tending. The Chilean fauna, though taxonomically similar, apparently includes neither. It would be a perilous strategy to be a specialist where seed set or climatic suitability for growth of large aphid populations is unpredictable from year to year. Additionally, MacArthur (1972: p. 21) has said: "if food is scarce enough just 1 year in 20 to cause severe competition between two bird species, the inferior one is eliminated, and if the area of scarcity is large, the inferior species may take more than the next 19 years to reinvade." This suggests that climatic unpredictability could function in concert with the isolation of Chile to maintain low species numbers. The effect of low immigration rate would be reinforced by periodic extinctions. The extinction rate for ants may, in fact, be higher in Chile than California because of climatic unpredictability (see Figure 15).

The within-year and within-day temperature fluctuations could affect resource partitioning, especially among generalist scavengers. I have noted repeatedly in my studies that ant species are responsive to temperature, that each species has its apparent temperature preferendum, and that no species is sufficiently broad in temperature tolerance to be active over a broad range of temperatures. The greater amplitude of the fluctuations in California could indeed engender a finer partitioning of foraging activities than would be possible under the more constant Chilean regime.

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Resource partitioning among the ants I have studied involves four major components: food (though only at the level of identification of major groups or extreme specialists), nest site (the major component of habitat selection), foraging temperature preferendum, and foraging strategy. I suggest that future field ecological studies of ants emphasize and explore the contributions of temperature preference and foraging strategy to the within-habitat separation of species.

The suggested patchy distributions of *Solenopsis xyloni* and the soil-nesting *Camponotus* species and of the dominant-subdominant associations on oaks also deserve more careful study. Room (1971) reports that six ant species are numerically very abundant in cacao groves in Ghana and that these six species maintain mutually exclusive territories. This had been reported previously, but Room went further in carefully documenting subdominant species associations characteristic of each dominant's foraging area. The situation seems similar to the one that apparently exists with the two common species on oaks in Echo Valley. These species associations, particularly as detailed by Room, seem analogous to the alternate stable equilibria introduced by MacArthur (1972: pp. 247-251). The ant species associations are on a regional or microgeographic scale, whereas MacArthur proposed the alternate stable equilibria in discussion of faunal realms. Clearly these ant associations define systems that should be exploited more fully in the exploration of phenomena of coexistence in nature.

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# APPENDIX A

## Preliminary List of Chilean Ants†

### Subfamily PONERINAE

1. *Amblyopone chilensis* Mayr
2. *Amblyopone monrosi* Brown
3. *Heteroponera carinifrons* Mayr*
4. *Hypoponera opaciceps chilensis* (Forel)
5. *Hypoponera opacior* (Forel)
6. *Hypoponera* sp.
7. *Cylindromyrmex striatus* Mayr

### Subfamily MYRMICINAE

8. *Pogonomyrmex* (*P.*) *bispinosus* (Spinola)*
   a. var. *intermedia* Menozzi
   b. var. *semistriata* Emery
   c. var. *spinolae* Emery
9. *Pogonomyrmex* (*P.*) *vermiculatus* Emery
10. *Pogonomyrmex* (*Ephebomyrmex*) *angustus* Mayr*
11. *Pogonomyrmex* (*Ephebomyrmex*) *laevigatus* Santschi
12. *Pogonomyrmex* (*Ephebomyrmex*) *odoratus* Kusnezov*
13. *Pheidole* sp.
14. new genus *bidentatus* (Mayr)*
15. new genus *denticulatus* (Mayr)*
16. *Nothidris latastei* (Emery)
17. *Nothidris bicolor* Ettershank*
18. *Nothidris* n.sp.

† compiled by R. R. Snelling, from Snelling and Hunt (in preparation).
* species collected by J. H. Hunt

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19. *Monomorium floricola* (Jerdon)
20. *Solenopsis gayi* (Spinola)*
21. *Solenopsis germaini* Emery
22. *Solenopsis helena* Emery
23. *Solenopsis latastei* Emery*
24. *Solenopsis patagonica* Emery
25. *Solenopsis* sp.*
26. *Tetramorium caespitum* (Linne)
27. *Tetramorium guineense* (Fabricius)

Subfamily PSEUDOMYRMICINAE

28. *Pseudomyrmex* sp.
29. *Pseudomyrmex lynceus* (Spinola)*

Subfamily DOLICHODERINAE

30. *Iridomyrmex humilis* (Mayr)*
    a. var. *oblonga* Santschi
31. *Dorymyrmex antarcticus* Forel* (=sp.No.5)
32. *Dorymyrmex minutus* Emery
33. *Dorymyrmex chilensis* Forel* (=sp.No.6)
34. *Dorymyrmex tener* Forel* (=sp.No.2)
35. *Dorymyrmex mucronatus* Emery
36. *Dorymyrmex* sp. No.1*
37. *Dorymyrmex* sp. No.3*
38. *Dorymyrmex* sp. No.4*
39. *Dorymyrmex* sp. No.7*
40. *Dorymyrmex* sp. No.8*
41. *Tapinoma antarcticum* Forel*

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Subfamily FORMICINAE

42. *Lasiophanes hoffmanni* (Forel)*

43. *Lasiophanes nigriventris* (Spinola)

44. *Lasiophanes picinus* (Roger)*

    a. var. *bruchi* (Forel)

45. *Lasiophanes uxorius* (Emery)

46. *Lasiophanes valdiviensis* (Forel)

47. *Myrmelachista chilensis* Forel

48. *Myrmelachista hoffmanni* Forel*

49. *Myrmelachista mayri* Forel

    a. var. *Monticola* Mayr

50. *Myrmelachista rectinota* Forel*

51. *Brachymyrmex giardii* Emery*

    a. var. *nitida* Santschi

52. *Brachymyrmex levis* Emery*

53. *Camponotus chilensis* (Spinola)*

    a. var. *ovaticeps* (Spinola)

54. *Camponotus distinguendus* (Spinola)*

    a. var. *tenuipubescens* Santschi

55. *Camponotus morosus* (F. Smith)*

    a. var. *hellmichi* Menozzi

56. *Camponotus ruficornis* Emery

57. *Camponotus spinolae* Roger

58. *Paratrechina* sp.

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## APPENDIX B

### Field Notes on the Ants of Chile

#### Subfamily PONERINAE

The only ponerine that I encountered was *Heteroponera carinifrons*. Two colonies of these ants were found under stones in a mixed *Nothofagus* forest in Parque Nacional Nahuelbuta on 14 December 1972. The habitat is under snow at least six months of the year. Each nest had large, well-defined galleries. Larvae and pupae were collected. Galleries of one nest were closely adjacent to those of a colony of *Nothidris latastei* that was nesting under the same stone. I know nothing of the foraging habits of these ponerines.

#### Subfamily MYRMICINAE

*Pogonomyrmex*. I have encountered three species of *Pogonomyrmex* in Chile. *Pogonomyrmex* (*P.*) *bispinosus* is fairly common at Punta Los Molles, but it is not an abundant ant in the other areas I have visited. The species forages in an open, conspicuous fashion, as do North American *Pogonomyrmex* species. It seems to include seeds as a large but not exclusive part of its diet. The other two *Pogonomyrmex* I have collected are *P. angustus* and *P. odoratus*, both in the subgenus *Ephebomyrmex*. Colonies of both species of these black ants were found under stones in moist *Nothofagus* forest sites. The ants moved very slowly and seemed completely dissimilar ecologically from *Pogonomyrmex* (*Pogonomyrmex*) species. The *Ephebomyrmex* species were found in sites where seed harvesting would not seem a profitable endeavor.

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*Pheidole*. The only verified record of a species of this genus in Chile is of specimens taken in or near Arica in the heart of the Atacama Desert. I have not seen the species myself, and I am confident that *Pheidole* is probably not present in the central or southern regions of the country.

New Genus (formerly *Nothidris*). My only encounter with these species was in *Nothofagus* forests of southern Chile. *G.n. bidentatus* nests under stones and was noted to be a very slow moving ant. *G.n. denticulatus* was found more commonly. It nests commonly under stones; one colony was taken from a very wet, rotting log; one nest under a stone had a few moist carton partitions. Nothing is known about the foraging habits of these species.

*Nothidris*. A single *N. bicolor* forager was taken in woodland leaf litter at Fundo Santa Laura. I know nothing more about the species. The only species of this genus that I commonly encountered was *Nothidris latastei*, found in the southern *Nothofagus* forests. This handsome, bicolored species nests beneath stones. I know nothing of its foraging habits. Studies of resource division among the several similar ant species that nest beneath stones in *Nothofagus* forests would be a challenging ecological problem.

*Monomorium*. I did not encounter *Monomorium* during my studies.

*Solenopsis*. *Solenopsis gayi* is probably the most common ant species in Mediterranean regions of Chile. It is found throughout matorral habitats. These ants have large colonies and swarm aggressively on baits. Nests are in the soil, frequently under stones. Nest sites in matorral are frequently difficult to locate. I saw one mating swarm of this species on 15 November 1972, about 30 km south of Coquimbo. Male and female alates and many workers were

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swarming about the nest entrance about one hour after the first morning sun reached the nest. Within 15 minutes of my finding the swarm, all of the alates had flown. It was a warm, cloudless, windy day. *Solenopsis latastei* is a small species that nests in soil. I know very little about its foraging habits; it may be a thief ant. *Solenopsis* sp. is the smallest ant species I encountered in Chile. I found a small group of these in a cell about 10 cm below the soil surface. I was excavating a *Dorymyrmex* at the time. This species must almost certainly forage as a thief ant.

*Tetramorium*. I did not encounter ants of this genus during my studies.

Subfamily PSEUDOMYRMICINAE

*Pseudomyrmex*. *Pseudomyrmex lynceus* is encountered uncommonly in matorral habitats. It is an obligate hollow twig nester, though no well developed ant - plant mutualisms are known for this species. I found one colony nesting in dead *Puya* flower stalks at Punta Los Molles. I have also seen the ant foraging on several species of matorral shrubs.

Subfamily DOLICHODERINAE

*Iridomyrmex*. *Iridomyrmex humilis* is a common household pest in Mediterranean regions of the country. I found no colonies of this species in natural habitats.

*Dorymyrmex*. The genus *Dorymyrmex* poses perhaps the most complex (or at least widespread) taxonomic and ecological problems among the ants of Chile. The eight species now known from Chile are found throughout the central and southern regions of the country, and they are frequently difficult to distinguish from one another in

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the field. Most are bicolored red and black. *D. tener* is common atop Cerro Roble where it nests under large, exposed stones. It is a comparatively large species, and is the only *Dorymyrmex* I found that aggressively attacked and bit me when disturbed. Alates and workers were seen swarming about nest entrances atop Cerro Roble on 22 October 1972. The swarming was very late in the evening; the reproductives probably fly at night. The other *Dorymyrmex* species nest in soil, usually with a small crateriform tumulus about the nest entrance. *D. antarcticus* is common in matorral habitats northwest of Santiago. *D. sp.3* is common in coastal matorral north of Valpariso. *D. sp.1* is common in the deserts of the Norte Chico. *D. sp.4* was found in a dry desert valley near Vicuña together with *D. sp.1*. *D. sp.7* is known only from near Paposo, both in the fog forest and on the coastal flats. *D. sp.8* was found abundantly in a Monterrey Pine plantation in Cajon del Maipo. I encountered only one nest of *D. chilensis*, in a second-growth area at Fundo Santa Laura. I have not seen *D. minutus* or *D. mucronatus* during my studies.

*Tapinoma*. *Tapinoma antarcticum* is in some Mediterranean regions more common than *Solenopsis gayi*, but it is less widespread. The species is active in warm weather, moves rapidly in active columns, swarms on bait, and changes nest site frequently. It seems identical in every ecological comparison to *Iridomyrmex pruinosum* of the southwestern United States. In fact, Roy R. Snelling (personal communication) informs me that the two species are probably congeneric, with neither *Tapinoma* nor *Iridomyrmex* being the appropriate taxon.

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Subfamily FORMICINAE

*Lasiophanes*. These species nest in soil or in rotting wood on the soil surface and are found in forest habitats. These ants seem common only in the southern *Nothofagus* forests, and I know little of their foraging behavior. These ants probably emphasize honeydew in their foraging.

*Myrmelachista*. These species occur in Mediterranean regions of the country and are found nesting in hollow cavities of standing trees. Due probably to the wood-gathering habits of European man they are very, very uncommon. I found one colony of *M. hoffmanni* in a dead branch of a large *Lithrea caustica* and have found occasional strays in several sites plus strays of *M. rectinota*. I know nothing of their foraging ecology.

*Brachymyrmex*. These are small, inconspicuous, soil nesting ants. The two species in Chile are difficult to distinguish in the field. Both sometimes nest under stones and sometimes have large colonies. *B. giardii* has (at least in some colonies) "honeypot" repletes. I dug one nest of this species and found the repletes, their abdomens swollen to the size of a small pea, hanging from the roof of nest chambers about 30 cm below the soil surface. These species, then, would emphasize honeydew in their feeding.

*Camponotus*. *Camponotus* species are generalized scavengers. The two Chilean species that I am familiar with are soil-nesters of the subgenus *Tanaemyrmex*. *C. chilensis*, with its handsome golden gaster, is common in woodland and densely shrubby areas of the Mediterranean region. I also found it, however, in a *Salicornia* - sand dune area near Huasco and an *Acacia* - *Atriplex* desertic area near Copiapo. *C. distinguendis* is found in more open habitats throughout the

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Mediterranean region. Its behavior of running with the gaster held erect is easily observed if the ants are disturbed. I saw (but did not collect) a few *C. distinguendis* - like workers near Putre in the northern Andes. *C. distinguendis* has morphologically highly variable populations throughout Chile, and *C. morosus* could not be distinguished from among them. I did not encounter *C. ruficornis* or *C. spinolae* during my studies.

*Paratrichina.* I did not encounter these introduced ants during my studies.

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## APPENDIX C

### Ants of California - A List of the Genera[†]

PONERINAE - 6 species

*Amblyopone* 1

*Proceratium* 1

*Hypoponera* 3

*Odontomachus* 1

DORYLINAE - 8 species

*Neivamyrmex* 8

MYRMICINAE - 94 species

*Myrmica* 2

*Paramyrmica* 1

*Manica* 4

*Pogonomyrmex* 12

*Stenamma* 9

*Aphaenogaster* 5

*Novomessor* 1

*Pheidole* 18

*Cardiocondyla* 1

*Crematogaster* 7

*Monomorium* 2

*Solenopsis* 7

*Myrmecina* 1

*Leptothorax* 12

*Tetramorium* 2

*Xiphomyrmex* 1

[†] compiled by R. R. Snelling

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MYRMICINAE (Cont.)

*Trichoscapa* 1

*Smithistruma* 1

*Cyphomyrmex* 1

*Acromyrmex* 1

PSEUDOMYRMICINAE - 2 species

*Pseudomyrmex* 2

DOLICHODERINAE - 8 species

*Liometopum* 2

*Iridomyrmex* 2

*Forelius* 1

*Conomyrma* 2

*Tapinoma* 1

FORMICINAE - 86 species

*Brachymyrmex* 1

*Plagiolepis* 1

*Camponotus* 22

*Prenolepis* 1

*Paratrechina* 4

*Lasius* 7

*Acanthomyops* 3

*Myrmecocystus* 17

*Formica* 26

*Polyergus* 1

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## APPENDIX D

### Field Notes on Ants of Southern California

Subfamily DORYLINAE

*Neivamyrmex* - 2 species. These are army ants. They have legionary habits and are predaceous. Nest sites are temporary and include crevaces in soil and sites under stones. These ants, when seen above ground, run very rapidly in distinct columns. The single colony found at Pendleton was active during daylight. The single colony found at Echo Valley was active at night, which is typical for these uncommon ants. The Laguna record is of dead ants found under stones. These may have been casualties of a raid on a colony of *Crematogaster californica*, since several dead ants of this species were also found.

Subfamily MYRMICINAE

*Paramyrmica* - 1 species. Four nests of this rare ant have been found in Echo Valley. All were shallowly situated under small (fist-sized) stones in an oak grove. Food and foraging habits are unknown.

*Pogonomyrmex* - 2 species. These are the conspicuous red harvester ants familiar to most persons who go afield in southern California. Seeds are important in their diet. Nests of these species are in soil, typically in exposed areas. This is possibly due to a preference for insolation warmth. The ants are active during the day and forage the soil surface among chaparral shrubs as well as in more exposed areas. *P. subnitidus* is more abundant than

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*P. californicus* at the Echo Valley site, with *P. californicus* apparently in more disturbed sites.

*Stenamma* - 2 species. These small ants are represented by only a few strays picked up at the Echo Valley site. There has been no opportunity to study their ecology. Western North American species of *Stenamma* have recently been monographed by Snelling (1973b).

*Veromessor* - 2 species. *V. andrei*, like the similar looking *Pogonomyrmex* species, is a conspicuous crepuscular seed gatherer. Of the large harvesters studied, this species forms the most distinct columns, and its nests in Echo Valley are characterized by a large ring of chaff about the opening. In Echo Valley the species is intermediate in abundance between the two *Pogonomyrmex* species. The species is common at Punta Banda, but only one colony was found (in a road) at Pendleton. *V. stoddardi*, at the margin of its geographic range, is represented by a single colony in a very exposed roadside site in Echo Valley.

*Pheidole* - 4 species. These are small harvesting ants with distinctive and characteristic size dimorphism. Majors of these species have much larger heads than the more abundant minors. Nests are in the soil, with the opening frequently marked by a small crateriform tumulus. *P. hyatti* nests have been found among rotting stumps and under stones. *P. hyatti*, the largest of the species studied, is common at all sites, though less so at the coastal than the inland sites. *P. californicus* is common in Echo Valley, which marks the southernmost locality for the species. *P. pilifera pacifica* is known from a single nest. Foragers of the single *P. clementensis* colony found in a road at Pendleton were seen carrying unidentified small seeds, flower parts, and dead insects.

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*Crematogaster* - 3 species. Ants of this genus are easily recognized by the characteristic heart-shaped gaster. *C. californica* nests in soil (often among plant roots) and is common at all sites. *C. mormonum* nests in galleries in dead wood of oak trees in Echo Valley. *C. nocturna* is known from only a few strays, but its nesting habits are presumed to be similar to *C. mormonum*. Food habits of these ants are not well known but probably include scavenge and some honeydew. *C. californica* is occasionally seen on fresh coyote scat.

*Monomorium* - 1 species. *M. minimum* is a minute black species whose habits at the sites are not known. By virtue of its small size it may be primarily a thief ant.

*Solenopsis* - 2 species. *S. xyloni* is the most abundant species at the coastal sites. The small to medium-sized workers of this fire ant are aggressive, and they sting. Nests are in soil, frequently under stones. The diet is most probably scavenge, perhaps with some seeds included. *S. molesta* is the smallest species encountered at the sites. No field observations have been made of this minute soil and litter dweller, though, like *Monomorium minimum* , it may be a thief ant.

*Leptothorax* - 4 species. Habits of these small ants are not well known. *L. rugatulus* is common on oaks in Echo Valley. Its nests are in dead wood galleries of the trees. *L. andrei* is frequently seen on shrubs though nests have not been found. *L. nevadensis* nests in soil. Only one stray of *L. gallae* has been found (crawling on my arm). Tandem running (see Wilson, 1959b) has been seen once in both *L. rugatulus* and *L. nevadensis*. These ants seem to forage as insinuators.

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Subfamily PSEUDOMYRMICINAE

*Pseudomyrmex* - 1 species. This arboreal ant is restricted to nest sites in hollow shrub stems. At Pendleton a colony was found in *Salvia* stems. At Echo Valley foragers have been seen on *Quercus dumosa*. The species is probably a predator-scavenger. No well developed ant-plant symbioses are known from the chaparral as are known with some tropical members of this genus.

Subfamily DOLICHODERINAE

*Iridomyrmex* - 1 species. *I. pruinosum* is a small, yellow soil nester frequently seen foraging in distinct, active columns. Food probably includes both scavenge and honeydew. I once saw this species carrying rolled oats into its nest. The introduced Argentine Ant, *I. humilis*, has been seen at Torrey Pines State Park but not at any of the study sites.

*Conomyrma* - 2 species. These ants nest in soil. A small crateriform tumulus about each nest opening is distinctive. The ants forage diurnally, frequently in columns. Food includes scavenge and honeydew. The two species are broadly sympatric. *C. bicolor* is the more common at higher elevations.

*Liometopum* - 1 species. This species is one of the most characteristic and conspicuous ants in oak grove and woodland habitats. It is exceedingly common in the oak grove at the Echo Valley site, where it may be represented by a single enormous colony. The colony galleries are abundantly scattered in dead wood of the trees, in fallen logs, and probably also in soil. The ants are aggressive, they bite, and they frequently forage in columns. Food includes

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scavenge plus honeydew from the abundant aphids on the oak foliage. These ants are not active at night.

*Tapinoma* - 1 species. This soil-nesting species is common in all habitats. It is a generalized scavenger whose foragers appear abundantly on baits. This small black ant is easily distinguished from *Conomyrma* spp. by its very pungent dolichoderine odor.

Subfamily FORMICINAE

*Camponotus* - 13 species. These ants are food generalists, taking both scavenge and honeydew. This complex assemblage of species is perhaps more easily understood if divided into subgenera.

*Camponotus* (Camponotus) - 2 species. *C. quercicola*, the largest species encountered in the study, nests in dead wood galleries of large *Quercus agrifolia* and *Q. kelloggii*. This ant forages only at night, when the large, black workers may be seen stalking the tree trunks. *C. n.sp. 395* is a much smaller, shiny brown species. It is common in Echo Valley, where it nests in soil in the chaparral, sometimes under stones. It is the only *C.* (Camponotus) species known to nest in soil (Snelling, personal communication).

*Camponotus* (Myrmaphaenus) - 1 species. This ant, an undescribed new species, is an obligate hollow twig nester with phragmotic majors. One nest has been found in the basal portion of a dead *Adenostoma*. Foragers have been taken both during the day and at night.

*Camponotus* (Myrmentoma) - 5 species. These medium-sized ants typically nest in dead wood or twig galleries. *C. anthrax*, which nests in soil, is exceptional. *C. anthrax* is abundant in Echo Valley. Nests of *C. clarithorax* and *C. n.sp.* have been found in dead *Quercus agrifolia* branches. I have not located nests of *C. nearcticus*. A

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*C. hyatti* nest was found in the basal portion of a dead *Quercus dumosa*. The four twig-dwelling species are largely arboreal and presumably emphasize honeydew in their diets.

*Camponotus* (Tanaemyrmex) - 5 species. These ants nest in soil, frequently under stones. They are the conspicuous, large, size-polymorphic carpenter ants of the chaparral. *C. dumetorum* is the most abundant chaparral ant in Echo Valley and is active during the day. *C. vicinus* and *C. n.sp.*nr. *vicinus* are much less common and seem to be largely crepuscular. I cannot distinguish between these two species in the field. *C. semitestaceous* is frequently found foraging at night during warm seasons. *C. festinatus* is common at Punta Banda. But I know nothing of its foraging habits.

*Prenolepis* - 1 species. This ant is uncommon at the sites. It has repletes in its nest and so would emphasize honeydew in its food gathering.

*Acanthomyops* - 1 species. This ant is entirely subterranean in habits. It is common at Laguna, though one never sees it without digging or turning rocks. The Echo Valley record is of two founding queens and of one forager captured in a pitfall trap.

*Myrmecocystus* - 3 species. These are honey ants having large repletes in their deep-galleried soil nests. The foraging habits of these species are fascinating, for the three study site species could not be more dissimilar. *M. flaviceps* is pigmented with shades of red and grey. Foragers of this ant are active by day but are exceedingly difficult to collect. They run rapidly and erratically; they are probably the fastest ants I have encountered. Among the terrestrial ants they are also the most tolerant of high soil

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surface temperatures. I have seen these ants run rapidly from pebble to twig to grass stem and so on and cross sand with a surface temperature of 50°C. By contrast, *Camponotus anthrax* workers shaken from shrubs onto this same sand died in a matter of seconds. *M. testaceous*, the other Echo Valley species, is pale yellow in color. Foragers of this species gather at the nest opening at twilight, and the species forages at night. All foragers return to the nest soon after sunrise. When active at night, however, these ants are abundantly scattered about the nest entrance; many seem just to be standing around. *Camponotus semitestaceous*, which also forages at night, is similar in this regard. No diurnal species have these habits. *M. mimicus*, taken at Punta Banda, is black. The foragers I saw were active by day and were ordinary enough in running rate that I managed a capture success of at least 95% with my fingers and forceps. The Echo Valley species, then, seem ideal examples of palatable ants that employ foraging strategies that minimize exposure to vertebrate predators, especially lizards. The Punta Banda species, however, now stands as an enigma seriously in need of further observation.

*Formica* - 2 species. *F. pilicornis*, like *Liometopum occidentale*, is common and conspicuous in oak grove and woodland habitats. Nests are in soil, and large groves of trees seem less a requirement than for *Liometopum*. Food includes scavenge and honeydew from aphids on the oaks. *F. occidua* is virtually indistinguishable in the field from its congener. It is apparently more common in chaparral habitat Echo Valley than *F. pilicornis*, though I have not documented the coexistence pattern.

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*Polyergus* - 1 species. This ant is a slave-maker; it cannot feed itself. *Formica occidua* is its slave in this region. One colony was found under a stone at Laguna. A single worker was taken from a can trap in the oak grove at Echo Valley.

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## APPENDIX E

### Preliminary List of the Ants of Arizona

[right-hand column gives literature source on which inclusion is based]

| | | |
|---|---|---|
| | **Subfamily PONERINAE** | |
| 1. | *Amblyopone pallipes* (Haldeman) | Creighton, 1950 |
| 2. | *Hypoponera opaciceps* Mayr | " |
| 3. | *Hypoponera opacior* Forel | " |
| 4. | *Odontomachus coninodis* Wheeler | " |
| 5. | *Odontomachus desertorum* Wheeler | " |
| 6. | *Cerapachys* (Parasychis) *augustae* Wheeler | " |
| | **Subfamily DORYLINAE** | |
| 7. | *Neivamyrmex agilis* Borgm. | Watkins, 1972 |
| 8. | *Neivamyrmex andrei* | " |
| 9. | *Neivamyrmex carolinensis* | " |
| 10. | *Neivamyrmex fallax* | " |
| 11. | *Neivamyrmex harrisi* (Haldeman) | " |
| 12. | *Neivamyrmex leonardi* Mann | " |
| 13. | *Neivamyrmex melanocephalum* (Emery) | " |
| 14. | *Neivamyrmex microps* | " |
| 15. | *Neivamyrmex minor* (Cresson) | " |
| 16. | *Neivamyrmex nigrescens* (Cresson) | " |
| 17. | *Neivamyrmex opacithorax* | " |
| 18. | *Neivamyrmex pilosus mandibularis* (M. R. Smith) | " |
| 19. | *Neivamyrmex rugulosus* | " |
| 20. | *Neivamyrmex swainsoni* (Shuck.) | " |

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| | | |
|---|---|---|
| | Subfamily DORYLINAE (Cont.) | |
| 21. | *Neivamyrmex texanus* Watkins | Watkins, 1972 |
| 22. | *Neivamyrmex macropterus* Borg. | " |
| | Subfamily PSEUDOMYRMICINAE | |
| 23. | *Pseudomyrmex pallida* F. Smith | Creighton, 1950 |
| 24. | *Pseudomyrmex apache* Creighton | Creighton, 1952 |
| | Subfamily MYRMICINAE | |
| 25. | *Myrmica emeryana tahoensis* Wheeler | Creighton, 1950 |
| 26. | *Myrmica lobicornis lobifrons* Pergande | " |
| 27. | *Myrmica whelleri* Weber | " |
| 28. | *Paramyrmica rugiventris* (M. Smith) | " |
| 29. | *Pogonomyrmex apache* Wheeler | Cole, 1968 |
| 30. | *Pogonomyrmex bicolor* Cole | " |
| 31. | *Pogonomyrmex rugosus* Emery | " |
| 32. | *Pogonomyrmex californicus* (Buckley) | " |
| 33. | *Pogonomyrmex desertorum* Wheeler | " |
| 34. | *Pogonomyrmex magnacanthus* Cole | " |
| 35. | *Pogonomyrmex maricopa* Wheeler | " |
| 36. | *Pogonomyrmex occidentalis* (Cresson) | " |
| 37. | *Pogonomyrmex* (Ephebomyrmex) *huachucanus* Wheeler | " |
| 38. | *Pogonomyrmex* (Ephebomyrmex) *imberbiculus* Wheeler | " |
| 39. | *Pogonomyrmex* (Ephebomyrmex) *pima* Wheeler | " |
| 40. | *Stenamma chiricahua* Snelling | Snelling, 1973b |
| 41. | *Stenamma huachucanum* M. Smith | " |
| 42. | *Stenamma occidentale* M. Smith | " |

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Subfamily MYRMICINAE (Cont.)

| | | |
|---|---|---|
| 43. | *Aphaenogaster* (Attomyrma) *boulderensis* M. R. Smith | Creighton, 1950 |
| 44. | *Aphaenogaster* (Attomyrma) *huachucana* Creighton | " |
| 45. | *Aphaenogaster* (Attomyrma) *texana* Emery | " |
| 46. | *Aphaenogaster megommatus* M. Smith | Smith, 1963 |
| 47. | *Novomessor albisetosus* (Mayr) | Creighton, 1950 |
| 48. | *Novomessor cockerelli* (E. André) | " |
| 49. | *Veromessor andrei* (Mayr) | " |
| 50. | *Veromessor pergandei* (Mayr) | " |
| 51. | *Veromessor smithi* Cole | LACM* |
| 52. | *Pheidole* (Macropheidole) *rhea* Wheeler | Creighton, 1950 |
| 53. | *Pheidole barbata* Wheeler | " |
| 54. | *Pheidole ceres* Wheeler | " |
| 55. | *Pheidole cerebrosior* Wheeler | " |
| 56. | *Pheidole cockerelli* Wheeler | " |
| 57. | *Pheidole crassicornis tetra* Wheeler | " |
| 58. | *Pheidole desertorum* Wheeler | " |
| 59. | *Pheidole hyatti* Emery | " |
| 60. | *Pheidole macclendoni* Wheeler | " |
| 61. | *Pheidole micula* Wheeler | " |
| 62. | *Pheidole militicida* Wheeler | " |
| 63. | *Pheidole sciophila* Wheeler | " |
| 64. | *Pheidole spadonia* Wheeler | " |
| 65. | *Pheidole subdentata* Pergande | Gregg, 1958 |

*indicates specimens in collection of Los Angeles County Museum

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Subfamily MYRMICINAE (Cont.)

| | | |
|---|---|---|
| 66. | *Pheidole tepicana* Pergande | Creighton and Gregg, 1955 |
| 67. | *Pheidole titanis* Wheeler | Creighton, 1950 |
| 68. | *Pheidole vallicola* Wheeler | " |
| 69. | *Pheidole vinelandica* Forel | Gregg, 1958 |
| 70. | *Pheidole virago* Wheeler | Creighton, 1950 |
| 71. | *Pheidole xerophila tucsonia* Wheeler | " |
| 72. | *Rogeria huachucana* Snelling | Snelling, 1973a |
| 73. | *Crematogaster* (Orthocrema) *arizonensis* Wheeler | Creighton, 1950 |
| 74. | *Crematogaster* (Orthocrema) *minutissima smithi* Creighton | " |
| 75. | *Crematogaster* (Acrocoelia) *depilis* Wheeler | " |
| 76. | *Crematogaster* (C.) *browni* Buren | Buren, 1968 |
| 77. | *Crematogaster* (C.) *colei* Buren | " |
| 78. | *Crematogaster* (C.) *dentinodis* Forel | " |
| 79. | *Crematogaster* (C.) *emeryana* Creighton | " |
| 80. | *Crematogaster* (C.) *hespera* Buren | " |
| 81. | *Crematogaster* (C.) *isolata* Buren | " |
| 82. | *Crematogaster* (C.) *larreae* Buren | " |
| 83. | *Crematogaster* (C.) *navajoa* Buren | " |
| 84. | *Crematogaster* (C.) *nocturna* Buren | " |
| 85. | *Crematogaster* (C.) *opuntiae* Buren | " |
| 86. | *Crematogaster* (C.) *punctulata* Emery | " |
| 87. | *Monomorium minimum* Buckley | Creighton, 1950 |
| 88. | *Monomorium viridum peninsulatum* Gregg | " |

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Subfamily MYRMICINAE (Cont.)

| | | |
|---|---|---|
| 89. | *Solenopsis aurea* Wheeler | Creighton, 1950 |
| 90. | *Solenopsis xyloni* McCook | " |
| 91. | *Solenopsis* (Euopthalma) *huachucana* Wheeler | " |
| 92. | *Solenopsis* (Diplorhoptrum) *molesta* (Say) | " |
| 93. | *Solenopsis* (Diplorhoptrum) *salina* Wheeler | " |
| 94. | *Solenopsis* (Diplorhoptrum) *truncorum* Forel | LACM |
| 95. | *Myrmecina americana* Emery | Creighton, 1950 |
| 96. | *Macromischa polita* M. R. Smith | " |
| 97. | *Leptothorax andrei* Emery | Smith, 1967 |
| 98. | *Leptothorax carinatus* Cole | " |
| 99. | *Leptothorax curvispinosus* Mayr | Smith, 1958 |
| 100. | *Leptothorax rugatulus* Emery | " |
| 101. | *Leptothorax silvestrii* (Santschi) | " |
| 102. | *Leptothorax stenotyle* Cole | " |
| 103. | *Leptothorax tricarinatus* Emery | Smith, 1967 |
| 104. | *Leptothorax crassipilis* Wheeler | Creighton, 1950 |
| 105. | *Strumigenys louisianae* Roger | Brown, 1953 |
| 106. | *Xiphomyrmex spinosus* Pergande | Creighton, 1950 |
| 107. | *Smithistruma sp.* | LACM |
| 108. | *Cryptocerus rohweri* Wheeler | Creighton, 1950 |
| 109. | *Cyphomyrmex rimosus* (Spinola) | " |
| 110. | *Cyphomyrmex wheeleri* Forel | " |
| 111. | *Trachymyrmex arizonensis* (Wheeler) | " |

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Subfamily MYRMICINAE (Cont.)

| | | |
|---|---|---|
| 112. | *Trachymyrmex desertorum* (Wheeler) | Creighton, 1950 |
| 113. | *Atta mexicana* | Byars, 1949 |
| 114. | *Acromyrmex* (Moellerius) *versicolor* (Pergande) | Creighton, 1950 |

Subfamily DOLICHODERINAE

| | | |
|---|---|---|
| 115. | *Liometopum apiculatum* Mayr | Creighton, 1950 |
| 116. | *Liometopum luctuosum* Wheeler | " |
| 117. | *Liometopum occidentale* Emery | " |
| 118. | *Iridomyrmex humilis* (Mayr) | " |
| 119. | *Iridomyrmex pruinosum analis* (E. Andre) | " |
| 120. | *Forelius foetida* (Buckley) | " |
| 121. | *Conomyrma insana* (Buckley) | " |
| 122. | *Conomyrma bicolor* Wheeler | " |
| 123. | *Tapinoma sessile* (Say) | " |

Subfamily FORMICINAE

| | | |
|---|---|---|
| 124. | *Acropyga epedana* Snelling | Snelling, 1973a |
| 125. | *Brachymyrmex depilis* Emery | Creighton, 1950 |
| 126. | *Camponotus modoc* Wheeler | " |
| 127. | *Camponotus laevigatus* (F. Smith) | " |
| 128. | *Camponotus noveboracensis* (Fitch) | " |
| 129. | *Camponotus schaefferi* Wheeler | " |
| 130. | *Camponotus* (Tanaemyrmex) *acutirostris* Wheeler | " |
| 131. | *Camponotus* (Tanaemyrmex) *festinatus* (Buckley) | " |

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Subfamily FORMICINAE (Cont.)

| | | |
|---|---|---|
| 132. | *Camponotus* (Tanaemyrmex) *ocreatus* Emery | Creighton, 1950 |
| 133. | *Camponotus* (Tanaemyrmex) *sansabeanus* (Buckley) | " |
| 133a. | *Camponotus* (Tanaemyrmex) *sansabeanus bulimosus* Wheeler | " |
| 133b. | *Camponotus* (Tanaemyrmex) *sansabeanus torrefactus* Wheeler | " |
| 134. | *Camponotus* (Tanaemyrmex) *vafer* Wheeler | " |
| 135. | *Camponotus* (Tanaemyrmex) *vicinus* Mayr | " |
| 136. | *Camponotus* (Myrmentoma) *nearcticus* | LACM |
| 137. | *Camponotus* (Myrmentoma) *sayi* Emery | Creighton, 1950 |
| 138. | *Camponotus* (Colobopsis) *papago* Creighton | Creighton, 1952 |
| 139. | *Camponotus* (Myrmobrachys) *mina* | Creighton, 1965 |
| 140. | *Camponotus* (Myrmobrachys) *trepidulus* Creighton | " |
| 141. | *Camponotus* (Myrmaphaenus) *ulcerosus* Wheeler | Creighton, 1950 |
| 142. | *Paratrechina melanderi* (Wheeler) | LACM |
| 143. | *Paratrechina vividula* (Nylander) | " |
| 144. | *Prenolepis imparis arizonica* Wheeler | Creighton, 1950 |
| 145. | *Lasius* (L.) *alienus* (Foerster) | Wilson, 1955 |
| 146. | *Lasius* (L.) *niger* (Linné) | " |
| 147. | *Lasius* (L.) *pallitarsus* (Prov.) [= "*sitkaensis*"] | " |
| 148. | *Lasius* (L.) *sitiens* Wilson | " |
| 149. | *Lasius* (Cantolasius) *flavus* (Fabr.) | " |
| 150. | *Lasius* (Cantolasius) *fallax* Wilson | " |

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Subfamily FORMICINAE (Cont.)

| | | |
|---|---|---|
| 151. | *Lasius* (Chthonolasius) *umbratus* (Nylander) | Wilson, 1955 |
| 152. | *Lasius* (Chthonolasius) *subumbratus* Viereck | " |
| 153. | *Acanthomyops interjectus arizonicus* (Wheeler) | Creighton, 1950 |
| 154. | *Myrmecocystus depilis* Forel | Snelling, in prep. |
| 155. | *Myrmecocystus flaviceps* Wheeler | " |
| 156. | *Myrmecocystus kennedyi* Cole | " |
| 157. | *Myrmecocystus mendax* Wheeler | " |
| 158. | *Myrmecocystus mexicanus* Wesmael | " |
| 159. | *Myrmecocystus mimicus* Wheeler | " |
| 160. | *Myrmecocystus navajo* Wheeler | " |
| 161. | *Myrmecocystus placodops* Forel | " |
| 162. | *Myrmecocystus yuma* Wheeler | " |
| 163. | *Formica altipetens* Wheeler | Francoeur, in prep. |
| 164. | *Formica argentea* Wheeler | " |
| 165. | *Formica canadensis* Santschi | " |
| 166. | *Formica densiventris* Viereck | " |
| 167. | *Formica foreliana* Wheeler | " |
| 168. | *Formica fusca* Linné | " |
| 169. | *Formica neoclara* Emery | " |
| 170. | *Formica neorufibarbis* Emery | " |
| 171. | *Formica occidua* Wheeler | " |
| 172. | *Formica podzolica* Francoeur, ms. | " |
| 173. | *Formica xerophila* M. Smith | " |
| 174. | *Polyergus breviceps* Emery | Creighton, 1950 |

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