

An Ecological Comparison of Small Mammal Communities in California and Chile¹

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Similar climates often seem to favor the evolution of similar organisms, and the Mediterranean-climate regions of the world have provided numerous examples of such evolutionary convergence. Of the five regions with this climate, California and Chile have been compared very extensively (Mooney 1977), particularly in terms of the morphological, physiological, and ecological attributes of their dominant organisms. Striking similarities between these two regions have been found in their vegetation structure and community patterns (Mooney and Dunn 1970; Parsons and Moldenke 1975; Parsons 1976), their birds (Cody 1973 and 1974), and their lizards (Fuentes 1976).

In a variety of projects during the past decade (Meserve 1972, 1976a, 1976b, 1981a, 1981b; Glanz 1977a and 1977b; Meserve and Glanz 1978), we have studied certain communities of small mammals in the Mediterranean zones of California and Chile. In this paper we will summarize our results by comparing our three best-documented sites on each continent. We will outline some aspects of these communities that suggest convergence in morphology and ecology. Our emphasis, however, will be on the ecological differences that we have found between the two regions, especially those relating to community diversity, habitat use, and diet. These dissimilarities suggest some major differences in the functional roles of mammals in these communities, some contrasting responses of these animals to vegetation structure, natural predators, and human disturbance, and some potentially important differences in the evolutionary histories of the two regions. We hope that our discussion of these topics will stimulate further research on these ecosystems and their small mammal faunas.

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Abstract: Our studies in similar scrub habitats in California and Chile reveal some interesting differences between these two regions in the structure of their small mammal communities. The Chilean fauna is less diverse, with fewer species per site, and possibly more extreme density fluctuations. Chilean rodents are more strongly associated with areas of high shrub and rock cover, while California species show a greater variety of habitat preferences. Chile has more insectivorous species, and California has more seed-eating specialists. Some of these differences may be related to biogeographic and climatic factors, while others may reflect a longer history of human disturbance in Chile.

FIELD SITES AND METHODS

We have ecological data from a variety of communities in each region, but will restrict our discussion here to results from three vegetational types which we have studied intensively: dry coastal scrub, moist coastal scrub, and evergreen chaparral. For each of these, the vegetation structure and life forms at our sites were closely matched between continents.

The dry coastal scrub localities were studied by Meserve near Irvine, Orange County, California in 1970-71 and at Fray Jorge National Park, Coquimbo Province, Chile in 1973-74. Detailed descriptions were provided by M'Closkey (1972) and Meserve (1972 and 1976a) for the California site, and by Fulk (1975) and Meserve (1981a) for the Chilean site. Both study areas were at about 200 m elevation, within 5 km of the coast, and were located on sandy, well-drained soils. Although mean rainfall at the California site (about 300 mm) was considerably greater than at the Chilean site (127 mm), their similar topography, seasonality, and soils apparently produced remarkably convergent vegetation, with approximately 60 percent shrub cover dominated by drought-deciduous species.

The moist coastal sites studied by Glanz (1977a and 1977b) were at Camp Pendleton Marine Base, San Diego County, California, and at Zapallar and Los Molles (two sites), Aconcagua Province, Chile. Although the rainfall at these localities (225 to 350 mm) was comparable to that of the California dry coastal site, they were on slopes more directly facing the ocean and received more coastal fog. This greater moisture plus the higher clay content of the soils resulted in greater average shrub cover (74 percent), also dominated by drought-deciduous species, but including more evergreen shrubs than the dry coastal sites. All study areas were between 20 and 60 m elevation and within 1 km of the coast.

The evergreen chaparral sites sampled by Glanz (1977a and 1977b) were at Echo Valley, near Descanso, San Diego County, California, and

at Fundo Santa Laura, near Tilttil, Santiago Province, Chile. Both were at 900 to 1000 m elevation, had 550 to 600 mm mean annual rainfall, and were dominated by evergreen sclerophyllous shrubs. Plots trapped at these sites averaged 75 percent shrub cover. Many additional aspects of the evergreen chaparral and moist coastal sites were studied during the Mediterranean Scrub Project of the International Biological Program, and are described in detail in Thrower and Bradbury (1977).

Our field techniques were designed to sample most mammal species up to 500 gm body size in each community. Populations were live-trapped on large (1.4 to 2.2 ha) grids at all sites except the Chilean moist coastal localities, and snap-trapped on small (usually 0.4 ha) grids at all sites except to California dry coastal area. Population densities were determined by mark-recapture techniques, and by correlating snap-trap success with live-trapping results. A variety of physical and vegetational measurements were used to characterize the habitat preferences of each species. Meserve (1976b, 1981b) categorized each trap station according to its shrub, herb, and bare ground cover values, and then conducted 2 x k association analyses (Simpson, Roe, and Lewontin 1960) between presence/absence data of each species at trap stations and categories of vegetation cover. Glanz measured 30 habitat variables at each trap station, scored each mammal capture for the characteristics of that trap station, and then compared the habitat measures of stations selected by each mammal species with those of all stations trapped at each site. To assess the degree of habitat differentiation among species at each site, Glanz also conducted discriminant analyses using capture records and programs in the SPSS computer library.

Meserve compared arboreal vs. terrestrial habitat utilization at the dry coastal sites using smoked cards placed on the ground and at 25, 50, 100 and 200 cm above ground in the most common shrub species. Tracks on the cards were identified to species and individual using foot characteristics and toe-clip marks (Meserve 1976b and 1981b).

Food habits were assessed by microscopic examination of stomach contents and fecal pellets at most sites, and by fecal analysis only at the California dry coastal site. Meserve (1976a and 1981a) homogenized the sample first, subsampled and boiled the material in Hertwig's solution (Baumgartner and Martin 1939), and then identified cell fragments under a microscope at 100X. Glanz (1977) quantified stomach content fractions first at 40X, subsampled each fraction, and then followed the above procedure. These variations in methods may limit the precision of our comparisons, but should not alter the general conclusions we present in this paper.

FAUNAL COMPOSITION AND DIVERSITY

The species of small mammal recorded from

Table 1. Occurrence of each small mammal species at the California (above) and Chilean (below) sites. Sites are dry coastal (DC), moist coastal (MC), and evergreen chaparral (EC). Abundance values are: X = present, but uncommon; L = locally common; C = common or abundant. Species Codes are used in figures 1 and 2.

Species (and Code)	Community Type		
	DC	MC	EC
<u>CALIFORNIA</u>			
INSECTIVORA			
Soricidae			
<u>Notiosorex crawfordi</u>	X	X	
RODENTIA			
Sciuridae			
<u>Eutamias merriami</u>			X
<u>Spermophilus beecheyi</u>		L	L
Geomysidae			
<u>Thomomys bottae</u>		X	X
Heteromyidae			
<u>Dipodomys agilis</u> (Dpa)	C		C
<u>Perognathus californicus</u> (Pgc)		X	X
<u>Perognathus fallax</u> (Pgf)	X	C	
<u>Perognathus longimembris</u> (Pgl)	C		
Cricetidae			
<u>Microtus californicus</u> (McC)	X	C	X
<u>Neotoma fuscipes</u> (Ntf)	L	C	C
<u>Neotoma lepida</u> (Ntl)	X	C	X
<u>Peromyscus boylii</u> (Pmb)			L
<u>Peromyscus californicus</u> (Pmc)	C	C	C
<u>Peromyscus eremicus</u> (Pme)	C	C	X
<u>Peromyscus maniculatus</u> (Pmm)	C	C	C
<u>Reithrodontomys megalotis</u> (Rtm)	C	X	X
Muridae			
<u>Mus musculus</u>	X	X	
Total Species	12	13	13
Common Species	7	8	6
<u>CHILE</u>			
MARSUPIALIA			
Didelphidae			
<u>Marmosa elegans</u> (Mae)	X	C	X
RODENTIA			
Abrocomidae			
<u>Abrocoma bennetti</u> (Abb)	X		C
Octodontidae			
<u>Octodon degus</u> (Ocd)	C	X	C
<u>Octodon lunatus</u> (Ocl)		L	L
<u>Spalacopus cyanus</u>		L	X
Cricetidae			
<u>Akodon longipilis</u> (Akl)	C	C	C
<u>Akodon olivaceus</u> (Ako)	C	C	X
<u>Oryzomys longicaudatus</u> (Orl)	X	X	X
<u>Phyllotis darwini</u> (Phd)	C	X	X
Muridae			
<u>Rattus rattus</u> (Rra)			L
Total Species	7	8	10
Common Species	4	5	5

each community are listed in table 1. Several points are obvious from this list. First, both faunas are dominated by rodents; the only excep-

tions are one shrew, Notiosorex crawfordi, in California and one mouse opossum, Marmosa elegans in Chile. Next, the two faunas are phylogenetically distinct. Among the rodents, only one native family (Cricetidae) is shared between the two regions, although each also contains species of murid rodents introduced by humans from Eurasia. The cricetid rodents of the two areas, moreover, are quite distantly related. Following Hershkovitz (1969), all the Chilean cricetids are placed in the tribe Sigmodontini, while the genus Microtus is in the subfamily Microtinae, and all California species are in the tribe Peromyscini. Similarities between these unrelated groups, then, may be considered evidence for evolutionary convergence; dissimilarities, however, may be due to either phylogenetic or ecological factors.

It is also evident from this list that the California fauna is much more diverse, including 17 species at these sites in contrast to only 10 species at the Chilean sites. This difference was not unexpected, as Greer (1965) and Baker (1967) have noted that the regional faunas of Chile are depauperate in comparison with those of similar areas in North America. They related this low diversity primarily to the geographic isolation of Chile, and to the restricted area of temperate biomes in southern South America.

If similar ecological opportunities are available in the two Mediterranean climate regions, one might expect similar numbers of small mammal species in analogous communities. This prediction is not supported, however, as each Chilean site produced fewer species than its counterpart in California (table 1). Thus, the Chilean fauna is less diverse even when comparing local communities.

POPULATION DENSITIES

Given this pattern of a depauperate Chilean mammal fauna with fewer species per community, one might predict that individual species in Chile might be replacing several analogous species in California, and that total densities of all species in comparable communities would be similar. Such "density compensation" (MacArthur and others 1972) is difficult to test on these Mediterranean-climate communities, as total densities at certain sites varied by more than 10X between years. Nevertheless, the evergreen chaparral and moist coastal sites appear to refute this prediction, as the average densities per snap-trapping grid were significantly lower in Chile for each vegetation type ($p < .05$ for both comparisons; Mann-Whitney U-test). The evergreen chaparral live-trapping densities were also lower in Chile (mean = 5.3/ha) than in California (mean = 9.6/ha), but because of great seasonal variability they were insignificantly different ($p > .05$). Density compensation, however, may be occurring at the dry coastal sites, as average total densities were actually higher in Chile (mean = 58.7/ha) than in California (mean = 41.4/ha), and insignificantly different between

the two continents ($p > .10$; U-test). The Chilean site had more extreme variations (coefficient of variation = 48.9 in Chile, 16.8 in California), with Akodon olivaceus declining from high densities (32/ha) early in the study and Octodon degus reaching 120/ha near the end (Meserve 1981b). Fulk (1975) live-trapped the Fray Jorge site in 1972-73 (prior to Meserve's study), and found even higher populations, with A. olivaceus and Phyllotis darwini densities combined exceeding 300/ha. Glanz (1977) also found higher average densities and much greater variability at another Chilean dry coastal site (near Guanaqueros, Coquimbo Province) than at its climatic counterpart in North America. Pefaur and others (1979) reported on a rodent outbreak in north-central Chile in 1972-73, which was dominated by Oryzomys longicaudatus and P. darwini. These data, then, indicate that small mammal densities are highly variable in these Mediterranean-type ecosystems, but that the fluctuations in Chile may be more extreme. Some Chilean sites never achieved densities as high as their California counterparts, but we have data from at most two years for each site, and further long-term studies may find that these populations also occasionally show rodent outbreaks.

MORPHOLOGICAL COUNTERPARTS

Several of the Chilean small mammal genera strikingly resemble certain California genera in morphological characters. The Chilean leaf-eared mouse, Phyllotis darwini, and the rice rat, Oryzomys longicaudatus, are very similar to the North American Peromyscus species, all being small mice with large eyes, large ears, and long tails. All are in the family Cricetidae, however, and also resemble other genera that inhabit other habitats, so their morphological similarity may not necessarily indicate convergence. A more striking example of morphological convergence involves the California woodrats, genus Neotoma, and the Chilean hystricognath rodents of the genera Abrocoma and Octodon. These large rodents are very distantly related, but are very similar in ear and tail length, body size, and coloration. The most obvious morphological counterparts are the fossorial rodents of these regions, the gopher Thomomys bottae in California and the coruro Spalacopus cyanus in Chile. Both have reduced eyes, ears, and tail, elongated claws, and stout incisors and cranial structure, all of which are characteristics found in unrelated groups of burrowing rodents throughout the world. They therefore exhibit convergence, but in a way that is not specific to Mediterranean-type ecosystems.

Most other small mammals of the two regions are more difficult to match with a morphological counterpart on the other continent. The shrew Notiosorex and the mouse opossum Marmosa show virtually no anatomical resemblance, but both have dental adaptations for handling insects and other animal prey. The Chilean cricetid mice of the genus Akodon vaguely resemble North American

meadow mice, genus *Microtus*, both having relatively short ears and tails, stocky bodies, long claws, and little dorso-ventral countershading. *Microtus*, however, is much more extreme in all of these features and has a highly specialized herbivorous dentition, while most *Akodon* species are morphologically generalized mice, showing no major differences from other cricetids. The California Sciuridae, including the chipmunks (*Eutamias*) and the ground squirrels (*Spermophilus*) have no obvious morphological equivalents in Chile. The Chilean hystricognath *Octodon degus* is diurnal, social, and a rough ecological analog of many North American ground squirrels (Fulk 1976; Glanz 1977b), but is much smaller in size, and more similar to the woodrats in body proportions. Perhaps the most conspicuous absences from the Chilean fauna are counterparts for the North American kangaroo rats and pocket mice, family Heteromyidae. No Chilean rodent has the cheek pouches, large auditory bullae, and adaptations for bipedal locomotion of the California heteromyids, nor their specializations for seed-eating and water retention (Glanz 1977a; Meserve 1978).

This brief review suggests that although some groups on each continent are morphologically convergent, the Chilean fauna has a lower diversity of structural adaptations. The California communities have more species with morphological characteristics that have no counterpart in Chile. A more rigorous morphological analysis (Glanz 1977a) confirms these general conclusions.

HABITAT SELECTION

Although the data on species diversity and morphological adaptations suggest some important differences between the small mammals of California and Chile, they do not deal directly with the ecological roles of these animals in their communities. In the next sections we will discuss the patterns of resource use by small mammals in the two regions, focusing primarily on the utilization of habitat and food.

Intercontinental comparisons of habitat selection can be difficult if great differences exist in the available habitat features. In our studies, for example, Chilean sites often had more herbaceous cover and a higher proportion of spiny shrubs than their California counterparts, and therefore selective use of these habitat types may have been more likely to evolve in Chile. To simplify our discussion here, we will consider only certain features that were comparable between analogous sites.

Percent shrub cover was virtually identical between our analogous sites, but the community response to this habitat variable was noticeably different in the two regions. Meserve's (1976b and 1981b) 2 X k association analysis of the dry coastal sites found that *Peromyscus californicus* and *P. eremicus* were associated with trap stations having high shrub cover (>75 percent) in California.

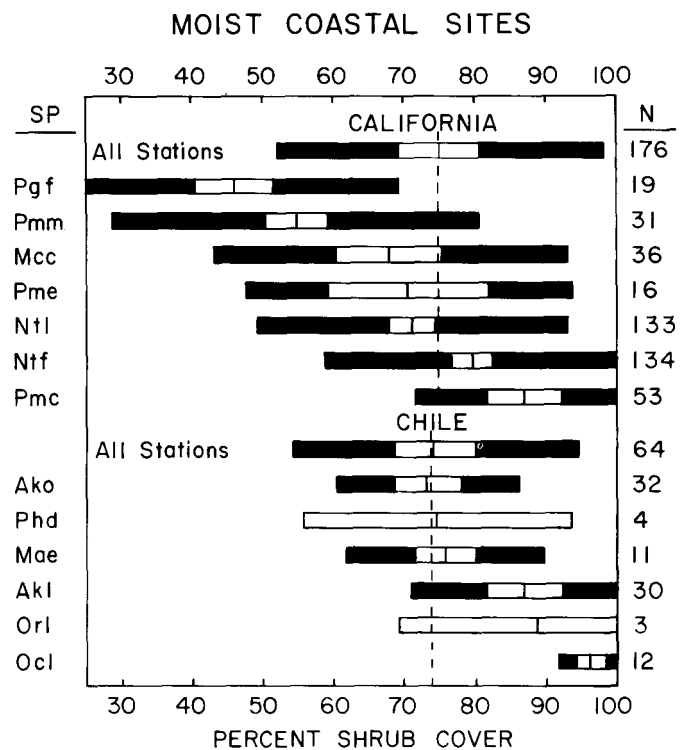


Figure 1. Comparison of shrub cover values (mean, 2 standard errors, and 1 standard deviation) of capture locations for each species with those of all trap stations at each moist coastal site. Species codes are from Table 1.

P. californicus and a third species, *Neotoma fuscipes* were much more common in dense shrublands adjacent to the more open study site, which also implies preferences for high shrub cover. In contrast, stations with low shrub cover (<50 percent) were significantly preferred by two other species, *Dipodomys agilis* and *Peromyscus maniculatus*. At the Chilean dry coastal site, two species, *Akodon longipilis* and *Phyllotis darwini*, showed associations with moderate to high cover (51 to 100 percent), but no species preferred stations with low shrub cover.

Shrub cover selection by small mammals at the moist coastal sites (Glanz 1977a) is depicted in figure 1, and it shows a similar intercontinental pattern. At the California site, *P. californicus* and *N. fuscipes* chose trap stations with shrub cover significantly higher than the site average, while two other species, *Perognathus fallax* and *P. maniculatus* significantly preferred stations with low shrub cover. At the corresponding Chilean sites, two species, *A. longipilis* and *Octodon lunatus*, were trapped at stations with shrub cover significantly above the site mean, while no species significantly chose low-cover stations. An analysis of shrub cover selection at the evergreen chaparral sites (Glanz 1977a) produced similar results. Preferences for high cover stations were significant for certain species on both continents, with *Peromyscus boylii*,

P. californicus, and N. fuscipes selecting such habitats in California, and Rattus rattus, A. longipilis, O. lunatus, and O. degus doing so in Chile. Preferences for low-cover stations, however, were again evident only in California, by D. agilis and P. maniculatus.

Several consistent patterns emerge from these data. First, species that prefer dense cover are relatively predictable from site to site within continents; these usually include some of the larger mice (notably P. californicus in California and A. longipilis in Chile) and the large woodrat N. fuscipes or its analogs (especially O. lunatus). Most of these high-cover species have ranges closely associated with Mediterranean scrub and associated forest and scrub ecosystems. Next, Chile very obviously lacks species that prefer low-cover habitats, while California has several. Finally, at all the California sites the species that choose open habitats always include one heteromyid (Dipodomys or Perognathus species) and one small cricetid, P. maniculatus. Heteromyids are dominant members of desert rodent communities in North America, while P. maniculatus is very widespread on the continent and frequently occupies arid and marginal habitats.

Rocky habitats also provide important cover to many species. The dry coastal sites had very few rocky stations and this variable was not studied there. At the moist coastal sites, three Chilean species (O. lunatus, P. darwini, and A. longipilis) were usually trapped near rocks, but these preferences were not significant, possibly because of few rocky trap stations. More rocky habitats were sampled at the evergreen chaparral sites, and the two communities showed contrasting trends. While both localities had species with significant preferences for rocky cover (P. boylii, P. eremicus, and Perognathus californicus in California, O. lunatus and M. elegans in Chile, California had two that significantly avoided rocky stations (D. agilis and P. maniculatus) and Chile had none. Other evidence from the small snap-trap plots suggests Chilean mammals favor rocky areas. Average density on these grids in Chile tended to increase with percent rock cover ($r=.51$; $.05 < p < .10$), while no such relationship was evident in California ($r=-.09$).

Meserve's smoked-card tracking data (1976b, 1981b) revealed differences in another pattern of habitat use, arboreal activity. In California, 20.4 to 28.5 percent of all tracking records were in the shrub foliage, while only 3.1 percent of all Chilean records were above ground, a striking difference in the utilization of these habitat zones.

These patterns in the use of shrub cover, rocky cover, and above-ground habitats suggest that Chilean communities of small mammals utilize a smaller range of habitats, preferring those with greatest cover, and that individual species may be more similar in their habitat preferences than in

California. Detailed analyses of habitat overlap by Meserve (1981b) and Glanz (1977a) support this generalization. Glanz's discriminant analyses of microhabitat selection, for example, found that 93 percent of all species pairs in California showed significant differences in habitats used, while only 68 percent of all Chilean pairs could be significantly distinguished by habitat features alone.

FOOD HABITS

Assuming that the similar vegetation patterns and climates of these regions produce similar varieties of potential foods for mammals, one would expect to find similar dietary patterns in these communities. Our analyses of mammal food habits, however, show some remarkable contrasts. Meserve (1976a, 1981a) compiled dietary data throughout the annual cycle at the dry coastal site, while Glanz (1977a) restricted his analyses to spring and summer seasons only. Since food habits vary considerably over the seasons, we will restrict our comparisons here to just spring and summer results. Figure 2 summarizes the diets of most species at the three site types. Spring and summer results have been averaged, and the food types have been combined into three general categories: vegetative parts of plants, seeds and fruits, and animal material. In this figure, each apex represents a diet composed entirely of that food type. The further a species is from an apex, the lower the proportion of that food type in the diet.

Several points are immediately apparent from these diagrams. First, most communities had one to three leaf-eating species, and these always included the larger genera Abrocoma, Octodon, and Neotoma. The diets of these "woodrat" analogs, thus, seem to have converged on leaves, particularly shrub foliage, as the principal food. The Octodon species, however, ate more herb leaves, and in some seasons seeds and fruits comprised up to 45 percent of their diet (Glanz 1977a; Meserve 1981a).

Most communities also included species that fed largely on seeds, but California sites usually had more species in this category. The heteromyid genera Dipodomys and Perognathus were always seed specialists at these sites, as they usually are in most arid communities. Most California Peromyscus were more omnivorous, but still fed extensively on seeds, particularly at the evergreen chaparral site. Two species, P. eremicus and P. maniculatus, ate substantial proportions of leaves or insects at each of the coastal sites, but averaged between 45 and 70 percent seeds in every community. In contrast to the emphasis on granivory in California, only two Chilean species, O. longicaudatus and P. darwini, fed primarily on seeds. Neither was as specialized on seeds as the heteromyid species at comparable California sites, and Phyllotis was seasonally very herbivorous at the evergreen chaparral site. Thus, in food habits as in the comparisons of habitat use, Chilean Mediterranean scrub communities seemed to lack an analog for the kangaroo rats and pocket mice of North America.

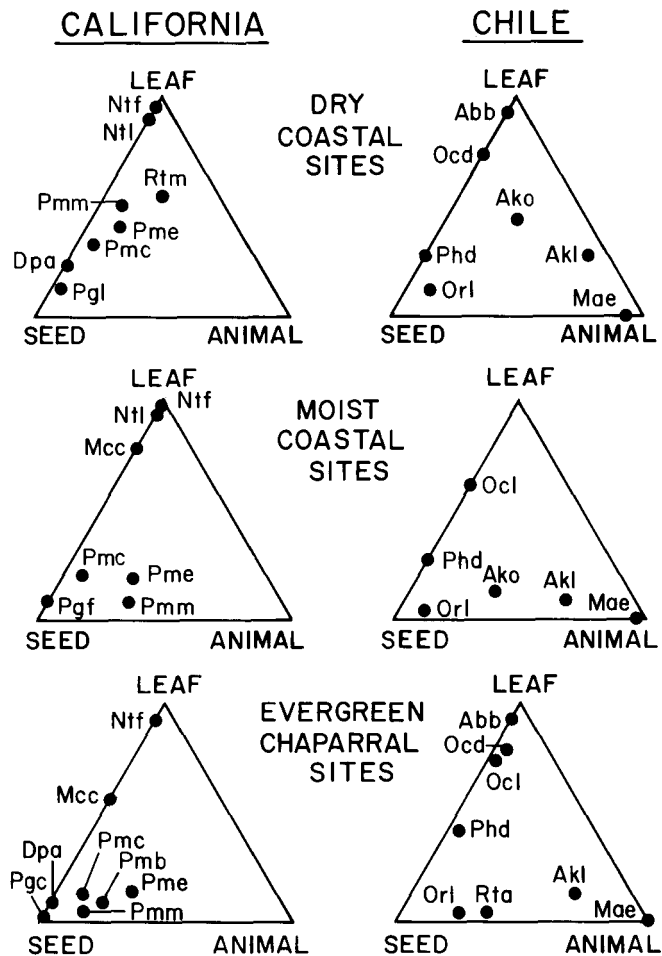


Figure 2. Food habits of small mammals at each site expressed as proportions of diets for each food type. See text for detailed discussion. Species codes are from Table 1.

A final point is even more obvious from Figure 2. California had no primarily insectivorous species, while Chile had two. The mouse opossum, *M. elegans*, was almost entirely insectivorous, while *A. longipilis* fed seasonally from 33 to 73 percent on invertebrates. *A. olivaceus* showed similar, but more omnivorous feeding trends, with insects comprising from 13 to 55 percent of its seasonal diets. In addition to invertebrates, small lizards were occasionally found in the diets of both *M. elegans* and *A. olivaceus*. These Chilean species, then, are trophically distinct from the small mammals studied in California.

DISCUSSION

The preceding data outline some possible examples of ecological convergence, but emphasize some interesting cases of "nonconvergence" in the organization of these mammal communities. These patterns raise numerous questions regarding the evolutionary pathways followed by the different mammal lineages, and the relative importance of

environmental vs. phylogenetic factors on such evolution. We would now like to present several major questions raised by our data and speculate on some alternative answers to these questions.

First, why are small mammals in Chile so insectivorous? Conceivably other animals could be assuming this trophic role in California. Shrews, for example, are the dominant insectivorous mammals elsewhere in North America, and we certainly did not sample adequately our one species, *Notiosorex crawfordi*. Considering how infrequently we trapped, sighted or found evidence of this species, however, we doubt that it is as common as *Marmosa* and *Akodon* species are at corresponding sites in Chile, but we urge further study of this interesting shrew. Insects may be more abundant and more predictable in Chile, and therefore may offer more opportunities for dietary specialization by mammals. Comparative data on flying insects of the two regions (Mooney 1977, p. 174) seem to support this idea, but more data on ground-dwelling species would be helpful. Alternatively, Chilean small mammals may represent lineages that tend toward insectivory irrespective of available resources. Elsewhere in South America, most small marsupials and many akodont rodents are also insectivorous (Hershkovitz 1969; Glanz 1977a; Pizzimenti and DeSalle 1980), but the diets of relatively few species have been studied. Morton (1979), in his comparison of North American and Australian desert mammals, found a strong bias toward insectivory in the marsupial-dominated Australian fauna.

Why is the Chilean fauna less diverse? We have mentioned above the hypotheses of Baker (1978) relating faunal size to geographic isolation and the relatively small area of temperate South America. The mammal fauna of Chile's scrub zone, then, may be a subsample drawn from a more depauperate zoogeographic source than for the California fauna. Clearly, more studies of their phylogenetic relationships to other temperate and tropical faunas will be necessary to properly test this idea. Equally important will be studies of faunal isolation through time. The Chilean Mediterranean zone is currently separated from other scrub habitats by the Atacama desert, the Andes, and the Valdivian forests, but it is unclear how important these barriers have been in limiting dispersal by different mammal groups. Speciation patterns within Chile may also have limited mammal diversity (Fuentes and Jaksic 1979) and certainly require more study.

Finally, why have no Chilean mammals evolved into a heteromyid analog, specializing on seeds and open habitats? First, Mares (1976) has found that no South American rodents are as morphologically specialized for open habitat as the heteromyids, and that historical factors provide plausible explanations for this contrast. Nevertheless, some rodents of other South American scrub areas, such as *Eligmodontia typus* of Argentine deserts, show more arid adaptations than any Chilean rodent, so additional factors may have influenced the Chilean fauna. Perhaps the extreme fluctuations of rainfall

in the semi-arid zones of Chile (Fulk 1975; Mooney 1977) produce less dependable food supplies in open habitats than in California. More likely, the availability of these open areas may have been different through evolutionary history. The California flora has many fire-adapted species (Mooney 1977), and fires have probably been frequent in the past, creating open habitats with which many rodents have coevolved (Quinn 1980). In contrast, the Chilean flora has few fire adaptations, fire has probably been less important there, and no rodents have coevolved with such disturbance. Most open habitats in the present scrub zones of Chile may be associated with recent land use practices by humans (see Bahre 1979; Mooney 1977), and the local mammals have not specialized on these disturbances. Finally our data show that certain opportunistic species (especially *P. darwini* and *A. olivaeus*) do use these open habitats, but primarily at peak densities, when other habitats are also occupied. They thus may be analogs of the similarly opportunistic and eruptive *P. maniculatus*, which occupies low-cover habitats in California. Additional ecological and behavioral comparisons of these species might prove very interesting.

The small mammal faunas of California and Chile, thus, show some striking differences in certain ecological features. We hope that our discussion of these examples of "nonconvergence" will stimulate further research on these animals.

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