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POPULATION ECOLOGY OF RODENTS IN THE SEMIARID SHRUBLANDS OF CHILE

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The mammalian fauna of the arid Pacific coast of South America reveals remarkably little diversity. Baker (1967) reported that it contains between one-half and one-sixth as many species as equivalent zones in North America. Mooney (Mooney and Dunn, 1970, 1971; Mooney *et al.*, 1970) reported remarkable similarities between California and Chile between the latitudes 30 and 40° with respect to climate, soil, and vegetation. Both areas have a Mediterranean climate with aridity increasing toward the equator, and along these moisture gradients both areas have equivalent vegetational communities. The ecology of rodent communities in semiarid shrublands of Chile is herewith described and compared to similar communities in southern California. Data for this comparison come from my live-trapping studies of two sites in Chile and similar studies by M'Closkey (1972) and MacMillen (1964) in the coastal scrub of southern California. This comparison draws attention to the effect diversity of the faunal assemblage has on the organization of a community.

The Mammals of Chile by Osgood (1943) clarified the nomenclature and taxonomy of Chilean mammals and provided an excellent base for ecological studies. However, few such studies have been made. These include two regional studies, Greer's (1965) work in south-central Chile and Mann's (1945) in the extreme north, and three studies on single species, *Dromiciops australis* (Mann, 1955, 1958) and *Spalacopus cyanus* (Reig, 1970). There are no studies on a single rodent community over a period of several months in Chile.

STUDY SITES

I conducted live-trapping studies at two sites. The southernmost site, locally known as Rinconada de Maipú, is within the grounds of the experiment station of the School of Agronomy, University of Chile, 15 kilometers west of Santiago (70°50'W, 33°31'S), Santiago Province. The other site is 308 kilometers to the north, at Fray Jorge National Park (71°40'W, 30°38'S), Coquimbo Province. In addition, I sampled small mammal populations with snap traps at four coastal sites (see Table 12); data from which will be reported in detail elsewhere but are mentioned in the results and discussion of this paper when they are of special interest.

The trapping grid at Rinconada was inside a 5-hectare enclosure that had excluded livestock for three years prior to my study. This enclosure was surrounded by land modified by grazing and by experimental plantations of forage shrubs. Analysis of four 40-meter transects showed the shrub cover to be 54 per cent, 95 per cent of which was *Proustia cuneifolia*. There was a good cover of grasses with almost no bare ground.

Fray Jorge National Park consists of about 3000 hectares, much of which has been ungrazed for 30 years. Muñoz and Pisano (1947) described the flora and vegetation of the park. Schamberger and Fulk (in press) reported on the broad habitat affinities of the mammals in the park. The live-trapping grid was in the middle of a large inland area of uniform vegetation, at the base of a coastal ridge that rises 500 meters above sea level. Two 4-meter transects at each grid point showed the shrub cover to be 44 per cent, of which 65 per cent was *Porlieria chilensis*, 16 per cent *Adesmia bedwettii*, 15 per cent *Proustia pungens*, and 4 per cent other shrubs. This corresponds, both in plant composition and location, to the *Porlieria-Adesmia* association of Muñoz and Pisano (1947). The herbaceous cover was considerably less dense than at Rinconada.

The climate of central Chile is characterized by summer aridity and winter rains that fall almost entirely between the months of May and September. As one goes north in Chile, annual rainfall is reduced, concentrated into fewer months of the year, and more variable (Gastó, 1966). The variability of annual rainfall is especially important in the semiarid zone north of Santiago (Gastó and Contreras, 1972). The mean annual rainfall for Santiago is 360 millimeters (Gastó, 1966), although Rinconada is somewhat drier with a mean of 304.1 millimeters (Gastó and Lazen, 1966). The mean (1928 to 1946) at Talinay, 10 kilometers south of Fray Jorge, was 209.4 millimeters of rainfall (Muñoz and Pisano, 1947). At Fray Jorge, a

TABLE 1.—Annual rainfall (in millimeters) at Fray Jorge National Park and at the Qunita Normal station in Santiago. Data from Oficina Meteorológica de Chile except where indicated.

Year	Fray Jorge	Santiago
1973	39.0	172.0
1972	255.3	580.6
1971	72.1	247.8
1970	27.3	326.6
1969	11.4	177.3
1968		69.2
1967		172.3
1966		365.0
1965	326.0*	415.6
1964	59.5*	203.0

*From Kummerow (1966).

period of exceptionally low rainfall lasting at least three and probably five years was broken by the high rainfall of 1972, when my study began (Table 1). At Santiago, the same pattern held except that the period of dryness was alleviated somewhat in 1970.

Coastal fog acts to alleviate water stress in plants at Fray Jorge. On the top of the ridge, Kummerow (1966) found that coastal fog increased tenfold the water available to plants, resulting in a humid rain forest. No dramatic increase in moisture was noted on my grid, inland to the ridge. Muñoz and Pisano (1947) stated that the *Portieria-Adesmia* association is the typical climax community for this altitude (100 meters) and is free of the fog-condensing influence of the forest. But, where I trapped, coastal fog may have had some effect on the plants.

METHODS

The grid at Fray Jorge was 50 by 100 meters (0.5 hectare), with points spaced 10 meters apart. Two traps baited with corn were placed at each point. Three types of traps were used: a sheet-metal trap with a spring-activated door (similar to the Sherman trap) and two types with gravity-drop doors, one made of wire screen, the other of wood. All traps were similar in size to a large Sherman trap (7.5 by 8.5 by 22.5 centimeters), and all were handmade. There was considerable individual variation in their effectiveness. If the same pair of traps were left at each station for an entire trapping period, the relative trap success of each grid point would have been influenced greatly by the variation in trap effectiveness. This source of error was elimi-

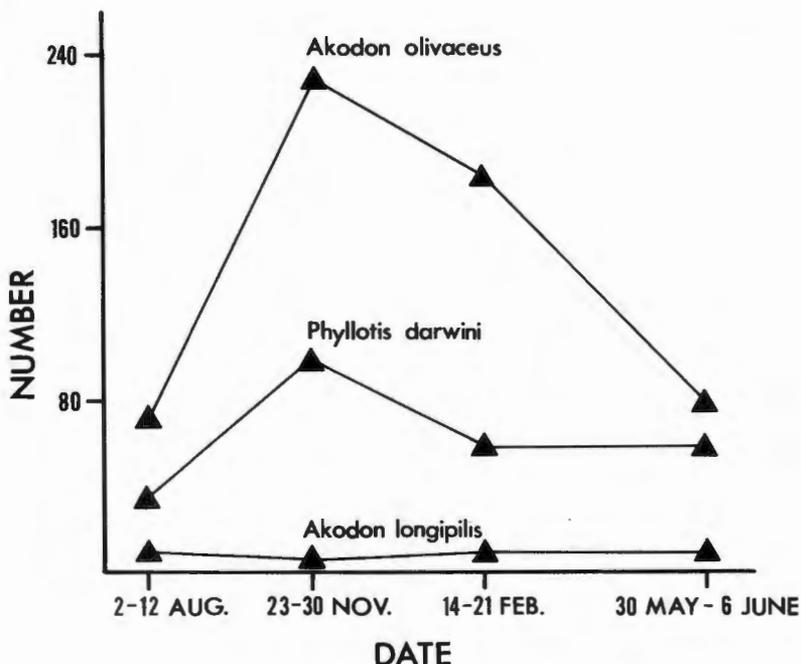


FIG. 1.—Number of individuals on the study area at Fray Jorge for each principal species of rodent. Note that intervals between trapping periods (horizontal axis) are not equal.

nated by rotating traps daily so each point received a new pair of traps.

I trapped for a minimum of eight nights at approximately three-month intervals (see Fig. 1 for precise dates). Traps were inspected in the morning, closed during the day, and set again in the evening, with the exception of the first trapping period when traps were continually set and inspected in the morning and evening. On 10 and 11 August, traps were inspected every 5 hours for 25 hours.

Animals were toe clipped for individual recognition, weighed, and checked for reproductive condition. The position of the testes was noted, and the following conditions were noted in females: lactation; pregnancy (by palpation); vagina perforate, imperforate, or with plug. Information on reproduction was supplemented by autopsy of animals taken with snap traps in areas removed from the grid but in similar habitat.

Weight was used to separate young and older age groups, because juvenile pelages were not clearly distinctive. Small mammals reach adult size rapidly, and the heavier weight classes may well contain

many juveniles (sexually immature animals). In this paper, animals in the lighter weight classes (less than 20 grams in the case of *Akodon olivaceus* and less than 40 grams in the case of *Phyllotis darwini*) are called juveniles and heavier animals are called older. The exception to this procedure, animals caught in November, is justified in the results.

Similar methods were employed at Rinconada, with the exceptions that the grid was 100 by 100 meters (one hectare), with only one trap at each station, and only three trapping periods (1 to 14 September, 14 to 29 December, and 27 March to 6 April). At both sites, animals were removed from the grid by intensive snap trapping at the end of the study.

The per cent of the total body weight consisting of digestive tract (stomach and intestines) was determined for *Akodon olivaceus* ($N=34$) and *Phyllotis darwini* ($N=34$). Stomachs also were weighed separately for most of these animals. Body weights were measured to the nearest gram and digestive tract and stomach weights to the nearest half gram. I also examined the external morphology of the caecum and measured the length, in millimeters, of the major divisions of the gut for three representatives of each species.

Collection of animals for digestive tract weights was done with a line of 66 snap traps operated during three trips to Fray Jorge in the spring of 1973. Data from these trap lines were compared to data obtained in November 1972 to indicate changes in reproduction, species composition, and density.

The numbers of animals on the study area were estimated using the method described by Marten (1970). This method uses the regression of the cumulative number of marked animals on the estimated number of unmarked animals. It is independent of trap shyness and trap proneness but assumes that the animal response to traps (catchability) does not change during sampling. If catchability is not constant, the regression will not be linear. I found that animals were caught more easily after an initial period of trap shyness. To meet this assumption, the first few days of each trapping period were considered prebaiting (that is, animals were caught and handled as usual and the data used for home range and survivorship but not for density estimates). After responses to the traps stabilized, as determined by the point where the regression became linear, the period of prebaiting was terminated. The number of days of prebaiting varied from one to three, depending on season and species. In cases where the number of recaptures was too low to use this method, density was considered equal to the total number of individuals caught. The estimate was

considered unreliable when more than one-fourth of the total was caught in the last two days of a trapping period.

The points of capture of all animals caught more than twice were plotted, and the maximum distance between captures, including half the distance to the next trap, was measured. The mean of these distances for a group of animals was then considered an estimate of the home-range length for that group. Unless otherwise stated, home-range lengths are based on animals caught three or more times in the case of *P. darwini*, or four or more times in the case of *A. olivaceus*, because more frequent captures failed to increase significantly the mean maximum distance between captures. The geometric center of the capture points for an animal is called its center of activity.

I considered the area sampled equal to the area of the grid plus, at Fray Jorge, a border strip of 20 meters if no edge effect was evident, or 40 meters if an edge effect was evident. I judged the edge effect evident if the outer rows of traps accounted for significantly more first captures than did the inside traps (Chi-square test, $\alpha \leq .05$). Edge effect was computed separately for each species and season. The size of the border strip was justified by the results of five 80-meter assessment lines perpendicular to the edge of the grid, with points spaced 10 meters apart. On the assessment lines, two snap traps per point were operated for three days at the termination of the study simultaneously with two traps per point on the grid. No marked animals were caught farther than 20 meters from the grid, a distance roughly equal to one-half the home-range length for all species. The edge effect for this month was not significant. At Rinconada, no assessment lines were operated, and the border strips used were equal to approximations of one-half the home-range lengths. For *Octodon degus*, home-range data were not available from trapping, but visual observations suggested ranges 100 meters long. *Marmosa elegans* was considered to have a range equal to that of *Phyllotis darwini*.

To calculate survivorship, a marked animal was considered to be on the grid during a given month, whether or not caught, if it was recaptured subsequent to that month.

The null hypothesis that a species' use of traps was independent of the type of vegetation around the traps was tested. Each grid point at Fray Jorge was given two ranks: one based on density of shrub cover, and the other based on herbaceous cover. Data for the ranks came from two 4-meter transects at each point. At 10-centimeter intervals along these transects, herbaceous cover was assigned to one of five categories. These categories were determined by clipping several 10-centimeter-square plots placed where the herbaceous cover seemed

most dense. The above ground vegetation was weighed, and the maximum weight (160 grams) was divided into five equal segments. These determined the limits of five categories used to measure herbaceous density. Prior to sampling, several plots were selected at random, visually assigned to a density category, and then clipped and weighed to check accuracy. This was done until accurate judgments could be made. Weights of herbaceous cover along the transects were then estimated visually and these estimates formed the bases for ranks assigned to each of the 66 points. Ranks for shrub cover were assigned according to the length of the transect covered by shrubs. This analysis of vegetation was done at the end of May, a few weeks before herbaceous plants had attained maximum growth. Ranks for use by each of the two principal rodent species were assigned to each point according to the frequencies of captures at that point. Spearman's ranked correlation coefficients, corrected for ties, were calculated for various combinations of the following parameters: shrub cover, grass cover, and capture frequencies of *Akodon olivaceus* and *Phyllotis darwini*.

At Rinconada, transects were not used at each grid point; but a trained observer, using five density categories, visually estimated shrub cover at each point. For each rodent species, Chi-square was used to test the null hypothesis that animal captures were distributed the same among the five density categories as were traps. All other frequency data were analyzed with the Chi-square test and differences between means with the *t*-test. Means are reported plus or minus one standard error.

Diversity was calculated by Brillouin's formula,

$$H = 1/N \log (N! / N_1 \dots N_s)$$

where s is the number of rodent species, N_i the abundance of the i^{th} species, and $N = \sum_{i=1}^s N_i$. Evenness of the species abundance dis-

tribution was measured by the ratio H/H_{max} , where H_{max} is the diversity attained if all the species were of equal abundance. M'Closkey (1972) discussed the use of these formulae with such data. My calculations differ from his only in that I used numbers of animals per hectare for values of N_i instead of numbers of animals on the study area. Diversity and evenness also were calculated separately for each month for MacMillen's data (1964, table 8, p. 35) using number of animals on the plot.

Study skins and skulls of representatives of all species from both sites were prepared and deposited at The Museum, Texas Tech University, Lubbock, Texas.

TABLE 2.—Number of animals per hectare by season at Fray Jorge for the three principal species. Number of individuals of other species also indicated.

Month	Principal species				Total	Other
	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>	<i>Akodon longipilis</i>			
August	30.3	29.4	8.7	68.4	1 <i>Abrocoma bennetti</i> , 4 <i>Oryzomys longicaudatus</i>	
November	97.0	42.3	4.8	144.1	1 <i>Octodon degus</i> , 1 <i>Marmosa elegans</i>	
February	78.6	46.0	7.1	131.8	2 <i>O. longicaudatus</i> , 2 <i>M. elegans</i>	
May	62.7	46.0	7.9	116.7	4 <i>O. longicaudatus</i> , 2 <i>M. elegans</i> , 1 <i>O. degus</i>	
Mean				115.2		

RESULTS

The number of recaptures during a single trapping session, as well as the numbers of animals known to have survived from a previous session, were extremely low at Rinconada. For this reason, I emphasize data from Fray Jorge and mention data from Rinconada only in comparisons.

Density

Recaptures were sufficient to use Marten's (1970) method of density estimation for *Akodon olivaceus* and *Phyllotis darwini* at Fray Jorge in all seasons and at Rinconada in September. In all cases where Marten's method was used, the estimated density was only slightly above or below the total number of individuals caught.

At Fray Jorge, *Akodon olivaceus* and *Phyllotis darwini* showed similar population changes, both reaching their maximum density in November (Fig. 1). However, *A. olivaceus* showed greater seasonal fluctuation than did *P. darwini*. *Akodon longipilis* maintained a stable, low density.

Other species present on the grid, in numbers too low to estimate, are shown in Table 2. Dense shrubland is suboptimal habitat for most of these species (see Discussion).

The European hare, *Lepus capensis*; the rabbit, *Oryctolagus cuniculus*; and the fossorial rodent, *Spalacopus cyanus* were not captured. At both sites, hares were observed frequently, and, at Rinconada, the rabbit also was abundant. The park manager at Fray Jorge said *Spalacopus cyanus* was formerly more abundant but had been reduced greatly during the recent dry years. In the more open parts of the shrubland I observed what appeared to be abandoned tunnel systems of this species.

Table 3 shows the densities of rodents at Rinconada. Several of the density estimates are unreliable, and seasonal trends are not meaningful due to the low densities in December, which may have been the result of a brush fire that burned the surrounding hillsides nearly to the edge of the enclosure. However, the greater relative abundance of *Oryzomys longicaudatus* and *Octodon degus* and the lower relative abundance of *Phyllotis darwini* and *Akodon longipilis* probably represent real differences between the two sites.

At Fray Jorge, edge effect was significant for *A. olivaceus* during every month except May, and for *P. darwini* only in November (Table 4). This corresponds to the apparent reluctance of *P. darwini* to enter traps, based on inspection of catch curves. Animals from different sex and age groups showed differential immigration

TABLE 3.—Densities of rodents at Rinconada by species and trapping session. \hat{N} = estimated number on the area sampled, \hat{N}/ha = estimated number per hectare (not given if less than one).

Species	Trapping session					
	September		December		March	
	\hat{N}	\hat{N}/ha	\hat{N}	\hat{N}/ha	\hat{N}	\hat{N}/ha
<i>Akodon olivaceus</i>	33	15.9	19*	9.2*	13	6.3
<i>Oryzomys longicaudatus</i>	17*	7.6*	0		14	6.2
<i>Octodon degus</i>	13*	3.3*	10*	2.5*	20*	5.0*
<i>Phyllotis darwini</i>	14	4.4	2*		10	3.2
<i>Marmosa elegans</i>	1		5*	1.5*	4	1.2
<i>Akodon longipilis</i>	0		1*		0	
Totals		31.2		13.2		21.9

*Unreliable estimates, see text.

onto the grid (Table 4). *Akodon longipilis* at Fray Jorge and all species at Rinconada failed to show a significant edge effect, even if the results were summed over all seasons.

Densities per hectare for Fray Jorge and Rinconada are shown in Tables 2 and 3, respectively. The number of small mammals per hectare at Fray Jorge ranged from 68.4 in August to 144.1 in November. The mean value is 115.2, considerably higher than at Rinconada, 21.9. Similarly, biomass was higher at Fray Jorge (Table 5).

At Fray Jorge, data from lines of snap traps indicated that rodent densities declined sharply in the spring of 1973. In November 1972, an effort of 120 trap nights gave a trap success of 67 per cent. In the spring of 1973 (between 6 September and 23 November), 396 trap nights resulted in a success of only 12 per cent.

Snap trapping in 1973 also showed that the relative abundances of *P. darwini* and *A. olivaceus* changed in that year. In early September

TABLE 4.—An index of edge effect, outside trap success/inside trap success, considering first captures only at Fray Jorge by month for the two principal species; level of significance; and sex of animals causing most of the edge effect, if significant.

Month	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>
August	1.72** males	0.60
November	1.27* adults	1.69** adults
February	1.37* females	1.08
May	1.40	1.10

* $P < .05$.

** $P < .025$.

TABLE 5.—*Biomass of rodents (in kilograms per hectare) at Rinconada and Fray Jorge.*

Date	<i>Akodon longipilis</i>	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>	<i>Oryzomys longicaudatus</i>	<i>Octodon degus</i>	Total
Fray Jorge						
August	.476	.992	1.929			3.397
November	.256	2.707	1.798			4.761
February	.362	2.296	2.463			5.121
May	.368	1.655	2.205			4.228
Mean	.365	1.912	2.099			4.376
Per cent	8.3	43.7	48.0			100
Rinconada						
September		.502	.184	.284*	.700*	1.670
March		.158	.191	.144	.815*	1.308
Mean		.330	.187	.214	.757	1.488
Per cent		22.2	12.6	14.4	50.9	100

*Unreliable estimates; see text.

1973, before reproduction, *A. olivaceus* was more abundant than was *P. darwini*, the former accounting for 44.8 per cent of the total catch and the latter, 20.7 per cent. When young of both species became trappable in November, *P. darwini* became the more abundant, accounting for 37.8 per cent of the total, and *A. olivaceus* for 33.3. This is in marked contrast to the situation exactly one year earlier (November 1972), when live trapping showed that *A. olivaceus* was more than twice as abundant as was *P. darwini*, and 72 of 80 animals taken in snap traps were *A. olivaceus*.

Diversity

Table 6 shows diversity, number of species, and evenness of species-abundance distribution for each trapping period at both sites. The means and standard errors of these measurements from the two southern Californian studies (MacMillen, 1964; M'Closkey, 1972) are also shown. Diversity and evenness were higher at Rinconada than at Fray Jorge. The Chilean sites showed lower diversity, fewer species, and lower evenness than did the Californian studies, except that Rinconada showed evenness values comparable to those in California.

Reproduction

Fray Jorge.—Most reproductive activity of *Akodon olivaceus* seemed to occur during the months of November and December. In August, 69 per cent of the males had scrotal testes, and 83 per cent of

TABLE 6.—Diversity (*H*), number of species (*s*), and evenness for each trapping period at Fray Jorge and Rinconada, and means of these values from two studies in southern California.

Date	<i>H</i>	<i>s</i>	Evenness
Fray Jorge			
August	1.480	5	.687
November	1.114	5	.493
February	1.308	5	.580
May	1.496	6	.514
Mean	1.349	5.25	.569
Rinconada			
September	1.592	5	.789
March	1.762	5	.826
Mean	1.677	5	.807
California			
Mean ^a (\pm SE)	2.022 (\pm .062)	7 (\pm .4)	.837 (\pm .017)
Mean ^b (\pm SE)	1.900 (\pm .075)	6.25 (\pm .2)	.770 (\pm .025)

^aFrom M'Closkey (1972).

^bFrom MacMillen (1964).

the females had perforate vaginas. No females were pregnant, although one had a vaginal plug. Data from snap-trapped animals confirmed these trends. The weight distribution (Fig. 2) suggests no juveniles in August. In November, 59 per cent of the population was juvenile, born since the last trapping period, probably during the previous six weeks. Because many of the animals with weights of 30 or more grams were recaptures from August, whereas only one animal of less than 30 grams was a recapture, animals weighing less than 30 grams were considered juveniles. In November, 87 per cent of adult males had scrotal testes; 54 per cent of the adult females was apparently pregnant; and 34 per cent of the adult females was lactating. Embryo counts in nine pregnant females taken in snap traps had a mean of 5.5 (\pm 0.27). There was a sharp decline in reproduction by February. Less than one per cent of the males had scrotal testes and only six per cent of the females was thought to be pregnant. Three individuals (0.2 per cent of the total) were juveniles. In May, the situation was similar: no males with scrotal testes, no females pregnant, and two juveniles (0.3 per cent).

In 1973, after the live trapping was concluded, three brief trips were made to the park (6 to 7, 29 to 30 September, and 22 to 25 November). Autopsies of animals taken in snap traps indicated the reproductive season began in the same month as it had in the previous year. In all three trips, all adult males had scrotal testes, but the

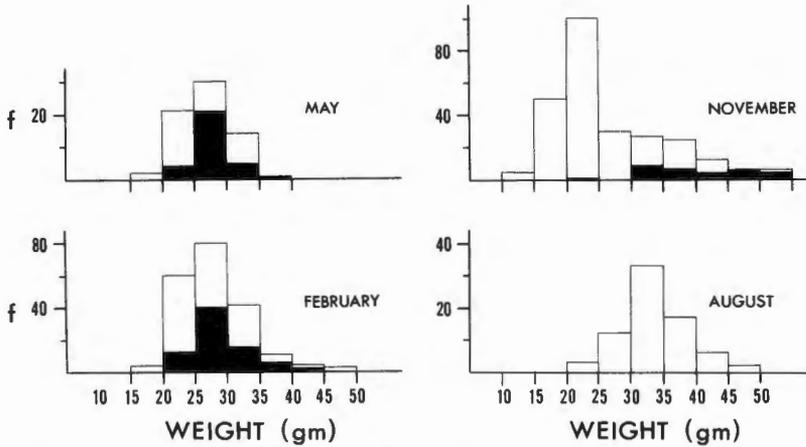


FIG. 2.—Weight distributions of *Akodon olivaceus* at Fray Jorge during the four trapping periods. Black bars represent animals marked in a previous month; open bars, animals caught for the first time.

females showed the following changes: all perforate, all pregnant, one pregnant and the other lactating in the first, second, and third trips, respectively. At the end of November 1973, only 31 per cent of the population was juvenile. The proportion of juveniles to adults was lower in 1973 than in the same week of 1972 ($P < .05$).

The pattern of reproduction in *Phyllotis darwini* was similar to that of *Akodon olivaceus*. In August, many males had scrotal testes (only 22 per cent of those trapped alive but 87 per cent of those snap-trapped); none of the females was pregnant, although 27 per cent had perforate vaginas. In November, animals weighing less than 50 grams were considered juvenile, inasmuch as none in this weight class was a recapture from August. Juveniles accounted for 71 per cent of the November population.

Classes of two different sizes (5 and 10 grams) were used to plot the weight distribution for animals caught in November and weighing less than 50 grams (Fig. 3). Upon inspection of the 5-gram classes, the distribution appears to be bimodal, suggesting two groups of litters: a younger group of 12 animals and an older group of 49 animals. Five pregnant females obtained from snap traps had a mean embryo count of 5.2 (± 0.58). Prior to February, reproduction declined sharply—none of the males had scrotal testes, and only 9 per cent (two animals) of the adult females was thought to be pregnant. Juveniles accounted for 10 per cent of the animals. In May, adults showed no sign of reproductive activity and again 10 per cent of the population was juvenile.

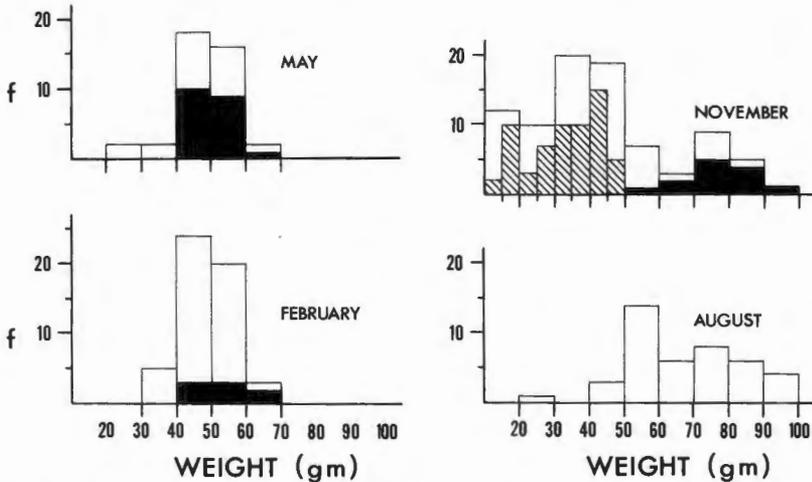


FIG. 3.—Weight distributions of *Phyllotis darwini* at Fray Jorge during the four trapping periods. Black bars represent animals marked in a previous month; other bars, animals caught for the first time. In November, 5-gram classes (bars with diagonal lines) and 10-gram classes (open bars) are used for animals weighing less than 50 grams.

After the conclusion of live trapping in the second year, snap-trap data for *P. darwini* from three subsequent trips showed that the reproductive cycle was similar to that of the first year. The percentage of the November 1973 population that was juvenile was only slightly lower than that in 1972.

There were slight differences between *A. olivaceus* and *P. darwini* in their reproductive patterns. After November, the ratio of juveniles to older animals was higher for *P. darwini* than for *A. olivaceus* (February and May pooled, $P = .06$), indicating recruitment of young continued later into the summer in *P. darwini*. In contrast, this ratio in November was greater for *P. darwini* ($P < .05$). This was probably due to differences in mortality, not reproduction; prior to November, *P. darwini* produced fewer young per female (3.6) than did *A. olivaceus* (7.3). The number of young in November and number of females in August were used to obtain these values.

Few *Akodon longipilis* were caught, so reproductive data are not detailed. In comparison to the other species, the reproductive rate in *A. longipilis* was lower and more consistent from season to season. In all months except May, a sizable portion of the adult males had scrotal testes. Pregnant females were taken in August and February. Juveniles were taken in November and May.

Only 10 *Oryzomys longicaudatus* were caught. Juveniles (two) were taken only in February.

Rinconada.—In spite of small sample sizes, it is evident that reproduction for most species at Rinconada began earlier in the spring and continued later into the summer and fall than it did at Fray Jorge.

Evidence of breeding in *Akodon olivaceus* was found in all samples (from early September through March). Always, the majority of the adult males had scrotal testes, and at least 20 per cent of each sample was juvenile. Pregnant or lactating females were present in every sample. The weight distribution in September was distinctly bimodal, indicating that the young of the year had not yet reached adult size and that reproduction had recently begun. Most adult females that month had perforate vaginas.

Phyllotis darwini showed a pattern similar to that of *A. olivaceus*. The majority of adult males had scrotal testes in every sample. Juveniles and females that either were pregnant or with a vaginal plug were taken in September and March (only adult males were taken in December). When I trapped in early September, the weight distribution of animals caught was bimodal (with none weighing from 30 to 60 grams), indicating that reproduction had recently begun. In every sample, it appeared that the ratio of juveniles to adults was smaller for *P. darwini* than for *A. olivaceus*.

Oryzomys longicaudatus differed markedly from the other species inasmuch as it seemed to breed principally in late summer and autumn. All nine of the *O. longicaudatus* taken in September showed no sign of reproductive activity. No animals were taken in December. In March, five of the seven adult females were pregnant (embryo counts obtained were 3, 4, 5, and 6) and most males had scrotal testes. The smallest of this sample weighed only 10 grams.

In *Octodon degus*, evidence of reproductive activity was found only in September, when, of eight females examined, four were lactating, two were pregnant, one had a perforate vagina, and one showed no sign of reproductive activity. No juveniles were taken.

Other coastal sites.—Snap trapping at other coastal sites showed that animals were still reproducing farther north after reproduction had ceased at Fray Jorge. At Fray Jorge, in the autumn before live trapping began (29 April 1972), a large sample taken in snap traps failed to show any sign of reproductive activity in adults or in any juveniles. However, one week later and 117 kilometers to the north at Buenas Herbas (locality in Table 15), 64.7 per cent of 17 *A. olivaceus* were obviously juveniles, as were 31 per cent of 32 *P. darwini*. Sexually active males and pregnant or lactating females of both species were caught. In February 1973, 90.3 per cent of the *P. darwini* at Fray Jorge weighed more than 40 grams, whereas in the same week at Huasco, 247 kilometers to the north, only 50 per cent of

TABLE 7.—Percentages of all animals, regardless of age or sex, surviving from one trapping period to the next for each of the principal species at Fray Jorge; absolute numbers of animals shown in parentheses.

Period	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>	<i>Akodon longipilis</i>
August to November	48.7 (36)	31.7 (13)	45.4 (5)
November to February	28.6 (72)	12.4 (10)	83.3 (5)
February to May	21.9 (40)	34.0 (18)	60.0 (6)

20 *P. darwini* had attained this weight, and three of five adult males had scrotal testes.

Survivorship

Data on survivorship were obtained only at Fray Jorge; at Rinconada, there was nearly a complete turnover (90 to 100 per cent) in the rodent population between trapping periods.

Table 7 shows the percentages of all animals, regardless of age or sex, that survived from one trapping period to the next. *Akodon olivaceus* showed its lowest survival rate from February to May, whereas *Phyllotis darwini* showed its lowest survival rate from November to February. *Akodon longipilis* showed a high survival rate throughout the year.

Figure 4 presents survivorship curves for adults caught in August and for young caught in November. To reduce variation in age within the young cohorts, only heavier juveniles (20 to 29 grams in *A. olivaceus* and 20 to 49 grams in *P. darwini*) were considered. *Phyllotis darwini* and *A. olivaceus* differed in their distributions of young in this cohort over the three months ($P < .05$), suggesting a difference in their patterns of survivorship. Young *P. darwini* showed lower survival in the first period (November to February) but higher survival in the second (February to May). Adult *P. darwini* showed lower survival rates in each period compared to *A. olivaceus*, but the pattern of decline did not differ significantly ($P < .1$) in the two species.

When sex-specific survival is considered, females of *A. olivaceus* showed greater survival than did males from August to November ($P < .25$) and from November to February ($P < .05$). No such trends were evident in *P. darwini*.

Consideration of age-specific survival from November to February shows that: in *A. olivaceus* older animals (over 20 grams) had better survival than did younger animals ($P < .25$), whereas the opposite seemed to be true for *P. darwini*.

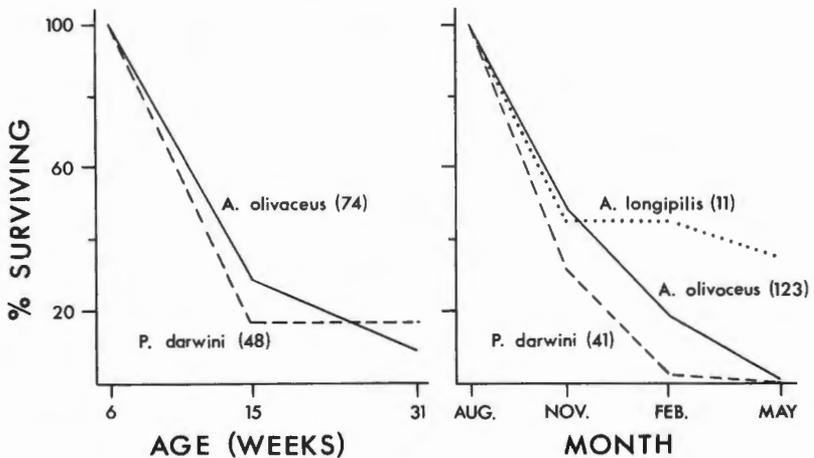


FIG. 4.—Survivorship of young caught in November (left) and adults caught in August (right) for species of *Akodon* and *Phyllotis* at Fray Jorge. Number of animals equal to 100 per cent are shown in parentheses.

Weight Changes

Change in weight of an animal from one season to the next, if not due to pregnancy (in females) or growth (in young), can be considered an index of general health. Data sufficient to indicate seasonal trends were gathered only for *Akodon olivaceus* at Fray Jorge. From November to February, when density was the highest, all 17 animals (young and females excluded) lost weight (mean weight loss, 5.9 grams). From August to November, when density was the lowest, only 20 per cent of 20 animals lost weight (mean, 4.5 grams). From February to May, 39 per cent of 36 animals lost an average of 2.5 grams.

Movement

The home-range lengths of *A. olivaceus* for each trapping period at Fray Jorge are shown in Fig. 5. Sexually active males showed larger home ranges than did females in August and November ($P < .05$). This was especially evident in November, when many females were pregnant or lactating and had reduced home ranges. Males continued to have larger ranges in February and May than did females, but not significantly so.

At Fray Jorge, ranges of male and female *P. darwini* showed seasonal trends similar to those of *A. olivaceus*, although the sample size was not adequate to show significant differences. The range size was also similar in the two species. The mean home-range length for all *P. darwini* varied from 36.3 meters (± 2.42) in February to 41.4

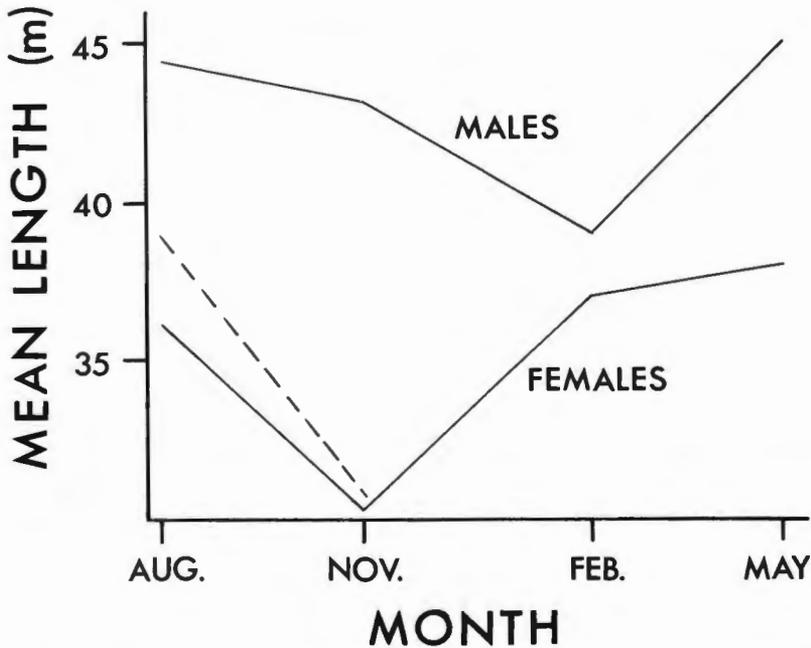


FIG. 5.—Mean home-range length, in meters, of *Akodon olivaceus* at Fray Jorge for each trapping period. Home ranges of sexually inactive males (broken line) are shown separately from other males in August and November.

meters (± 7.57) in November. *Akodon longipilis* seemed to have a larger home range, the mean length being 46.8 meters (± 9.39) for all months, although the sample size (11) is small.

At Rinconada, *A. olivaceus* showed a slightly larger home range (mean, 54.0 meters ± 4.26) and *P. darwini* a much larger range (mean, 76.9 ± 9.00). The mean home-range length for *Oryzomys longicaudatus* was 51.4 meters (± 10.80). Data from animals caught three or more times were included because of small samples.

The centers of activity were plotted for each animal caught in two consecutive trapping periods, and the distance that this point moved from one trapping period to the next was measured. Generally, for *A. olivaceus*, an animal's center of activity remained remarkably consistent; the average shift was about one trap station (means vary from 8.9 meters to 15.5 meters, depending on sex and season). The exception to this was the period from August to November, when males were sexually active and females were producing young. During this period males shifted their centers of activity an average of 21.3 meters (± 5.6); females, an average of only 7.1 (± 1.86). Both variances (*F*-test) and means differ significantly ($P < .001$). *Phyllotis darwini* males

TABLE 8.—Extent of home range overlap in females of *Akodon olivaceus* and *Phyllotis darwini* at Fray Jorge in months when overlap was not extensive; T=total number of ranges; 0=number with no points in common with another; 1=number with one point in common with another.

Species	November			August			May		
	T	0	1	T	0	1	T	0	1
<i>Akodon olivaceus</i>	12	4	4	16	7	5			
<i>Phyllotis darwini</i>	10	5	5	8	6	2	10	4	6

and females showed a pattern similar to that in *A. olivaceus*, but the sample sizes were smaller and the differences were not significant.

In *Akodon olivaceus* from November to February, young animals (weight less than 30 grams in November) shifted their center of activity less than adults, the means being 14.06 meters for young and 19.11 for adults, although this difference may be due to chance ($P < .07$).

Home ranges for the animals at Fray Jorge were plotted using the exclusive boundary strip method (Stickel, 1954), and examples of intraspecific nonoverlap were noted. If fewer than 20 per cent of the ranges were exclusive, the overlap was called extensive. In *A. olivaceus*, *A. longipilis*, and *P. darwini*, home ranges of males overlapped extensively with those of other males and females. In females of *P. darwini* and *A. olivaceus*, however, home ranges generally did not overlap with those of other females (Table 8) during the breeding season (August and November).

Ranges of female *Akodon longipilis* (Fig. 6) did not overlap with those of other conspecific females and were remarkably consistent in their location from one season to the next. Throughout the entire study, there was only one point where two adult females were caught, and these capture dates were six months apart. In May, two juveniles had their home ranges entirely within that of female number 3043, suggesting they were her offspring.

Time of Activity

In August at Fray Jorge and in September at Rinconada, traps were inspected twice daily, in the morning, not later than three hours after sunrise, and in the evening, not earlier than one hour before sunset. The percentages of captures that occurred in the evening inspection are shown in Table 9. At both sites the majority of *A. olivaceus* captures occurred during the daylight hours. All other species were largely nocturnal. For one 24-hour period at Fray Jorge, traps were

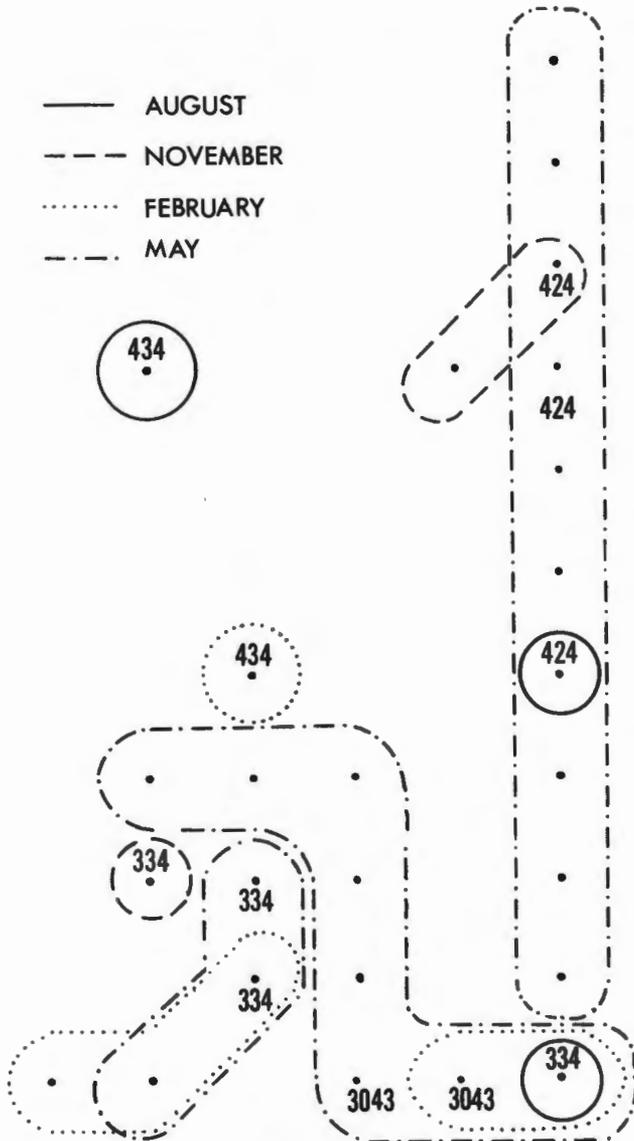


FIG. 6.—Home ranges of female *Akodon longipilis* caught two or more times at Fray Jorge. Numbers identify individuals.

inspected about every five hours (that is, five hours elapsed from the midpoint of one session of trap tending to the midpoint of the next). Data in Table 10 show *A. olivaceus* active during daylight, as well as at night, although rain appeared to suppress nocturnal activity. *Phyllotis darwini* was active only at night.

TABLE 9.—Percentages of captures in the evening check of traps (per cent diurnal) at Fray Jorge and Rinconada in August; number of captures equal to 100 per cent in parentheses.

	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>	<i>Akodon longipilis</i>	<i>Oryzomys longicaudatus</i>
		Fray Jorge		
Per cent diurnal	54 (302)	8 (100)	1 (21)	0 (6)
		Rinconada		
Per cent diurnal	59 (59)	0 (53)		4 (29)

Use of Grid Points

At Fray Jorge, competition for traps was an important factor affecting the frequency of capture at a given point. In all months except August, the number of animals on the grid exceeded the number of traps (132) and animals entered the traps readily. A trap often was heard to close less than two minutes after it was set. Trap success of 80 per cent was common, and many of the traps without animals were nonfunctional. In the keen competition for traps, *Akodon olivaceus* had an advantage over *P. darwini*, because the former was already active when traps were set in the evening, whereas *P. darwini* did not become active until about one hour later. At Rinconada, competition for traps was less important, inasmuch as the number of traps well exceeded the number of animals, and trap success was low, usually less than 10 per cent.

Spearman's ranked correlation coefficients were calculated between use by *A. olivaceus* and by *P. darwini* and the indices of shrub and grass cover (Table 11). Generally, use by *A. olivaceus* was correlated positively with both shrub cover and grass cover, whereas use by *P. darwini* was correlated negatively with grass cover; response to shrub cover was mixed. However, few of these correlations approach significance at the 0.05 level (see Table 11 for probability values). The correlation between shrub and grass cover was -0.183 and not significant. The correlations between use by *A. olivaceus* and use by *P. darwini* were negative and significant ($P < .01$) for all months except August, the month of lowest population density (Table 11).

To analyze the relation of capture frequency and vegetation for all species at Rinconada and for *A. longipilis* at Fray Jorge, grid points were separated into one of five categories of shrub cover varying from little cover (category one) to dense cover (category five). Numbers of captures per point for each species are shown for each category of shrub cover in Fig. 7. At Rinconada no points fell into category one. Density of shrub cover had a clear effect on capture frequencies for

TABLE 10.—Number of animals caught per hour during five time intervals over a 24-hour period in August at Fray Jorge.

Time interval	Species				Conditions
	<i>Akodon olivaceus</i>	<i>Phyllotis darwini</i>	<i>Akodon longipilis</i>	<i>Oryzomys longicaudatus</i>	
8:52 to 13:30	5.4	0	0.4	0	daylight
13:30 to 16:55	4.4	0	0	0	daylight
16:55 to 22:30	3.2	1.3	0.4	0	3.5 hrs. darkness
22:30 to 4:00	0.9	2.0	1.1	0	rain, 5.5 hrs. darkness
4:00 to 9:00	1.4	1.1	0.4	0.2	rain, 3.0 hrs. darkness

TABLE 11.—Sign and probability of difference from zero of Spearman's ranked correlation coefficients between vegetational cover of grid points and frequency of rodent captures; correlations between frequencies of *Akodon olivaceus* and *Phyllotis darwini* captures also are shown; NS indicates probability greater than .20.

Month	<i>A. olivaceus</i>		<i>P. darwini</i>		<i>A. olivaceus</i> - <i>P. darwini</i>
	Grass	Shrub	Grass	Shrub	
August	+NS	+ $P < .1$	- $P < .005$	+ $P < .1$	+NS
November	+NS	+ $P < .1$	-NS	+ $P < .1$	- $P < .01$
February	+NS	+NS	-NS	-NS	- $P < .01$
May	+ $P < .07$	-NS	-NS	-NS	- $P < .01$

two species: for *Octodon degus*, captures increased with decreasing shrub cover ($P < .05$), and *A. longipilis* was caught principally at the most densely covered points ($P < .025$). Less clear are the tendencies of *P. darwini* to prefer less densely covered points and for *A. olivaceus* to prefer more densely covered points. *Oryzomys longicaudatus* showed no definite pattern. *Phyllotis darwini* and *A. olivaceus* seemed to differ in their response to shrub cover ($P < .06$).

Alimentary Tracts

In *Akodon olivaceus*, 20.8 per cent of the total body weight consisted of digestive tract; for *P. darwini*, the corresponding value was 23.6. This difference is significant (Mann-Whitney U -test, $P = .032$). If the weights of the stomachs are subtracted from the digestive tracts, the difference is more pronounced ($P < .02$).

In three specimens of each species, *A. olivaceus* always had a relatively longer small intestine and shorter caecum and large intestine. Mean lengths, expressed as percentages of the mean length of the entire intestinal tract, are as follows (*A. olivaceus* followed by *P. darwini*): small intestine, 69.7, 61.3; caecum, 12.3, 15.6; large intestine, 51.7, 66.3. Based on the six specimens, *P. darwini* had a caecum with three folds, whereas *A. olivaceus* had only two (Fig. 8).

Other Coastal Sites

Four coastal sites were inventoried with snap traps, and the results for *P. darwini* and *A. olivaceus* are presented in Table 12. These results illustrate how Fray Jorge fits into the general pattern for the zone. All sites were trapped between 15 March and 12 May 1972 except the northernmost, Huasco, visited on 17 February 1973. Data for Fray Jorge are from Schamberger and Fulk (in press) and were

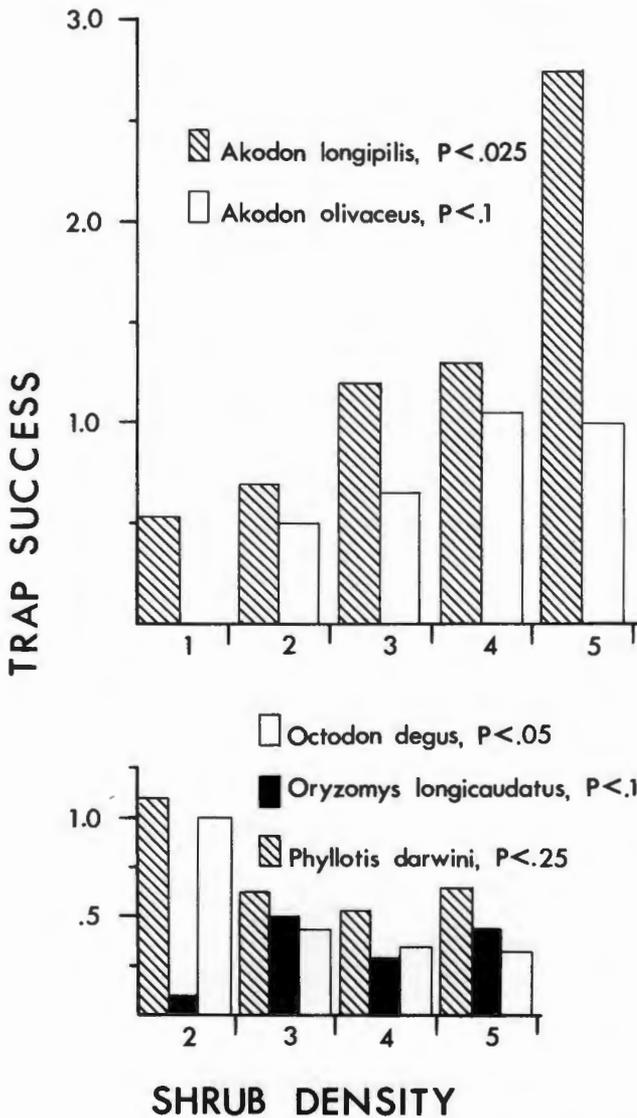


FIG. 7.—Trap success (captures per point) at points with various degrees of shrub cover. Data are from Rinconada, except those for *Akodon longipilis* from Fray Jorge. The probability that the actual distribution deviates from the expected based on equal trap success in each shrub cover category is given for each species.

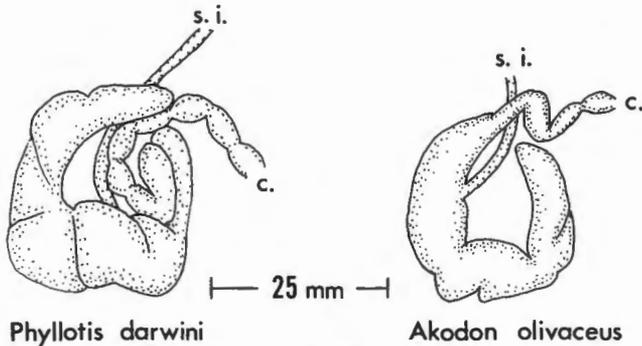


FIG. 8.—Caeca of two species of rodents; s. i.—small intestine; c.—colon.

collected from 26 to 30 April 1972, with a small grid of snap traps in the same plant association as the live-trapping grid. *Akodon olivaceus* and *P. darwini* were the two most abundant species at each coastal site except at Los Molles, where *Marmosa elegans* was unusually abundant. Northward into more arid conditions, there is a general trend for *P. darwini* to increase and *A. olivaceus* to decrease in abundance.

DISCUSSION

Three comparisons are made: Fray Jorge to Rinconada, *Phyllotis darwini* to *Akodon olivaceus*, and the two Chilean sites to other arid zones, especially southern California.

Fray Jorge and Rinconada

The rodent fauna on the live-trapping grid at Rinconada does not represent well a typical rodent community on an undisturbed site in the Central Valley. The enclosure was small and the influence of the surrounding modified land considerable. It did not appear to support a stable resident rodent community. However, Rinconada may be considered typical of the habitat actually available to rodents, inasmuch as the Central Valley is intensively cultivated and undisturbed habitats are rare.

Fray Jorge is an excellent example of an undisturbed climax community in the more arid zone of the north. Because the grid was placed in a large area of similar habitat, the influence of other plant associations was minimal.

These differences between the two sites invalidate many possible comparisons between them, but differences in species composition, reproductive season, and home-range size are of interest.

TABLE 12.—Relative abundance (per cent of total catch) of *A. olivaceus* and *P. darwini* and number taken at five coastal sites in north-central Chile.

Locality	Km. N Santiago	Description	% <i>Phyllotis darwini</i> (number)	% <i>Akodon olivaceus</i> (number)	% <i>A. olivaceus</i> % <i>P. darwini</i>	
3 km. N Los Molles, Aconcagua Prov.	142	shrub cover dense, canopy height 1.5 m.	14.0 (10)	29.5 (30)		2.11
Las Palmas, 95 km. N Los Vilos, Coquimbo	238	shrub cover moderate, canopy height .5 m.	42.0 (56)	23.0 (30)		.53
Fray Jorge Nat'l Park, Coquimbo	308	shrub cover dense, canopy height 1.5 m.	43.0 (78)	41.0 (74)		.95
Buenas Herbas, 35 km. N La Serena, Coquimbo	425	rocky, shrub cover sparse, cactus	52.6 (30)	35.0 (20)		.67
2 km. S Huasco, Atacama	550	cactus dominate, few shrubs	81.8 (9)	18.2 (2)		.22

Differences in relative abundance of various species are better understood when the geographic ranges and habitat affinities of these species are considered. *Oryzomys longicaudatus* does not extend north into the Atacama Desert, and Fray Jorge is in the northern part of its range (Osgood, 1943). At Fray Jorge, it was a minor component in all but the humid fog forest and forest ecotone (Schamberger and Fulk, in press). In Malleco Province, closer to the center of its range, rainfall is more than 10 times greater. Here, Greer (1965) found *O. longicaudatus*, along with *A. olivaceus*, to be the most abundant rodent in the Central Valley. Rinconada receives an intermediate amount of rain and it is not surprising that *Oryzomys longicaudatus* is more abundant here than at Fray Jorge.

The opposite situation holds for *P. darwini*. This species extends as far north as central Perú (Hershkovitz, 1962). In Perú (Pearson, 1951), as well as in southern Chile (Greer, 1965), it prefers dry rocky places. In Coquimbo Province, I found it to be the most abundant rodent on dry, north-facing slopes. Of all the species studies, *P. darwini* occupied the most xeric habitat, and it was more abundant on the drier of the two live-trapping sites.

In central Chile, Osgood (1943) found *A. longipilis* only along the coast. The Central Valley site of Rinconada, where I caught a single individual, is probably the eastern edge of its range. Greer (1965) also failed to find this species in the grasslands of the Central Valley in Malleco.

The greater abundance of *Octodon degus* on the grid at Rinconada as compared to that at Fray Jorge likely resulted from sampling error rather than to geographic variation in the abundance of this species in dense shrublands. The abundance at Rinconada was probably a result of the proximity of large colonies in pasture land bordering the enclosure. At Fray Jorge, *Octodon degus* might have been slightly more abundant than the live trapping indicated. Four individuals were taken in the assessment lines near the grid. However, visual observation of this diurnal species and inspection for burrows suggested that *Octodon degus* prefers more open plant communities and that dense shrublands are probably suboptimal habitats. This hypothesis is supported by a greater frequency of capture of *Octodon degus* at points with low shrub cover at Rinconada.

For *A. olivaceus* and *P. darwini*, reproduction began later and was concentrated into fewer months at Fray Jorge than at Rinconada. At Fray Jorge, reproduction began abruptly in late September and declined sharply between November and February. This is in marked contrast to the situation at Rinconada, where reproduction occurred over a seven-month period (September through March). Mooney

and Dunn (1970) suggested that in Mediterranean climates there is only a short time in the spring when vigorous plant growth is possible, because winter is too cold and summer and autumn too dry. They further pointed out that the time for vigorous plant growth becomes shorter as aridity increases with lower latitudes. If one assumes that rodent reproduction occurs principally during this time of increased plant production, one would expect that the length of the reproductive season would be shorter at more northern latitudes in Chile. This hypothesis is supported by my data and by those of Greer (1965). Greer, working in a Mediterranean climate in southern Chile (latitude: 37°15' to 38°55' S), found pregnant females over a six-month period (November through April). The fact that reproduction began later (November) in Greer's study than at Santiago (September) could be the result of colder spring temperatures in the south.

North of Fray Jorge, reproduction continued later into the autumn than at Fray Jorge. Because it is not known when reproduction began at these northern sites, this evidence neither adds nor detracts from the hypothesis that the reproductive season decreases in length as the latitude decreases.

Reproductive data for the other species of rodents were not complete enough to show any pattern of geographic variation. The facts that *Oryzomys longicaudatus* reproduced later in the summer than did the other species (Rinconada data) and that *Akodon longipilis* seemed to extend its reproductive activity over a greater part of the year (Fray Jorge data) suggest that these species differ from others in reproductive strategy.

At Fray Jorge, where rodent density was high, *A. olivaceus* and *P. darwini* had home ranges of similar size. At Rinconada, where density was low, both species had larger ranges, *A. olivaceus* only slightly so but *P. darwini* considerably so. An inverse relationship between home-range size and density has been frequently reported for small mammals (Stickel, 1968). The much greater increase in home range for *P. darwini* as compared to the modest increase for *A. olivaceus* with similar decreases in density may have occurred because *P. darwini* is a larger animal and has a much larger home range than does *A. olivaceus* under normal densities. Pearson and Ralph (1974), working with populations of much lower densities than those at Fray Jorge, found that ranges of *P. darwini* varied from 36 to 103 meters in length. A multiple regression involving the numbers of rodent refugia (places where rodents can hide) and the number of annual plants accounted for 98 per cent of this variation. Probably the densities they encountered were not great enough to affect home range size. On the two sites where *P. darwini* and a species of *Akodon* co-

existed, *P. darwini* had larger home ranges than did the species of *Akodon*.

The smaller home ranges reported by Greer (1965) for *A. olivaceus*, *A. longipilis*, and *Oryzomys longicaudatus* probably resulted largely from the short trap spacing (6.4 meters) and small grids that he used. Contreras (1972), using 10-meter spacing (equal to mine), reported that *O. longicaudatus* had a home-range length of 53.0 meters for females and 56.2 meters for males, a length similar to 51.4 meters that I report.

Principal Species at Fray Jorge

Although *P. darwini* and *A. olivaceus* both reproduced and reached their maximum densities at the same time of the year and were abundant in the same habitat, some differences existed between them. For example, *Phyllotis darwini* had a lower reproductive rate, but recruitment of young continued later into the summer. Adult mortality appeared higher in *P. darwini* than in *A. olivaceus*, and the former produced only enough young to replace dying adults. *Akodon olivaceus* produced an excess of young, which experienced a high mortality rate in the period immediately following reproduction. *Akodon olivaceus* showed its lowest rate of survival from February to May, when conditions were the driest and seeds and insects were probably least abundant, whereas *P. darwini* experienced its lowest survival from November to February, when rodent densities were the highest.

The two species also differed in their pattern of relative abundance along the coast (Table 12). As conditions became more xeric to the north, populations of *P. darwini* increased in relative abundance as those of *A. olivaceus* decreased. At a given latitude, I also found that *P. darwini* was more abundant on drier, north-facing slopes and *A. olivaceus* was more abundant on south-facing slopes.

Under the low density conditions at Rinconada, the two species seemed to differ in their response to shrub cover; *A. olivaceus* was caught most frequently at points with dense shrub cover, and the opposite was true for *P. darwini*. Under the greater densities at Fray Jorge, analysis of capture frequencies suggests a competitive interaction; *P. darwini* correlated negatively to grass cover whereas *A. olivaceus* correlated positively. The two species had a negative correlation to each other. This competition may have been for space or for traps.

The two species also differed in their alimentary tracts. Vorontsov (1960) pointed out that a larger alimentary tract, longer caecum and colon, shorter small intestine, and a more complex caecum are char-

acteristics often associated with a low-energy diet, that is, vegetative parts of plants. The opposite characters are associated with high-energy diets, such as those consisting of seeds and insects. The evidence suggests, then, that *A. olivaceus* is more adapted to a high-energy diet and that *P. darwini* is better able to utilize low-energy food, although their food habits probably show great overlap.

These two species also seem to differ in their proclivity for digging and climbing. When *A. olivaceus* was caught in a wire-floored trap, the trap usually was filled with sand. The same was not true for *P. darwini*. Furthermore, in habitats where *A. olivaceus* was abundant, the sandy soil often was riddled with small excavations. These observations suggest that digging, perhaps for seeds, is important for *A. olivaceus*. *Phyllotis darwini*, on the other hand, seems more adapted for climbing, the tail and hind feet being relatively longer. Four nests, between 1 and 2 meters off the ground in cactus and shrubs, were found to contain *P. darwini*. Several other similar nests were found, apparently unoccupied.

Most of these differences can be synthesized into a single hypothesis. *Akodon olivaceus*, with a higher reproductive rate and an alimentary tract adapted to a high-energy diet, is best able to exploit the sudden increase in seeds and insects that follows the rains, whereas the abundance of *P. darwini* is related to the density of permanent vegetative cover, especially shrubs. Thus as aridity increases to the north, shrubs increase and grasses decrease; likewise, *P. darwini* increases and *A. olivaceus* decreases in numbers. Furthermore, at a single site, *P. darwini* would show a relative increase after a year of below normal rainfall. Indeed this seems to have been the case in the spring of 1973, a year of below normal rainfall in Coquimbo Province. Comparison of snap-trap data from November 1972 and November 1973 showed that *P. darwini* increased markedly, whereas *A. olivaceus* decreased in relative importance. The age structure of the 1973 population suggests this was due to the lower reproductive success in *A. olivaceus* as compared to the previous year.

On the other hand, the more xeric affinities of *P. darwini* relative to *A. olivaceus*, as evidenced by the greater relative abundance of *P. darwini* populations in drier habitats and apparently during drier years, may be unrelated to differences in the food habits of the two species. Perhaps *P. darwini* has physiological adaptations enabling it to maintain higher densities under drier conditions. Such adaptations may be totally unrelated to adaptations for a low-energy diet.

In an arid environment where moisture, the principal limiting factor, shows great annual variation, it is advantageous that poten-

tially competing species differ in their response to changes in rainfall. The stability of the physical environment has a great effect on biological communities (see discussion in Miller, 1969; and Slobodkin and Sanders, 1969). Variability of rainfall, perhaps more than low average rainfall, greatly influences community organization. The variation in the response of various species of grasses to drought in the Great Plains (Weaver and Alberston, 1956) is an excellent example of a system similar to the one for Chilean rodents. Obviously studies on food habits, long term changes in species composition, and behavior of these species are needed to test the ideas I propose.

Akodon longipilis, which maintains low but stable densities by means of low mortality, low reproductive rates, and possibly a longer reproductive season, fits in well with the strategies employed by the two dominant species.

Chile and Other Arid Zones

The density estimates at Fray Jorge (mean, 115 animals per hectare) are fairly conservative, inasmuch as the assessment lines showed that rodents previously caught on the grid did not range more than 20 meters from the grid; when data indicated greater immigration onto the grid, I doubled the border strip. Nevertheless, this density is several times greater than most values previously reported for arid zones. In a review of the literature (Blair, 1943; Chew and Butterworth, 1964; Chew and Chew, 1970; Cockrum and Hoagstrom, 1973; MacMillen, 1964; Packard, 1971, 1972; Pearson and Ralph, 1974; Turner, 1973), maximum rodent densities were below or close to 20 animals per hectare, except in two cases: Chew and Chew (1970), with 29 per hectare, and Packard (1971), with 58 per hectare. Walter G. Whitford (personal communication) found a maximum density of 140 animals per hectare in 1973 at the Jornada site of the IBP Desert Biome after a 14-month period of above normal rainfall. At Fray Jorge, the maximum density was 144 per hectare. The densities at Rinconada (mean, 22 animals per hectare) compare more favorably with the above mentioned studies.

From trap success at coastal sites in Coquimbo, I received the impression that rodent densities were high throughout the province. Sterling Miller (personal communication) saw large numbers of *P. darwini* crossing the road at night near La Serena in the summer of 1973. Pearson and Ralph (1974) reported "plague" densities of *P. darwini* in March 1973 at a coastal site in southern Perú. Many farmers in the transverse valleys of Coquimbo Province (Ríos: Elqui, Limari, and Choapa) complained of rodent damage in the summer

and autumn of 1973. Outbreaks of rodents have been known to occur in Chile (see discussion in Hershkovitz, 1962:42). Above normal rainfall (Table 1) and possibly lower grazing pressure by domestic animals (Jurgen Rottman, personal communication) made conditions ideal for rodents in 1972. However, in August (Table 3) and April 1972 (Schamberger and Fulk, in press), before reproduction began, densities were already high at Fray Jorge; therefore, the high densities could not be due solely to favorable conditions in 1972. Reduced rainfall in the winter of 1973 was probably the major cause of the low densities observed in the spring of 1973. McCulloch (1962), Packard (1972), and Whitford (personal communication) all found substantial decreases in rodent density apparently caused by reduced food supplies subsequent to a drought.

The density estimates at Rinconada, live-trapping studies by William Glanz (personal communication), and mammal survey of Melvin Schamberger (personal communication) suggest that the high densities in Coquimbo Province and areas farther north did not extend as far south as Santiago.

Because of the similarity between Chile and California (Mooney *et al.*, 1970), the studies of M'Closkey (1972) and MacMillen (1964) in southern California are of special interest. The major differences between the sites in California and Fray Jorge are that the latter is closer to the equator ($30^{\circ}38'S$) than are the California sites ($34^{\circ}8'$ and $33^{\circ}36'N$), receive less rainfall, and have a shorter rainy season (see Klimadiagrammen in Mooney *et al.*, 1970). The rainfall pattern at Rinconada ($33^{\circ}32'S$) is more similar to that of the Californian sites.

Californian rodent communities are much more diverse than are the Chilean communities (Table 6). Coquimbo Province and Santiago fall into the northern edge of the Nothofagian sector (*sensu* Baker, 1967), which contains 35 species of mammals, whereas the Californian sites are in the North Eremian sector, with 114 mammalian species.

The low diversity in Chile is again apparent in the comparison of my sites with those of Crespo *et al.* (1970) at a similar latitude, $33^{\circ}50'$ to $34^{\circ}35'S$, in Argentina. The comparison is marred by differences in the habitats: the Argentinian sites receive more rain (802 millimeters annually) than do the Chilean sites and are grasslands rather than shrublands. Crespo *et al.* (1970) gave values for diversity but did not indicate how they were calculated. I used their data (fig. 9 in their paper) to calculate diversity and evenness as defined here, and the results (diversity = 2.23, evenness = .863) compare favorably with the Californian studies but are much greater than the values in

my study. The lower community diversity in Chile is again accompanied by lower faunal diversity. There are 63 species of mammals in Chile and 160 in Argentina (Greer, 1965).

The species distribution was the least even at Fray Jorge in comparison with those at Rinconada and the Californian sites. This low evenness was due to the unusually large number of *A. olivaceus* and *P. darwini* and accounts for the lower diversity at Fray Jorge as compared to Rinconada. Tramer (1969) suggested that when evenness rather than the number of species determines diversity, the environment is unpredictable and the species involved are "opportunistic" (*sensu* MacArthur, 1960). This hypothesis seems to be supported here, inasmuch as Gastó (1966) showed that rainfall is less predictable near Fray Jorge than it is near Santiago (that is, a normal year is less frequent).

Consideration of seasonal changes in density reveals additional differences between the Chilean and Californian rodent communities. Species in these studies may be placed into one of three groups according to when they reach their peak density: in early summer, early winter, or low densities and no distinct peak (Table 13). Although classification by this scheme is arbitrary in a few cases, most species fall easily into one of these groups, for example, *Peromyscus eremicus* in M'Closkey's (1972) study could be considered to show a summer peak rather than no distinct peak. *Dipodomys agilis*, in M'Closkey's study (1972), showed an unusual pattern of continual decline and is not placed into any of the three groups. In all three studies, most species had low densities with no clear peaks. At both Californian sites, *Neotoma lepida* showed a summer peak, and two other species showed winter peaks. Further evidence of asynchronous changes in density was reported by M'Closkey (1972); out of 15 possible correlations between monthly densities of various species, only eight were positive (four significantly so) and six were negative. In Chile, no such asynchrony was shown, with the possible exception of *Oryzomys longicaudatus*, breeding principally in late summer instead of in spring; both principal species reached their maximum densities in early summer. Asynchrony in density changes alleviates interspecific competition. The synchronous changes in Chile increased the possibility of interspecific competition.

In the absence of special mechanisms, maximum densities should occur during the reproductive season or, allowing time for the young to become trappable, shortly after. Reproduction occurred principally in spring at all four sites. In M'Closkey's study (1972), the mechanisms that caused densities to peak in winter were: high mortality in

TABLE 13.—Comparison of Chile and California with respect to seasonal changes in the population densities of rodent species at Fray Jorge and at two sites in southern California.

Seasonal pattern	California					
	Fray Jorge		M'Closkey (1972)		MacMillen (1964)	
	N	Species	N	Species	N	Species
Low, stable	3	<i>Akodon longipilis</i> , <i>Marmosa elegans</i> , <i>Oryzomys longicaudatus</i>	3	<i>Neotoma fuscipes</i> , <i>Peromyscus californicus</i> , <i>Peromyscus eremicus</i>	4	<i>Neotoma fuscipes</i> , <i>Perognathus fallax</i> , <i>Peromyscus californicus</i> , <i>Peromyscus maniculatus</i>
Winter peak	0		2	<i>Peromyscus maniculatus</i> , <i>Reithrodontomys megalotis</i>	2	<i>Dipodomys agilis</i> , <i>Peromyscus eremicus</i>
Summer peak	2	<i>Phyllotis darwini</i> , <i>Akodon olivaceus</i>	1	<i>Neotoma lepida</i>	1	<i>Neotoma lepida</i>

spring and summer, low winter mortality, and high rates of immigration onto the grid in winter. In MacMillen's study (1964), species having winter density peaks tended to show high levels of intraspecific aggression, whereas *Neotoma lepida*, which peaked in summer, was intraspecifically more compatible. Prevention of maximum densities from occurring during the reproductive season may reduce intraspecific competition during this critical time of the year. At Fray Jorge, mechanisms that prevented the population density from greatly increasing during the reproductive season were absent or ineffective.

Akodon olivaceus and *P. darwini* had larger embryo counts than did rodent species in the Californian studies. MacMillen (1964) reported that four species in his study had mean embryo counts ranging from 2.9 (± 1.2) to 2.5 (± 0.8), and the remaining species, 4.3 (± 1.3). I found that *A. olivaceus* had a mean embryo count of 5.5 (± 0.3), and *P. darwini*, 5.2 (± 0.6).

The extremely high density in 1972, the apparently much lower density in 1973, the lack of asynchrony in density changes, the fact that reproduction produced an immediate increase in density, and the uneven species-abundance distribution all suggest that the rodent community at Fray Jorge shows little self-regulation. In Fray Jorge as compared to California, forces arising from within the rodent community itself are less important in the determination of rodent densities, and environmental forces (rainfall and food supply) are more important. This hypothesized difference between the two rodent communities does not mean that Chilean rodents are less adapted to the environment.

SUMMARY

Two rodent communities in north-central Chile were live trapped over a nine-month period in 1971-72. Snap trapping provided additional information. At the northern site (Fray Jorge), the average rodent biomass was 4.376 kilograms per hectare, 91.7 per cent of which was accounted for by *Akodon olivaceus* and *Phyllotis darwini*. The average rodent density, 115 animals per hectare, was about five times greater than is common in arid zones. It is suggested that this outbreak of rodents was widespread in Coquimbo Province but did not occur near Santiago, where the mean density was 22 animals per hectare (biomass, 1.488 kilograms per hectare). Populations in the north declined sharply in 1973, a year of low rainfall.

At Fray Jorge; *A. olivaceus* and *P. darwini* both reached their maximum densities in November, the month of greatest reproductive

activity. *Akodon olivaceus* showed a greater seasonal fluctuation and produced more young per female. In *P. darwini*, adult mortality seemed to be higher and the number of young produced per female lower. *Akodon longipilis* maintained a low but stable population with low mortality and low reproduction.

With the exception of *Oryzomys longicaudatus*, which bred later than the others, all species bred principally in spring. The reproductive season was shorter at the more northern live-trapping site. It is suggested that this is a result of the shorter period of vigorous plant growth in the north. North of Fray Jorge, rodent reproduction extended later into the summer, but it is not known when reproduction began at these northern sites.

In *Akodon olivaceus*, the digestive tract constitutes a smaller percentage of the total body weight than it does in *Phyllotis darwini*; also, the caecum is less complex. This suggests that *A. olivaceus* is adapted to high-energy food, such as seeds and insects, which would be more available during a rainy year. This food habit, together with the high rate of reproduction, may cause the relative abundance of *A. olivaceus* to increase during rainy years and decrease during dry years. This hypothesis is supported by the relative increase in the population density of *P. darwini* as one goes north into drier habitats and by the shift in species composition at Fray Jorge from November 1972 to November 1973.

At the southern site (Rinconada), the mean maximum distance between captures was 76.9 meters for *P. darwini*, 54.0 for *A. olivaceus*, and 51.4 for *Oryzomys longicaudatus*. Home ranges of the first two species (especially *P. darwini*) were smaller at Fray Jorge, where densities were higher.

At Fray Jorge, home ranges varied considerably with season. Males of *Akodon olivaceus* had larger home ranges than did females, especially during the reproductive season, when home ranges of females were reduced. Females of *Phyllotis darwini* and *A. olivaceus* showed intraspecific nonoverlap of home ranges during the reproductive season. During the months of greatest reproductive activity (August to November), males of *A. olivaceus* shifted their centers of activity an average of 21.3 meters, a greater shift than at other times of the year and much greater than that of females, for which the centers of activity shifted little (mean, 7.1 meters) during the reproductive period. *Akodon longipilis* females showed consistent and nonoverlapping home ranges throughout the study.

At Rinconada, *Octodon degus*, and to a lesser extent *Phyllotis darwini*, were frequently caught at points with sparse shrub cover,

whereas the opposite seemed to be true for *Akodon olivaceus*. At Fray Jorge, *Akodon longipilis* was caught with greatest frequency at sites with the most dense shrub cover, but data suggest competition between *Akodon olivaceus* and *Phyllotis darwini* either for space or for traps or both.

The findings of this study are compared to similar studies in southern California (M'Closkey, 1972; MacMillen, 1964), where climate and vegetation are very similar to those in Chile (Mooney *et al.*, 1970). At both Chilean sites, the mammalian diversity was lower than that found in California. This was due to fewer species at Rinconada and to both fewer species and a more uneven species-abundance distribution at Fray Jorge. Density changes in southern California showed some asynchrony, but at Fray Jorge density changes were synchronous. In Chile, the two species that showed a distinct seasonal peak in density did so during the breeding season; in California, two species reached maximum densities well after the breeding season and one species, *Neotoma lepida*, during the breeding season. Based on these comparisons and on the high density at Fray Jorge and subsequent sharp decline, it is suggested that the rodent communities in north-central Chile are less well regulated than those in southern California.

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