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THE DIVERSITY AND ABUNDANCE OF VERTEBRATES ALONG AN ALTITUDINAL GRADIENT IN PERU

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I N D E X

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ABSTRACT

The number of species of plants, Foliage Profile, Plant Species Diversity, Foliage Height Diversity, percent ground cover, and number of small mammal refugia (safe retreats) were measured in eight arid or semi-arid plant communities in Peru on a transect from the coast to 4,500 m elevation in the Andes. These measurements were then related to the number of species, Species Diversity, population density, and biomass of the birds, mammals, and lizards living in the eight communities.

Number of species of birds was highly correlated with Plant Species Diversity, number of species of plants, and Foliage Height Diversity. The formula: $-42.55 + 14.087$ log (Foliage Profile x number of species of plants) accounts for 95% of the variance in number of species of birds in the eight habitats. If the exceptional *Tillandsia* community in omitted, 99% of the variance in number of species of birds in the remaining seven communities is occounted for by the formula: $-.62 + 21.52$ (Foliage Height Diversity) $+.44$ (% ground cover). After allowing for differences in measuring techniques, this equation also seems to predict fairly well the number of species in Kalahari habitats. Peruvian habitas in general support about the same number of bird species as comparable habitats elsewhere; the bunchgrass habitat in Peru supports more. The individuals are more equitably distributed than in most communities on other continents.

Most of the Peruvian communities support a greater Bird Species Diversity than expected on the basis of Foliage Height Diversity appropriate to Chile or North America. Bird densities varied from 0.3 to 33 per ha; these are in general comparable to those in other countries. The formula: $-26.70 + 1.224$ (number of species of plants) $+.016$ (Foliage Profile) accounts for about 84% of the variance in bird density. Bird biomass correlates most highly with the number of species of plants and exceeds the biomass of small mammals in six of the eight communities.

Number of species of small mammals varied from 0 to 6 and correlated positively with altitude. Compared with similar habitats in North America, the number of species in the Peruvian desert and western slope was low, probably because desert-adapted forms have failed to evolve, and the number of species at high altitude was relatively high. Mammal Species Diversity was best predicted by the formula: $-1.04 + .00027$ (altitude) $+ .028$ (% ground cover). The highest small mammal densities were 5.45/ha; they correlated well with Plant Species Diversity and number of species of plants. The greatest biomass of small mammals was in the Tola community (352 g/ha); 297 g of this, however, was subterranean herbivore (*Ctenomys*). The subterranean herbivore niche is a profitable one in North America also. No environmental attribute correlated well with mammal biomass, but if *Ctenomys* is omitted, biomass correlated well with number of species of plants and Plant Species Diversity. Ninety-seven % of the variance in biomass is accounted for by the formula: $-46.0 + 3.85$ (number of species of plants) $+ 1.79$ (% ground cover).

Community evolution is not tending to equalize biomass or energy flow among species of mammals.

Microhabitat preferences of several species of mammals were quantified in terms of those habitat characteristics measured.

The number of refugia varied from 224/ha to 2,300/ha. Traps set near refugia were not more successful than traps set elsewhere when refugia were as abundant as 2,300/ha, but when the density of refugia dropped below 1,300/ha, trapping success was greater near refugia. Even a density of refugia as low as 224/ha (48/mouse) seemed to limit neither the number of species of mammals nor the density of individuals.

The size of the home range of *Phyllotis darwini* was highly correlated $(r = -.97)$ with the number of species of small annual plants; 98% of the variance in home range is accounted for by the formula: $115 - 2.27$ (number of species of annuals) -6.26 (Refuge Index).

None of the study sites supported more than two species of lizard. Except for the very dense population of a single species in the Loma community, densities and biomasses were much lower than in desert habitats on other continents. Lizard biomass exceeded that of birds or mammals in only one community.

The average biomass, combining all communities was: birds 259 g/ha, mammals 143, lizards 88 — a ratio of 2.9:1.6:1. The most significant correlation of total vertebrate biomass was with the number of species of plants. Ninety-two % of the variance in biomass of vertebrates is accounted for by the formula: $72.6 + 25.90$ (number of species of plants) $- 641.89$ (Foliage Height Diversity).

The number of species of birds in a community is unrelated to the number of species of mammals; one class does not gain at the expense of the other. Number of species of birds, however, is highly correlated with density of small mammals, showing that where birds add species, mammals add individuals.

Most measures of the vertebrate populations increased with altitude. This probably results from increased precipitation with increasing altitude (and consequent increase of vegetation), and from more successful speciation of birds and mammals at high altitude than in the coastal deserts.

INTRODUCTION

The Pacific slope of the Andes of southern Peru supports a variety of biotic communities, some of which are unique and some of which are ecologic analogs of communities found on other continents. Because quantitative descriptions of the fauna and flora of these communities are lacking, because some of the communities are so widespread as to be of economic importance in Peru, Bolivia, Argentina, and Chile, and because together they provide an interesting altitudinal sequence, we have attempted to describe quantitatively a series of eight selected communities. These communities lie along an Andean transect in southern Peru extending from latitude 18° S, on the coast, east to the city of Tacna, and thence north-northeast along the Tacna-Ilave road over the continental divide into the Lake Titicaca Basin (Fig. 1). Our eight communities include study sites in the coastal desert, at the intermediate elevations dominated by shrubs, and at high altitude in the mountain and plateau regions called the puna or altiplano. Analysis of these communities provides insight into the relative importance of altitude, of various features of vegetative cover, and of shelter in determining the number of species and the population densities of the vertebrates present.

Important earlier studies are those of Koepcke (1954) and Koepcke and Koepcke (1953), who have provided a qualitative description of the vegetation and birds on a transect from the coast to the high mountains in central Perú. Mann (1960) briefly described various ecologic regions of a transect in northern Chile. An important geographic study of the region is that of Bowman (1961), and vegetational studies are those of Weberbauer (1945) and Tosi (1960). The notable work of Terborgh (1971) and Terborgh and Weske (1969) on forest birds on the Amazonian side of the Andes of Peru in a world of constant moisture, lush vegetation, and a multitude of bird species seems to have emanated from
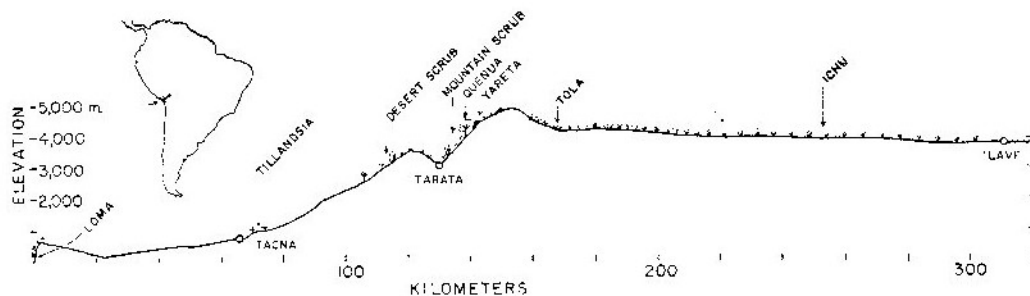

Fig. 1. Transect from the coast at 18° S latitude east to Tacna, thence NNE to Lake Titicaca showing the location of the eight habitats studied and the distribution of the kinds of vegetation. The descriptions in the text are presented in sequence from west to east.

a different planet. Pearson (1951) has written about the biology of mammals at high altitude in Peru, and Dorst (1967) about birds.

The climate and biology of coastal Peru are controlled by the cold Humboldt Current to the west and the Andes to the east, both of which shield it from moisture-bearing winds. Few coastal localities average as much as 5 cm of rain per year, and many receive essentially none. Precipitation increases northward and with altitude. At the latitude of Lima, a scanty, fog-nourished coastal vegetation gives way inland to sterile desert, but, beginning at about 1,000 m elevation, scattered shrubs, cacti, and annuals appear. At the latitude of our transect in southern Peru 1,000 km to the south, similar vegetation does not appear until 2,500 m elevation, leaving a broad "lifeless" zone between the coast and high in the mountains. Another 1,000 km to the south, at the latitude of Copiapó in Chile, the "lifeless" zone extends from the coast to the continental divide above 4,700 m.

At the latitude of our transect in southern Peru, the vegetation reaches its greatest height and complexity at about 3,700 m. Above this elevation, factors associated with altitude rather than with precipitation limit the vegetation.

Almost all of the rain, snow, or hail falls during the Southern Hemisphere summer months (December to March). The increased moisture at that season, accompanied by the warmer nights that result from increased cloud cover, renews plant growth. Most vertebrates reproduce during that season.

The actual measurements of our communities were made from September 17 to November 20, 1971. During this time no precipitation fell on any of our study areas and, with one exception, the annual increase of vertebrates had not yet been added to the populations. Comparisons of population densities at the different sites should, therefore, be valid. The one exception is the coastal Loma study site. The Loma vegetation if fog-nourished, with a growing season beginning in May or June. Young mice had already been added to the population in the Loma, and many birds were nesting.

ACKNOWLEDGEMENTS

METHODS

The study grids. Having decided to quantify a particular biotic community, we selected as large an area as possible that displayed as uniformly as

possible the desired plant formation and then staked out a study grid within it. The choice of a site for the grid was influenced by (1) appropriate species composition and uniformity of the vegetation, (2) proximity to an acceptable camp site, (3) flat enough topography to permit establishment of a sufficiently large, reasonably square census grid within the chosen plant formation, (4) freedom from molestation during the trapping period, and (5) a definite bias toward sites that appeared, on the basis of previous experience in southern Peru, to be "good" habitat for small mammals.

Six of the eight study sites (*Tillandsia* and Yareta excepted) are heavily grazed by cattle, sheep, horses, burros, goats (up to 3,700 m), llamas (down to 3,000 m), or alpacas (down to 3,700 m). Since the human population has kept livestock for centuries, and we know of no ungrazed or even lightly grazed areas, we are content to consider grazing to be an integral part of the plant-animal association in this region. In the absence of cultivation and of industry, people were scarce.

The study grids contained between 1.57 and 3.24 ha. Numbered stakes or other markers were set up at measured 15-m or 20-m intervals, providing us with 90 to 110 fixed points that could be defined by two coordinates. These points were used to determine the vegetation sampling points and the trap positions. Vegetation was analyzed at 30 to 48 of these stations evenly distributed over the grid. The number of sampling stations was chosen taking into account the size of the grid and the uniformity of the vegetation. At each of these sampling stations we determined, as described below, the foliage density profile, the percent of ground covered by vegetation, the number of species of plants present, and the number of refugia available to small mammals.

Foliage Profile. To estimate the density of the vegetation we used a 25 X 180 cm board marked off into 12.5 X 10 cm squares; it was held vertically 4 m away from a chosen grid stake. An observer at the grid stake then estimated the proportion of the board covered by vegetation at the following levels: 0-1/2 m, 1/2-1 m, 1-2 m, 2-3 m, and 3-4 m. The observer put his eye at the midpoint of each layer of vegetation. The board was held perpendicular to his line of sight and was placed on a predetermined diagonal of the grid squares (to avoid trampled vegetation along the grid lines). If this diagonal fell over a sharp drop, the board was moved to the side until it was no longer obscured by this drop. Rocks that covered part of the board were "seen through," since we wished to measure the profile of the vegetation, not the topography. If the vegetation was higher than the board, which it rarely was, we lifted the board to the height necessary to record the density at the 2-3 m level, or, one occasion, the 3-4 m level.

The decision to divide the vegetation into layers at the 1/2, 1, 2, 3, and 4-m levels was imposed by consideration of the fact that we wished to relate the resulting data to both bird and small-mammal populations. Consequently, our measurements of foliage height density and diversity are not directly comparable

with those in earlier studies, such as those of MacArthur and MacArthur (1961), Rosenzweig and Winakur (1969), Tomoff (1974), and Willson (1974). So that our units at least will be in a standard and reproducible form, we have converted our field observations (percent of board obscured by foliage at the different levels) to cm² per m³ with the equation

$$\text{cm}^2\text{m}^3 \text{ of space} \;=\; -\;\log_e (1 - q)/L - \lambda$$

where q is the percent of the target board obscured by foliage, L is the distance from the eye of the observer to the board, and λ is the distance from the observer within which obscuring objects were avoided. We assume that the observer would move his head if some twig or leaf only a few centimeters from his eye obscured a large fraction of the board. Ten centimeters seemed to be a reasonable estimate for λ, making $L - \lambda = 390$ cms. Copies of the derivation will be supplied by the authors upon request. It is based on the fact that the probability that a random piece of vegetation would lie in a particular plane between the observer and the target board is proportional to the area available in that plane within the pyramid bounded by the oberver's eye and the board. This measurement of amount of vegetation is closely related but not identical with Willson's (1974) PCVC (the sum of the percent vegetation cover for all layers of foliage). Both are functions of the volume of vegetation present.

　　Throughout this paper we shall capitalize Foliage Profile when referring to the sum of the densities calculated as described in the two preceding paragraphs. Foliage Profiles of the eight study sites may be compared in Figure 2. The statistical significance of comparisons of Foliage Profile and of percent ground cover in Table 7 were made with the *t*-test.

Foliage Height Diversity. This measure was calculated by the formula — $\Sigma p_i \log_e p_i$ where p_i is the proportion of Foliage Profile in each of the layers
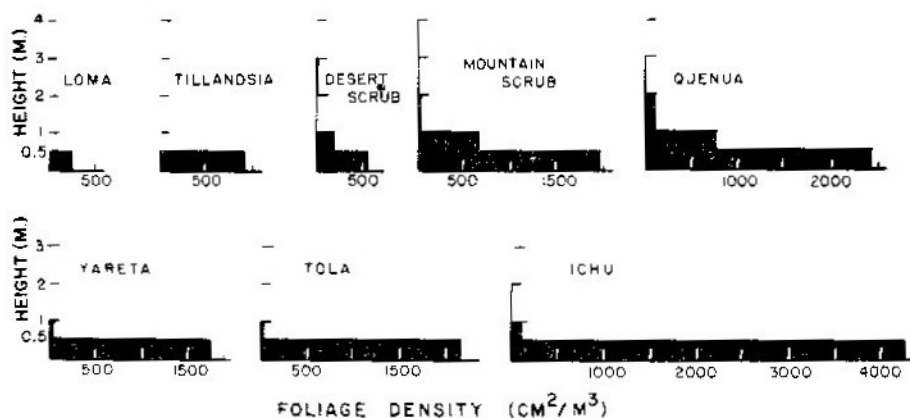

Fig. 2. Foliage density profiles at the eight study sites.

after doubling the calculated densities in the layers above 1 m to compensate for the fact that the two lowest layers were only 1/2 m deep).

Ground cover. Along the same diagonal as that used for the profile measurement a hoop enclosing 1 m² was placed on the ground, its center 2 m from the grid stake. The percent of the ground inside the hoop covered by each species of plant was estimated by two observers, and their estimates were averaged. A plant was considered to cover all of the ground below the circle (or other figure) defined by the periphery of its canopy. This gives as much importance to slender light plants as to thick mats of to plants such as cacti with much different biomasses. The total percent cover within the hoop was also noted, subtracting when necessary from the sum of the separate species to allow for overlap. Dead vegetation was included in the total cover.

Plant Diversity. Our measures of plant diversity are based on the total number of species represented in 30 or more hoop samples (see above) distributed evenly over the grid. We distinguished the different species within each hoop sample and christened them with temporary names. Specimens of the important species were collected for later identification because at the time of our study (end of dry season) most species are without flowers, seeds, or other diagnostic features. For this reason we are especially grateful to Dr. John Strother for aid in plant identifications. We know that on some of the grids, fairly important species of plants escaped representation in the hoop samples, but we have made no correction for these omissions.

Plants were also classified somewhat arbitrarily as to life form: tree, shrub, bush, cactus, moss or lichen, fern, large annual, mediumsized annual (10-30 cm), or tiny plants (less than 10 cm). "Tiny plants" were mostly small, dry annuals but included some low, non-mat perennials, especially at the higher study areas.

Four measures were used to reflect the species complexity of the plants in each community: the total number of species appearing in the hoop samples (Number of Species of Plants in later discussions); the mean number of species per hoop (ranged from 0.73 in *Tillandsia* to 10.20 in Mountain Scrub); the mean number of species per hoop, but lumping all small annuals as one species and all medium-sized annuals as another species (ranged from 0.73 in *Tillandsia* to 6.70 in Mountain Scrub); and Plant Species Diversity (using the formula — $\Sigma p_i \log_e p_i$). The latter index was based on the number of hoop samples in which each of the fourteen most common species in any community appeared. Commonness was based on the number of hoop samples in which each species appeared. The cutoff at 14 species penalized the index of Plant Species Diversity of those communities with more than 14 species of plants, but the penalty was probably of little importance biologically because of the scarcity of the remaining species.

Refugia. On the assumption that the number of available refugia, or hideholes, might influence the number of species of small mammals or the number

of individuals present on the area, we counted the number of refugia within 2.2 m of each of the stakes at which we also measured the vegetation, as well as at some additional stakes. Refugia were defined as retreats into which a frightened mouse could escape and be almost completely safe from capture by a fox or a human. Refugia were usually burrows or small caves under or between large rocks, but sometimes were under large cacti, between stems at the base of spiny thorn bushes, in dense *Tillandsia* mats, or, at the Tola study site, tunnels made by a burrowing rodent (*Ctenomys*). Refugia were not necessarily suitable for nesting. The average number within 2.2 m of the stakes on any one grid we have called the Refuge Index for that habitat. It can be converted to refugia per hectare by multiplying by 658. A plot of the frequency of the number of refugia is not distributed normally and so, when testing for the significance of differences between Refuge Indices (Table 7), we have used the Mann-Whitney U test.

Weather. Using a maximum-minimum thermometer, air temperatures were recorded in the shade at each of the study sites. Humidity was measured with a sling psychrometer at three times of day: approximately 6 a.m., noon, and 6 p.m. Because of the great altitudinal range, the relative humidities reported here have been corrected for altitude by multiplying the wet-bulb depression, before entering the relative humidity tables, by the quotient of: atmospheric pressure at campsite in mm Hg. divided by 760. This correction at high altitudes raises the values of relative humidity greatly and thereby conceals how little water vapor the air actually contains and how low its vapor pressure is. The wet bulb was sometimes as much as 16°C colder than the dry bulb. Humidities usually were not measured when the air was below freezing circumstances under which it is certain that the water vapor pressure will be very low.

Mammals. Small mammals were censused by mark-and-recapture for three to six successive days and nights. This trapping effort gave rise to the figure used for Number of Species present. The population size was then estimated from simple Lincoln Index calculations using the percentage of marked mice of each species obtained on the last day of trapping. Home ranges (mean maximum distance between points of capture) were calculated, and a border strip equal to the average home range of each species was then added to the periphery of the study area to arrive at an estimate of the area actually being utilized by the population during the census period, and consequently the population density. Approximately equal numbers of small (50 X 65 X 165 cm) galvanized and large (77 X 90 X 228) folding aluminum Sherman live traps were used, one set within 2.2 m of each stake. Occasionally a trap was set somewhat farther from a stake. To avoid recapturing the same individual twice in succession at the same site and thereby recording a home range of zero, traps that caught a mouse during one night were not reset until 24 hours later. All traps were baited with rolled oats. Mortality in the traps was very low in spite in of nighttime temperatures as low as —14 C at three of our camps. On those study areas

where some species were active during the daytime, the traps were shaded from the hot sun.

Some species of small mammals were represented by capture of only one or two individuals on the study area. Since this did not provide enough data for reliable home range measurements, and consequently reliable estimation of the area occupied, we have used home range measurements of the same species in other areas or, in the absence of such data, have added a border strip 30 m wide.

Biomass of small mammals on each study area was calculated by multiplying the population density of each species by the mean body weight of individuals of that species caught on or near the study grid. Mammal Species Diversity was calculated from the estimated population density of each species (number per ha) rather than from the numbers actually trapped.

Foxes (*Dusicyon*) and, probably, skunks (*Conepatus*) utilized all of the study areas. Since it was impossible to census them and since they were so widespread, we have omitted them from all calculations. Vizcachas (a rodent weighing about 1.2 kg) lived in the cliffs close to three of our grids and, judging from the presence of numerous droppings, visited one of the grids frequently. It would be impossible to calculate densities, and so they have been omitted also.

In addition to live-trapping on the grid, considerable trapping was carried out nearby. In this way specimens were obtained for positive identification and for information on the age structure and reproductive status of the populations. This peripheral trapping frequently revealed species not trapped on the grid itself, but only the species actually trapped on the grid were used in defining the species composition of the grid and in calculating Mammal Species Diversity. The mammal censuses were carried out by Oliver Pearson.

Birds. To determine for the season of the study the number of species of birds using the study area (Bird Inventory), a list was made of all species seen on the grid or in adjacent similar habitat during the 3 to 5 days of study. Field identification down to species was not always possible, but were are confident that we distinguished between the different species, so that the number of species counted is accurate. The total does not include, of course, all species that ever occur on the census area and does not necessarily represent the number of species using the area in the breeding season. However, virtually all species in most of the communities are resident throughout the year. Nomenclature follows Meyer de Schauensee (1970).

To measure the relative abundance of species at each site (Bird Density and Bird Species Diversity), a strip census was carried out. After the grid to be used for small mammal census and vegetation analysis had been set up and the kind of vegetation it included thereby defined, a trail was paced off through the grid and adjacent similar habitat such that the area covered during a census would be 3 ha. The width of the trail was set according to the density of the vegetation and the shyness of the birds so that all birds within the trail would be

perceived and censused. This width was usually about 30 m, so the trail was about 1 km long, within the accuracy of pacing. Censuses were made by walking slowly along the trail, stopping when necessary, and recording all birds within the prescribed distance. Birds that merely flew over, unless they were aerial feeders or raptors, were not counted. At each study site two censuses were made at the time of maximum activity or visibility, which was usually early morning just after sunlight reached the census area. An additional census was made later in the morning to record species with different activity schedules. At most of the study areas this census had to be made before the daily winds started. The final estimate of the Density of each species at a site was the maximum number of individuals seen on any one of the three census runs, divided by three to reduce it to a per-ha basis. These final abundances were summed to give Bird Density and were used to calculate Bird Species Diversity. We used the maximum, rather than the average number of individuals seen on the censuses, to avoid giving undue weight to early-morning, as opposed to late-morning, species.

At the Loma study area, young birds were subtracted from the count to make the figures comparable to those of the other study sites, where breeding had not started. This assumes that the birds remain in the Loma during the non-breeding season, and at least some of them do (Koepcke, 1954).

The estimates of bird populations may have been low for sneaky, ground-living species such as furnariids, and high for flocking species such as fringillids that happened to pass through during the census. Emlen (1971) has pointed out the deficiencies of this and other methods of censusing birds. We have made no correction for differences in detectability of different species, relying more on the narrowness of the census strip in these open habitats to permit detection of most individuals. The number of species represented in these strip censuses was, in all communities except Tola, close half the number recorded in the Bird Inventory. This indicates that the censuses are probably reliable for comparing abundances of species in each site and between our different study sites but cannot be relied upon to compare with more accurate censuses, especially those of breeding birds which take into account the size of the territories.

The Bird Density figures for each species were multiplied by average body weight (taken from labels on museum specimens) to arrive at biomass per hectare (Bird Biomass). The bird inventories and censuses were made by Carol Ralph.

Reptiles and amphibians.-- Lizards were so scarce on all except the Loma grid that they were formally censused only in that habitat (by color-marking followed by Lincoln Index calculations of subsequent resightings). At the other study areas occasional sightings of lizards during dozens of man-hours on the grids were recorded on a map of the grid and, at the end of the study, these sightings were used to estimate the actual number of individuals seen; such estimates are probably minima. They also may be considered minima, at least at the high altitude sites, because the study was conducted near the end of the

"winter" season when the lizards are less active (Pearson, 1954). Species seen or collected nearby but not recorded on the grid were not included in the species count.

No amphibians were seen on any of the study grids. This reflects an absence of suitable water on any of the sites, because frogs and toads were present in suitable habitat close to several of the grids.

Note that for mammals and reptiles the species counts and density estimates are based only on individuals actually living on the study grid, whereas for birds the species Inventory figures are derived from species utilizing similar habitat nearby as well as those utilizing the grid itself. Furthermore, the bird density figures are derived from strip censuses that extended into similar habitat beyond the limitis of the grid itself.

LOMA STUDY AREA

At many places along the coastal desert of Peru, a local configuration of hills causes ocean fog to condense in sufficient quantity and for a long enough period to support growth of a remarkable seasonal flora that may contain plants up to the size of bushes and even small trees. The measurable annual precipitation in usually only a few centimeters. Grasses are scarce, endemic forms are frequent. The seasonal flush of green vegetation supports grazing by goats, cattle, horses, and burros. Such areas are known as *lomas* (Weverbauer, 1945; Ferreyra, 1953; Goodspeed and Stork, 1955; Holdridge, 1967; Hughes, 1970). Using the climatic system of Holdridge, Tosi (1960) includes these lomas in the plant formation *chaparral bajo montano bajo*. Holdridge considered the loma at Lachay in central Peru to be a *Cloud Chaparral Association* of the Subtropical Desert Scrub Life Zone.

On November 7 we selected a study area on a sloping, rock-strewn terrace 60 m above the rocky beach at Morro Sama, 65 km west of Tacna (Plate 1). The vegetation was beginning to dry up. Some days were foggy all day, others partly foggy or cloudy-bright, and others clear. Maximum temperatures were 25 C, 28, 25, 27; minima 14, 15, 16, 15, 16, 17; relative humidities in the morning 74%, 70, 67; noon 61, 42, 54, 65; evening 71, 74. At Punta Islay, 175 km up the coast, rainfall averages 20.5 mm per year, and the mean annual temperature is 18.2 C. At Arica, 80 km down the coast, the corresponding figures are < 3 mm and 18.6 C. Potential evapotranspiration at these two places is, respectively, 74 and 72 cm (Papadakis, 1961).

The percent of ground covered by vegetation (see legend for Figure 3) was about the same as that on five of the other study areas, and the presence of 32 species of plants in the hoop samples represents a diversity about midway in the range encountered in our other habitats. The mean number of plant species per hoop, 4.81, was relatively high. The Loma vegetation presented by far the smallest value for profile of any of the habitats studied. This reflects a scarcity of "substantial" plants. There were only a few bushes (*Grindelia*), and a

slender caper (*Cleome chilensis*), which covered only 1.9% of the ground, was the most abundant other plant more than 30 cm tall. In contrast, the percent of ground covered by small annuals was 10 times as great as in any of the other habitats studied (34.6%). Filaree (*Erodium cicutarium*), an introduced weed, covered, for example, 13.2% of the ground, and a beggar tick (*Bidens* sp.) covered 11.2%. Both of these were setting large numbers of seeds.

Sandy slopes adjacent to the study area were speckled with many species of blooming annuals only a few centimeters tall. On the steep slopes and cliffs immediately above the study area, rivers of green cucumber vines (*Sicyos bade-roa* and *Cyclanthera* sp.) poured down the talus below and between the cliffs. The top of the ridge (580 m) was covered with *Grindelia* bushes in bloom.

The lomas of coastal Peru vary from a seasonally lush, broad-leafed flora, even with bushes and trees, to one with a very sparse sprinkling of delicate annuals; our study area was intermediate.

The study grid (Plate 1) covered 135 X 150 m (2.025 ha) and included 110 trapping sites spaced 15 m apart. Numerous boulders and large quantities of angular rocks provided an abundance of refugia.

Mammals.— The grid was trapped for six nights and produced only one kind of mouse, *Phyllotis darwini,* a species with an enormous geographical and altitudinal range. The genus is the Andean equivalent of the North American *Peromyscus.* Twenty-five individuals were captured on the grid; Lincoln Index calculations indicated a population of 30. Twentyfive recaptures of 12 individuals gave a home range (mean maximum movement) of only 36 m. After adding a border strip of 36 m to the Loma grid, the population density becomes 6.52 per ha the highest density of small mammals measured on any of our study areas. This comparison of densities is biased by the fact that the growing season for plants in the *lomas* is 6 months out of phase with that at our six mountain study areas, and breeding seasons of the animals are shifted accordingly. Consequently, a crop of young *Phyllotis* had been added to the population in the Loma. If these young mice are omitted, the population density becomes 3.85 adults per hectare a density more like that of the combined species of small mammals on the other study areas. The biomass of the entire mouse population amounted to 206 g/ha; the adult population was 166 g/ha.

This habitat is capable, at least on rare occasions, of supporting enormous densities of mice (see section on Numbers of Mammals per Hectare).

Trapping nearby with Museum Special traps disclosed the presence of *Mus musculus* (house mouse) along the rocky shoreline as well as in the dense cucumber vines and bushes at the base of the cliffs high above the study grid. Examination of pellets of burrowing owls and droppings of foxes showed that they had been eating not only *Phyllotis* and *Mus*, scorpions and other invertebrates, but also another species of mouse (*Akodon*) and mouse opossums (*Marmo-sa*). These were probably caught in the denser vegetation higher up the slope. Foxes (*Dusicyon griseus*) were seen and trapped only 100 m from the study grid.

The number of refugia at 32 stakes where mice were caught averaged 3.75, and 3.32 at 31 stakes where no mice were caught. The difference is small, probably because refugia were so abundant-more abundat than on any of the other study areas.

Birds.— The spring chorus of sparrows (*Zonotrichia*), sierra finches *Phrygilus*), and wrens (*Troglodytes*) that started at dawn and could be heard in the study area all day was misleading. Most of this song was floating down the hill, and on the actual study area birds were neither abundant nor diverse. The small birds present were taking advantage of the abundant insects available at this season. *Phrygilus* was in pairs or families, some incubating, and some feeding nestlings. Conebills (*Conirostrum*) were feeding young, and a nightjar (*Caprimulgus*) was sitting on an egg. One pair of wrens had fledglings. Young birds seen on the census were excluded from the population estimate so that this census could be compared more directly with censuses on the other study areas.

We do not know how many these birds are present in the dry season. There must be a fair supply of seeds available for them later in the year, since most of the vegetation consists of seed-producing annuals. During a brief visit in March of 1973, vultures, condors, burrowing owls, wrens, and *Phrygilus* were noted. The raptors surely are permanent residents. *Cathartes* and *Vultur* both live primarily off of the nearby seacoast with its sea lions and guano birds (*Phalacrocorax boungainvillii*). The vultures roosted in good numbers among the sea lions, and about 20 condors roosted on the cliff above the study area. A buzzard-eagle (*Geranoaetus*) was nesting on the cliff. On top of the ridge among the denser bushes were some species of birds, such as *Zenaidura auriculata*, that did not come down to the study area while we were there, as well as greater numbers of the same species that were present down below on the study area. Censuses took 55 minutes to 1 hour 15 minutes.

Of the 16 species in the Inventory, 9 occur also in the mountains at least to the level of 3,000 m (but not necessarily on our study sites). Only four are coastal or low Andes species. Three are not identified well enough to say what their ranges are. Most are species with enormous latitudinal and altitudinal ranges, notably *Speotyto cunicularia, Troglodytes aedon, Falco sparverius, Vultur gryphus, Cathartes aura,* and *Zonotrichia capensis.* Koepcke (1963) states that the latter, at least in central Peru, is a temporary visitor in the lomas during the breeding season.

Reptiles.— The Loma grid supported many more lizards than any of the other study areas. Only one species was represented, *Tropidurus peruvianus,* an omnivorous, polymorphic species that weighed, at this season, from 12 to 46 grams. Four censuses were carried out by noosing as many individuals on the grid as possible (28 by the time of the fourth census), color-marking and releasing them, then having a team of five evenly-spaced observers make slow sweeps across the area, recording the numbers and locations of marked and

unmarked individuals. Lincoln Index calculations were then applied to these counts and indicated populations of 84, 79, 145, and 112 individuals. The last was considered to be most reliable. Mean maximum movement, based on 50 re-sightings of 24 lizard, was 22 m. Adding a border strip of this width gives an area censused of 3.47 ha, a density of 32 lizards per hectare, and a biomass of 652 g/ha. The number of lizards visible varied considerably depending upon the presence of sun or fog, but the Lincoln Index procedure should minimize errors arising from this.

This number and biomass of lizards exceeded not only the number and biomass on any of the other study areas but also exceeded the number and biomass of small mammals on any of the grids. The mildness of the temperature and abundance of refugia (more than at any of the other sites) probably contributed to the suitability of this habitat for lizards. In most North American desert communities the population density of lizards is much lower than in the Loma community (Pianka, 1967), but in some places such as in desert scrub in Texas (Tinkle, 1967) and Nevada (Turner *et al.*, 1970) a species of much smaller lizard (*Uta stansburiana*) reaches much higher densities. *Tropidurus peruvianus* in the Loma habitat, however, achieves a greater biomass per hectare than any population of lizards elsewhere with which we are familiar except for a population of the large, herbivorous chuckawalla (*Sauromalus obesus*), which reached a biomass of 1.67 kg/ha in the Mojave Desert of California (Nagy, 1971). Preliminary measurements at the Jornada Validation Site in New Mexico indicate that the lizard *Cnemidophorus tigris* may exceed even this (Whitford, 1972).

Two specimens of a colubrid snake, *Dromicus tachymenoides*, were captured in cucumber vine tangles not far from the study grid. This species is venomous, oviparous, and said to be fond of eating lizards (Donoso-Barros, 1966).

Summary.—This Loma community presented a low Foliage Profile, a low Foliage Height Diversity, a moderate Plant Species Diversity, and an average percentage of ground covered by vegetation. An unusually large percent of the ground was covered by small, seed-bearing annuals. Refugia were more abundant than in any of the other communities. Only a single species of mammal and a single species of lizard occupied the study grid, but they were present in large numbers. A moderate number of bird species was present, with the individuals at rather low densities. The mouse, the lizard, and almost all of the birds belonged to extremely wide-ranging species. Resources were available for supporting a large biomass of vertebrates, but the mammals and reptiles had not divided them among related species, several of which were living nearby. This was the only community in which the biomass of lizards exceeded that of the birds and of the mammals. Judging from the relatively low biomass of birds, it is probably safe to say that this was the only community in which birds were bioenergetically the least important class of vertebrate.

TILLANDSIA STUDY AREA

Tillandsia is a genus that includes more than 350 species of tropical and subtropical bromeliads, many of which, such as Spanish moss, are epiphytes. At many places in coastal Peru where ocean fogs are persistent enough and high winds lacking, one or more species of *Tillandsia* form fairly dense pure stands. In many regions, such as at our study site, the plants are completeley rootless and rest unattached on the surface of the desert, deriving all of their moisture and nourishment from fog. Individual plants live for decades.

We chose an area 6 km north of Tacna at 1,000 m elevation and, on October 9, set up a study grid 150 X 150 m with 15-meter spacing between stakes (Plate 2). The only species of vascular plant present was *Tillandsia werdermannii*. No *Tillandsia* plants were blooming or fruiting at this time, and no seedlings were present. Flowers, fruits, and seedlings were absent also in September, 1971, in January, 1972, and in March, 1973; indeed, this species may be viviparous (MacBride, 1936). The plants themselves on our grid appeared to be thriving, but is should be noted that this *Tillandsia* community was unusually far from the coast (46 km) and consisted of a narrow band bordered on both sides by absolute desert, thereby giving the appearance, problems, and opportunities provided by small islands.

During our measurements at the *Tillandsia* site days were clear, but some nights were foggy. A light breeze blew toward the mountains during the day and toward the sea at night, causing moisture to settle on the north (mountain) side of the *Tillandsia* leaves. Maximum temperature on one day was 24 C; minima 2, 1; relative humidity in the morning 90%, 52%; noon 62%; evening 89%. The minimum temperatures were lower than those encountered at our Desert Scrub site 2,000 m higher. Nearby at Tacna the mean annual rainfall is 32 mm, and the mean annual temperature 16.3C (Tosi, 1960). Potential evapotranspiration is 110 cm (Papadakis, 1961).

Our study area lies in the **desierto montano bajo** formation of Tosi (1960).

Because the habitat was so uniform, we did not consider it necessary to distribute the vegetation sampling points evenly, as on the other study areas. Instead, we sampled at 30 stations located at 15-m intervals along both diagonals of the grid. Living *Tillandsia* covered 18.9% of the ground, and mats of dead stems and leaves covered 11.2%. The plants grow in rows or crescents as much as 7 m long (Plate 2). The direction of growth is toward the south, regardless of the slope of the substrate, so that an advancing front of live *Tillandsia* leaves a mat of dead stems and leaves behind in to the north. The Foliage Profile averaged 967 cm^2/m^3 in the lowest 1/2m. This appears to be a sparse profile, compared with that of several of the other communities, but it reflects merely a complete absence of foliage higher than 40 cm. Below this height the plant profile was fairly dense, and plant biomass was undoubtedly great. The only other live macroscopic plants seen in the general area were a small dormant succulent (*Calandrinia pachypoda*) and a lichen (*Teloschistes exiles*) that

resembled a tuft of rusty steel wool. The lichen appeared in only one of the 30 hoop samples. No example of the succulent was seen anywhere on the grid itself.

The Refuge Index of 2.2 reflects a relatively large number of potentially safe shelters among the tightly packed leaves of the living *Tillandsia* mats. There were no rocks, small caves, or burrows on the grid. In fact, the only relief from monotony was provided by a single small travelling sand dune about 1 m high that was moving from south to north across the grid leaving behind a trail of smothered Tillandsia plants.

To assess the diversity and number of macroscopic animals of all kinds living in such a simple habitat, we marked off what appeared to be a typical 15 X 15 m section of the study grid, estimated the area covered by the 57 mats of *Tillandsia* growing there, then overturned and shook them in search of animal life. The mats totalled 37 m² (16 percent groundcover). Underneath them we found 20 small and medium-sized spiders, 2 small thysanurans, and one pseudo-scorpion. This represents a much sparser fauna than that found in *Tillandsia latifolia* in central Peru, where the ecosystem included an abundance of thysanurans, spiders, scorpions, three or more species of mice, two species of foxes, and species of lizards (Pearson, ms).

Mammals.—We trapped the grid for three consecutive nights and caught nothing. Additional evidence of the absence of mice was provided by the fact that no mouse footprints could be found in the fine dry soil, a substrate that would preserve prints clearly for many days or weeks. One or more foxes visited the grid each night. Droppings collected nearby revealed that they were eating primarily invertebrates such as scorpions, but included also a bird, a mouse, garbage, a large lizard, and a viscacha (*Lagidium*). The viscacha must have been caught many kilometers away.

Mice were living nearby, however. Twenty-five Museum Special traps set in a steep gulley about 150 m from the grid for two nights caught one house mouse (*Mus musculus*). We attribute its presense there to the abundance of rocks, since pure *Tillandsia* and a small number of rocks suppported many *Mus* on the study area central Peru (Pearson, ms). *Mus* has also invaded other desert habitats in coastal Peru (Koford, 1968).

Birds.—There were no resident birds regularly using the study area. The ground-feeding flycatcher seen during the census belongs to a widespread South American genus (*Muscisaxicola*) of many similar species, most of which have altitudinal migrations, latitudinal migrations, or both. The individual seen foraging between the *Tillandsia* mats was too shrouded in morning fog to permit identification to species. It was not seen again, so must have been a visitor. The other species in the Inventory (swallow and turkey vulture) were also just passing through but are species that eat wherever they happen to find food, so they were considered to have been foraging over the area. The Inventory was brief; only three days, but only a few other ground-feeding species could be

expected. A nightjar was flushed from the grid in March of 1973 and a seed snipe was heard; *Geositta* might also be expected. There certainly is nothing to support a granivorous bird. Koepcke (1954) observed only the following in *Tillandsia* in central Peru: sparrow hawk, *Geositta*, *Muscisaxicola*, swallows, nighthawks, and, once, a combduck (*Sarkidiornis*).

The census trail was 600 X 50 m, and each census was one hour long.

Reptiles.—No reptiles or reptile tracks were found on the study grid. However, specimens of two species of lizards (*Tropidurus peruvianus*, *Ctenoblepharis* sp.) and one species of gecko (*Phyllodactylus gerrhopygus*) were captured within 150 m of the grid, always associated with rocks or surface objects. Geckos were fairly abundant wherever flat rocks lay on the ground. The *Tillandsia* mats, however, did not seem to be adequate shelter for them.

Summary.—The *Tillandsia* community is a monoculture that surely approaches the state of being the simplest possible terrestrial ecosystem. The number of species of vertebrates present is much less than would be expected in view of the amount of vegetation (see later in this paper, especially Figure 7). It is tempting to attribute the scarcity to the remote-small-island effect inherent in this pach of *Tillandsia* surrounded by desert. This explanation fails for mammals and lizards, however, because there were one or more species living only meters away, and it fails for birds because during the intensive study of a different *Tillandsia* site in central Peru, we saw only two species of birds on the ground (*Burhinus* and *Pezites*) in spite of proximity to habitat occupied by many species. We conclude that pure *Tillandsia* is not attractive to birds, probably because of inadequate food supplies, and is not attactive to mice and lizards because of lack of adequate shelter, such as rocks and surface objects, and possibly food. The thick mats of *Tillandsia* that we judged to be sabe refugia for mice apparently did not fulfill some of the thermal requirements of lizards and some nesting or other requirements of mice.

DESERT SCRUB

Tillandsia continues to grow for a few kilometers toward the mountains northeast of our *Tillandsia* study area, but then for more than 20 km and a thousand meters of increasing elevation the landscape is devoid of vegetation (Fig. 1). As one ascends into the mountains a few scattered shrubs appear in the dry washes, then a few tree cacti on the slopes. Not until the 3,000 m level was there enough vegetation to encourage us to set up a study plot, which we have called Desert Scrub. On September 17 at 16 km south of Tarata we laid out a 165 X 105 m grid (15-m spacing), one-third of which was the flat bottom of a dry wash, one-third a sloping bench about 5 m above the dry wash, and one-third a steep (22°) east-facing slope (Plate 3). The grid was trapped for three days.

Days were brilliantly sunny and dry with a steady breeze up the canyon in the morning and down the canyon in the evening. Nights were clear and cool. Maximum temperatures were 26 C, 20, 18; minima 5, 6, 4; relative humidity in the morning 40%, 45, 52; noon 45, 42, 37, 40; evening 52, 63, 60. At vegetationally similar Arequipa, mean annual temperature is 14.9 C and mean annual rainfall 138 mm (Tosi, 1960); potential evapotranspiration is 122 cm (Papadakis, 1961).

The vegetation at this site suggests that it lies in Tosi's **Maleza desértica montano bajo,** although in his map and text (1960) this formation does not reach quite this far south. Our study area corresponds to the columnar cactus community of the lower zone of the **Serranía esteparia** of Koepcke (1954), which in central Peru is at about 1800 m elevation.

Vegetation in the dry wash primarily scattered bushes (*Baccharis* cf. *petiolata*) and tobacco seedlings and saplings up to 4.3 m tall (*Nicotiana glauca*). One clump of bushy pepper trees (*Schinus molle*) grew at the edge of the dry wash. A stone retaining wall beyond one border of the grid but well within the home range of mice increased the amount of shelter available for mammals and birds. On the bench above the dry wash a sparse mixture of bushes such as *Lycium* and *Franseria*, candelabra cacti, and small annuals provided most of the plant biomass; in a few places they provided patches of impenetrable thicket. Refugia were found under boulders, piles of stones, and at the base of large cacti and bushes. The nearest water a small seep about 1/2 km down the dry wash. Dense tall bushes grew in a steep, narrow section of the canyon a few hundred meters down the canyon.

The percent of the ground covered by vegetation was much less than that on any of our other study areas and less than in many North American desert habitats (Table 1). Nevertheless there were many species of plants and a high Plant Species Diversity. Foliage Profile was not great (Fig. 2), but Foliage Height Diversity was large as a result of the actually infrequent but **relatively** abundant columnar cacti and tobacco plants reaching to 2 or 3 meters. Most of the ground cover was provided by bushes such as *Franseria* (4.3%), *Baccharis* (3.3%), and *Lycium* (1.75%); less than one percent was covered by the 20 species of small annuals. Grasses covered only 0.1 percent.

Mammals.—The dominant small mammal was *Phyllotis darwini*. Lincoln Index calculations indicated that we were sampling a population of 17 individuals. Fourteen recaptures of 11 individuals gave a mean home range of 60 m and a resulting density of 2.65 individuals per hectare. The average weight of 12 specimens from the grid or near it was 38.6 g. Two specimens trapped near the grid were juveniles weighing only 10 and 16 grams.

A single *Phyllotis magister* was also captured in a dense patch of large dead cacti. At this latitude the species is ordinarily found in denser brush. No free water was available to these mice, but they presumably made use of water in the tissues of the cacti. Both species of mice were nocturnal.

Other species of small mammals caught within a few hundred meters and that could be expected to occur at least occasionally on the grid were *Marmosa elegans* (mouse oppossum) and *Akodon berlepschii*. A bat was seen hunting over the area, vizcachas were heard nearby, and a wildcat skeleton was found. The mammal fauna in general is one derived from higher altitude and one that needs neither free water nor grass.

Mammalogists familiar with North American deserts, when shown the Desert Scrub study area in Peru, or photographs of it, anticipate the presence of many more than two species of small mammals and a much higher population density. Table I summarizes a number of studies in arid habitats in North America for comparison. We have subtracted rabbits from the data of those studies in which they were originally reported because no ecological equivalent of rabbits is available in the Peruvian Andes, but we have retained ground squirrels whenever possible because an equivalent (guinea pig) is potentially available to some of our Peruvian study grids (even though none was actually recorded on any of our grids). Slight discrepancies remain in the table because some studies included gophers and others did not. Nevertheless, it is apparent that the Desert Scrub and Mountain Scrub in Peru are near the low end of the range of species richness. It should be pointed out that in the *Larrea* desert in Arizona, an especially important community with which additional comparisons will be made later in this paper, the six species listed in the table include neither five species of rodents listed as "transients" by Chew and Chew (1970) nor two species of rabbits nor one species of gopher.

Table 1 indicates also that densities and biomasses were relatively low in these Peruvian communities.

Birds.—In spite of the sparse Foliage Profile and ground cover, this community supported a moderate number of bird species and a moderate Bird Species Diversity. The census trail went through the lower half of the grid (dry wash with bushes and tobacco in bloom) and then doubled back through the upper half (cacti and small bushes), with extensions beyond the grid making the trail 630 X 50 m. Because of the bare terrain, all birds coud be seen 25 m away and one could avoid counting twice a bird that moved during a census from the lower half to the upper. Each census took one hour. The trail was designed to have the same proportion of dry wash and hillside as on the study grid. In addition to the ground-feeding granivores and insectivores, this community had a few gleaners that exploited the larger bushes along the dry wash and occasionally moved to the cactus on the hillsides. The tobacco in the dry river bed was the main attraction for the three species of hummingbirds, although these also fed at the flowers of *Psittacanthus cuneifolius* and caught flying insects. The *Sicalis* were attracted to the area by holes in the rock retaining walls of the road, the banks cut by the road and river, and rock outcrops on the hillsides. They roosted at night in these refugia, sang near these holes in the morning when the sun reached them, and disappeared for the day. Perhaps they spent the day

1/2km down the canyon at the water hole, but they foraged on the census area also. Other than the singing of *Sicalis*, we noted no evidence of breeding. The fringillids flocked at the water hole, but other birds occurred singly or in pairs.

Lizards. Only one individual of one species (tentatively identified as *Liolaemus pantherinus*) was recorded on the study grid, which gives a density of 0.6 per hectare and a biomass of about 13 g/ha. Numerous other individuals were caught nearby, and a probable second species was seen a few meters outside of the grid boundary but was not collected. *L. pantherinus* is said to be herbivorous and viviparous (Donoso-Barros, 1966).

Summary. In this community near the lower limit of vegetation on the west slope, mammals and reptiles were relatively scarce, clearly with fewer species and individuals than would be found in comparable vegetation in North America. The mammal species were ones extending down from higher altitude. The bird fauna was comparatively rich and, in species composition, was not as closely related to the *loma* avifauna as would be expected on the basis of Koepcke's data from central Peru (1954). This is probably accounted for by the fewer miles of extreme desert separating the two habitats in central Peru. On the basis of biomass, birds clearly dominated the community.

MOUNTAIN SCRUB

The Mountain Scrub study site was chosen to represent the elevation at which the vegetation appeared to be most dense, complex, and diverse. On September 24 we set up a 75 X 210 m grid containing 90 trapping stations (15-m spacing) on a ridge 3.2 km northeast of Tarata, 3,500 m. Steep topography of the entire region imposed the rectangular shape. An irrigation canal about 1 m wide ran through part of the grid. This water nourished, for one or two meters on either side of the canal, a strip of taller bushes (Plate 4), occasional trees, and a few kinds of plants not found elsewhere in the area, such as *Equisetum*. Nine of the 90 grid stations fell within the richer vegetation along the irrigation canal. This canal has probably been full of water for hundreds of years, and so we have considered it to be a permanent part of the habitat. Similarly, the grid included about 60 m of stone walls supporting long-abandoned terraces. Rocks and boulders also were common on much of the grid and these, together with burrows under large cacti and thorny bushes, provided a moderate number of refugia for mice.

Skies were clear throughout our study. A breeze blew irregularly up the valley during the day and down the valley at night. Maximum temperatures wes 22 C, 20, 19, 20; minima -1, -3, -3, -4; relative humidities in the morning 32%, 36, 59, 40; noon 29, 35,33, 35; evening 48, 55, 52, 47.

The Mountain Scrub site and the next higher site (Queñua) are the only communities in our transect with appreciable amounts of plant profile

more than one meter above the ground (Fig. 2). The total Foliage Profile
(2,845 cm²) is somewhat less than at the Queñua site and, surprisingly, less
than that at the Ichu bunchgrass habitat. The Ichu compensated for
lack of height with the most dense first half-meter (4,258 cm²). The
percent of ground convered by vegetation on the Mountain Scrub grid (36.5%)
was similar to that in several of the other habitats. In other words, in spite of
the apparent richness of the vegetation, two-thirds of the ground was not covered
by canopy of any sort. The species that provided most of the ground cover were
the bushes *Grindelia* sp. (7.8% coverage), *Erigeron* sp. (7.7%), and another
Compositae bush (2.7%). Because of their height, bulk, and flowers, tal bushes
of *Cantua candelilla* (0.9% ground cover), *Colletia spinosissimus* (0.6%), and
Cereus cactus (less than 1%) are probably much more important than their
percent cover figures suggest. Twenty-three species of small annual forbs covered
3.4%, and six species of grasses covered about 1%.

The Mountain Scrub community was outstanding in number of species of
plants. Nearly twice as many species appeared in our 45 hoop samples as in any
of the other habitats, and the average number of species appearing in each hoop
sample was 10.20 - twice the number recorded in any of the other communities.
Approximately 23 of the 60 species were small annuals, but 9 or more species of
bushes of the family Compositae provided over half of the ground cover. One of
the most widespread plants, and possibly one of importance to the mice, was a
small cactus with sphrical joints which appeared in 17 of the hoop samples. This
frequency was exceeded by only two species, both of them frail, small annuals.

The grid supported five kinds of cacti, and two others grew nearby. The
candelabra cacti were up to 2 m tall. *Cantua* and *Colletia* bushes were as much
as 2 m tall away from water and to 4-1/2 m along the irrigation ditch.

The difference between the vegetation of this community and that of the
Desert Scrub community at 3,000 m is one of degree. The higher site supported
taller and denser vegetation. It is actually a dense desert scrub, but we have
distinguished it by the name Montain Scrub. It corresponds to the *Estepa ar-
bustiva* of the **serranía esteparia baja** of Koepcke (1954), which is found
between 2,300 and 2,600 m elevation in central Peru.

Mammals. Census trapping on the grid for four day captured 14
Phyllotis darwini, 10 *P. magister*, 3 *Akodon berlepschii*, and 1 *Akodon boliviensis*.
P. magister is restricted to the brushy zone on the western slope of the Andes,
the other three species are common at higher elevations. *A. boliviensis* is
basically a grassland mouse and appeared on the grid only because of the green
vegetation bordering the irrigation ditch. The species descends at least another
500 m of elevation, where it is common in the retaining walls of irrigated pastures
near Tarata. *Akodon berlepschii* avoids grassland. This mammalian fauna is
clearly derived from that of the altiplano. *Akodon berlepschii* is largely diurnal,
Akodon boliviensis is active day and night, and both species of *Phyllotis* are
nocturnal.

In addition to the four species captured on the grid, we saw within a few hundred meters one bat and, on previous expeditions, captured specimens of the mouse opossum (*Marmosa elegans*) and a brush-inhabiting rat (*Andinomys edax*).

Lincoln Index calculations indicate a population of 14.6 *Phyllotis darwini*. Home ranges based on 20 recaptures of 11 individuals averaged 54 m. When a border strip of this width is added to the area, a density of 2.51 *darwini* per hectare is obtained. For *P. magister*, 14 recaptures of 8 individuals indicated an average home range of 44 m; density was 2.06 *magister* per hectare. Not enough recaptures of *Akadon berlepschii* were made to calculate the home range, but using a figure of 45 m found on the Queñua grid, the density of *berlepschii* becomes 0.61 per hectare. Total number of mice per hectare, including *Akodon boliviensis*, is estimated to be 5.45, and biomass 112.1 g. The biomass figure incorporates an average weight of 37.9 for 16 specimens of *P. darwini* and 59.5 g for 15 specimens of *magister*.

Birds. The Mountain Scrub community had more birds, more bird species, and a higher Bird Species Diversity than any of the other Peruvian communities. Large flocks of fringillids, with a few accompanying furnariids, foraged on the ground among the dry composite bushes. These flocks spent long periods in the middle of the day resting in the dense shrubs along the irrigation canal. Flocks of 3 to 40 doves followed the same schedule. These dense bushes, especially the blooming *Cantua candelilla*, were the main attractant at his season (September) for the many hummingbirds and a few *Diglossa*. By November, when *Cantua* had almost finished blooming, hummingbirds were much scarcer. Hummers also fed at *Psittacanthus cuneifolius*, abuelito cactus, *Dunalia lycoides*, and *Mutisia*, and caught insects. A short-billed hummer, *Metallura*, that cannot reach nectar at the bottom of the long corollas of *Cantua*, landed on the flowers and hung on while it perforated the base of the corolla to feed. High in the shrubs along the irrigation canal were numerous bulky twig nests of spinetails (*Asthenes*) from previous years, and the spinetails were working on new nests. Other than this building activity, the only signs of beginning breeding were singing goldfinches (*Spinus*), but these were still in flocks. Other fringillids and doves were flocked also, and *Zonotrichia*, a sparrow that is conspicuous when breeding, was very quiet.

Water in the irrigation ditch flowed so swiftly that it provided no food for birds. Since the irrigation ditch did provide a different habitat from the dry hillsides, we proportioned the bird census area to include the same proportion (6.4%) of canal habitat as did the mouse census grid. This resulted in 250 m of the 1,000 m of census trail being along the canal. However, it will be shown later (see Discussion) that the number of bird species can be predicted fairly accurately using only vegetation measurements, without including the presence of water as a parameter. Therefore, the high number of birds at this site is

mostly in response to the relatively rich vegetation rather than to the simple presence of water on the study area.

The censuses took 1 hr 27 minutes to 1 hr 35 minutes.

Lizards. Three individuals of *Liolaemus alticolor* were recorded on the grid, giving a density of 1.9 per hectare and a biomass of 6 g/ha. This species has an altitudinal range on the transect from about 3,000 m to 4,500 m and prefers brushy situations. It is said to be omnivorous and viviparous (Donoso-Barros, 1966).

Summary. The vegetation of this community has great structural complexity, compared to most of the other areas studied, and has by far the greatest number of species of plants. At only a slightly higher elevation many of the species of small annuals drop out, which provides one of the clearest breaks between the low-altitude and high-altitude floras. The mammals, birds, and reptiles of the Mountain Scrub community, however, in spite of this low-altitude aspect of the flora, are derived from a high-altitude fauna. Presumably in response to the relatively rich vegetation, the number of species of birds, and the number individual birds and mammals were higher than on any of the other areas. The lizards, which in North American deserts respond to the volume diversity of foliage available (Pianka, 1966), were represented by only a single species at low density. The biomass of birds clearly exceeded that of the mammals and lizards.

QUEÑUA

Queñua is the native name for the only tree (*Polylepis tarapacana*) that grows at high altitudes at this latitude. On our transect in occurred only between 3,650 and 4,300 m, although a few kilometers from our Tola study area it flourished up to about 4,600 m. At the site chosen for our study at 3,900 m, 6 km northeast of Tarata, the queñua trees were rather shrubby, rarely more than 3 m tall, and many were heavily polled by natives who use the wood for fuel and construction. The trees remind one of mountain mahogany (*Cercocarpus ledifolius*) in California. A few trunks were as much as 25 cm in diameter. One "trunk" 8 cm in diameter contained 37 growth hings, and another 17 cm in diameter contained more than 48 rings, so growth is not rapid. On our grid the trees were interspersed with Compositae bushes and small annuals (Plate 5). The bushes were mostly species from higher altitudes, such as *Lepidophyllum quadrangulare* (in bloom), *Baccharis microphyllum,* and *Chuquiraga.* Small annuals of many kinds are here approaching their upper altitudinal limit, and three reliable indicators of high-altitude altiplano conditions here reach their lower limit: yareta, *Chinchillula, Abrocoma.*

Neither this community nor any of our higher sites fit neatly into Tosi's scheme of life zones (1960). We find it more practical to rely upon the presence

of certain indicator plants. *Lepidophyllum quadrangulare, Azorella compacta, Festuca orthophylla,* and *Stipa ichu* are especially useful.

On October 13, on a ridge between two steep canyons, we set up a 120 X 150 grid with 99 trapping stations spaced 15 m apart. The nearest water was at the bottom of these canyons more than 200 m elevation below the study area. The grid included one rock outcrop and a moderate number of boulders and rocks. These, as well as the bases of some of the denser clumps of bushes, provided the small-mammal refugia, which were not as abundant as on most of the other study areas.

Skies were clear during our visit. A breeze blew down the valley during the days and up the valley at night. Maximum temperatures were 13 C, 14, 14; minima -3, -3, -2; relative humidity at noon 37%, 40, 37.

The Foliage Profile was quite similar to that of the Mountain Scrub community (Fig. 2) in spite of a quite different species composition. Foliage Height Diversity was almost identical in these two communities. The most important species contributing to the 31 percent ground cover were Queñua (14 3%), *Erigeron* bushes (4.1%), *Baccharis microphyllum* (3.4%), *Lepidophyllum quadrangulare* (2.7%). Grasses contributed only 2% although they were present in 32 of the 40 hoop samples and were fairly conspicuous on the steep slopes falling away from the study grid. On the grid itself, heavy grazing by herds of passing llamas probably supresses the grasses. Small and medium-sized annuals covered 2.3% of the ground.

The number of species of plants present was only half that in the Mountain Scrub community and was about the same as in the Loma and Desert Scrub communities. Plant Species Diversity was lower than in either the Mountain Scrub or the Desert Scrub communities.

Mammals. Trapping was carried out for three nights and two days. In spite of a fairly abundant and diverse plant cover, only two species of small mammal were trapped on the grid: *Phyllotis darwini* and *Akodon berlepschii.* Both of these were also living in the Mountain Scrub community and in or near the Desert Scrub study area regardless of the quite different plant composition at these other places. Also trapped in similiar habitat within a few hundred meters of the Queñua grid on this or previous expeditions were the rodents *Abracoma cinerea, Chinchillula sahamae, Phyllotis magister,* and the mouse opossum (*Marmosa elegans*). Vizcachas (*Lagidium*) were seen about 150 m from the grid. This fauna is clearly one derived primarily from higher altitude.

Akodon berlepschii and *Lagidium* are diurnal, the other species are nocturnal.

Lincoln Index calculations indicate a population of 9 *Phyllotis darwini,* and nine recaptures of five individuals revealed an average home range of 68 m. Combining these figures gives a density of 2.20 *Phyllotis* per hectare. Mean weight of 11 individuals was 30.0 g. The calculated population of *Akodon berlepschii* was 17.8 mice; average home range based on 25 recaptures of 11

individuals was 45 m, and the resulting density per hectare was 3.53. Mean weight of 6 specimens was 21.5 g.

Birds. Although only 3 km distant and 400 m higher, the Queñua supports a bird fauna with a much greater high-altitude component than at the Mountain Scrub area. In the Queñua community, 65% of the species occur on both the northeast and southwest sides of the divide at this latitude (within the length of the transect). That is, 65% live at the highest altitudes or cross them. This compares with 46, 41, and 48% in the Loma, Desert Scrub, and Mountain Scrub communities, respectively. These high altitude birds aret tinamous, birds of prey, and fringillids.

The fringillids here are taking advantage of the seed-producing bushes and forbs, and the shrubs and rocks provide shelter for the furnariids (*Asthenes, Upucerthia*). Among the species that glean foliage for insects is *Oreomanes fraseri*, which pokes nuthatch-like under the shreds of bark of the *Polylepis* and which is probably the species most dependent upon these Queñua trees. This species was recorded on 11 September but was not recorded during the study period. The four species of hummingbirds present were represented by fewer individuals than at the Mountain Scrub site. On a small, bare pampa close to the grid, but which the census trail avoided, miners (*Geositta tenuirostris*) and ground tyrants (*Muscisaxicola*) foraged during the day, and lapwings (*Ptiloscelys*) spent the night.

In this habitat, as in the Mountain Scrub and Ichu areas, birds were concentrated in feeding flocks, basically of fringillids, but including a few furnariids. This flocking indicates that these fringillids were not breeding. However, two different juveniles of *Upucerthia ruficauda* were seen, and *Asthenes* was singing in the mornings, so perhaps were starting to nest, as at the Mountain Scrub area two weeks earlier. A count of singing *Asthenes dorbignyi* along the 1-km census trail came to nine pairs; only some of these pairs used the area within 30-m width of the trail. Another breeding species was *Caprimulgus longirostris*, which was sitting on two eggs in its "nest" on the steep side of the canyon below census area.

Censuses took 1 hr 13 min and 1 hr 43 min.

Lizards. No lizards were seen on the grid, but a *Liolaemus multiformis* lived about 200 m from the grid, and *L. alticolor* would be expected to occur in this habitat.

Summary. The most obvious difference between this habitat and the Mountain Scrub is the presence of Queñua "trees" and a reduction in the number of species of plants. Queñua forests are said to have covered a much larger area of the altiplano in earlier times than they do now, but in spite of this the do not seem to have brought about significant speciation of vertebrates. The mammals and lizards on and near the Queñua grid are species found also in other

quite different habitats at high altitude, and almost all of the birds are high-altitude, open-country types rather than "forest" types. The number of bird species was, related to vegetation complexity (Figs. 8 and 9), but bird Density, while fairly high compared with densities at the other study sites or in North America, was lower than expected on the basis of the amount and complexity of the vegetation (Fig. 11). Mammal density was fairly high, probably as high as one would expect to find in equally dense and complex vegetation on other continents, but biomass of mammals was exceeded by that of birds.

YARETA

Yareta is a native name widely applied to several species of mat or cushion plants belonging to the family Umbelliferae. The species on our study area is *Azorella compacta,* which, in this region, is restricted to elevations above 3,950 m. It grows in dense, hard, coral-like heads formed of tightly packed, resinous leaves and stems. When dried, these heads, often 0.6 m in diameter, are used for fuel.

Our study area was at 4,500 m, 13 km northeast of Tarata. On October 1 we laid out a grid 90 X 180 m, with 15-m spacing between stakes, on a north-facing slope at the base of a cliff. The area supported more yareta than any other place known to us (Plate 6). The habitat is clearly equivalent to Koepcke's (1954) Cushion Plant Community and probably falls into the category **maleza desértica subalpino** of Tosi (1960). The soil was gravel with numerous boulders. Moderate numbers of refugia were under boulders, un der heads of yareta, or in dense mats of the low bush, *Lepidophyllum quadrangulare.*

During our censuses some days were clear, some partly cloudy, and a few flakes of snow fell one afternoon. A breeze blew irregularly up the valley during the day, and nights were calm. Maximum temperatures were 12 C, 9, 12, 11; minima -10, -15, -13, -6; relative humidity at noon 28%, 32, 34. The great range in nighttime minima reflects the presence or absence of clouds. Weather conditions were probably similar to those at Paucarani, a village at the same elevation as the Yareta study area and 19 km southeast of it. At Paucarani the mean annual temperature is 1.6 C and the mean annual precipitation 364 mm.

The 46 hoop samples enclosed 10 species of plants. Two additional species (a small *Senecio* and a *Nototriche*) grew on the grid in modest numbers. About 200 m downhill began extensive areas of bunchgrass (*Festuca orthophylla*), and 1 km away in opposite directions were two seeps of water with associated different vegetation. Only one of the species of plants on the area was a small annual, a dramatic departure from the situation at lower elevations, and it appeared in only two of the hoop samples. Grasses appeared in only four hoops and provided less than 0.2% ground cover. Yareta covered 20.0% of the ground (including 7.1% coverage by dead yareta), and *Lepidophyllum quadrangulare,* a low Compositae shrub (in bloom) covered 14.0%. It rarely exceeded 45 cm in height, and yareta rarely exceeded 100 cm (average depth of yareta was 26

cm). A species of cushion cactus (*Opuntia*) covered 0.5% of the ground. The Plant Species Diversity and average number of plant species per hoop (only 1.28) are considerably lower than at most other areas, probably reflecting extreme daily temperature fluctuations, very porous soil, and absence of water. Almost all of the Foliage Profile was provided by yareta and *Lepidophyllum*, which, although not high, have very dense foliage.

Mammals. Trapping revealed only *Phyllotis darwini* and *Akodon andinus* living on the grid. *Akodon andinus* is restricted to very high altitude in Peru, Bolivia, northern Chile, and northern Argentina. Vizcachas were seen frequently in the boulders and cliffs above the grid and left their droppings in many places on the grid, but have not been included in the census because they were never actually seen on the grid and because of the impossibility of assigning a density to them. Antelope-like huemuls (*Hippocamelus bisulcus*) were seen about 200 m from the grid, and *Auliscomys boliviensis* (a diurnalmouse) were abundant at one of the springs 1 km away. Traps set in rocky habitats nearby did not catch any of several other high-altitude genera that might be expected in the area.

Trapping for four successive days nights revealed the presence of 11 *Phyllotis darwini* and 4 *Akodon andinus* on the grid. Lincoln Index calculations indicated populations of 12 and 4 individuals, respectively. Twelve recaptures of 8 *darwini* gave an estimate of home range of 103 m and resulted in an estimate of 2.2 per ha. Three recaptures of two *andinus* gave a home range estimate of 50 m and a consequent density of 1.2 per ha. *Phyllotis*, as elsewhere in its range, was nocturnal and wide-ranging. *Akodon andinus* was active in the daytime.

The biomass of small mammals (51.3 g/ha) was less than half that on any of the other grids (except the completely unoccupied *Tillandsia* grid). The average weights of 12 *darwini* captured on or near the grid (36.5 g) and six *andinus* (17.8 g) were used to calculate the biomass.

The scarcity of mice on the grid, in spite of relatively large figures for Foliage Profile, percent of ground covered by vegetation, and plant biomass, may be due to the fact that none of the vertebrates seems to prefer yareta for food. Its chief role seems to be to provide shelter under dead or hollow heads, or to provide perches for birds. Important food items were blossoms of *Lepidophyllum* and seeds of cushion cacti (*Opuntia*). Captive *Phyllotis* and *Akodon* ate cactus seeds avidly, and *Phyllotis* ate cactus fruits and *Lepidophyllum* twigs also. *Akodon* ate a few yareta seeds when no other food was available.

Birds. At this highest study area birds are equally visible at all times of day, but almost all are quiet birds that spend most of their time on the ground, among rocks, bushes, and yareta. The census trail was, by accident, too short, 550 X 50 m, making only 2.75 ha, so we included a fourth census for the population estimate. Censuses were of 1 hour to 1 hr 5 minutes. The bird Inventory

covered four days, but because of great mobility of many of the species in this habitat and because of the sneaky habits of some, it is probably a bit low.

Being near the summit, this area has the highest percent of high-altitude species, 92%. At the Tola site, a little lower but across the divide, 90% of the species likewise are ones that cross the divide.

Notable residents on or near the Yareta grid were a pair of *Falco femoralis* nesting on a 100-m cliff, nesting hummingbirds (*Oreotrochilus*), and tinamous (*Tinamotis*) that called daily from the *Festuca* bunchgrass below the study area. Some additional species (*Cinclodes, Attagis, Thinocorus, Diuca*) were at the springs a kilometer away.

Lizards. One *Liolaemus mocquardi* and 6 *L. alticolor* were recorded on the grid, giving a density of 4.3 per hectare and a biomass of about 21 g per hectare. Almost all of the *alticolor* were seen close to *Lepidophyllum* bushes whereas *mocquardi*, which was fairly abundant nearby, lived in more open and in rocky places. At four grid locations where *alticolor* was recorded, the percent ground cover was slightly greater than the average for the grid, Foliage Profile was much greater, and the number of refugia much greater. Both lizard species are omnivorous and viviparous (Pearson, 1954; Donoso-Barros, 1966).

Yareta inert? Since we found no evidence in the field that vertebrates made any specific use of yareta plants, which were the dominant vegetation at the Yareta study site, in our analysis of vegetation correlates with vertebrate populations (see Discussion), we ran a set of multiple regressions with the data from the Yareta site altered by omitting yareta plants from the Plant Species Diversity, number of species of plants, percent ground cover, Foliage Profile, and Foliage Height Diversity. The resulting regressions for birds (number of species, BSD, Density) were changed very little. For mammals, the regressions for number of species, Species Diversity, and biomass including tuco-tucos were slightly but appreciably improved while the regressions for number of mammals per hectare and for biomass omitting tuco-tucos remained the same.

Since introduction of irrelevant measurements would be expected to reduce the precision of a regression, and since inclusion of yareta measurements did not alter appreciably the correlations with various characteristics of the bird populations, it appears that the yareta plants do have some significance to the birds. Perhaps the few insects attracted to the tiny but numerous yareta flowers are a source of food. Since introduction of yareta measurements reduced the correlations with several characteristics of the mammal populations, it seems that yareta, as for as mammals are concerned, is ecologically inert.

Summary. At this highest of the study sites, the vegetation was sparse and unusual because of the remarkable growth form of the dominant species of plant. The number of species and individuals of birds and lizards was fairly high. The number of species of mammals on the grid (two), while comparable with that on the grids on the western slope, is notably less than on the altiplano

grids to the east. We expected more representatives of the rich altiplano mammalian fauna. Density and biomass of mammals were lower than on any of the other grids (except *Tillandsia*, which supported no mammals). Nevertheless, the mammalian biomass was greater than that of the lizards on the Yareta site and only moderately lower than that of the birds.

Perhaps because of sparse vegetation and scarce food, home ranges of *Phyllotis darwini* were much larger than at any of the four other study sites where it was found.

We know of no similar habitats elsewhere with which to compare the fauna.

TOLA

Tola is the Andean equivalent of sagebrush and usually consists of relatively flat expanses of bushes of one or more species of *Lepidophyllum* or *Baccharis*. It is found only at high altitude in the drier portions of the altiplano, where it is widely harvested for fuel. At decreasing elevations to the east of our study site (Fig. 1) it grades into bunch grass (*Stipa ichu*).

Our study area was 1 km west of Challapalca, 4,300 m, Department of Tacna. The grid began about 150 m south of the Rio Maure and was 180 X 180 m (3.24 ha.) with 20 meters between stakes (Plate 7). Noteworthy features were the uniformity of the vegetation, the low number of plant species, heavy grazing by llamas and alpacas, deep sandy soil, almost total absence of rocks, underground tunneling activities of the tuco-tuco (rodent genus *Ctenomys*), and the fierce afternoon wind. Almost all of the refugia were burrows made by tuco-tucos.

During our measurements (October 20-24) skies were continually clear, mornings and evenings were relatively calm, but the wind coming down the valley in the afternoon was overpowering. Maximum temperatures were 17 C, 17, 16; minima -14, -13,-13, -12; relative humidity at noon 46%, 42, 31, 38, 42. During one 31-hour period the temperature regime was as shown in Figure 3. The great range, repeated day after day, is typical at high altitude during the dry season. During the daily cycle illustrated, the temperature remained above freezing for 12-3/4 hours and below freezing for 11-1/4 hours. The total degree-hours above freezing were 1.5 times the degree hours below freezing. To an observer the daytime maxima appear to underestimate the "real" temperature because of the intense sunshine.

Vegetation. Foliage Profile measurements showed a substantial amount of vegetation in the lowest half-meter, but no plants were as tall as 1 meter. Almost all were less than 1/2 m. Most of the Foliage Profile was *Festuca orthophylla* and *Lepidophyllum lucidum*, since they were the only plants more than a few centimeters tall. Bunchgrass (*Festuca*) covered 16.8% of the ground, tola (*Lepidophyllum*) 9.7%, a diminutive tuftgrass (*Calamagrostis* sp) 4.8%,
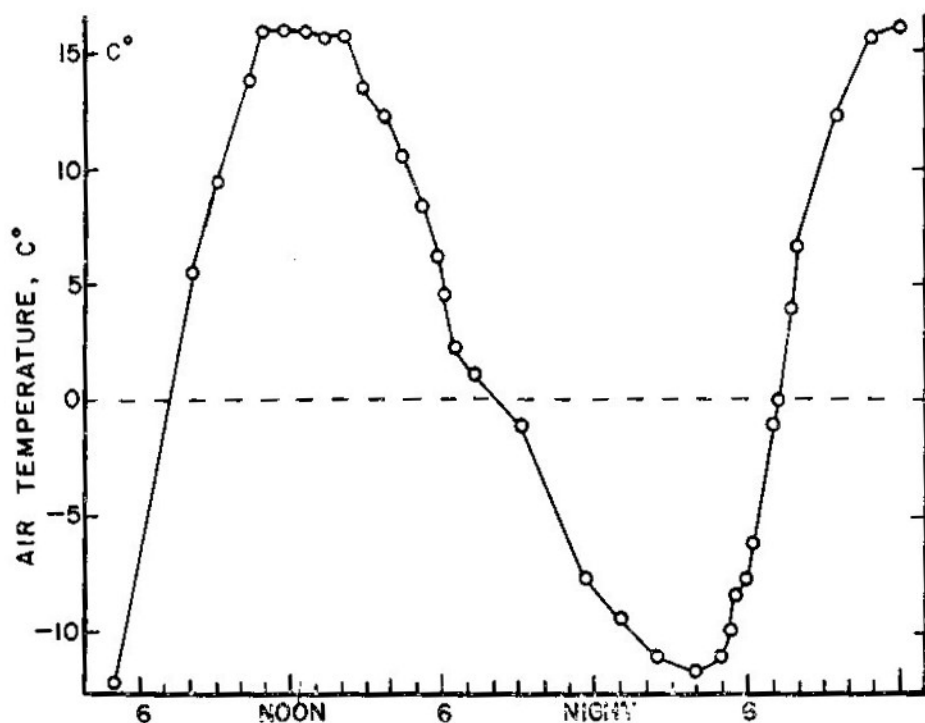
Fig. 3. Shade temperatures at the Tola site, 4,300 m. October 23-24, 1971.

and flat mats of a *Senecio*-like composite (2%) and of *Pycnophyllum tetrasti-chum* (1%). The last seems to be little utilized for food by vertebrates.

It spite of a considerable amount of vegetation, only eight species of plants appeared in our hoop samples. Plant Species Diversity was almost as low as on the Yareta grid, but the average number of plant species per hoop was higher (2.85) than on the yareta grid(1.28). Only three species of plants on the tola grid were small, seed-producing annuals. One small plant (*Nototriche*) has a nutritious, corrit-like root, but is was relatively scarce and appeared in only two of our hoop samples. The tola was blooming; the bunchgrass and tuftgrass were dry.

Mammals. This simple habitat supported more species of mammals than any of the other habitats. *Eligmodontia typus*, possibly the most desert-adapted South American mouse and here at the northern limit of its range, was the most abundant small mammal. Also trapped were 3 *Auliscomys sublimis*, 2 *Akodon andinus* (both near the only large rocks on the grid), 1 *Akodon berle-pschii*, and 1 *Abrocoma cinerea*. All of these species have either quite small, very high-altitude ranges restricted to the arid western portions of the altiplano,

or are living at the northern limit of a larger distribution. *Auliscomys sublimis* will tolerate thick bunchgrass, but the other species avoid dense vegetation. They are essentially a subset of the high-altitude fauna, a subset that is successful in the absence of rocks and dense grass.

Three other species were trapped within 150 m of the study grid: *Phyllotis darwini*, *Calomys lepidus ducillus*, and *Auliscomys boliviensis*. The proximity of, respectively, rocks, dense bunchgrass, and water made possible their existence nearby; the absence of these resources on the grid reduced the probability of their occurrence there.

Trapping for four consecutive nights revealed the presence of 12 *Eligmo- dontia*. Lincoln Index calculations indicated a population of 13.4 individuals. Average home range based on 15 recaptures of 9 individuals was 92 m; when a border strip of this width is added to the grid, a density of 1.01 *Eligmodontia* per hectare is obtained. Average weight of 21 individuals was 24.38 g, giving a biomass of 24.6 g per hectare. Densities of the other species were estimated to be: *Auliscomys* 0.52/ha; *Akodon andinus* 0.26/ha; *Abrocoma* 0.17/ha; and *Akodon berlepschii* 0.14/ha. Total biomass of these species was 55.2 g/ha.

The Tola was the only site to support a population of tuco-tucos (*Ctenomys opimus*), a subterranean rodent remarkably similar in morphology and habits to North American pocket gophers but belonging to a separate suborder. The presence of tuco-tucos was not dependent upon the presence of tola, however, because they live in nearby habitats without tola (Pearson, 1959). When tola is present they use its branches for food, which gives them in this habitat the unusual status of being fossorial browsers. Since only one *Ctenomys opimus* lives in each burrow system (Pearson, 1959), it was possible to census them by plotting on a map the location of fresh earth mounds each day and, by opening up a large number of closed burrows and noting whether a tuco-tuco reclosed any of them, increase the number of positive observations. Some tuco- tucos utilized burrow openings as much as 40 m apart, and a trail of increasingly weathered mounds indicated that some had gradually shifted their center of activity as much as 80 m in recent weeks. Mapping indicated the presence of four tuco-tucos on the grid (1.23/ha). Since the average weight of tuco-tucos trapped nearby was 241 g, and no juveniles were present at this season, the contribution of these four individuals to the biomass of the grid was 296 g/ha. The fact that they were more abundant than any of the mice and that their biomass was five times as great as that of all of the mice combined suggests that the subterranean herbivore niche is an unusually profitable one. This suggestion is confirmed by several other observations: tuco-tucos are commonly found at even greater densities and biomasses (Pearson, 1959, Pearson *et al.*, 1968); *Spalax* is found at much greater densities in arid habitat in Israel (Nevo, 1961); and pocket gophers (*Thomomys*) are found at much higher densities and biomasses in annual grassland in California (Howard and Childs, 1959), and in mountain meadows in Colorado (Hansen and Remmenga, 1961; Vaughan, 1969). The latter report is particularly valuable for comparison because it contains

density measurements for small, above-ground mammals as well as for gophers. From the densities of small mammals trapped early in the summer before populations had increased to their peaks, I have estimated biomasses and find that in each the three years of Vaughan's study gophers weighed more than any one of the other species present. The average weight of gophers in the three years was 55% of the total weight of all resident small mammals. In other words, in the Colorado meadow as in the Peruvian Tola, the single species of burrowing herbivore outweighed all of the other small mammals combined.

The contribution of the tuco-tucos to the ecosystem is even greater than their biomass indicates, for their hundreds of meters of occupied and of abandoned tunnels provided almost the only refugia on the grid. These refugia made possible the existence of so many species of small mammals in this rather monotonous area of few plant species and few rocks

The similar appearance of the Tola community and various desert communities in the western United States invites comparison (Table 1). Although there are seasonal differences in mouse density, and although the number of mammalian species reported for some of the comparison areas are more properly compared with the number on our grid **plus** the surrounding area, nevertheless it is probably permissible to state that the number of species (6) living in the Tola habitat at 4,300 m elevation does not differ greatly from the number living in vegetationally similar habitats in North America.

The best-documented of the comparison areas in the creosote bush desert shrub community studied by Chew and Chew (1970). Their much greater density and biomass (Table 1) result from very dense populations of the kangaroo rat, *Dipodomys merriami*. This desert rat seems to have made a breakthrough that South American mice have not matched. The success of *D. merriami* in exploiting this kind of habitat is confirmed by Kay (1972) and Reynolds (1958).

Species Diversity of small mammls in Tola greatly exceeds that of this North American analog where the resident species consisting of four species of mice and two species of ground squirrels give a mammal Species Diversity Index of only 0.966 (Chew and Chew, 1970). This is only 54% of the maximum Species Diversity possible with six species — a result of the fact that *Dipodomys merriami* far outnumbered all other species combined. These calculations do not take into account a few pocket gophers that were not censused by the Chews but whose analog (tuco-tucos) were included in our Tola census.

Birds. In this uniform, windy habitat birds were few and widely spaced, giving only four individuals on the census. A high percentage of the 16 species represented in the Inventory are ground feeders that stay close to the ground, probably because of the high winds. The census trail, about 750 X 40 m, was covered in a zig-zag manner, taking 1 hr 10 min to 1 hr 23 min. Only three of the 16 species in the Inventory appeared in the census, whereas on all of the other study areas about half of the species in the Inventory appeared in the

TABLE 1

COMPARISON OF POPULATIONS OF RESIDENT SMALL MAMMALS IN DESERT SCRUB AND IN TOLA-LIKE COMMUNITIES. WE HAVE CALCULATED SOME OF THE ENTRIES FROM DATA GIVEN IN THE PUBLISHED REPORTS

Community	% Ground Cover	No. Sp. Mammals	Sp. Div. Index	No./ha	g/ha	Reference
Desert Scrub, Peru	15	2	.254	2.85	112	This study
Mountain Scrub, Peru	36	4	1.120	5.45	240	" "
Tola, Peru	33	6	1.504	3.33	352	" "
Larrea, Arizona	23	6	.966	15.94	553	Chew and Chew, 1970
Larrea, New Mexico	±28	5	1.143	42.2	1,951	Kay, 1972
Larrea, New Mexico		9				Blair, 1943
Larrea, Nevada	>8	8				Bradley and Mauer, 1973
Larrea, California		9				Johnson et al., 1948
Larrea Cassia, California	>6.6	6	.287	>16.2	>585	Soholt, 1973
Semi-desert, California		7	1.568	24.3	1,814	MacMillen, 1964
Larrea-yucca-bunchgrass	±27	7		±1.2		Chew and Butterworth, 1964
Shortgrass-yucca, Texas		10				Blair, 1940
Santa Rita Range, Arizona		10	±1.099	±17		Reynolds, 1958
Huachuca Mtns., Arizona		14				Hoffmeister and Goodpaster, 1954
Atriplex, New Mexico		6				Blair, 1943
Atriplex, Utah	11	6	.765			Fautin, 1946
Tetradymia, Utah	21	8	1.180			" "
Sarcobatus, Utah	22	6	1.434			" "
Artemisia, Utah		6	1.434			" "
Artemisia, California		10	1.917			Johnson et al., 1948
Coastal Sage Scrub, California		7				M'Closkey, 1972
11 Desert Scrub habitats in Arizona	1-6	av. 3.04	0.1-720 av. 1.018			Rosenzweig and Winakur, 1969
18 Stabilized Dune habitats in California, Nevada, Utah	1-8	av. 5.28	0-1.800 av. 1.158			Brown, 1973

census. Such a low percentage in the Tola suggests that perhaps we should have increased the census area. However, birds were so sparse in the surrounding similar habitat that we should have had to add many hectares to bring this percentage up to that of the other habitats. The river, 300-400 m distant at the point nearest the bird census area, small rock outcrops, and a stone corral were features of the general area not represented on our study grid or bird census area but close enough to be relevant to birds. The bird Inventory did not seem to be inflated by birds associated with the rives. Of the species present at the water (e.g., *Cinclodes*, *Larus serranus*, *Lessonia rufa*, various ducks, *Thinocorus*, *Ptiloscelys*), all except the last two stayed close to the water. Those species seen on the census area could all be found farther still from water. *Thinocorus*, a grazing, granivorous grouse-like bird, roosts in the tola; the lapwings, *Ptiloscelys*, go there when disturbed along the river.

Birds were solitary or in pairs, not feeding in flocks as at other camps. A few showed signs of breeding: the shrike-like tyrannid (*Agriornis*) and the miner (*Geositta*) were carrying nesting material, and spinetails were in pairs and singing. This habitat shares with the *Tillandsia* area the distinction of being without hummingbirds, and these are the two areas with the lowest Bird Density. At another locality (Pampa de Ancomarca) only 12 km from the Tola area and similar to it but with many small rocks, birds were much more abundant, especially miners (*Geositta*) using the tuco-tucos burrows.

In crossing the pass from the Yareta study area to the Tola area, there was a turnover in species of Furnariids. The two spinetails, earthcreepers, and miners are different on the two sides of the divide. In other families this change did not occur.

The Tola site at 4,300 m bears a remarkable resemblance to the creosote bush community studied by Raitt and Maze (1968) at 1,300 m in New Mexico. The height of bushes on their area (primarily *Larrea divaricata*) was similar to the height of *Lepidophyllum* on our area, and the percent of ground covered by bushes (19%) was somewhat less than the coverage by *Lepidophyllum* and *Festuca* on our area (Singh, 1964). They list 14 species of birds breeding on or adjacent to their 640-acre study area over 2 years, and their ceususes enabled us to calculate a Bird Species Diversity of 1.31 for their area. The corresponding figures for our Tola area in a single non-breeding season are 16 species and a Bird Species Diversity of 1.04.

Lizards. One *Liolaemus multiformis* and 8 *L. alticolor* were recorded on the grid, giving a density of 2.78 per hectare and 12.5 grams per hectare. In a similar habitat 12 km to the northeast and at a similar altitude we found a shed snake skin (probably *Tachymenis*). No other reptiles are known from the region.

Summary. This high, windy habitat of little vegetational complexity was populated by more species of mammals than any of the other habitats. All

species were high-altitude endemics, presumably resulting from the rich Pleistocene speciation described by F. Vuilleumier (1969) and B. Vuilleumier (1971), and Bianchi *et al.* 1971). Density of small mammals was low, however, and biomass would have been very low except that exploitation of the subterranean herbivore niche by tuco-tucos brought the biomass to a higher level than in any of the other communities studied. Even without their contribution to the biomass, the Tola community is the only one studied in which the mammals outweighed the birds and the lizards.

The birds also were high-altitude species. A moderate number of species at very low densities gave a low Bird Species Diversity.

Two species of lizards were present at low density.

ICHU

Ichu is the native name applied to "soft" bunchgrass, usually *Stipa ichu*. It dominates a vast area between 3,800 m and 4,100 m where it and, especially, the smaller grasses and forbs between the bunches, are the basis of an important grazing economy (sheep, llamas, cattle). At higher elevations ichu is replaced by the coarser, more spiny *Festuca orthophylla*.

On October 29 we laid out a 105 X 165 m grid (15-m spacing) on a fairly steep (27°) slope facing west-northwest toward the Rio Huenque about 1 km away (Plate 8). The site was on Hacienda Ontave at 3,900 m, 40 km south of Ilave, Department of Puno. It is at the upper altitudinal limit of cultivated crops. Grazing pressure was intense. The collecting localities illustrated in Figures 3 and 5 of Pearson (1951) and called Hacienda Pairumani are only a few hundred meters away. An irrigation canal only a few centimeters deep and about 20 cm wide ran 30 m away from one corner of the grid, but no water was on the grid proper. The influence of this water on the vegetation was to create a band of green matted forbs and grass only a few centimeters wide. A number of small rock outcrops on the grid provided almost the only refugia; the bunches of ichu were not dense enough to serve as safe retreats for mice. Consequently, this community provided by far the smallest number of refugia of any of the eight areas studied.

During our measurements one day was overcast, the others partly or completely clear. One day with little wind was almost stifling although the thermometer reached only 22 C. Maximum temperatures were 17 C, 22, 21, 22; minima -5, -12, -15, -13, -11 relative; humidity in the morning 67%; at noon 42, 30, 35, 28; in the evening 66. Mean anual precipitation, estimated by interpolating between the values for the nearest weather stations in the Titicaca Basin, is probably about 600 mm and mean annual temperature about 5 C. Potential evapotranspiration at Puno, 82 km away on the shore of Lake Titicaca, is 87 cm (Papadakis, 1961).

Only a small fraction of the vegetation reached above 1 m (Fig. 2), but the Foliage Profile was denser in the lowest half-meter (4,258 cm² / m³) than in

any of the other communities. Bunchgrass provided almost all of the Foliage Profile. Foliage Height Diversity, however, was low.

The percent of ground covered by vegetation (50%) was higher than in any of the other communities. Ichu provided 25.5% cover, *Calamagrostis* cf. *rigescens* 9.3%, and a small tuftgrass (*Muhlenbergia fastigiata*) 6.6%. Nine species of small annuals were present and together provided only 0.7% ground cover. The number of species of plants present in hoop samples (19) and the Plant Species Diversity (1.859) were moderately low.

Mammals. As in the Tola habitat, the vegetationally monotonous Ichu area supported a relatively large number of species of small mammals. All of these are high-altitude forms. One of them, *Phyllotis osilae*, is tied closely to ichu all the way from south-central Peru to Argentina and could serve as an indicator species of ichu habitat. *Akodon amoenus* is also a bunchgrass mouse but of much more restricted distribution. *Akodon berlepschii* and *Calomys lepidus ducillus* were taken in sparsely vegetated portions of the grid. Captured nearby on this visit or in previous years were the following species, listed together with their special habitat requirements: *Neotomys ebriosus* (dense grass near water), *Akodon boliviensis* (rocks and grass), *Akodon jelskii* (rocks and grass), *Phyllotis darwini* (rocky open places), *Chinchillula sahamae* (rocky cliffs), *Auliscomys pictus* (bunchgrass, as for *P. osilae*), *Galea musteloides* (rocks or burrows). All of these except wide-ranging *Phyllotis darwini* are high-altitude species.

Traps were run on the grid for four successive nights. Eight *Akodon amoenus* were caught; Lincoln Index indicated a population of eight, and six recaptures of five individuals indicated a home range of 41 m. Density was 1.73/ha, and average body weight was 21.7 g. Six *Phyllotis osilae* were caught, and Lincoln Index indicated a population of 6.67 individuals. Home range based on 7 recaptures of three individuals was 40 m, giving a density of 1.47/ha. Average weight of 12 individuals was 32.1 g. Densities of the remaining three species were *Calomys lepidus ducillus*, 0.81/ha; *Akodon berlepschii*, 0.40/ha; and *Auliscomys sublimis*, 0.27/ha. The total number of individuals per hectare was fairly high compared to the other areas studied. The biomass was almost identical with that found in the Desert Scrub and in the Queñua communities.

Compared with mammal populations in various grasslands in the Northern Hemisphere (Table 2), the number of species on the Ichu grid in close to the average, and the Species Diversity Index is far above average. The Index at five of the Northern Hemisphere sites was depressed by the fact that a single species outnumbered all of the others combined, whereas partitioning was more equitable in Ichu. Population density and biomass were definitely low in the Ichu community. This may be due in part to the fact that many of the Northern Hemisphere comparison areas were trapped at the end of the breeding season when populations were high, but it is also due to the absence from Ichu of opportunistic species that build up to high numbers. The Jornada and Osage

TABLE 2

COMPARISON OF SMALL MAMMAL POPULATIONS IN VARIOUS GRASSLANDS

Community	No. Sp. Mammals	Sp. Div. Index	No./ha	g/ha	Reference
Ichu Bunchgrass, Peru Desert Grassland	5	1.410	4.68	115	This study
Jornada, New Mexico Blue Grama	7	.923	21.5	1,208	Grant, 1971
Pantex, Texas Short-grass Prairie	8	1.234	16.4	288	" "
Pawnee, Colorado Tall-grass Prairie	4	1.252	4.5	243	" "
Osage, Oklahoma Mountain Bunchgrass	8	.743	34.9	1,111	" "
Bridger, Montana Wheatgrass	3	.776	11.6	354	" "
Cottonwood, South Dakota Mixed Grass Prairie	6	1.494	2.9	100	" "
Dickinson, North Dakota Broomsedge	7	1.769	4.5	179	" "
Savannah River, South Carolina Upland Grass	5	.936*			Golley et al., 1965
Savannah River, South Carolina Lowland Grass	4	.500*			" " " "
Savannah River, South Carolina	3	.782*			" " " "

* Calculated from number of individuals caught, rather than from density.

habitats, weith their very high biomasses, were dominated by *Dipodomys* and *Microtus*, respectively; these highly adapted and very successful genera belong to families that have never reached the Andes and have no analogs among the native species. It is probable that if introduced they would dominate some Andean habitats - with unpredictable effect on the native species.

Birds. This community, third in number of bird species, was second in density due to large flocks of *Phrygilus plebejus* and other fringillids that fed in the early morning sun in protected places. One such place on the census area was also attractive because it had more of the turfy plants found near water; this turf provided more open space among the bunchgrass and more manure piles, since livestock prefer this more palatable vegetation. The 1,000 X 30 m census trail had to pass through this zone because, despite vast stretches of ichu, the study grid and adjoining similar habitat were boxed in by a creek, an irrigation

canal, a cluster of huts, and rocky outcrops. The inclusion of the more turfy area near the creek (30 m from it) is reasonable because creeks and seeps are handy to birds throughout this region, because is was only a small part of the entire census area, and because its vegetation profile and composition did not differ greatly from those measured on the grid. The earth banks and rock faces associated with the creeks were important refuges where the birds roosted at night and spent much of the day. Many of the birds nested in holes in these banks and rocks, but the only signs of breeding during our visit were a pair of swallows attending one egg and a pair of earthcreepers (*Upucerthia*) carrying nesting material. The sparrow *Zonotrichia* again was silent. All birds that are not aerial feeders or raptors are of necessity ground feeders in this habitat, since there are no bushes. The hummingbird *Oreotrochilus* fed on insects on the ground. The spinetails were especially sneaky and were almost impossible to see in the dense ichu.

Since censusing the large number of fringillids in flocks presented problems, an extra census was made to permit a more careful estimate of the numbers of *Phrygilus plebejus* in them. For other species only the official three censuses were used. Censuses lasted 1 hr 14 min to 1 hr 45 min.

With the elevation of the Ichu area being the same as that at the Queñua area across the divide, the proportion of high-altitude, dividecrossing species of birds dropped back to 65%. The bird fauna was completed by some altiplano species such as the two tinamous *Nothoprocta* and *Nothura*, and a different assortment of furnariids.

Twenty-four species of birds were seen on the area, and 11 species entered into the density counts (85 individuals) and into the calculations of Bird Species Diversity (1.084). In comparison, Cody (1966) surveyed birds in numerous North American and South American grasslands and found a remarkably uniform 5 to 11 species present and an average Bird Species Diversity (of the passerines) of about 1.01. Wiens (1971) also found an average Bird Species Diversity of about 1.0 in seven grassland study sites in central and western United States; those sites supported 3 to 10 breeding species.

Lizards. One small lizard of undetermined species was seen on the grid, giving a density of 0.6 lizards per hectare and an assumed biomass of 3 g/ha.

Summary. The bird and mammal faunas of the Ichu community are clearly dominated by altiplano endemics. Bunchgrass provided a dense Foliage Profile in the lowest half-meter and a high percent of ground cover. It supported an unusually high number of species of birds, compared with grassland habitats elsewhere, and a high number of individuals, compared with the other habitats on the Peruvian transect. Number of species of small mammals was relatively high, but density and biomass were moderate, compared with other Peruvian habitats, or low when compared with North American grasslands. Reptiles were of little importance.

TABLE 3

COEFFICIENTS OF CORRELATION BETWEEN THE ANIMAL POPULATIONS AND THE ENVIRONMENT AT THE EIGHT STUDY SITES

	No. Sp. Birds (Inventory)	No. Sp. Birds (Strip Census)	Bird Spec. Div.	Bird Density	Bird Biomass	No. Sp. Mammals	Mammal Spec. Div.	Mammal Density	Mammal Biomass	Mammal Biomass (Excl. Tucos) Lizards	No. Sp. Lizards	Lizard Density	Lizard Biomass	Biomass all Vertebrates	Darwini Biome Pairs
No. Species Plants	.784	.850	.733	.695	.816	.106	.054	.736	.311	.338	.132	.133	.187	.882	.655
Foliage Profile	.623	.514	.162	.677	.522	.638	.764	.592	.165	.195	-.047	-.526	.528	.148	.322
Plant Species Diversity	.831	.739	.841	.516	.553	.330	.219	.816	.455	.817	.222	.226	.223	.725	-.734
Foliage Height Diversity	.776	.778	.708	.504	.654	.081	.078	.535	.139	.551	-.285	-.402	.374	.343	.083
Altitude	.507	.386	.356	.336	.306	.674	.765	.315	.279	.036	.434	.673	.725	-.114	.817
Percent Ground Cover	.168	.134	-.144	.445	.226	.425	.527	.382	.127	.190	.121	.161	.137	.306	-.039
Number of Refugia					-.428	-.452	-.587	-.301	.160	.051	.096	.752	.742	.158	-.626

• Coefficients greater than .707 depart significantly (P < .05) from 0.

DISCUSSION

A field biologist surveying an unfamiliar habitat is consciously or subconsciously making estimates of the diversity and abundance of animals living there. What environmental characteristics is he integrating to arrive at his estimate? We annotate below our attempts to define and quantify various attributes of the environment that influence such estimates. In the absence of contrary evidence we surmise that the animals themselves in their own inscrutable ways are integrating the same characteristics.

We measured and tested a dozen different characteristics and found almost all of them to be useful in predicting one or more characteristics of the populations of vertebrates. The challenge was to identify the ones that were most effective. It is certain that some unmeasured parameters would have been equally useful or more useful, such as weather, food supplies, kind of soil, and presence of rocks. Adequate weather data, however, are not available for any of our study sites and, because of the steep topography, weather data from stations even a few kilometers away may not be relevant. Consequently, climate enters our analyses only indirectly, in measurements of altitude and vegetation. Food supplies are difficult to quantify even under the best of conditions; for a fauna whose food habits are not even known, it is futile to attempt appropriate measurements. We consider it surprising that some of our regressions were so successful in the absence of any direct input concerning diet.

Number of species of birds: Comparisons within the transect. The relationship between measurements of vegetation and the number of species of birds recorded at each of the eight study sites was analyzed first by studing simple linear correlations (Table 3). In general the greater the "complexity" of the vegetation the greater the number of species of birds. Elements of complexity that seem to be important are: number of kinds of plants (measured as number of species of plants and as Plant Species Diversity), amount of plant material (measured as Foliage Profile), and vertical distribution of foliage (measured as Foliage Height Diversity). The positive correlation between number of species of birds and altitude is partly a result of a rich speciation of the high-altitude avifauna and partly a result of an increasing amount of vegetation up to about 3.700 m, which in turn depends upon precipitation increasing with altitude. The two correlations between number of species of birds and number of species of plants (Table 3) agree fairly well with similar measurements made in island communities (Abbott, 1974, Antarctic islands, r=.71; Harris, 1973, Galapagos Islands, r=.85; Power, 1972, California Islands, r=.86).

An attempt was then made to develop an equation that would predict the number of species of birds living in an Andean habitat. A computer using Ariel Library Routine G2 CAL COVA printed a matrix of correlation coefficients, then Routine G2 CAL REGRESS performed a stepwise multiple regression, the object of which was to choose a series of predictors (environmental variables) that

would best predict the criterion or dependent variable (number of species of birds). The calculations proceed as follows: from a number of sets of environmental measurements (potential predictors) made at each study site, the computer program chooses first the one correlated most highly with the criterion variable. From the remaining potential predictors it then selects the one that will produce the greatest increase in the coefficient of multiple corelation and calculates the appropriate regression statistics. From the remaining potential predictors in then selects the one that will again give the greatest increase to the coefficient of multiple correlation, etc. The choice for the second, third, etc. predictor is usually not intuitively obvious because the program avoids using predictors that are themselves highly correlated with predictors already used, even if they have a high simple correlation with the criterion variable itself.

For predicting number of species of birds recorded in the Inventory in each of the eight communities, the highest simple correlation ($-.831$) was with Plant Species Diversity, followed by number of species of plants, Foliage Height Diversity, Foliage Profile, and altitude (see Table 3). The potential bird fauna seemed to be little influenced by the fact that some sites had only 14.8% ground cover and others as much as 50% ($r = -.168$). Figures 4, 5 and 6 illustrate the stepwise procedure making use of, successively, Plant Species Diversity, Foliage Profile, and Foliage Height Diversity. The best predictive equation is given at the bottom of each graph.

PREDICTED NUMBER OF SPECIES OF BIRDS
3.15 + 9.00 (PLANT SPECIES DIVERSITY)
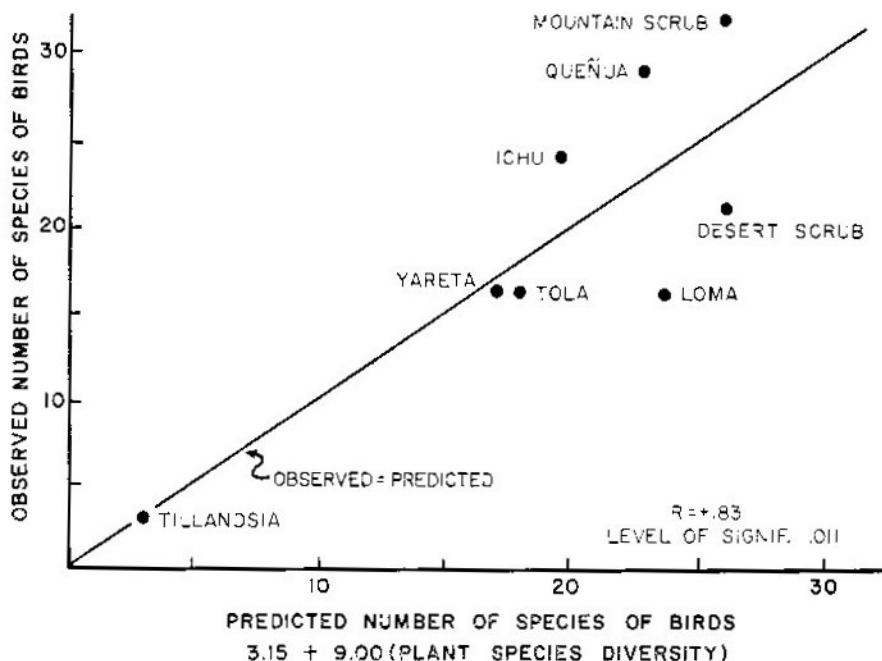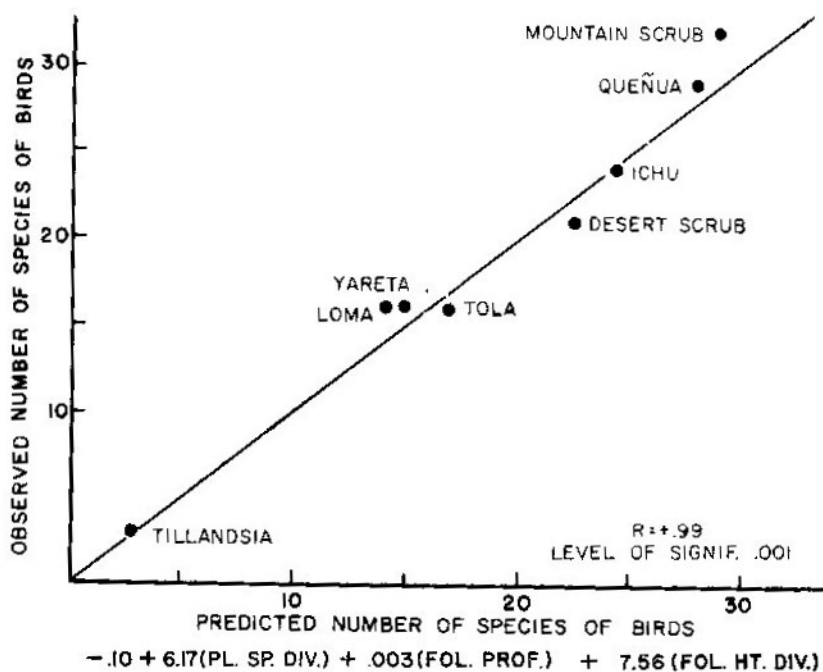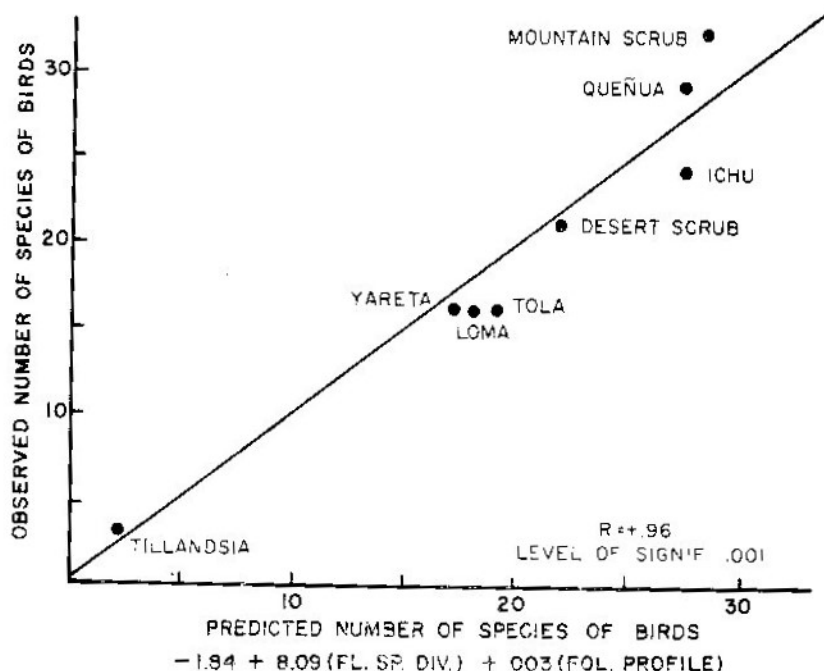
Figs. 4, 5 and 6. The observed numbers of species of birds recorded in the Inventories at each of the eight study sites (vertical axes) plotted against the numbers predicted by the formulae making use of one, two, and three predictors (horizontal axes). The coefficients of multiple correlation are printed at the lower right.

Because of high cross-correlations between some of the predictors (Table 4), regression analysis is able to provide good equations for predicting number of species of birds even when deprived of some of its most informative data. For example, when information on Plant species Diversity and Foliage Height Diversity is withheld, it can still generate an equation:

No. species birds $= 3.98 + .35$ (No. sp plants) $+$

$.003$ (Foliage Profile)

for which the coefficient of multiple correlation is .946.

TABLE 4

CROSS-CORRELATIONS BETWEEN VARIOUS ENVIRONMENTAL CHARACTERISTICS AT THE EIGHT STUDY SITES

	Fol. Prof.	Plant Spec. Div.	Fol. Height Div.	Alt.	% Ground Cover	Refuge Index
No. Species Plants	.124	.794	.730	—.016	—.048	.037
Foliage Profile		.171	.276	.684	.615	—.879
Plant Species Diversity			.633	.247	—.075	—.048
Foliage Height Diversity				.365	—.415	—.310
Altitude					.106	—.725
Percent Ground Cover						—.337

By using more predictors, the fit of points to the regression line improves and soon achieves a very satisfying coefficient of multiple correlation, such as .999. However, as the number of predictors approaches the numer of criterion variables, one approaches a condition of biological and statistical absurdity. The use of more than three predictors for estimating the number of species of birds at eight study sites is probably ridiculous.

The routine of generating a predictive equation through multiple regression, using available environmental measurements, was strained by the inclusion of the *Tillandsia* community (Fig. 7). In spite of a considerable amount of vegetation present (reflected in percent ground cover and Foliage Profile),, only three species of birds were recorded there (including vulture and swallow). This awkward situation almost demanded that any predictive equation include some environmental measurement for which *Tillandsia* had a very low score. Foliage Height Diversity, Plant Species Diversity, and number of species of
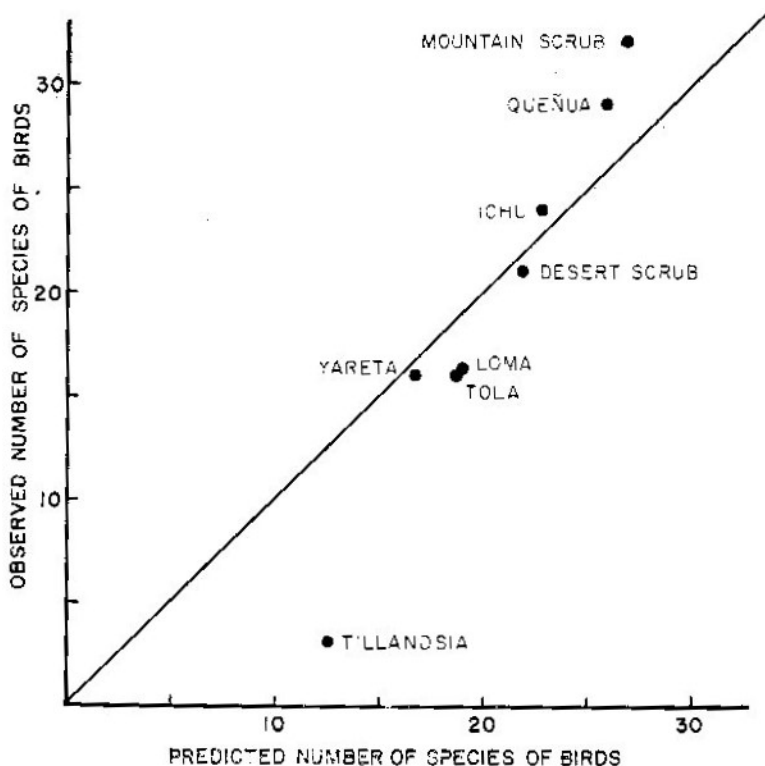
Fig. 7. Goodness of fit of number of species of birds at each of eight study sites to a composite regression line calculated using data from the other seven sites. The regression is based on two predictors: Plant Species Diversity and Foliage Profile.

plants were such parameters. When the multiple regression routine was spared the necessity of including the *Tillandsia* community, it generated for the remaining seven communities a new set of coefficients of correlation (Table 6) and the following equation with a coefficient of multiple correlation of $+.997$:

No. species birds $= -.62 + 21.52$ (FHD) $+ .44$ (% Ground cover).

Note that percent ground cover is now a useful predictor, although its own coefficient of correlation with number of species of birds is low. Foliage Height Diversity has also replaced Plant Species Diversity as the best single predictor

If one is convinced that the *Tillandsia* community is so isolated or suffers from so many other constraints that its bird fauna is controlled by different factors, then this equation (Fig. 9) could be expected to have better predictive power for Andean habitats in general than the preceding equations that included the *Tillandsia* habitat.

Statistical theory states that the multiple regression illustrated in Figure 5, with a coefficient of multiple correlation of .964, can be expected to account

for 93% ($=.964^2$) of the observed variance in number of species of birds. Not being convinced that Plant Species Diversity and Foliage Profile (or any other two parameters) could really account for so much of the observed variance, we attempted to assess how successfully in actual practice these two measurements could be expected to predict the number of species of birds at some different, sitll-unmeasured habitat. The best way to test this would be, of course, to return to the Andes and repeat the procedures at a large number of differente sites. As a more practical alternative, we have pretended that we never visited one of the eight sites and calculated and graphed the regression for the other seven sites. Then, using our environmental measurements for the eighth site, we have predicted how many species of birds "should" have been there. By repeating this procedure omitting one site each time, we obtained eight predictions of the number of species of birds that could then be compared with the numbers actually recorded. Figure 7 documents this exercise, using Plant Species Diversity and Foliage Profile to define the regression line for each of the seven sites. The average departure of the observed number of species from the predicted number at each of the eight sites is 3.25 species; the standard error of estimate is 4.27. When three predictors are used, the average error of prediction improves only slightly to 3.1 species. As a result of this test of the ability of the multiple regression procedure to predict the number of species present in a habitat that we had already studied, we are disposed to accept predictions of the number of species of birds living in still-unmeasured Andean habitats, as well as predictions of other population attributes based on the multiple regression equations reported in subsequent sections of this report.

Since the birds (and mammals) were obviously responding to various attributes of the vegetation at the eight study sites, intuitively it seemed that by combining some measure of amount of vegetation and some measure of plant diversity we could contrive a single superpredictor that would simplify and perhaps improve prediction. On the average, Plant Species Diversity, Foliage Profile, number of species of plants, and Foliage Height Diversity were, in that sequence, the most effective single predictors for the various characteristics of the bird and mammal populations being investigated. After juggling various combinations and various ways of combining these, using number of species of birds as the dependent variable, one superpredictor emerged: log (Foliage Profile X number of species of plants). We have called this Plant Wealth. Its effectiveness in predicting number of species of birds is shown in Figure 8. Unfortunately, it did not prove to be useful for any of the other population measurements except for Bird Density. We have not attempted to develop superpredictors for other population characteristics under study.

Number of species of birds: Comparisons with other countries. The number of species of birds detected on the study grids and in nearby similar habitat (Bird Inventory) varied from three in *Tillandsia* to 32 in Mountain Scrub. Censuses restricted to a 3-ha strip of uniform habitat varied from one species in *Tillandsia* to 19 in Mountain Scrub. These counts are composed
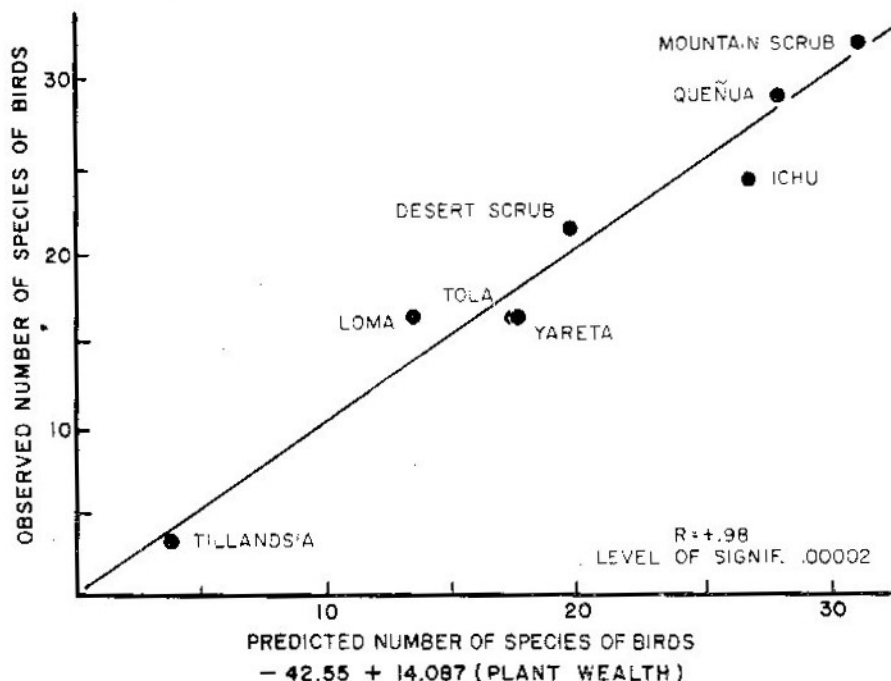
Fig. 8. Correlation of number of species of birds with Plant Wealth, which is Log_{10} (Foliage Profile X number of species of plants).

primarily of non-breeding birds, almost all of them resident species. Counts made by other people in other regions sometimes include only nesting species, sometimes non-nesting residents, and sometimes migrants; their censuses also cover areas of different sizes. Considering these differences in methods, when we compare, in a very general way, our tallies in Peru with counts elsewhere, the number of species in the Peruvian habitats equals or exceeds the number in similar habitats elsewhere. This statement is based primarily on comparison with data found in the following reports: Pianka and Pianka, 1970 (Australia); Recher, 1969 (Australia); Vuilleumier, 1972 (Patagonia); Cody, 1970 (Chile); Cody, 1966, 1968 (grasslands); Howell, 1971 (Nicaragua); Pianka and Huey, 1971 (Kalahari); Udvardy, 1957 (North America); Willson, 1974 (Illinois); Johnson, 1970 (Illinois); Karr, 1968 (Illinois); Karr, 1971 (Illinois and Panama); Karr and Roth, 1971 (Illinois, Texas, Panama); Wiens, 1969, 1971 (grasslands); Kricher, 1972 (New Jersey); Fautin, 1946 (Utah); Raitt and Maze, 1968 (New Mexico); Dixon, 1959 (Texas and Chihuahuan Desert); Emeln, 1972 (Texas); Hensley, 1954 (Arizona); Tomoff, 1974 (Arizona); Johnson, Bryant, and Miller, 1948 (California); Stewart, 1972 (California); Wing, 1949 (Washington).

The Loma, *Tillandsia,* and Yareta communities with their 16, 3, and 16 species of birds, respectively, are such unusual habitats that data from comparable communities elsewhere, if they exist, have not been gathered. The Desert Scrub, Mountain Scrub, and Queñua communities in Peru (21, 32, and 29 species, respectively) support at least as many species as do comparable habitats in most other regions, and the Tola community (16 species) falls about in the middle of the range of species abundance of other habitats such as *Larrea* in New Mexico (Raitt and Maze, 1968; Tomoff, 1974), *Sarcobatus, Atriplex, Tetradymia,* and *Artemisia* in Utah (Fautin, 1946), scrub grassland in Texas (Emlen, 1972), duneveld in Africa (Pianka and Huey, 1971), *Festuca-Mulinum* and *Nothofagus* steppes in Patagonia (F. Vuilleumier, 1972), and coastal heath in Australia (Recher, 1969). The most striking difference was in the Ichu bunchgrass community. The number of species here (24) far exceeds number in grassland elsewhere (references cited above). The number of passerines (15) is especially noteworthy. All of the birds in the Ichu community are thought to be year-round residents; all, with the possible exception of parakeets, feed to a large extent in or over the grassland, and many nest in the grassland itself. The remainder nest nearby in rock walls, mudbanks, or cliffs.

The remarkable constancy of the number of species of passerines and other groups of birds in numerous grassland habitats in the Northern and Southern Hemispheres led Cody (1966) to suggest that the number of niches in all grasslands is limited and filled to capacity. The fact that the Ichu bunchgrass habitat in Peru is able to support more species than grasslands elsewhere calls for a re-examination of Cody's hypothesis. It should be revealing to analyze in the manner of Cody (1968) and Wiens (1969) the feeding ecology of the passerine subset of the Ichu avifauna in search of an explanation of the species richness. Part of the explanation surely stems from the fact that the bird species in the Ichu habitat are drawn from an unusually rich, high-altitude avifauna (B. Vuilleumier, 1971; F. Vuilleumier, 1969) created by repeated waves of Pleistocene glaciation, but is is also clear that additional species (see list in legend to Plate 8) have packed themselves into the Peruvian Ichu by taking advantage of at least three of the four methods of resource division listed by Cody (1968): vertical habitat selection (swallow); food specialization (hummingbird, flicker); and difference in time (nightjar). The fact that three of these four species nest in nearby gullies or cliffs does not detract from the fact that they share the food resources of the grassland itself. The hummingbird is noteworthy not only because hummingbirds do not occupy grasslands elsewhere, but also because it has modified the traditional hummingbird niche by spending considerable time on the ground, feeding among the grass clumps (Carpenter, 1972).

It would be interesting to know whether our equations relating the number of species of birds in Peru to various environmental measurements would serve as well in other regions. The most nearly comparable study is one in nine different habitats in the Kalahari Desert of Africa by Pianka and Huey (1971).

In general their habitats were vegetationally similar to ours and contained similar numbers of bird species (16 to 41).

Their bird inventory was composed primarily of resident species and extended over many months. They found no significant correlation of number of species of birds with percent ground cover, number of species of perennial plants, rainfall, or plant species diversity (based on the volumetric proportion of each species). Plant height diversity, however, gave a significant correlation of +.795. They stratified the foliage in three layers: 0.3-0.6 m, 0.7-1.4 m, and >1.5 m. These layers are more like ours than are those of the Mac Arthurs and others, but differ especially in omitting vegetation below 30 cm. Nevertheless, the coefficient of correlation of our Foliage Height Diversity to number of species of birds was almost identical to theirs for Kalahari birds, and their regression line would serve almost as well for our points.

The most direct comparison of the Kalahari and Peruvian faunas can be made using the multiple regression equation for birds on the seven Peruvian
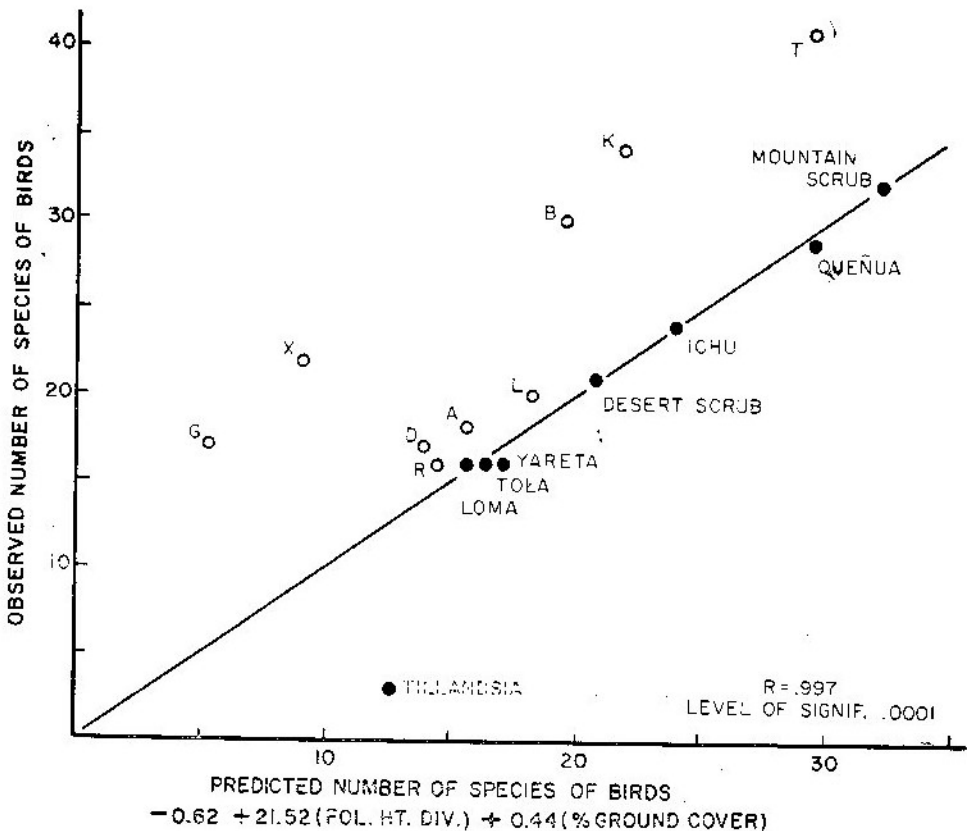

Fig. 9. Regression for number of species of birds at the Peruvian sites (solid circles), calculated without regard for the *Tillandsia* habitat. Open circles and letters refer to nine habitats studied by Pianka and Huey (1971) in the Kalahari Desert.

grids, omitting the *Tillandsia* grid (see previous section). This equation is appropriate not only because in Peru it gave a very tight correlation ($+.997$), but also because it is expressed in terms of Foliage Height Diversity and percent ground cover - measurements available in the Kalahari report (at least for perennial vegetation). When the Kalahari habitats are plotted into this Peruvian equation (Fig. 9), it is apparent either the number of species of birds in Kalahari habitats is greater than expected on the basis of Peruvian experience or that differences in methods of measuring Foliage Height Diversity or percent ground cover cause the Kalahari regression to be displaced to the left. If the inventory period in the Kalahari had lasted only a few days, as in the Peruvian study, instead of several months, the number of species tallied would have been fewer and the Kalahari had lasted only a few days, as in the Peruvian study, instead of several months, the number of species tallied would have been fewer and the Kalahari regression line would drop down closer to the Peruvian regression in Figure 9. Also, if annual vegetation had been included in the Kalahari measurements of Foliage Height Diversity and percent ground cover, the Kalahari regression would be shifted to the right, closer to the Peruvian regression. After correction for these differences in field techniques, we conclude that the species richness of the avifauna and its response to the vegetation are quite similar in the Kalahari and in Perú. Even without belaboring the comparison between the two avifaunas, it is clear that Foliage Height Diversity and percent ground cover are quite effective in predicting the number of species in the Kalahari (for this distribution of Kalahari points $R = +.823$) as well as in Peru.

Bird Species Diversity. Bird Species Diversity, calculated on the basis of the number of individuals of each species tallied on the 3-ha strip censuses, ranged from 0 in the *Tillandsia* to 2.528 in Mountain Scrub. The average for the eight study sites was 1.618. Such diversities are, taking into account differences in procedures, not grossly different from the diversities measured by other people in comparable, sparsely-vegetated habitats on other continents (see studies cited below). In spite of the relatively large number of species in the Ichu bunchgrass community, Bird Species Diversity in Ichu was about average for grasslands in other areas.

The best predictor of Bird Species Diversity in our communities was Plant Species Diversity (Table 3). The predictive equation (Fig. 10) is:

$$\text{Bird Species Diversity} = -.051 + .856 \text{ (Plant Species Diversity)}$$

Adding a second predictor variable (Foliage Height Diversity) makes only a slight improvement in predictive value.

MacArthur and MacArthur (1961) demonstrated a close linear relationship between Bird Species Diversity and Foliage Height Diversity among birds nesting in forests of various kinds in the eastern United States. The relationship was clearest when Foliage Height iDversity was based on three layers of foliage: herbs
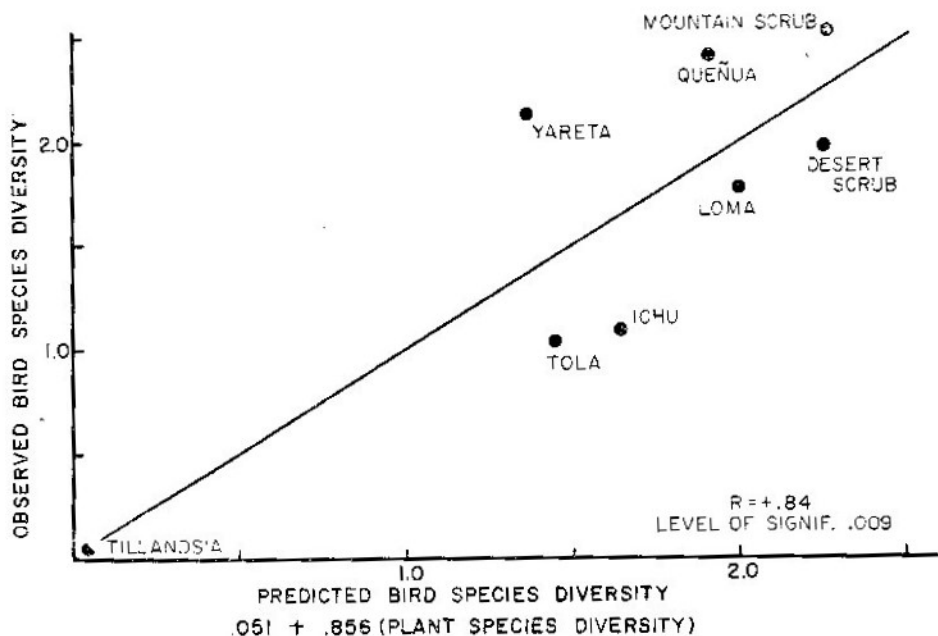
Fig. 10. Correlation of Bird Species Diversity with Plant Species Diversity.

(0-2 feet), shrubs (2-25 feet), and trees (above 25 feet). In their study Plant
Species Diversity did not account for any of the variation in Bird Species Diver-
sity unaccounted for by Foliage Height Diversity. The relationship between
Bird Species Diversity and Foliage Height Diversity has subsequently been
tested in other regions and, with a few exceptions such as Howell in Nicaragua
(1971) and Vuilleumier (1972) in Patagonia, found to be a fairly tight linear
one, although in different studies the slope of the regression line varies between
1.44 and 2.01, and the Y-intercept varies between 0.46 and 1.52.

Vegetation at the eight Peruvian sites rarely exceeded 2 m in height, and
consequently we were inclined to stratify the vegetation differently; bird censuses
also were not strictly comparable to those in many of the other studies, so it is
not surprising that our data do not cluster about the regression lines provided
by previous workers. Additionally, it would not be surprising if the bird species
themselves, because of the limited range of foliage height available, failed to
cluster closely about *any* regression line based on Foliage Height Diversity. The
coefficient of correlation between Bird Species Diversity and Foliage Height
Diversity on our eight study sites was only +.708 (Table 3); the regression
equation was:

$$BSD = 1.064 + 1.719 \text{ (Foliage Height Diversity)}$$

Perhaps by chance this regression, loose though it be, when plotted on a graph

falls midway between the low line of Willson (1974) for a variety of habitats in Illinois and the high line of Karr (1968) and Karr and Roth (1971) for various habitats in North and Central America. Cody's (1970) regression for Chilean habitats also falls between these two extremes.

Stratifying our vegetation into the same layers as in the work of the Mac Arthurs, Karr, Cody and others lowers the Foliage Height Diversity of all of our Peruvian sites, which then reveals that most of the Peruvian sites support a greater Bird Species Diversity than would be expected on the basis of Foliage Height Diversity appropriate to Chile or North America. The Bird Species Diversities in the Peruvian desert and high-mountain habitats are as great as in many northern communities with structurally more complex vegetation.

A closer correlation with Foliage Height Diversity was prevented especially by a much higher-than-predicted Bird Species Diversity at the lowest (Loma) and highest (Yareta) study sites, as well as by the very low (zero) Diversity Index at the *Tillandsia* site. The high value at the Loma site might have resulted from an unusually equitable distribution of species because of territorial behavior imposed by the nesting season at that site. In the Yareta community, a scarcity of seed-bearing plant species may have reduced the number of flocks of seed-eaters.

Contrary to the situation for breeding birds in forests of eastern North America (MacArthur and MacArthur, 1961), in the eight Peruvian habitats Plant Species Diversity (Fig. 10) correlated slightly better with Bird Species Diversity than did Foliage Height Diversity, as did also number of species of plant (Table 3). Cross correlation are high between all three of these measures, however (Table 4). If the unusual Tillandsia community is omitted (Table 6), then Foliage Height Diversity is indeed the best single predictor of Bird Species Diversity.

Tomoff (1974) found that Foliage Height Diversity, even when stratified in a manner appropriate to desert scrub, was not a good predictor of Bird Species Diversity. He used instead an index of vegetational complexity called the Physiognomic Coverage Density (PCD). The coefficient of correlation between this index and Bird Species Diversity in seven communities in Arizona was +.875. PCD correlated even better, according to our calculations, with the number of species of birds in Tomoff's desert scrub (+.918) and with bird density (+.936). It is clear that PCD in his study and Plant Species Diversity in ours added important information not provided by Foliage Height Diversity. Tomoff attributes this to the importance in desert scrub of a few individual plants of relatively rare species for nest placement. We agree that addition of some measurement of vegetational complexity such as PCD provides better prediction of Bird Species Diversity than does Foliage Height Diversity, but must point out that in the Peruvian communities the presumed critical vegetational features were holding diverse bird faunas in their communities during the non-nesting season as well.

Karr (1968) found that the logarithm of percent vegetation cover was neatly correlated with Bird Species Diversity on strip-mined land in Illinois. In our communities, including or excluding the *Tillandsia* community, correlation was very low between Bird Species Diversity and both percent ground cover and the logarithm of percent ground cover.

Species Diversity Indices are made up of two components: the number of species and the relative abundance of individuals representing each of the species. By comparing the observed Species Diversity Index of a large number of bird censuses with the maximum possible index that would be obtained if all species within each census were represented by an equal number of individuals, Tramer (1969) has shown that birds in a variety of habitats seem to arrange their populations in a manner so that the ratio between observed and maximum possible Species Diversity is about 0.86. The ratio varied from 0.72 in marshes to 0.92 in tropical woodlands. The coefficient of correlation between observed Species Diversity and maximum possible diversity in 267 censuses was .972; the slope of the regression line was .941. Tramer pointed out that high ratios might reflect well-developed intraspecific territorial behavior among breeding birds and also suggested that animals living under rigorous, unpredictable conditions would be expected to show low ratios.

We have calculated the observed/maximum ratio for the birds at seven of our eiht sites (*Tillandsia* was omitted because its Species Diversity Index for birds was 0). Excluding the Ichu bunchgrass habitat, for reasons described below, the ratios averaged .91 (range .86 to .97) and were neatly distributed with a coefficient of correlation of .99 and a slope of .57. These values suggest that the Peruvian birds were unusually successful in dividing the resources evenly among the species present. This success was occurring in spite of the fact that at only one of the sites was appreciable nesting in progress; the territorial behavior that accompanies nesting would be expected to increase equitability even more. According to Tramer's views, the Peruvian birds in these six communities were responding as though the habitats were predictable and nonrigorous. Chilean birds also are more equitably distributed among species than are birds in most other regions (Cody, 1970).

The ratio between observed and maximum possible Species Diversity among birds in the Ichu community was only .45. This reflects the presence of large feeding flocks dominated by a small finch. Some species were in flocks at the Mountain Scrub and Queñua sites also, but these flocks were smaller and formed a smaller proportion of the total number of birds present.

Density of birds. The number of individual birds tallied on the strip censuses varied from one in *Tillandsia* to 98 in Mountain Scrub. These counts convert to a range of 0.3 to 33 birds per hectare. Counts at the latter site were dominated by two species of finches (*Phrygilus fruticeti* and *plebejus*), but doves (*Gymnopelia cecilae*) contributed considerably to the biomass. Counts in the Ichu bunchgrass revealed almost as many birds (85) as in the Mountain Scrub, but 63 of the 85 individuals were *Phrygilus plebejus*, mostly in flocks. The other

sites had many fewer birds, especially the windswept Tola, without rocks, where only four individuals appeared in the censuses. An apparent scarcity of sites sheltered from the wind surely restricted the number of birds. We did not detect any of the birds retreating into tuco-tuco burrows as they do in some regions nearby.

Because of the vagaries of bird census procedures (Emlen, 1971), we hesitate to compare density of birds recorded in our counts with those of other workers. We feel, however, that our counts reflect with sufficient accuracy relative abundance on our different study sites and can with caution, and in a very general way, be compared with censuses made by other people in other regions. We have made such a comparison relying primarily on census data in Wiens (1969, 1971), Stewart (1972), Udvardy (1957), Dixon (1959), Emlen (1972), Johnson (1970), Karr (1968), Karr and Roth (1971), and o Raitt and Maze (1968). It becomes clear that in the Peruvian habitats that have counterparts on other continents, the density of birds, even at high altitude, is not less and, in many comparisons, is greater.

Of the environmental attributes measured, the number of plant species in the community correlated most highly with the number of birds tallied in the strip censuses (Table 3). Foliage Profile provided almost as good a correlation, and since cross-correlation between these two was low (.124), together they provided a multiple regression (Fig. 11) that can account for more than 80
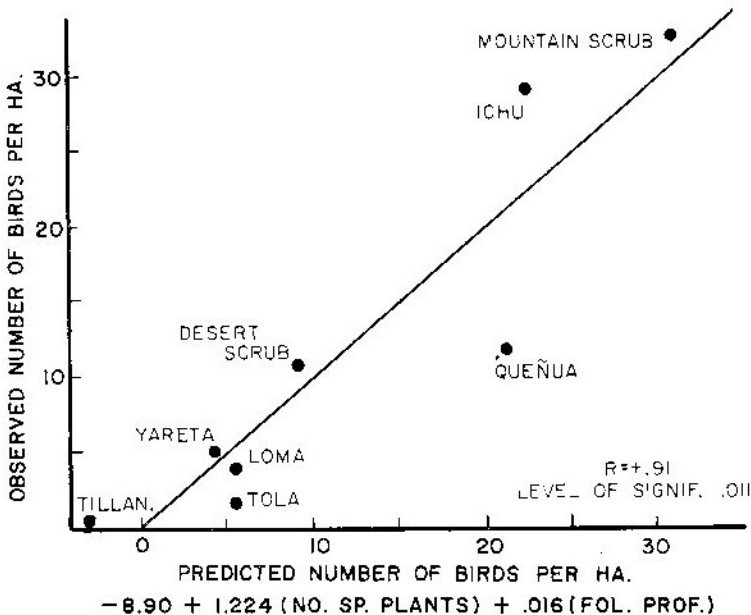

Fig. 11. Multiple regression of density of birds with two predictors: number of species of plants and Foliage Profile.

percent of the variance in bird density. The Queñua and Tola communities have few birds relative to the vegetational diversity available. Perhaps other factors such as wind or insect abundance at these sites prevent the birds from exploiting this diversity.

Biomass of birds. When considering the number of grams of birds occupying each hectare of habitat, one must keep in mind that all birds, even those using only part of the 3-ha strip, were counted. The biomasses are, therefore, overstated and must be considered upper limits. The biomasses of birds in one community can be compared with biomasses of birds measured in the same way in other communities but can be compared only with caution to the mammal and lizard biomasses, which are adjusted for partial use of a study area by a correction factor based on size of home range.

The biomass of birds, omitting raptors, swifts, and swallows, varied from 7 g/ha in *Tillandsia* to 890 in Mountain Scrub (see captions to Plates 1-8). Birds outweighed mammals in most of the communities. A notable exception was in the coastal Loma, where lizards and mice were unusually abundant among the cobbles and seed-bearing weeds, whereas the bird biomass was quite low.

Bird biomass in the different communities correlated most highly with the number of species of plants (as did mammal biomass without tuco-tucos) and correlated poorly with altitude and with percent of ground covered by vegetation (Table 3). Correlation is high, of course, between biomass of birds and bird density. and is moderate between bird biomass and mammal biomass (Table 5).

The biomass of wintering birds in four open habitats studied in a similar manner in Texas by Emlen (1972) ranged from 500 to 1,000 g/ha. It is clear

TABLE 5

COEFFICIENTS OF CORRELATION BETWEEN VARIOUS ASPECTS OF THE BIRD AND MAMMAL POPULATIONS OF THE EIGHT STUDY SITES

	Bird Density	BSD	Bird Biomass	No. Sp. Mammals	MSD	Mammal Density	Mammal Biomass[*]
No. Species Birds	.800	.798	.780	.463	.471	.827	.784
Bird Density		.406	.940	.452	.505	.788	.722
Bird Species Diversity			.598	.077	.083	.688	.694
Bird Biomass				.394	.430	.736	.781
No. Species Mammals					.966	.560	.225
Mammal Species Diversity						.520	.164
Mammal Density							.974

[*] Omits tuco-tucos.

that the biomasses in Peru are much more variable and average somewhat less than half those in Texas. If the migratory species (winter invader) in the Texas communities are omitted so as to make comparison with Peru closer, the biomass of birds in Texas is reduced about 13%. Bobwhite quail dominated the Texas habitats (50% to 68% of the biomass); if these are omitted, the Texas and Peruvian biomasses are more nearly equal. In three of the richest Peruvian habitas, however, finches of the genus *Phrygilus* dominated the bird biomass: 65% *P. plebejus* in the Ichu bunchgrass, 49% three finches in the Mountain Scrub, and 48% three finches in the Queñua. The scene in Texas consists essentially of a large biomass of resident quail and moderate weights of resident meadowlarks and winter-invading sparrows. In Peru the quail analog (the tinamou *Nothura*) is scarce or absent, resident finches are abundant, and much of the remaining biomass is composed of furnariids and doves. One wonders why quail are so successful in the Texas communities, or tinamous so unsuccessful in these Peruvian communities.

Number of species of mammals. The number of species of small mammals actually taken on the different study plots varied from 0 in *Tillandsia* to 6 in Tola. In those plant communities for which reasonably close analogs exist in North America, a comparison of species richness reveals some interesting differences. The Desert Scrub community in Peru yielded only two species, and the Mountain Scrub four, but similar habitat in the southwestern United States would be expected to yield two or three times this number drawn from genera such as *Peromyscus, Perognathus, Dipodomys, Reithrodontomys, Onychomys,* and *Neotoma* (Table 1). Two additional species were taken within a few hundred meters of the Desert Scrub grid in Peru, and two more species near the Mountain Scrub site but addition of even these to the faunas does not bring them up to the number of especies expected on similar areas in North America.

Climatically and vegetationally the coastal Loma area cannot be compared with communities elsewhere but its single species (and three other species nearby) seems to be a poor representation considering the quantity of food and cover available.

On the altiplano however the five species of small rodents in Ichu bunchgrass (and seven other species nearby) and the six in Tola (with three others nearby) equal or exceed the number of species expected in similar plant communities in North America (Tables 1 and 2); indeed they equal or exceed the number in temperate forests and in rain forest in Panama (Fleming, 1970, 1971). Since all of the species at the Tola and Ichu sites are high-altitude endemics, and seven out of ten of these are at the norther edge of their range, one is led to suspect that we are seeing the results of a successful radiation by high-Andean and Patagonian forms (Bianchi *et al.*, 1971; B. Vuilleumier, 1971) and lack of radiation by mammals along the coastal desert including the western slopes. No highly desert-adapted small mammal has evolved in South America. In many parts of the Peruvian desert, the introduced house mouse competes quite successfully.

Cody (1970) has pointed out that a characteristic of the avifauna of Chile is a tendency for each genus to be represented in each region by a single species. No such tendency exists among mammals in the Peruvian habitats considered in this report. Sympatry in species of *Phyllotis* is common in the desert, on the western slopes, and at high altitude (Pearson, 1958), and numerous species of *Akodon* co-exist. In bunchgrass habitat not far from that shown in Plate 8 but enriched by the presence of more rocks and some water, it is possible to capture ten species of mice that belong to only three genera: *Phyllotis, Auliscomys*, and *Akodon*.

In contrast to the case with birds, the multiple regression procedure was unable to relate closely the number of species of mammals with habitat measurements. Of the various environmental parameters measured, altitude provided the highest correlation with the number of species of small mammals ($+.674$). The greater number of species at high altitude reflects partly the increase in vegetation (up to 3,700 m) and partly the successful radiation of mountain species mentioned above. Foliage Profile showed a modest correlation with number of species ($+.638$), and percent ground covered by vegetation showed a low correlation ($+.425$). Number of species of plants and Foliage Height Diversity were quite unrelated to number of species of mammals, and the Refuge Index even showed a negative correlation ($-.452$). Since altitude and Foliage Profile were highly cross-correlated, the best multiple regression for predicting number of species was provided by combining altitude and percent ground cover (Fig. 12). The coefficient of multiple correlation was only $+.762$, and adding a third predictor (Refuge Index) increased the coefficient only slightly and lowered the level of significance. The Yareta community, with its high altitude and fairly high values of ground cover and Refuge Index, and yet only two species of small mammals, was especially troublesome to fit into the regression. Omission of the *Tillandsia*, site did not make prediction any better (Table 6).

The relatively poor predicting power of the regression for number of species of mammals clearly suffers from inadequate input. One knows that several species of altiplano mammals respond to the presence of grass, not the Foliage Profile or Foliage Height Diversity of grass but the physical and nutritional environment provided by grass. Other species of mammals require water; others require rocks, or sandy soil. None of these factors entered directly into our equations. Other species might depend upon the presence of certain plant species, as woodrats (*Neotoma*) and nesting birds depend upon cholla cactus in the desert scrub of the southwestern United States (Brown and Lieberman, 1972; Tomoff, 1974), but we know too little about requirements of the Peruvian fauna. These other unmeasured characteristics of the environment account for the remaining fifty percent of the variation in number of species of mammals not accounted for by altitude and percent of ground cover.

Species Diversity of small mammals. Species Diversity varied from zero in *Tillandsia* (no small mammals) and Loma (one species) to 1.504 in the
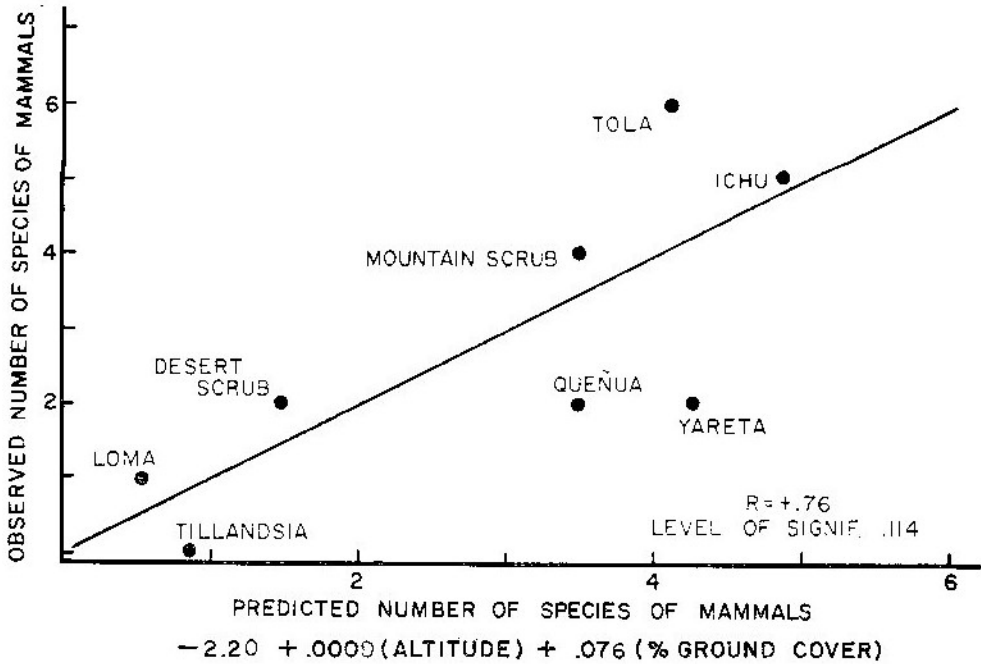
Fig. 12. Multiple regression of number of species of mammals with two predictors: altitude and percent of ground covered with vegetation.

TABLE 6

COEFFICIENTS OF CORRELATION BETWEEN THE ANIMAL POPULATIONS AND THE ENVIRONMENT AT SEVEN STUDY SITES (OMITS THE *TILLANDSIA* SITE)

	No. Sp. Birds	Bird Spec. Div.	Bird Density	No. Sp. Mammals	Mamm. Spec. Div.	Mammal Density	Mammal Biomass*
No. Species Plants	.726	.648	.631	—.209	—.220	.737	.951
Foliage Profile	.603	.139	.424	.582	.733	.506	.910
Plant Species Diversity	.565	.548	.414	—.369	—.462	.589	.794
Foliage Height Diversity	.803	.711	.424	.152	.116	.479	.445
Altitude	.232	—.052	.182	.533	.693	—.197	—.466
Percent Ground Cover	.103	—.387	.430	.423	.531	.352	.139
Number of Refugia				—.433	—.581	—.289	.189

* Omits *tuco-tucos*.

Tola community. The average for the six communities for which the index was not 0 is .925, which is probably not far from an average for uniform habitats elsewhere. It was shown earlier that the indices for Tola and Ichu were high (Tables 1 and 2) and were certainly not penalized by geographic, climatic, altitudinal, and faunal constraints of the Peruvian Andes. The three desert habitats at lower elevations, however, were distinctly impoverished.

Mammal Species Diversity, unlike Diversity of the birds living on the same areas, does not respond to Foliage Height Diversity, number of species of plants, or Plant Species Diversity (Table 3). Altitude, however, was positively correlated with Mammal Species Diversity ($+$.765), as was Foliage Profile ($+$. 764). Percent ground cover provided a moderate correlation ($+$.527), and Refuge Index a negative correlation (-.587). The best predictive equation was provided by altitude combined with percent ground cover (Fig. 13), the same two predictors preferred for predicting number of species of mammals. The predictive power is not great, however (accounting for only 76% of the variance in Mammal Species Diversity), and is not improved appreciably by adding a third predictor (Refuge Index). The Tola habitat supports a greater Species Diversity than predicted by the equation (Fig. 13), and the Yareta habitat supports a lower Species Diversity. If the percent of ground covered by the
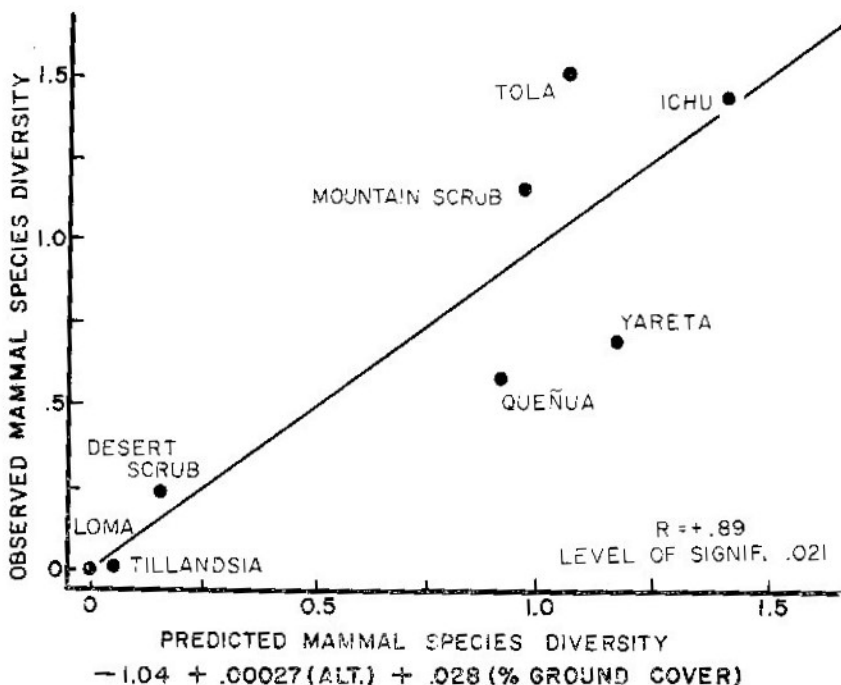

Fig. 13. Multiple regression of Species Diversity of small mammals with two predictors: altitude and percent ground cover.

relatively inert yareta plants in subtracted, the errant Yareta point is brought much closer to the regression line.

Our effort to relate Mammal Species Diversity to various aspects of the environment can be compared with that of Rosenzweig and Winakur (1969) in desert habitats in Arizona. They found, as did we, that the diversity of the mammal population was unrelated to Plant Species Diversity. Their measure of mammal diversity did correlate, however, with a vertical subdivision of the foliage into three layers (0.7.6 cm, 7.6-46, > 46), with a horizontal subdivision of foliage density, and with a measure of surface strength of the soil. By combining these three characteristics into a single measure of habitat complexity, they were able to account for 40% of the variance in diversity of mammals on their study sites (based on our calculation of the coefficient of correlation for their Figure 10). This is somewhat less effective than Foliage Profile or altitude on our transect and considerably less effective than our multiple regression (see above) based on altitude and percent ground cover. Their vertical and horizontal foliage measurements probably contain elements common to our Foliage Profile measument, and this would account for the fact that both studies found a positive correlation between mammal diversity and foliage density and complexity.

The species richness componet of the Diversity Index accounts for most of the variation in the index for small mammals at the different Peruvian sites. Omitting the Loma and *Tillandsia* sites (for which Diversity is undefined or 0), and omitting the Desert Scrub site (see below), the ratio between the observed Species Diversity and the maximum possible index varied from .81 in Mountain Scrub to .98 at the Yareta site. The coefficient of correlation between observed and maximum possible Species Diversities was .99 and the slope .55. According to the theory proposed by Tramer (1969), this indicates that the mammals at the higher sites on this transect are responding as though the environment is predictable and non-rigorous. On the other hand, the Desert Scrub community had a ratio of only .37. The small mammals seem to have been unable to divide up their resources as equitably as in the other communities, but rather than invoking unpredictability, this can be explained by the fact that the study area included only a couple of small patches of the dense bushes required by one of the two species of mice present. Probably the most climatically unpredictable of the habitats is the Loma community, dependent upon coastal fog and drizzle in most years to germinate seeds of annuals. It supported only a single species of mouse.

Density of small mammals. The density of small mammals in the Peruvian habitats varied from 0 in *Tillandsia* and 1.80 per hectare in Yareta to a maximum of 5.45 in the Mountain Scrub community (6.52 in Loma if one counts juveniles). Although densities were not measured during previous collecting trips to this region of the Andes, note was taken of trapping success during five previous seasons at the same or similar sites without detecting conspicuous

differences. We assume, therefore, that these populations are relatively stable from one year to the next.

A remarkable exception was revealed when the Loma study area was revisited in March, 1973. A plague of *Phyllotis* of two species was living among the shrivelled weeds remaining near the end of the dry season. One collector trapped 14 *Phyllotis* in a few hours - within reach of his sleeping bag.

The densities encountered in the various Peruvian communities do not differ greatly, in spite of sparse vegetation and high altitudes, from those found at the end of then non-breeding season in many temperate communities and even in tropical rain forest (Fleming, 1971), but they are clearly lower than in comparable arid habitats in North America (Tables 1 and 2). We have already mentioned that kangaroo rats and meadow voles have made evolutionary breakthroughs that enable them to reach, at least on occasions, higher densities than we encountered in these Andean habitats.

Densities of small mammals at the eight study sites correlated most highly (Table 3) with Plant Species Diversity (.816) and number of species of plants (.736). Altitude (.315) and percent ground cover (.382) correlated poorly, and the Refuge Index, suprisingly, was negatively correlated, although not significantly so. The overall picture is one of more individuals in communities with more abundant and more complex vegetation regardless of elevation above
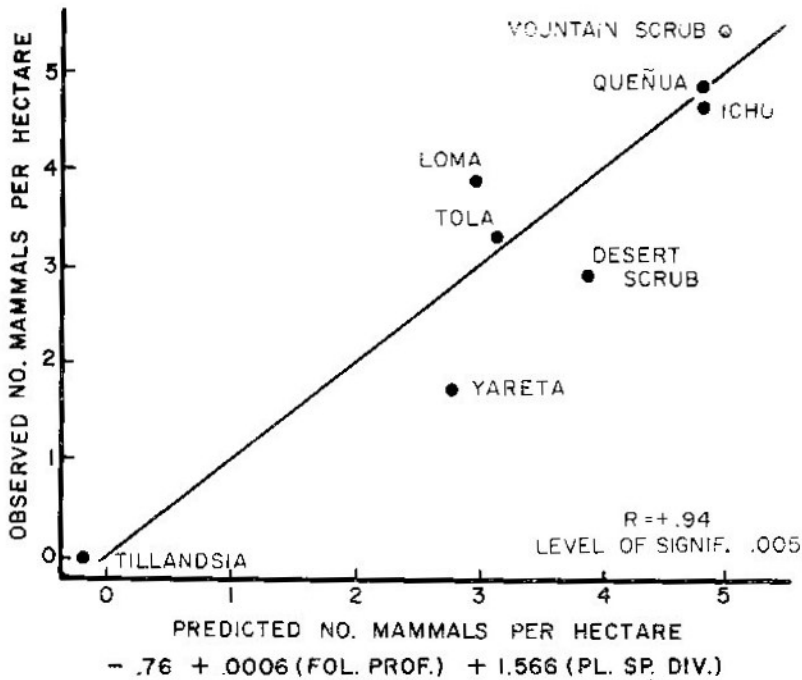

Fig. 14. Multiple regression of density of small mammals (including tuco-tucos) with two predictors: Foliage Profile and Plant Species Diversity.
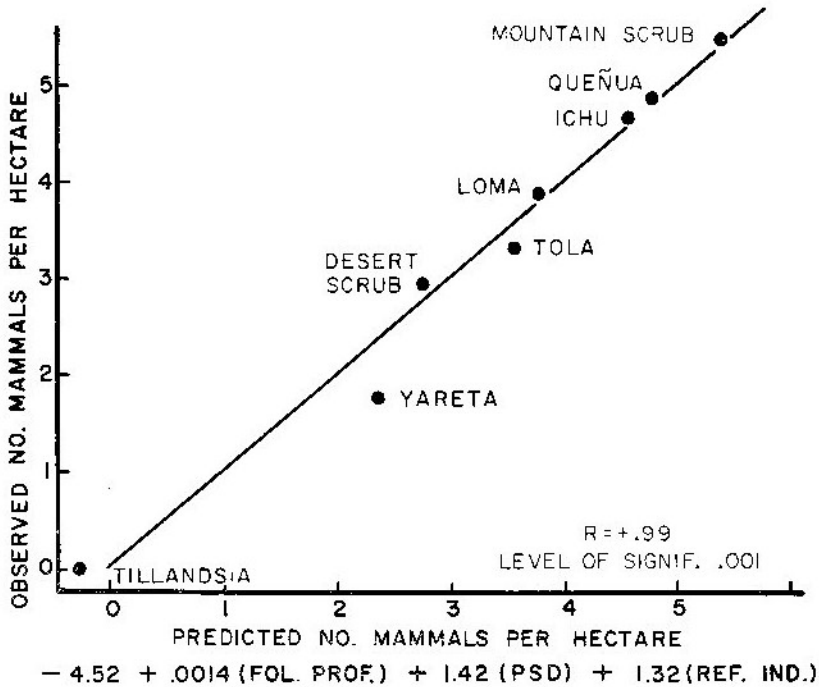
Fig. 15. Multiple regression of density of small mammals (including tuco-tucos) with three predictors: Foliage Profile, Plant Species Diversity, and Refuge Index.

sea level and regardless of the number of refugia. The *Tillandsia* habitat remains an exception, and the Yareta habitat supported fewer individuals than its vegetation measurements predicted (Figs. 14 and 15). If the yareta heads themselves are considered to be ecologically inert and left out of the calculations, the multiple regressions in Figures 14 and 15 are considerably tighter.

Biomass of small mammals. The live weight of small mammals per hectare varied from 0 in *Tillandsia* and 51 g in Yareta to 352 in Tola. Of the latter figure, 297 g were fossorial tuco-tucos. If these are omitted, then the highest biomass was found in the Mountain Scrub habitat (240 g/ha). It was noted earlier that biomasses on the Tola and Ichu areas were less than have been found on similar areas in North America, and this might again be attributed to absence of genera as resourceful as *Dipodomys* and *Microtus*, or it might stem also from lower plant productivity or more competition from livestock. We have no data concerning these possibilities.

The highest correlation between biomass of mammals and any of the environmental parameters measured was with Plant Species Diversity (only +.455), and no combination of predictors provided a useful multiple regression for predicting biomass. If, however, the tuco-tucos are omitted (they were present only on the Tola grid), a high correlation is obtained between biomass

of small mammals and number of species of plants (+.958). Adding percent ground cover provides an even more satisfactory predictive equation (Fig. 16). Plant Species Diversity, which is highly correlated with number of species of plants (+.794), also provided a high correlation with biomass of above-ground small mammals (+.817).

The fact that a satisfactory prediction can be made for biomass of small mammals minus tuco-tucos while no effective prediction can be made for biomass including tuco-tucos means either that tuco-tucos are responding to aspects of the environment that we did not measure or that hey are geographically excluded from many of the study sites. Actually, elements of both explanations are responsible. In this region tuco-tucos, for no obvious reason, do not cross the continental divide onto the Pacific slope and so are not presently available to colonize 6 of the 8 study sites, even though some provide suitable deep, sandy soil. At the other available site (Ichu), the soil was too heavy to provide favorable conditions.

Chew and Chew (1965, 1970) give data that permit testing the goodness-of-fit of small-mammal biomass in their *Larrea* area in Arizona to the regression shown in Figure 16. Just as this regression does not include tuco-tucos, the Chews did not include the analogous gophers (*Thomomys*). The Peruvian
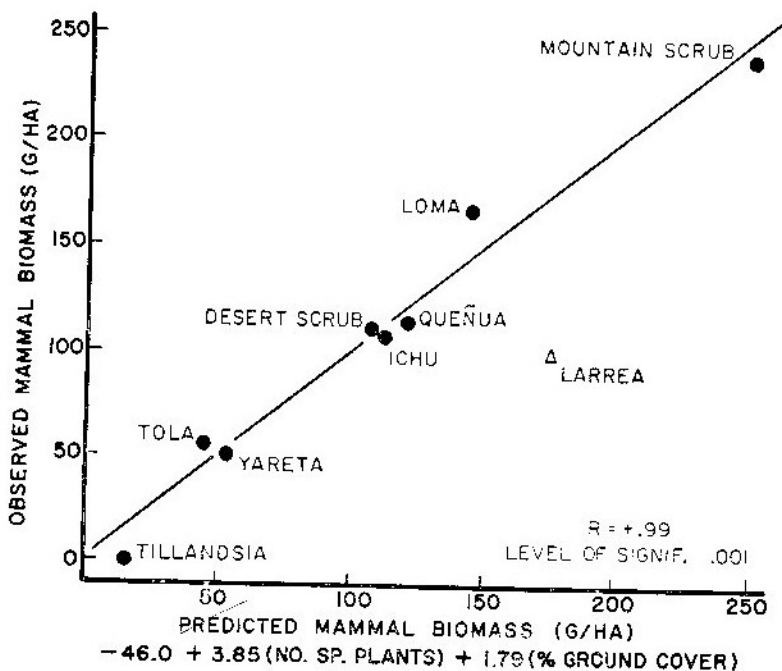

Fig. 16. Multiple regression of biomass of small mammals (excluding tuco-tucos) with two predictors: numbers of especies of plants and percent ground cover. The triangle represents the biomass (excluding kangaroo rats) in a *Larrea* community in Arizona (see text).

regression, based on number of species of plants and percent ground cover, predicts 176 g/ha in the Arizona *Larrea;* the actual biomass present in Arizona (omitting rabbits) was 553 g/ha. Of this, 100 g was composed of small mammals other than kangaroo rats. The remaining 76 predicted grams was not only filled by a single species of kangaroo rat but was exceeded by such an amount as to bring the total biomass of this kangaroo rat up to 453 of the total 553 g. These calculations confirm the idea that kangaroo rats in the Northern Hemisphere are filling a very profitable niche that in South America is either absent, unfilled or filled by quite different kinds of animals.

Chew and Chew (1970) noticed that on their *Larrea* study area the Diversity Index and its equitability measure increased in the sequence: population density < biomass < energy flow. This leads to the tempting theory that community evolution tends to maximize the share of energy captured by each species. We have no measurements of energy flow, but the data from our eight study areas indicate that there is no clear tendency for Biomass Diversities and their equitability indices to be higher than the Density Indices; in fact, they are on the average *lower*. In MacMillen's (1964) desert rodent community also, the Biomass Diversity Index was less than the Density Diversity Index. We conclude that community evolution among small mammals in probably *not*, as a general rule, tending to maximize equitability of energy flow.

Microhabitat preferences of mammals. Although each of the study sites was selected to provide as uniform a habitat as possible, a mosaic of microhabitats existed within the boundaries of each grid. By comparing various characteristics of the habitat at each marker stake where one species was caught with the characteristics at stakes where no mice were caught, or where other species were caught, it becomes possible to analyze microhabitat preferences of the different species (Table 7). For example, *Phyllotis darwini* at the Desert Scrub study area was trapped at sites with significantly greater than average Foliage Profile, percent ground cover, and number of refugia.

Phyllotis darwini and *P. magister* are sympatric at intermediate elevations in southern Peru. *P. magister* is said to prefer habitat that is more brushy, and at higher and lower elevations as the brush disappears, *darwini* replaces *magister* completely (Pearson, 1958). The Desert Scrub community is at the lower limit of the distribution of *magister* on the transect. It contains only a few clumps of dense brush, and the only *magister* caught was in one of these (Table 7). In the Mountain Scrub community, enough of the elements preferred by both *darwini* and *magister* were present to support the two species in about equal numbers. Table 7 reveals that *magister*, compared with *darwini*, is responding positively to Foliage Profile, especially profile in the vegetative layers above 1/2 m. Ground cover had much less effect on distribution of these two species; the difference in percent ground cover between *darwini* sites and *magister* sites was not significant. The difference between the Refuge Indices for the two species was also not significant. However, in both the Desert Scrub and the Mountain Scrub

TABLE 7

HABITAT CHARACTERISTICS AT GRID STAKES WHERE DIFFERENT SPECIES OF MICE WERE TRAPPED. NUMBERS IN PARENTHESES ARE THE SIZE OF SAMPLE. PAIRS OF SUPERSCRIPT SYMBOLS INDICATE DIFFERENCES SIGNIFICANT AT THE .05 LEVEL.

Community	Species	Foliage Profile (cm³)				% Cover	Refuge Index
		½m	1m	2-3m	Total		
Desert Scrub	Phyllotis darwini	2261	955	4	3220 (8)*	47.0 (7)*	2.6 (20)*
	Phyllotis magister	7683	131	0	7814 (1)	100.0 (1)	15.0 (1)
	No mice	295	89	9	334 (40)*	7.3 (40)*	0.8 (41)*
Mountain Scrub	Phyllotis darwini	1441	270	26	1737 (9)*	37.0 (9)	2.42 (24)*
	Phyllotis magister	2286	1105	105	3496 (13)*	26.1 (13)	2.76 (20)¹
	Akodon berlepschii	417	52	0	469 (3)	36.3 (3)	1.5 (4)
	No mice	2224	704	52	2980 (21)*	38.1 (21)	1.00 (20)*¹
Quenua	Phyllotis darwini	2047	1065	186	3298 (7)	28.6 (7)	1.50 (16)*
Quenua	Akodon berlepschii	3768	951	78	4797 (14)	36.6 (14)	1.87 (30)*†
	No mice	2105	572	78	2755 (21)	31.4 (21)	0.81 (21)*†
Yareta	Phyllotis darwini	1440	0	0	1440 (7)	38.0 (7)	1.53 (15)
	Akodon andinus	0	0	0	0 (1)	0 (1)	2.40 (3)
	No mice	1835	61	0	1896 (37)	32.6 (37)	1.66 (37)
Ichu	Phyllotis osilae	3309	588	0	3897 (4)	39.5 (4)*	1.0 (10)*
	Akodon orophilus	9456	52	0	9508 (4)	68.2 (4)*†	0.3 (10)
	No mice	3894	48	0	3942 (22)	47.9 (22)+	0.09 (22)*

communities, both species showed a strong tendency to frequent spots with far above-average numbers of refugia.

Phyllotis darwini and *Akodon berlepschii* were both present in the Queñua community in moderate numbers. The percent of ground covered by vegetation was almost the same at stakes where *Phyllotis* was caught, where *Akodon* was caught, and where no mice were caught. Foliage Profile at *Akodon* stakes was not significantly different than at *Phyllotis* stakes; the Profile for each species was greater than at stakes where no mice were caught, but not significantly so. The sites of capture of *Phyllotis* and *Akodon* had significantly more refugia than sites where no mice were trapped. It appears, therefore, that, both species are choosing a recognizable subset of the conditions available on the grid but that it is difficult to distinguish between the preferences of the two species. Behaviorally, however, the two species are distinct: *Phyllotis* is nocturnal and *berlepschii* is diurnal.

In the Yareta community *Akodon andinus* seemed to prefer dense patches of *Lepidophyllum* where these was more than the average number or refugia. At *Phyllotis* stakes the percent of ground covered by plants, the Foliage Profile, and the number of refugia were close to the average for sites where no mice were captured.

In the Tola comunity, *Eligmodontia* was the only mouse abundant enough to provide data on habitat preferences - and it showed no preference. Foliage Profile, percent ground cover, and Refuge Index were essentially the same at stakes where where *Eligmodontia* was caught and at stakes where no mice were caught.

Because of the scarcity of refugia in the Ichu community and consequent heavy use of most of them by mice, the average number of refugia at all stakes where mice were caught was almost seven times as great as at stakes where no mice were caught *Phyllotis osilae* seemed to be especially dependent upon refugia (Table 7). Foliage Profile and the percent of ground covered by plants at the stakes where *Akodon amoenus* was trapped were significantly greater than at stakes where no mice were trapped.

The data in Table 7 and the conclusions drawn from them concerning habitat preferences agree with our hunches developed on the basis of trapping experience - but such trappers' hunches have seldom been quantified. It is also encouraging to note that the capture of mice was clearly correlated with certain of our environmental measurements; therefore, in spite of the fact that these measurements were not notably successful in predicting the number of species of mammals in a community, they were obviously measurements of environmental attributes that were relevant to the mammals themselves. This conclusion is confirmed by the high correlations with mammal density and biomass.

Further study of the way in which each species exploits the patchiness of each habitat should lead to a better understanding of the community physiology underlying the demonstrated correlations.

Home range of *Phyllotis darwini*. Since *Phyllotis darwini* was common in five of the communities, it was possible to examine what environmental attributes are related to size of its home range (as measured by mean maximum movement). Altitude showed a high positive correlation, and Plant Species Diversity, number of species of plants, and number of refugia all showed negative correlations (Table 3), although, owing to small sample size, none of the coefficients can be proven to differ significantly from zero. An especially high and statistically significant correlation was obtained with number of species of small annual plants ($r = -.97$, $P = .006$). Since *darwini* is a seed-eater and the small annuals are important producers of seeds, it is not surprising to find that home ranges are small where seed-bearing annuals are abundant. When the number of species of small annuals is combined with a measure of shelter (Refuge Index) or with Plant Species Diversity, the multiple regression accounts for more than 98 percent of the variance in size of home range (level of significance .017):

Home range = 115 - 2.27 (Number of species of annuals) -

6.26 (Refuge Index).

Number of refugia. The Refuge Index varied from only 0.34 at the Ichu site (= 224 refugia per hectare) to 3.49 in the Loma (= 2,300 per hectare). Mice were clearly making heavy use of the limited number of refugia at the Ichu site because traps set at stakes with refugia nearby were much more successful than those without refugia nearby (Table 7). In the Desert Scrub, Mountain Scrub, and Queñua communities also, traps near refugia were much more successful. In the Loma habitat, however, refugia were so abundant that they did not seem to be related to the capture and presumably to the distribution of mice on the grid.

In view of a strong tendency for mice in four of the communities to be caught at stakes near which refugia were uncommonly abundant, and in view of a conviction that the number of refugia **should** be an important component of a mouse's environment, it was surprising to find (Table 3) that the number of refugia correlates poorly (or even negatively) with all of the measures of mammal populations. Apparently, the refugia on most of our study areas were scarce enough to be heavily utilized without being scarce enough to limit the number of species and they density of mammals.

If this is true, then it becomes possible to say that the number of refugia available per mouse on our study areas was "adequate" and that refugia become limiting only when the refugia/mouse ratio drops below 48, the lowest ratio encountered. The ratios were: Loma, 596; Desert Scrub, 443; Mountain Scrub, 215; Queñua, 159; Yareta, 621; Tola, 423; and Ichu, 48.

Number of species of lizards. None of the study grids supported more than two species of lizards, and even raising this figure by including those species known to be living nearby does not bring the total even close to the eight or more

species commonly found in desert habitats in North America (Johnson, Bryant, and Miller, 1948; Pianka, 1967), the 12 to 18 species found in various habitats in the Kalahari Desert of Africa (Pianka, 1971), or the two or three **dozen** species in Australian desert communities (Pianka, 1969). The reptilian fauna of the deserts of these other continents is even richer when snakes are included. No snakes were seen on any of the Peruvian grids.

Various coefficients of correlation between number of species of lizards and environmental characteristics are listed in Table 3 for completeness, but because of the small range in number of species little confidence can be placed in them. Most important, in view of Kiesters's 1971 study, is the evidence that altitude did not depress the number of species.

It is not clear why there are so few species of lizards on our transect. It seems fairly satisfying to attribute the abundance of species of birds and mammals at the higher study sites to several rounds of speciation at high altitude during a series of glacial and interglacial periods (F. Vuilleumier, 1969; B. Vuilleumier, 1971; Bianchi et al., 1971), but may one assume that poikilothermic lizards are constrained from speciating at high altitude? It seems unlikely that the evolutionary vigor of, for example, *Liolaemus,* a genus that has given rise to about 60 living species of lizards in Chile alone (Donoso-Barros, 1966), would be suppressed by the relatively mild climatic regime at 3,000 m elevation. Other theories as to possible mechanisms for the control of species density in lizard communities, such as those proposed by Pianka (1967), likewise do not provide a satisfying accounting for the few species at either high or low elevations on the Peruvian transect. The contrast, for example, between a pure stand of spinifex bunchgrass in Australia with its 20 species of lizards (Pianka, 1969) and the Peruvian Ichu bunchgrass with its single species is difficult to explain in terms of spatial heterogeneity, plant productivity, or the climatic regimes that produce these bunchgrass communities. Low temeprature, to be sure, prevents operation at high altitude of nocturnal species such as those that are so abundant in Australia and the Kalahari, but even our lowest-altitude site, Loma, supported only a single species (*Tropidurus peruvianus*). This is an omnivorous lizard in which males, females, and juveniles are of quite different appearance. In the Loma this species had expanded into an obviously favorable environment and had saturated it (see density figures under Loma habitat) with a polymorphic population of a single species.

A coincidence that may be important is the scarcity or absence of ants on most of our study sites. Does this reflect an absence of certain resources common in other deserts? Does it reduce the available lizard food?

Density and biomass of lizards. With the exception of the remarkably dense population of *Tropidurus* in the Loma community (see preceding section and section on the Loma), the abundance and biomass of lizards on the other grids was much lower than in arid regions of North America (compare Turner et al., 1969, 1970; Pianka, 1970). Two of the Andean study grids were without

lizards, and the greatest density and biomass of lizards (other than in the Loma habitat) was at the highest study site (Yareta), which supported 4.3 lizards per ha and 21 g/ha of two species. This biomass amounts to about 41% of the weight of small mammals and 27% of the weight of birds in that community. The metabolic impact of the lizards, of course, would be much less than this. At the Tola site, the biomass of lizards was one-third that of the birds, but at no other site (except Loma) did the lizards amount to more than a small fraction of the bird or mammal biomass.

Density and biomass in the eight communities both correlated most highly (Table 3) with the Refuge Index (.752 and .742, respectively, significant at the .03 level) followed by altitude (negative correlations). Foliage Profile and Foliage Height Diversity were negatively correlated (Table 3, significance not statistically certain). Stepwise regressions for density and biomass both made use of Refuge Index and percent ground cover, but achieved barely-significant coefficients of only .872 and .848, respectively.

The abundance of lizards at the Loma site and their scarcity at all of the others distorts the various regressions and reduces the credibility of any general conclusions. In general, it is apparent that biomasses and densities were low at all except one of the sites, were not closely related to most of the environmental characteristics measured, and, at those sites between 3,000 and 4,500 m, not related to altitude.

Biomass of all vertebrates. Calculating the biomasses of all three classes of vertebrates from all eight study sites reveals that the birds contribute on the average 259 g/ha, mammals 143 g/ha, and lizards 88 g/ha = a ratio of 2.9:1.6:1. When tuco-tucos are omitted, the figure for mammals is 106 g. This ratio should be interpreted keeping in mind the precaution, noted earlier, that the bird biomass is probably overstated.

The only significant single predictors of total vertebrate biomass were number of species of plants and Plant Species Diversity (Table 3). Various measures of the amount of foliage present were not relevant. A multiple regression combining number of species of plants and Foliage Height Diversity provides a satisfactory predictive equation (Fig. 17). In the Tola community the biomass of vertebrates exceeds the predicted by a considerable amount (Fig. 17) because of the presence of tuco-tucos. It was shown above that the tuco-tuco niche was not filled at the expense of the other mammals; Figure 17 suggests that likewise it was not filled at the expense of birds and lizards. The vertebrates of the Yareta community are underachievers, possibly because of the prevalence of the ecologically inert yareta plants themselves. The *Tillandsia* community was, as usual, unproductive.

Interclass competition. Table 5 was drawn up to reveal to what extent birds and mammals were responding in the same way to the constellation of environmental characters in the eight communities. It becomes obvious at once
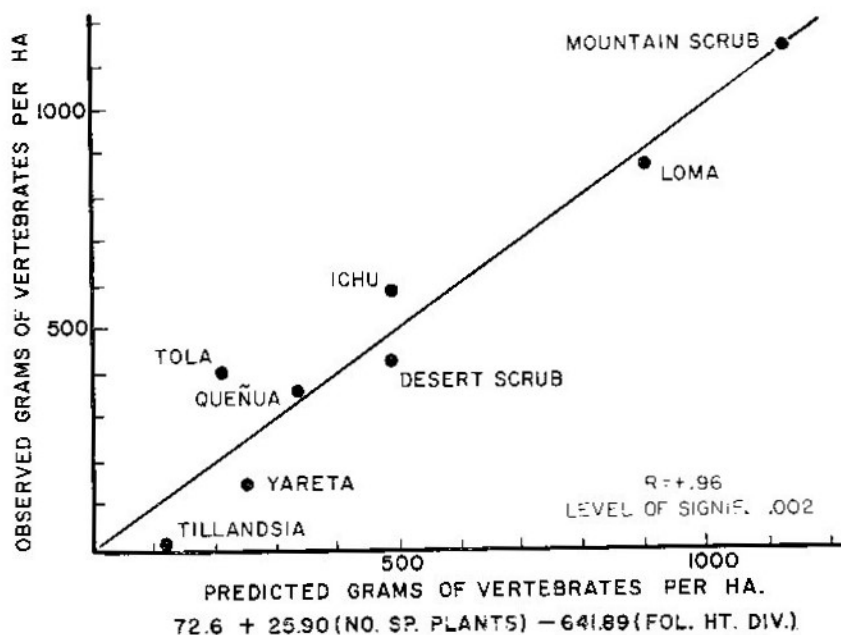
Fig. 17. Multiple regression of biomass of all vertebrates (including tuco-tucos) with two predictors: number of species of plants and Foliage Height Diversity.

that birds and mammals are playing the niche game in a totally different manner. The coefficient of correlation between number of species of birds and number of species of mammals is only .39 (not significantly different from 0), and between Bird Species Diversity and Mammal Species Diversity only .06. This means that knowing the number of species of one class in a community does not help to predict the number of species of the other class. The fact that the correlations are not negative indicates that the abundance of species of one class was not achieved at the expense of the other class.

The number of species of birds in a community, however, is highly correlated with the density of mammals (.93). This indicates that birds are likely to divide an increase of resources among many species; mammals are likely to monopolize it. An example is the Loma habitat. Apparently abundant food and shelter were being utilized by a dense population of mice of a single species, whereas a moderate number of species of birds, none at high density, were sharing the resources.

Kiester (1971) noted in a survey of mammals and reptiles in North America that there were many species of mammals in the mountains and many species of reptiles in the lowlands. This was reflected in a negative correlation between mammals and reptiles on east-west transects across North America. In our eight communities the correlations of number of species of lizards against number of

species of birds and number of species of mammals did not depart significantly from zero. Although our analysis is handicapped by the low number of reptilian species, it appears that no class is displacing another, nor are they adept at exploiting simultaneously the same resources.

Similarly, we plotted population density and biomass of mammals against those of lizards. In no case was there a clear positive or negative correlation.

Pianka (1971) has suggested that lizards may be at a competitive advantage over birds in arid habitats or in habitats characterized by unusual variability of primary production. When this suggestion is tested by graphing number of species of birds against number of species of lizards on our study areas and comparing this graph with a similar one for the deserts of North America, Australia, and Kalahari (Pianka, 1971), the Peruvian points form no meaningful pattern and do not fall anywhere near the points that represent lizard populations on other continents. The Peruvian habitas have numbers of species of birds comparable to those in North America, the Kalahari, and Australia but have only a fraction of the number of species of lizards of these other continents.

These comparisons indicate either that populations of the three classes are ordered and regulated by quite different environmental pressures or that biogeographic and evolutionary accidents in such a geologically and climatically young region as the Andes have overshadowed more subtle attempts by the different classes to dominate the different communities. The generous number of species of birds in the desert habitats on the western slope might be considered complementary to the unexpectedly small number of species of mammals and reptiles, but in the Ichu and Tola communities on the altiplano, the number of bird species remains high, by North American standards, in spite of the presence of many species of mammals.

Altitude. Table 3 demonstrates that in general the higher the altitude the greater the number of species and the greater the density of birds and of mammals. This correlation does not necessarily mean that birds and mammals prefer high altitude *per se*. It may reflect the increase with altitude of the amount and complexity of vegetation, especially Foliage Profile (Table 4). One should probably expect a *negative* correlation between altitude and abundance of birds and mammals on the Amazonian side of the Andes, where vegetation becomes more complex with decreasing altitude. The altitude entry of Table 3 *does* tell us, however, that the physical attributes of high altitude, such as low oxygen tension, low water vapor pressure, and large daily fluctuations of temperature, all of them so often assumed to be stressful, are not severe enough to override a modest improvement in other environmental factors at high altitude. Pearson (1951) notes that 10 species of small mammals lived in a valley at an elevation even higher than any of the communities on our transect. There is little doubt that many bird species also would live at extreme elevations if adequate vegetation were present.

Among lizards, the data are dominated by the results from the Loma habitat on the coast. In the other communities altitude reduces neither the number of species of lizards nor the density and biomass.

CONCLUSIONS

Number of species and species diversity. The arid and high-altitude communities quantified in this study seem in general to support at least as many and frequently more species of birds than vegetationally similar habitats on other continents. The high-altitude end of the transect is enriched by numerous species that evolved on the altiplano during cycles of Pleistocene glaciation, whereas the coastal end of the transect is populated by extremely wide-ranging species. The number of species of birds and Bird Species Diversity were positively correlated with Plant Species Diversity, number of species of plants, Foliage Height Diversity, and to some extent with Foliage Profile; in other words, with the amount and complexity of vegetation. The number of species of mammals (and Mammal Species Diversity) were not correlated with any of these environmental measurements. The distribution of mammalian species on the transect seems to be explained better by evolutionary and zoogeographical accident. The high-altitude end of the transect is populated by as many genera and species of mammals as would be expected in vegetationally comparable communities in North America, while the coastal and scrub zones on the Pacific slope support many fewer species than would be expected on the basis of North American experience. Speciation in the coastal deserts, as in other South American deserts, has lagged remarkably. The sharpest change in faunal composition on the transect seems to occur at about 3,900 m, the level above which small seed-bearing annual forbs become scarce.

The number of species of birds in a community was unrelated to the number of species of mammals, wich confirms that the two classes respond to the environment in different ways and that the richness of one class is not achieved at the expense of the other.

No study area supported more than two species of reptiles. This fall far short of the numbers found in vegetationally similar communities on other continents. The scarcity of species in the coastal desert and on the Pacific slopes is reminiscent of the scarcity of mammalian species in these habitats, but, unlike the mammals, the lizard populations at high altitude have not been enriched by an infusion of species evolved there.

Density and biomass. The densities and biomasses of the mammals on the transect were in general comparable to those in many kinds of habitat elsewhere but not match the densities and biomasses reached in North American communities where kangaroo rats or meadow voles are abundant. Effective mammalian analogs of the forms are absent from South America, and in the region of the Peruvian transect other animals that might perform their roles, such as ants or other arthropods, are scarce or absent. One must conclude either

that comparable niches do not exist in South America, that they are filled in some obscure manner, or that they are unfilled.

The subterranean herbivore niche was filled by tuco-tucos in only one of the eight communities. Their biomass exceeded that of the combined five species of mice living on the same study grid. In North America also the biomass of subterranean, herbivorous pocket gophers in many communities exceeds that of the mice. This seems to be a very profitable niche on several continents, but mammals have not subdivided it (Pearson, 1959).

Lizard population densities and biomasses were almost insignificant compared to those of North America, Africa, and Australia, with the exception of the coastal Loma population of *Tropidurus peruvianus*. This population reached a spectacularly high density and biomass, a feat made possible perhaps by its omnivorous, polymorphic nature.

The biomass of birds in most of the Andean communities exceeded (note reservations expressed above) that of the other vertebrates, but in the Loma, lizards were by far the most important, and in the Tola, the mammals, bolstered by tuco-tucos, outweighed birds and lizards combined. The total biomass of vertebrates in the communities correlated only with the number of species of plants and with the closely cross-correlated Plant Species Diversity. Since the figure for the number of species of plants was to a considerable extent composed of the number of small, seed-bearing annuals, it appears that the total standing crop of vertebrates may depend considerably upon the productivity of the annuals.

Birds vs. Mammals. The similarity of environmental needs for a diverse bird fauna and for a high density of mammals leads to a high correlation between the number of species of birds and the density of mammals (Table 5) and to the conclusion that in general the Andean birds respond to favorable conditions by packing more species into the community whereas mammals respond by packing in more individuals of a few species.

To guide future studies of this kind, we attempted to identify which were the most useful habitat characters measured. On the assumption that a high coefficient of correlation, either positive or negative, between some population attribute and some environmental measure indicates meaningfulness (and usefulness), we have added, ignoring sign, various combinations of the correlation coefficients in Table 3. For example, an ornithologist interested only in the number of species of birds present in a community, the Bird Species Diversity, the density, and the biomass of birds could remove from those four columns the appropiate four coefficients of correlation with number of species of plants, add them together, and find that this sum exceeds the comparable sum for Plant Species Diversity, which exceeds that for Foliage Height Diversity. The coefficients associated with percent of ground covered by vegetation have a much smaller sum and so presumably would be of less importance (although useful when combined with other characters). A mamalogist interested in the four listed attributes of above-ground mammal populations would find Plant Species

Diversity and Foliage Profile most interesting. In general, it appears that both bird and mammal comunities respond to the variety of plant species, but the birds respond more strongly to the vertical distribution of the vegetation than do mammals, which respond to the amount vegetation. It may never be known whether these responses are direct ones or whether the vegetation is merely integrating climate and non-biotic features of the environment that control the animal populations through other channels. However, here can be little doubt that appropriate measurements of the vegetation can be used to predict various properties of the animal populations. When similar measurements have accumulated from studies made on other continents, it will be interesting to learn whether the same predictor variables, and possibly the same coefficients, will be effective. Every agreement, or disagreement, should tell us something about the anatomy and physiology of communities of vertebrates.

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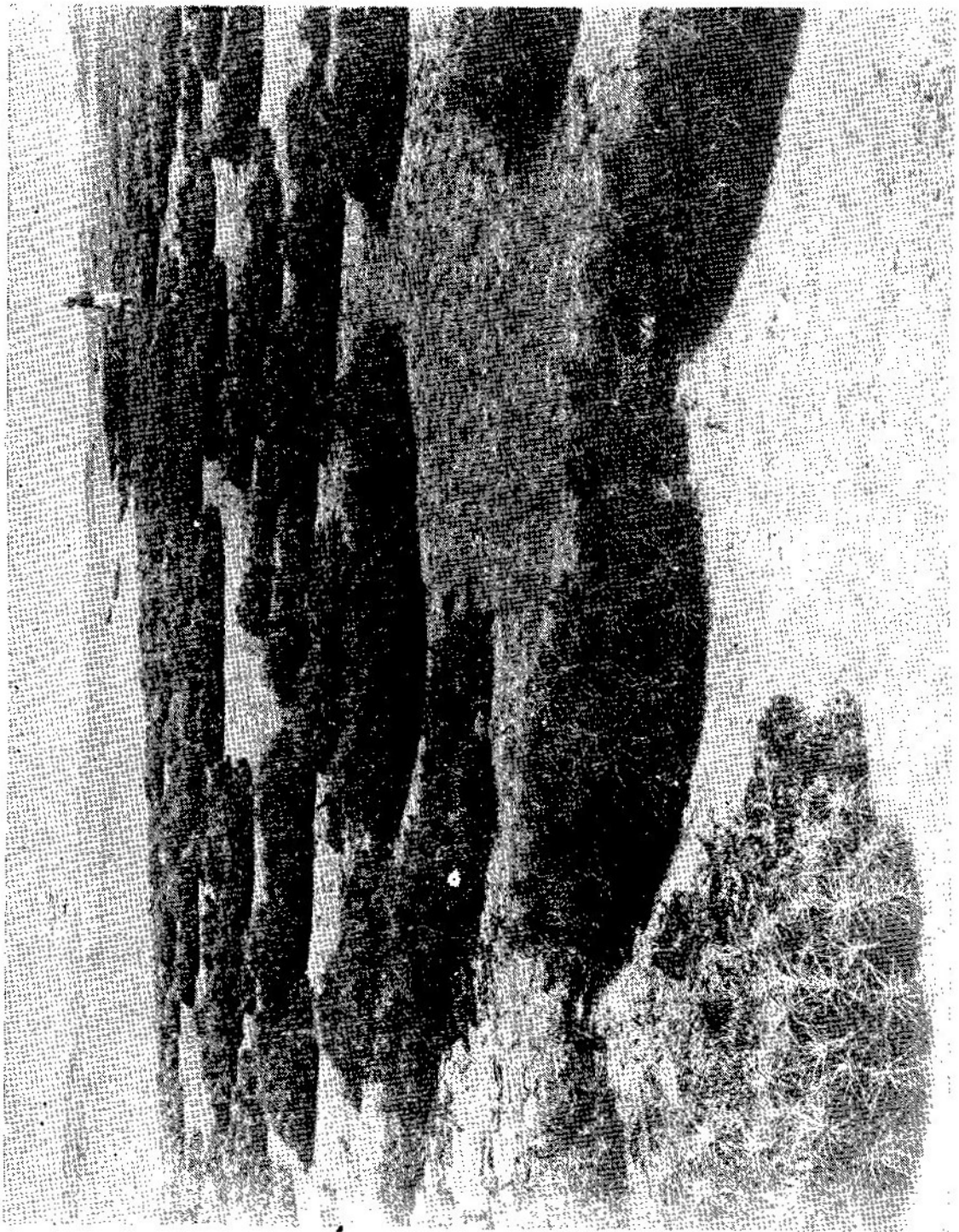Wing, L. 1949. Breeding birds of virgin palouse prairie. Auk 66: 38-41.

LAMINAS

PLATE 1

The Loma study site, 60 m elevation. Wild tomato in lower right corner, small annuals, and, at left margin and middle distance, *Grindelia* bushes. Guano-covered rocks in distance. The largest bushes are about 0.8 m tall.

Ground covered by plants (%)	36.8
Foliage Profile (cm²)	285
Foliage Height Diversity	0
Number of species of plants	32
Plant Species Diversity	2.279
Refuge Index	3.49
Number of small mammals per ha (adults)	3.85
Grams of small mammals per ha (adults)	166
Species Diversity of small mammals	0
Small mammals present: *Phyllotis darwini*	
Number of birds per ha	4.33
Grams of birds per ha	49.2

Bird Species Diversity	1.781
Bird species present: *Vultur gryphus*, *Cathartes aura*, *Geranoaetus melanoleucus*, *Buteo* sp., *Falco sparverius*, *Thinocorus rumicivorus*, *Speotyto cunicularia*, *Chordeiles acutipennis*, *Caprimulgus longirostris*, *Rhodopis vesper*, *Geositta* sp., *Troglodytes aedon*, *Conirostrum cinereum*, *Sicalis* sp., *Phrygilus alaudinus*, *Zonotrichia capensis*	
Number of lizards per ha	32
Grams of lizards per ha	652
Lizard species present: *Tropidurus peruvianus*	
Ratio of Bird: Mammal: Lizard biomasses 1 : 3.4 : 13.2.	

PLATE 2

The *Tillandsia* study site, 1,000 m elevation, showing live *Tillandsia* and residual mats of dead leaves and stems.

Ground covered by plants (%) 30.1
Foliage Profile (cm²) 967
Foliage Height Diversity 0
Number of species of plants 2
Plant Species Diversity 0
Refuge Index 2.23

Small mammals present: none

Number of birds per ha 0.33
Grams of birds per ha 7.1
Bird Species Diversity 0
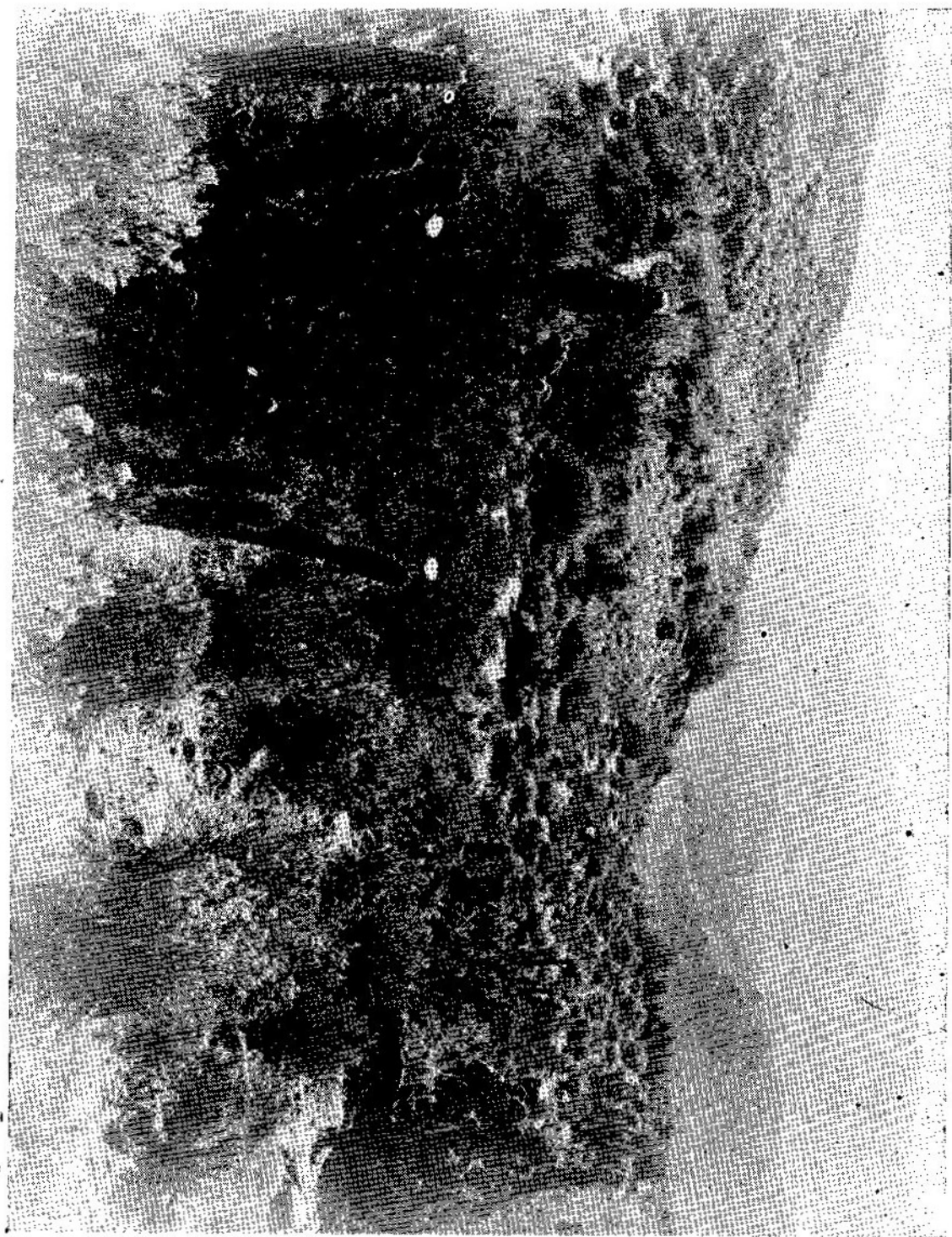Bird species present: *Cathartes aura*, *Muscisaxicola sp.*, swallow sp.

Lizard species present: none

PLATE 3

The Desert Scrub study site, 3,000 m elevation. One-third of the grid was on the floor of the dry wash and two-thirds on the bench and slope to the left. The tallest cacti are about 2 m tall, and the tallest tobacco shrubs in the wash are 4.3 m tall.
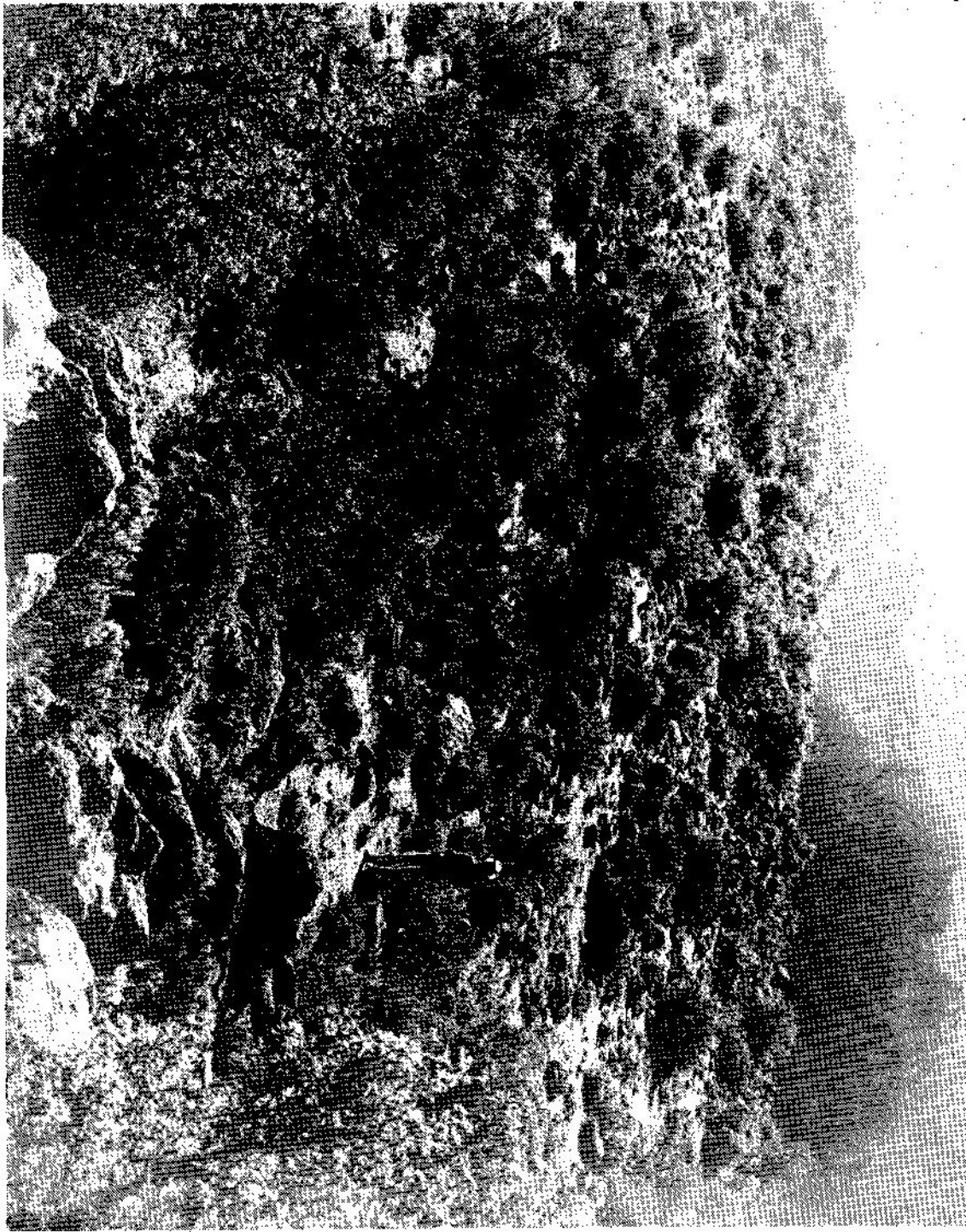
Ground covered by plants (%) 14.8

Foliage Profile (cm^2) 777

Foliage Height Diversity 0.665

Number of species of plants 33

Plant Species Diversity 2.576

Refuge Index 1.92

Number of small mammals per ha 2.85

Grams of small mammals per ha 112

Species Diversity of small mammals 0.254

Small mammals present, in order of abundance: Phyllotis darwini, P. magister

Number of birds per ha 9.66

Grams of birds per ha 302.5

Bird Species Diversity 1.978

Bird species present: Buteo sp., Falco femoralis, Metriopelia ceciliae, M. melanoptera, parakeets, Aeronautes andecolus, Oreotrochilus estella, Patagona gigas, Rhodopis vesper, Geositta sp., Upucerthia ruficauda, Leptasthenura striata?, Asthenes dorbignyi?, Ochthoeca leucophrys, Anairetes flavirostris, Conirostrum cinereum, Diglossa carbonaria, Sicalis sp., Phrygilus plebejus, P. fruticeti, Spinus magellanicus

Number of lizards per ha 0.58

Grams of lizards per ha 13

Lizard species present: Liolaemus pantherinus

Ratio of bird: mammal: lizard biomasses: 23.3 : 8.6 : 1

PLATE 4

The Mountain Scrub study site, 3,500 m elevation. *Erigeron, Grindelia* and other Compositae bushes are in the foreground. An irrigation ditch with its fringe of taller *Cantua* and *Colletia* bushes runs around the hill on the left side of the photo. The *Cereus* cactus is about 2 m tall, and the tallest bushes along the irrigation ditch are 4.5 m.

Ground covered by plants (%)	36.5
Foliage Profile (cm²)	2,845
Foliage Height Diversity	0.775
Number of species of plants	60
Plant Species Diversity	2.587
Refuge Index	1.73
Number of small mammals per ha	5.45
Grams of small mammals per ha	240
Species Diversity of small mammals	1.120

Small mammals present, in order of abundance: *Phyllotis darwini, P. magister, Akodon berlepschii, Akodon boliviensis*

Number of birds per ha	32.66
Grams of birds per ha	890.5
Bird Species Diversity	2.328

Bird species present: *Vultur gryphus, Geranoaetus melanoleucus,* hawk sp., *Falco femoralis, F. sparverius, Metriopelia ceciliae, M. melanoptera,* parakeet, *Aeronautes andecolus, Colibri coruscans, Oreotrochilus estella, Patagona gigas, Metallura phoebe, Rhodopis vesper, Geositta sp., Upucerthia validirostris, U. ruficauda, Leptasthenura striata?, Asthenes dorbignyi?, A.* sp., *Muscisaxicola sp., Ochthoeca leucophrys, Anairetes flavirostris, Petrochelidon andecola, Diglossa carbonaria, Sicalis sp., Phrygilus fruticeti, P. gayi, P. plebejus, Zonotrichia capensis, Spinus sp.,* "bushtit"

Number of lizards per ha	1.9
Grams of lizards per ha	6

Lizard species present: *Liolaemus alticolor*
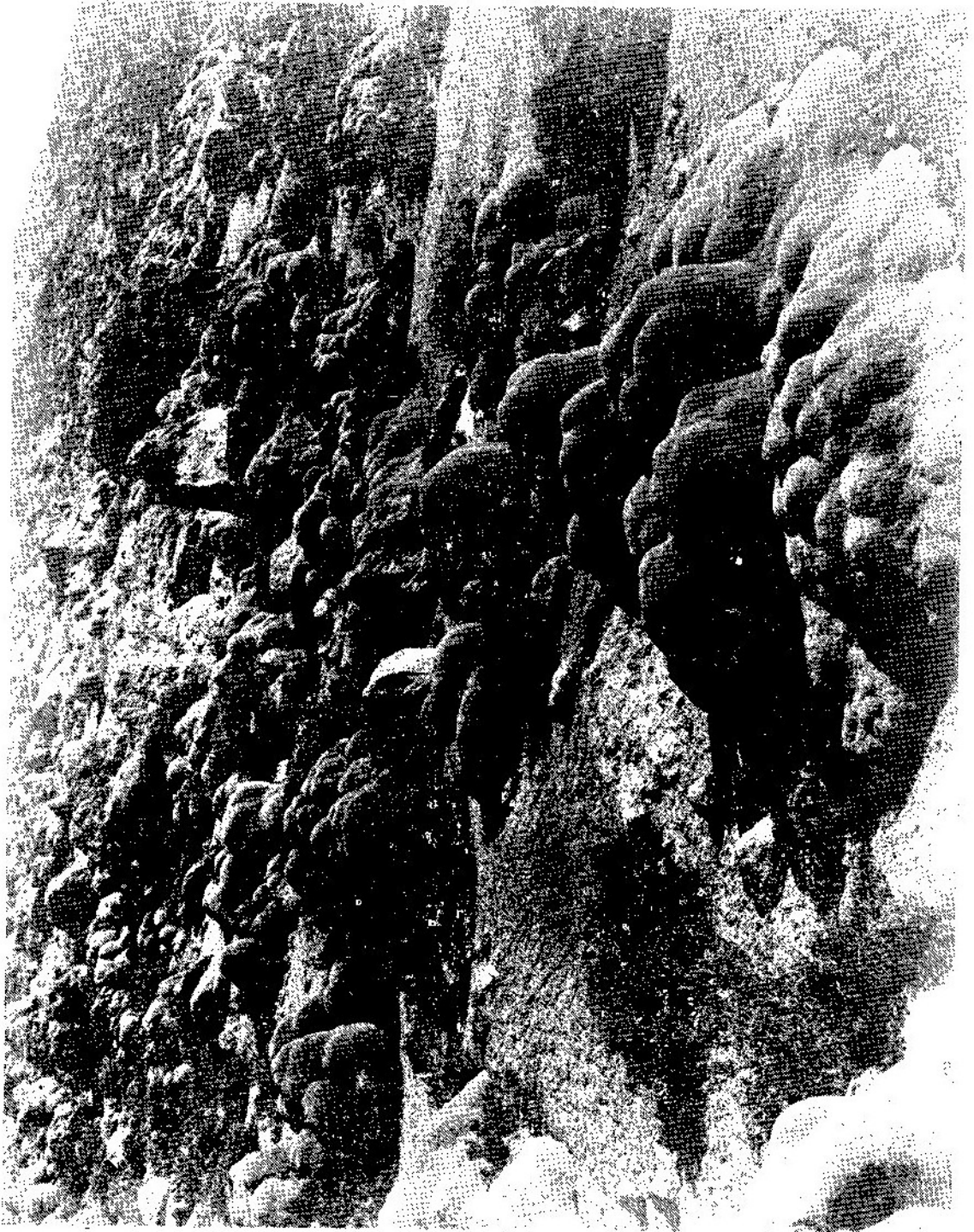
Ratio of bird: mammal: lizard biomasses: 148 : 40 : 1

PLATE 5

The Queñua study site, 3,900 m elevation. The larger shrubs are queñua "trees" (*Polylepis tarapacana*) about 3 m tall.

|	
Ground covered by plants (%)	31.0
Foliage Profile (cm²)	3,418
Foliage Height Diversity	0.764
Number of species of plants	29
Plant Species Diversity	2.176
Refuge Index	1.15
Number of small mammals per ha	4.75
Grams of small mammals per ha	113
Species Diversity of small mammals	0.581
Small mammals present, in order of abundance: *Akodon berlepschii*, *Phyllotis darwini*	
Number of birds per ha	11.66
Grams of birds per ha	241.2

Bird Species Diversity 2.401

Bird species present: *Tinamotis pentlandi*, *Vultur gryphus*, *Buteo poecilochrous*, *Falco sparverius*, parakeets, *Caprimulgus longirostris*, *Oreotrochilus estella*, *Patagona gigas*, *Metallura phoebe*, *Rhodopis vesper*, *Geositta tenuirostris*, *Upucerthia validirostris*, *U. ruficauda*, *Leptasthenura striata?*, *Asthenes d'orbignyi?*, *Agriornis* sp., *Muscisaxicola* sp., *M.* sp. 2, *Ochthoeca oenanthoides*, *Anairetes flavirostris*, *Petrochelidon andecola*, *Catamenia* sp., *Phrygilus gayi*, *P. fruticeti*, *P. plebejus*, *Spinus otratus*, *S. magellanicus*, *S.* sp., "bushtit"

Lizard species present: none

Ratio of bird: mammal: lizard biomasses: 2.1 : 1 : 0

PLATE 6

The Yareta study site, 4,500 m elevation. The tallest "heads" of yareta (*Azorella compacta*) are about 1 m high, and the shrubs (*Lepidophyllum quadrangulare*) are about 45 cm high.

Ground covered by plants (%) 34.0
Foliage Profile (cm²) 1,826
Foliage Height Diversity 0.124
Number of species of plants 10
Plant Species Diversity 1.540
Refuge Index 1.70

Bird Species Diversity 2.131
Bird species present: *Tinamotis pentlandi, Vultur gryphus, Buteo poecilochrous, Falco femoralis, Thinocorus orbignyianus, Oreotrochilus estella, Upucerthia ruficauda, Leptasthenura striata?, Asthenes* sp., *Muscisaxicola* sp. 1, *M.* sp. 2, *Ochthoeca oenanthoides, Petrochelidon andecola, Phrygilus unicolor?, Spinus atratus, S.* sp.

Number of small mammals per ha 1.80
Grams of small mammals per ha 51
Species Diversity of small mammals 0.680
Small mammals present, in order of abundance: *Phyllotis darwini, Akodon andinus*

Number of lizards per ha 4.3
Grams of lizards per ha 21

Lizard species present: *Liolaemus alticolor, L. mocquardi*

Number of birds per ha 5.33
Grams of birds per ha 78.2

Ratio of bird: mammal: lizard biomasses: 3.7 : 2.4 : 1
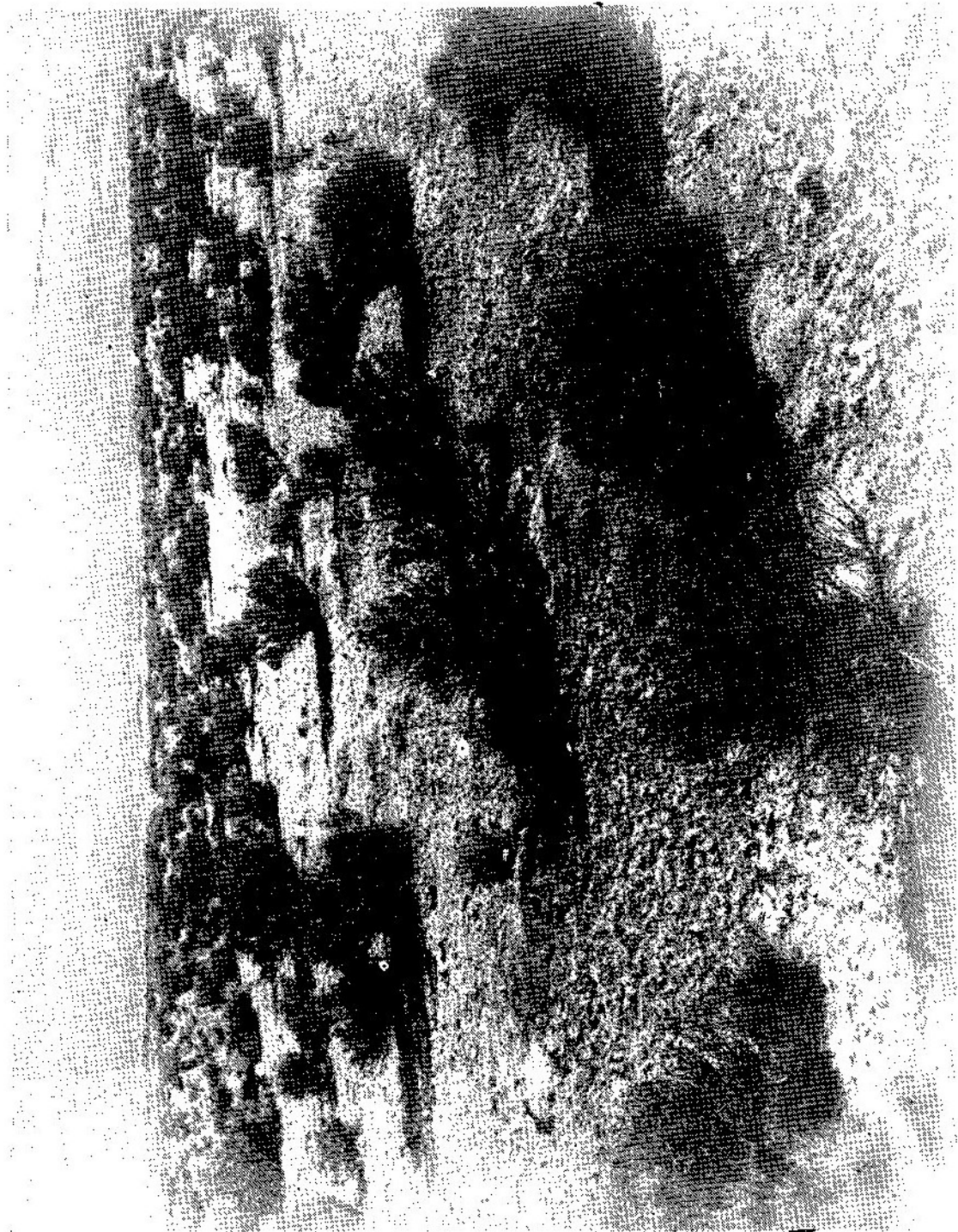
PLATE 7

The Tola study area, 4,300 m elevation. Clearly visible are tola bushes (*Lepidophyllum quadrangulare*), bunchgrass (*Festuca orthophylla*), and, front center, a pale mat of *Pycnophyllum tetrastichum*. Barely visible are small tufts of grass (*Calamagrostis* sp.). The tallest vegetation is less than 1 m.

Ground covered by plants (%) 33.3
Foliage Profile (cm²) 2,210
Foliage Height Diversity 0.110
Number of species of plants 8
Plant Species Diversity 1.623
Refuge Index 2.14

Number of small mammals per ha 3.33
Grams of small mammals per ha 352
Species Diversity of small mammals 1.504
Small mammals present, in order of abundance: *Ctenomys opimus*, *Eligmodontia typus*, *Auliscomys sublimis*, *Akodon andinus*, *Abrocoma cinerea*, *Akodon berlepschii*

Number of birds per ha 1.33

Grams of birds per ha 38.0
Bird Species Diversity 1.039
Bird species present: *Buteo polyosoma?*, *Phalcoboenus albogularis*, *Thinocorus orbignyianus*, *Metriopelia melanoptera*, parakeets, *Geositta punensis?*, *Upucerthia validiros tris*, *Leptasthenura striata*, *Asthenes modesta*, *Agriornis microptera?*, *Muscisaxicola* sp., *Petrochelidon andecola*, *Phrygilus gayi*, *P. plebejus*, *Spinus atratus*, *S. magellanicus*

Number of lizards per ha 2.78
Grams of lizards per ha 12.5
Lizard species present: *Liolaemus alticolor*, *L. multiformis*

Ratio of bird: mammal: lizard biomasses: 3.0 : 28.1 : 1

PLATE 8

The Ichu study site, 3,900 m elevation. The bunches of *Stipa ichu* are less than 1 m tall.

Ground covered by plants (%) 50.0
Foliage Profile (cm²) 4,367
Foliage Height Diversity 0.118
Number of species of plants 19
Plant Species Diversity 1.859
Refuge Index 0.34

Number of small mammals per ha 4.68
Grams of small mammals per ha 115
Species Diversity of small mammals 1.410
Small mammals present, in order of abundance: *Akodon amoenus, Phyllotis osilae, Calomys lepidus ducilla, Akodon berlepschii, Auliscomys sublimis*

Number of birds per ha 28.3
Grams of birds per ha 463.6

Bird Species Diversity 1.084
Bird species present: *Nothoprocta ornata, Nothura darwini,* accipiter, *Phalcoboenus albogularis, Metriopelia ceciliae,* parakeet, *Caprimulgus longirostris?, Oreotrochilus estella, Colaptes rupicola, Geositta* sp., *Upucerthia validirostris, Cinclodes* sp., *Asthenes modesta, A. humilis, Agriornis montana?, Muscisaxicola* sp., *Ochthoeca oenanthoides, Pterochelidon andecola, Sicalis uropygialis?, Sicalis* sp., *Phrygilus alaudinus, P. gayi, P. plebejus, Zonotrichia capensis*

Number of lizards per ha 0.6
Grams of lizards per ha 3
Lizard species present: one, unidentified

Ratio of bird: mammal: lizard biomasses: 154 : 38 : 1