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FLORA AND VEGETATION OF PAN DE AZUCAR NATIONAL PARK IN THE ATACAMA DESERT OF NORTHERN CHILE

FLORA Y VEGETACION DEL PARQUE NACIONAL PAN DE AZUCAR EN EL DESIERTO DE ATACAMA

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ABSTRACT

Pan de Azúcar National Park comprises a unique area of coastal fog desert and marine communities along the coast of northern Chile between Taltal and Chañaral in the II and III Regions. Created in 1985, the park protects a 43,754 ha area of diverse flora and fauna and spectacular coastal landscape. Pan de Azúcar, furthermore, is the only National Park along the entire coast of the Norte Grande. The flora of the park is known to include at least 207 species of vascular plants, with the Asteraceae (25 species) Nolanaceae (17 species) and Cactaceae (14 species) as the largest families. Six species are endemic to the park. Despite the significance of the rich plant communities which form in coastal loma formations along the upper face of the steep coastal escarpment, only about 26% of the flora of Pan de Azúcar is restricted to these fog zone communities. Dry bajadas, rocky slopes, dunes, and arroyo habitats below the fog zone support 66% of the vascular flora. Saline and freshwater springs provide special azonal habitats form the final 8% of the flora. Animal populations are also notable within Pan de Azúcar with large populations of resident guanacos (*Lama guanicoe*) and two species of resident foxes. Marine mammals are also well represented, with notable populations of the southern sea otter (*Lutra felina*) on Isla Pan de Azúcar. Bird diversity is also high with at least 27 resident species and 130 species overall reported. Both Humboldt and Magellanic penguins (*Spheniscus humboldti* and *S. magellanicus*) breed on Isla Pan de Azúcar, along with many other significant sea birds.

KEYWORDS: Pan de Azúcar National Park, Atacama Desert, northern Chile, lomas.

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RESUMEN

El Parque Nacional Pan de Azúcar abarca un área única de desiertos costaneros de neblina y comunidades marinas a lo largo de la costa del norte de Chile, entre Taltal y Chañaral en las regiones II y III. El parque, creado en 1985, protege una flora y fauna diversa y un paisaje costanero espectacular en un área de 43.754 ha. Pan de Azúcar es el único parque nacional a lo largo de toda la costa del Norte Grande. La flora del parque incluye por lo menos 207 especies de plantas vasculares, siendo las familias Asteraceae (25 especies), Nolanaceae (17 especies) y Cactaceae (14 especies) las más representativas. Seis especies son endémicas al parque. Sólo un 26 % de la flora de Pan de Azúcar se encuentra restringida a las comunidades de zonas de neblina a pesar de la alta biomasa de esta comunidad de plantas, que se disponen en forma de lomas a lo largo de la cara superior del profundo escarpado de la costa. Las bajadas secas, hondonadas rocosas y los habitats de los arroyos, que se encuentran por debajo de la zona de neblinas, sustentan el 66 % de la flora de plantas vasculares. Pozos salobres y de agua dulce proveen habitats azonales especiales para el restante 8 % de la flora. Las poblaciones animales del Pan de Azúcar también son notorias; en el parque residen grandes poblaciones de guanacos (*Lama guanicoe*) y dos especies de zorros. Los mamíferos marinos se encuentran bien representados, con poblaciones importantes de nutria marina (*Lutra felina*) en la Isla de Pan de Azúcar. La diversidad de aves también es alta, con por lo menos 27 especies residentes y 130 especies reportadas. En la Isla Pan de Azúcar se reproducen tanto pingüinos de Humboldt como de Magallanes (*Spheniscus humboldtii* y *S. magellanicus*), junto con muchas otras aves marinas de importancia.

PALABRAS CLAVES: Parque Nacional Pan de Azúcar, Desierto de Atacama, Norte de Chile, lomas.

INTRODUCTION

The Pan de Azúcar National Park forms an area of 43,754 ha along the coast of the II and III

Regions in northern Chile (Figure 1), extending from 25°53' to 26°15' S lat. and 70°29' to 70°40' E long. (CONAF 1990). This area lies about 20 km north of Chañaral and 80 km south of Taltal. The National Park was created in 1985 to preserve the diverse natural resources of flora and fauna which occur here, including both terrestrial and marine elements. Coastal fog vegetation is well developed in this area, representing one of the richest points for survival of the unique loma flora of northern Chile (Rundel *et al.* 1991). This richness in both plant cover and diversity provides significant resources for desert animal populations as well. Pan de Azúcar supports a large population of resident guanacos as well as two species of foxes, smaller mammals, and a diverse assemblage of terrestrial bird species. Marine resources are likewise rich. The offshore Isla Pan de Azúcar provides a rookery for Humboldt penguins and other seabirds, as well as areas for resident populations of fur seals and the southern sea otter.

HISTORY

There is abundant evidence along the coastal zone of Pan de Azúcar National Park that small numbers of indigenous people had lived in this area for thousands of years (CONAF 1990). Shell middens, burial sites, and remains of temporary shelters of stone are present in many regions of the park, and artifacts such as arrow points, tools, bone implements and ceramics have been found in a number of areas. The indigenous populations appear to have been largely hunters and fishermen, utilizing both marine resources of fish and sea mammals as well as guanacos inland.

Scientific studies in the area of Pan de Azúcar National Park began with the remarkable travels of R. A. Philippi (1860) who traversed a broad area of northern Chile in December of 1853 and January of 1854. Virtually nothing was known of the flora in northern Chile prior to this expedition. Working with little assistance, Philippi was able to collect large numbers of scientific specimens of all types which he later described. For the vascular flora of Pan de Azúcar included here, 34% of the species were first described by Philippi. This is a remarkable number for the limited time and restricted storage capability that he had on this journey.

Philippi left Chañaral in his journey on December 12, 1853, and traveled north up the coast to the Caleta de Pan de Azúcar. In this epoch, the small village of Puerto San José Pan de Azúcar existed at the Caleta where copper from the mines inland at Carrizalillo was transported by mule carts down the Quebrada Pan de Azúcar and transferred to ships. In the 1850's this village had a population of about 100, with a main street and three side streets (CONAF 1990). The ruins of a copper smelter, warehouses, a mill, and houses remain today. Leaving the caleta, Philippi turned inland and continued on to Aguada Grande in the Quebrada Grande, which he referred to as Cachinal de la Costa. Here he spent the night, and collected in this area during the following morning. He continued on northward beyond the park in the same afternoon.

Little scientific study was carried out at Pan de Azúcar for more than a half century after the visit of Philippi. The most notable historical event over this period was a small engagement during the War of the Pacific in 1879 when a Peruvian warship attacked the port of Pan de Azúcar and sank a number of small boats (CONAF 1990).

Carlos Reiche visited the area of Pan de Azúcar in 1909 during his studies of *Euphorbia lactiflua* as a potential source of rubber. On September 16 of that year he traveled north along the coast from Chañaral to Pan de Azúcar, and then turned inland to Las Bombas. Although he made relatively few collections, he provided useful information on the biogeographical and ecological distributions of many plant species (Reiche 1911).

Ivan T. Johnston visited the area of Pan de Azúcar National Park on December 14, 1925, entering from the north via a high pass in the Sierra Esmeralda and travelling along the Quebrada de la Cachina where he camped about 5 km from the coast at Aguada de la Cachina (Johnston 1929). The following day he explored the high sea cliffs toward the south as far as Cerro de la Cachina before returning to camp on the granite plain that stretches southward from Aguada de la Cachina. He collected in the area of his camp on December 16, and the following day traveled southward to spend the night at Aguada Grande. Here he collected in Quebrada Grande and along the crest of the sea cliffs in the fog zone above

near Las Lomitas. On December 18, he followed the Quebrada Las Chilcas south to Quebrada Pan de Azúcar where he continued westward to the coast at Caleta Pan de Azúcar and then south to Chañaral.

GEOMORPHOLOGY AND GEOLOGY

The western margin of Pan de Azúcar National Park is characterized by a coastal plain of old beach terraces which ranges from a few hundred meters to 2-3 km in width. This coastal plain, varying from rocky to quite sandy in substrate texture, terminates to the east in the abrupt escarpment of the coastal mountains which reach to just above 800 m in elevation. Although surprising flat at their summit, the steep gradient of the western face of these hills is virtually perpendicular in many areas, providing a focal point for the concentration of fog moisture at the upper margin of the escarpment (Figure 2). Winter camanchacas provide sufficient moisture to allow the development and survival of a moderately rich flora of loma species. It is at this point that the greatest plant cover and diversity of growth forms is present and where the largest group of vertebrate species are concentrated.

Back from the coastal escarpment, the coastal range in the central area of the park present a broad erosion plain with shallow arroyos breaking up an otherwise flat landscape. This area provides much of the home range for the guanaco populations of the park. Access to this area is provided by a dirt road to Las Lomitas at 805 m elevation where there is a rustic shelter.

The remaining topography of Pan de Azúcar National Park is dominated by a series of steep but low ranges of mountains which are sharply dissected by major arroyo systems. These ranges include the Sierra Las Tapias, Sierra Pan de Azúcar, and Sierra del Castillo, as well as the rounded Llanos de Castillo south of Quebrada de Castillo (Figure 1).

The northern boundary of Pan de Azúcar National Park is formed by the Quebrada de Cachina, while rugged mountains along the northeastern margin reach from 658 m at Cerro Negro near Quebrada de Cachina to nearly 900 m moving southeastward and finally 865 m at Cerro La Cachina (Figure 1). The highest elevation in the park is reached at 916 m along its southeast boundary. Isla Pan de Azúcar, lying close to the Caleta de Pan de Azúcar, reaches 155 m in elevation.

Geologic structures at Pan de Azúcar are complex (Mercado 1980). Stratified rock includes extensive metasediments of pre-Permian age as basement rock, intrusive metamorphic rocks of Permian and Jurassic age, and fossiliferous marine sediments of Tertiary and Quaternary age. Large outcrops of Triassic lava flows are present at several points along the coast. Extensive sediment movement down the major arroyo channels has produced deep strata of sand and gravels at the base of many of these channels in historical time. These sediments appear to be subject to rapid erosion at times of flooding, but nevertheless frequently support distinctive plant communities.

HYDROLOGY

The hydrology of Pan de Azúcar National Park centers on the drainage of the Quebrada Pan de Azúcar which crosses the southern half of the park and drains more than half of its area (Figure 1). This extensive arroyo system cuts across the relatively low coastal range of mountains at this latitude and reaches to the Central Valley at an elevation of about 830 m. There is abundant evidence of significant flows of water from the Andes across the Central Valley and out to the Pacific Coast through the Quebrada Pan de Azúcar in years with heavy rains and snow melt in the Andean Cordillera. A number of major arroyo systems feed into Quebrada Pan de Azúcar in the park, including Quebrada Los Chalices, Quebrada Agua Chica, Quebrada Quiscudo, and Quebrada Agua Salada. The northern 30% of the Pan de Azúcar National Park lies in the hydrological drainage of the Quebrada Grande which reaches the Pacific Ocean at the northern boundary near Esmeralda. The Quebrada El Quisco feeds into Quebrada Grande. The Quebrada de Castillo and Quebrada de las Piedras Blancas together drain about 15% of the park along its southern margin. Significant sediment movement occurs along all of the large major arroyo systems in years with relatively heavy rainfall.

Despite the extreme aridity of Pan de Azúcar National Park, springs are present at a number of locations, particularly at the lower margins

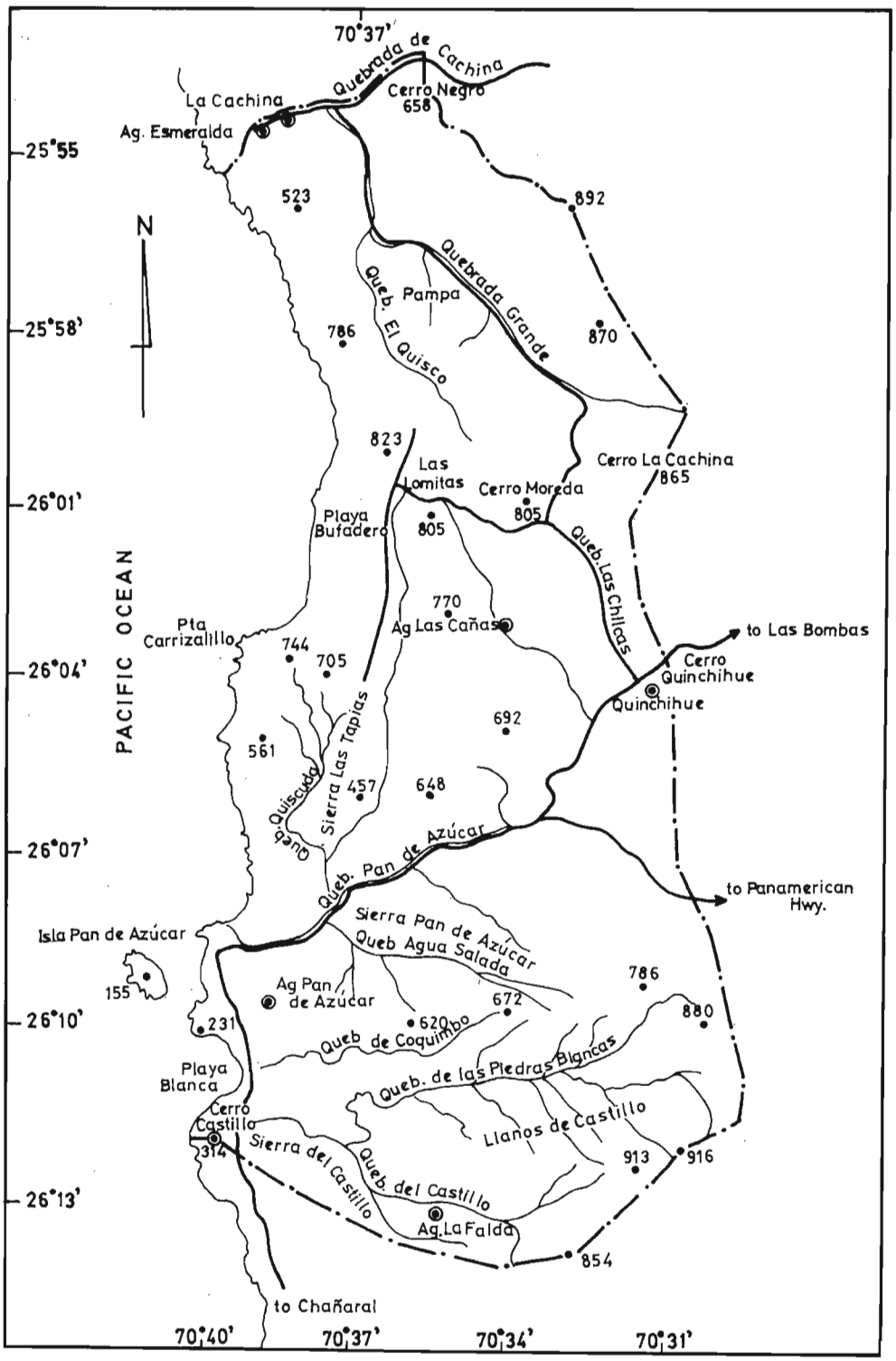


FIG. 1. Pan de Azúcar National Park.

of major arroyos where the channels narrow. Both saline and freshwater springs are present. Examples of such springs include those at Aguada Esmeralda and La Cachina in the Quebrada de Cachina, Quinchihue at the base of the Quebrada Los Chalices, Aguada Las Cañas in the Las Cañas sector of the central portion of the park, Aguada Pan de Azúcar below the mouth of Quebrada Pan de Azúcar, and Aguada La Falda in the upper reaches of the Quebrada del Castillo (CONAF 1990). Extensive areas of saline seepage are present outside the park to the east on the road to Las Bombas.

CLIMATIC CONDITIONS

The climatic conditions at Pan de Azúcar National Park broadly resemble those at Chañaral, 20 km to the south of the park headquarters, where long-term records are available for temperature, rainfall, and other climatic conditions. Temperature conditions along the coast in nortern Chile are moderated by frequent fogs and cool onshore winds from the sea. Both diurnal and seasonal changes in temperature are small. Mean monthly maximum temperatures range from a high of about 24°C in January and February to a low of about 17°C in June and July (Table 1). Extremes of high temperatures are virtually absent, with individual daily highs only rarely reaching to 27°C or above. Mean monthly minimum temperatures range from 17°C in summer to 11°C in winter. Thus seasonal and diurnal ranges of temperature have roughly equal magnitudes of 6-7°C.

Relative humidity conditions likewise change very little over the course of the year at elevations near sea level. Typical nocturnal humidities here reach to 80-85%, but generally remain below the dew point level along the coast. Mean monthly values of midday relative humidity remain at 60-70% throughout the year.

Mean annual precipitation at Chañaral and Taltal to the north averaged about 27 mm in the early part of this century, and these older climatic records appear in many discussions of climatic conditions in northern Chile. Mean annual precipitation for the period from 1926-1948 averaged 18 mm. The last half century has been one of extended drought for this region, however, and mean annual rainfall has dropped to less than 10 mm over this period.

Mean annual rainfall provides a relatively poor assessment of conditions of moisture availability for plant growth because of the extreme interannual variability in rainfall events. Periods of 5-7 years without measurable rainfall have occurred, offset by infrequent years of relatively intense rainfall associated with ENSO (El Niño-/Southern Oscillation) events. Such conditions in July 1987 brought 65 mm of rainfall within a single week, the second heaviest amount in records for this century for either Chañaral or Taltal to the north. In August 1930, 81 mm of rain fell in Chañaral for the heaviest monthly total of the century.

The camanchaca and the fog conditions it produces are generally restricted to a relatively narrow zone in northern Chile with both upper and lower elevational limits (Rundel and Mahu 1976; Rundel *et al.* 1991). At Pan de Azúcar the impact of the camanchaca is restricted to elevations above 200-300 m and reaches its peak at the upper elevations of the coastal escarpment at 700-800 m. Below this lower elevational limit, relative humidities seldom exceed much above 80% and dew point temperatures are seldom reached. This condition is readily apparent in the virtual lack of epiphytic lichens at lower elevations in the park compared to their luxuriant growth in the fog zone at higher elevations along the immediate coast. Vascular plants below the fog zone thus are largely dependent on irregular rainfall and concentration of hydrologic flow in arroyo systems for their water resources since fog moisture is not normally available for them.

Apart from rainfall, fog interception and dewfall provide important inputs of moisture within the upper camanchaca zone along the coast. The potential input of water from this source is significant, particularly in winter when the camanchaca is strongest. Fog collecting nets atop the coastal hills served as the primary source for park drinking water for many years. These collectors were able to condense about two liters of water per m^2 of collector per day under camanchaca conditions (CONAF 1990).

FLORA

The flora of Pan de Azúcar National Park described here is based on a variety of sources. We have relied heavily on our own field collections and observations made in the park in six

different years from 1987 to 1994. To this we have added records of species noted by Philippi (1860), Johnston (1929), and Hoffmann (1986). Where we have not seen actual collections and have questions, we have noted these in the appendix below. Our primary source for floristic distributions in the coastal regions of northern Chile is a specimen-oriented, computerized database (LOMAFLOR, Dillon unpublished). The database contains records from our field collections and observations and from specimen records entered at visits by one of us (MOD) to various herbaria (CONC, F, GH, MO, SGO, UC, US).

The flora of Pan de Azúcar includes 207 species of vascular plants (see Appendix). This total is made up of two ferns, one gymnosperm, 28 monocotyledons, and 176 dicotyledons. Only one of these species is exotic. The five largest families in the flora are the Asteraceae (25 species), Nolanaceae (17 species), Cactaceae (14 species), Poaceae (12 species), and Boraginaceae (11 species). Together these families make up nearly 40% of the total flora. The five largest genera are *Nolana* (Nolanaceae, 17 species), *Copiapoa* (Cactaceae, 6 species), *Tetragonia* (Aizoaceae, 5 species), *Cryptantha* (Boraginaceae, 5 species), *Heliotropium* (Boraginaceae, 5 species), and *Cistanthe* (Portulacaceae, 5 species).

This floristic diversity at Pan de Azúcar is unusually high for the coastal Atacama Desert in northern Chile. Only in the area around Paposo and north to Miguel Díaz are there more species present. Until a formal national park or reserve can be established around Paposo in this northern area, Pan de Azúcar remains the only area of protection for many rare species along the coast of the Norte Grande. Six species are only known from within the boundary of Pan de Azúcar National Park. These are *Domeykoa perennis* (Apiaceae), *Cryptantha argentea* and *Cryptantha romanii* (Boraginaceae), *Spergularia cremnophila* (Caryophyllaceae), *Linum cremnophilum* (Linaceae), and *Cristaria fuentesiana* (Malvaceae).

The greatest diversity of species at Pan de Azúcar does not occur in the fog zone where biomass reaches its highest level in the park. Rather the largest group of species are ones whose typical habitat is below the fog zone in relatively dry sites such as arroyos, bajada slopes, dry flats and coastal plains, and coastal dunes. For the native overall, only 26% of the species are largely restricted to the fog zone, while 66% are characteristic of drier habitats (Table 2). The final 8% of the species occur around saline or freshwater springs.

Shrubs and subshrubs with a woody or semi-woody growth-form a large proportion of the flora with 72 species, 35% of the flora (Table 2). The great majority of these would be considered chamaephytes since only a small number species reach sufficient heights to be classified as phanerophytes. More than 70% of these species occur in dry habitats. Herbaceous perennials include 71 species, 34% of the total. The greatest diversity of the herbaceous perennials occurs in the fog zone, including all seven of the native geophytes. Obligate annuals include 37 species (18%) at Pan de Azúcar, with all but one characteristic of dry habitats. Eight additional species may grow as annuals but survive into a second year if moisture is available, thereby becoming herbaceous perennials. This flexibility in annual growth habit appears to be relatively common in Chile (Arroyo *et al.* 1990), but is rare in desert areas of North America. A final group of interest, the succulents is made up Cactaceae and two shrubby species of terrestrial Bromeliaceae. The great majority of these are typical of dry habitats, but the two arborescent cacti (*Eulychnia saint-pieana* and *Echinopsis deserticola*), *Opuntia berteri* and *Puya boliviensis* are characteristically fog zone species.

The diversity of Cactaceae and Nolanaceae is a particularly notable aspect of the flora. Both of these families reach their highest point of diversity in northern Chile within the Pan de Azúcar National Park. Within the Cactaceae, the genera *Copiapoa* and *Neoporteria* are of particular interest because of the diversity of species and ecological variation present. Taxonomic concepts for these small cacti in northern Chile remain in a seemingly constant state of flux and will no doubt change in the future with more detailed study. Taylor (1981) suggests, for example, that the mound-forming *C. longistaminea* should be considered a variety of the highly variable *C. cinerea*. Hoffmann (1989), however, feels that the two forms are quite distinct in the field. Generic and species concepts within *Neoporteria* likewise remain controversial, and the literature is replete with a multitude of synonyms. We have followed Hoffmann (1989) in our species concepts presented here.

Taxonomic concepts for the large and complex genus *Nolana* are likewise controversial.

The Nolanaceae, as treated here, contains no fewer than 37 species in northern Chile and the 17 species of *Nolana* in the park make it the single largest genus. A phylogenetic analysis of this group is currently underway (Dillon, unpublished). Preliminary results indicate that species of *Nolana* in the park come from several independent lineages. These relationships suggest secondary sympatry for many of the species found growing in close proximity within the boundaries of Pan de Azúcar National Park.

VEGETATION

A variety of plant communities are present at Pan de Azúcar National Park. These include arroyo and bajada communities of shrub species, coastal terraces and bajada slopes dominated by a diverse group of cacti, and loma communities of semi-arborescent species in the coastal fog zone at higher elevations. Azonal communities are also present in sand dunes along the coast and at local areas of freshwater or saline springs.

ARROYO COMMUNITIES

A moderately diverse assemblage of shrub species form open communities along the major arroyo systems which drain Pan de Azúcar National Park (Figure 4). The size and diversity of these communities is largely determined by the hydrologic drainage basin feeding into each arroyo system. Thus relatively good communities of this type are present along the Quebrada Pan de Azúcar, Quebrada Grande, Quebrada de Castillo, and other major arroyo systems where run-on flows of water in years with rainfall can provide soil moisture reserves. Sediment movement can be significant in these drainage systems despite the irregular rainfall, and thus erosion can be an important factor in shrub establishment and survival.

Moving westward toward the coast down the Quebrada Pan de Azúcar from the eastern margin of the National Park, arroyo plant communities increase steadily in both diversity and cover. The drainage of margins of the Quebrada Pan de Azúcar and the Central Valley to the east of the National Park contain only scattered perennial vegetation. While rainfall events in 1987 led to extensive germination of *Nolana divaricata* (Nolanaceae), *N. leptophylla*, and the annual *N. aplocaryoides*, these scattered elements appear to be relatively short-lived.

Near the west entrance to the National Park at just above 500 m elevation, the Quebrada Pan de Azúcar assumes its first permanent shrub communities with open stands of low *Nolana divaricata* and scattered individuals of *N. leptophylla*. As one continues westward into the park, there is a steady addition of new shrub species, beginning with *Loasa chilensis* (Loasaceae), *Tetragonia maritima* (Aizoaceae) and *N. mollis*. Shrub cover is very light, however, and is limited to the main arroyo channel. About 3 km inside the park boundary at about 450 m elevation, however, there is a striking increase in the cover and diversity of shrub species as the large arroyo systems join the major Quebrada Pan de Azúcar. Shrub cover here averages about 5% and reaches to 20% in some areas, with a dominance by *N. mollis* and a secondary codominance by *Eremocharis fruticosa* (Apiaceae) and *Tetragonia maritima*. The former two species reach 2-3 m in diameter and 1-2 m in height, reflecting favorable growing conditions. Both were flowering abundantly in 1993, the second year of extended drought conditions. Eleven shrub species were present in this community, with eight of these reaching canopy diameters of 1 m or more. These included *Loasa elongata*, *Oxyphyllum ulicinum* (Asteraceae), *Ophryosporus triangularis* (Asteraceae), *Nolana leptophylla*, *N. divaricata*, and *Heliotropium linarifolium* (Boraginaceae). Two other semi-woody perennials, *Frankenia chilensis* (Frankeniaceae) and *Nolana salsoloides* were also present, but remain smaller. *Nolana mollis* (60%), *E. fruticosa* (26%), and *T. maritima* (9%) together comprised 96% of these large individuals. Herbaceous plant cover is relatively limited in dry years, but can be considerable in years with significant rainfall. Dense populations of two annual species, *Astragalus coquimbensis* (Fabaceae) and *Nolana aplocaryoides*, recruited into this area in 1987.

Plant community structure, however, appears to be highly dynamic in this community. Seedlings of shrub species which have become established since the rains of 1987 reflect the likelihood of a very different community structure in the future. Both *N. mollis* and *T. maritima* were highly successful in seedling establishment, providing together more than 80% of such individuals. *Eremocharis fruticosa*, a codominant to-

day in the community, has been virtually unable to recruit new individuals over the years since this heavy rainfall.

Similar communities of shrubs are present along all of the major arroyo systems in Pan de Azúcar National Park. As in the Quebrada Pan de Azúcar, local coverage, dominance, and diversity is highly variable, reflecting soil moisture availability as well as historical factors of seedling establishment and erosion form of extensive alluvial deposits of sediments lie below many of the steep arroyo systems that drain mountainous areas near the coast in Pan de Azúcar National Park. Distinctive communities of shrub species are present on these bajada slopes where run-on hydrology provides sufficient flows of water in years with rainfall to promote plant growth. These communities are most characteristic of areas within a few kilometers of the coast, suggesting the possibility that fog moisture inputs at higher elevations above may impact soil water resources below. Such a suggestion remains conjectural, however, and it seems more likely that hydrological basin size is the key factor.

Bajada Communities

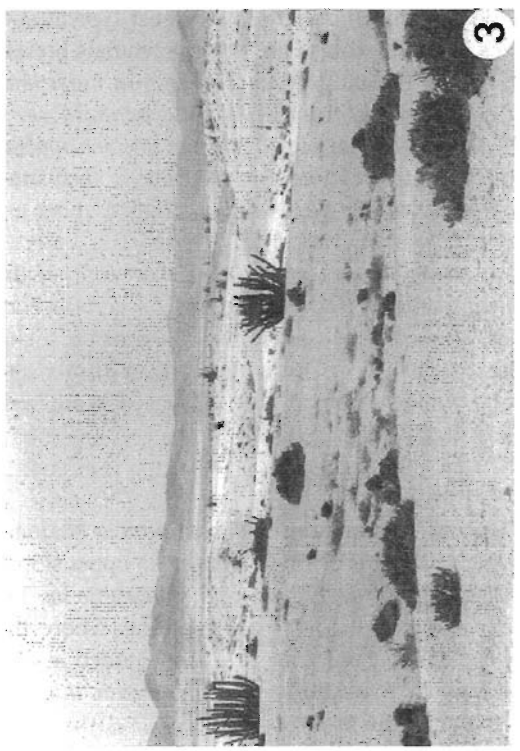
Bajada slopes near the coast where moisture collects from steep runoff channels in the hills contain distinctive plant communities dominated by woody shrubs (Figure 5). Plant cover generally reaches its greatest amount lower on the bajada slopes near the junction with the major arroyo systems. Soils on these slopes are rocky, but contain a considerable amount of fine textured material as well. The structure of a bajada community of this type has been described by Rundel *et al.* (1980) for a site along the margin of the Quebrada Pan de Azúcar 3 km from the coast at an elevation of about 100 m. The dominant species at this site was *Gypothamnium pinifolium* (Asteraceae), with *Nolana mollis* and *Heliotropium pycnophyllum* as important associates. Typical large shrubs here reached 1-2 m in diameter and 0.7 m in height. A broad survey of 487 individuals found 13 species of shrubs and subshrubs with *G. pinifolium* (40%), *N. mollis* (25%), and *Heliotropium pycnophyllum* (21%) collectively contributing 86% of all individuals. Next in importance was *Tetragonia maritima* (7%), followed by a group of more typically arroyo species (*Eremocharis fruticosa*, *Polyachyrus fuscus* and *Ophryosporus triangularis*) and small numbers of typical bajada and rocky slope specialists such as *Euphorbia lactiflua* (Euphorbiaceae), *Deuterocohnia chrysantha* (Bromeliaceae), and *Encelia canescens* (Asteraceae). The water relations and ecology of some of these dominant shrubs have been studied (Mooney *et al.* 1980; Rundel *et al.* 1980).

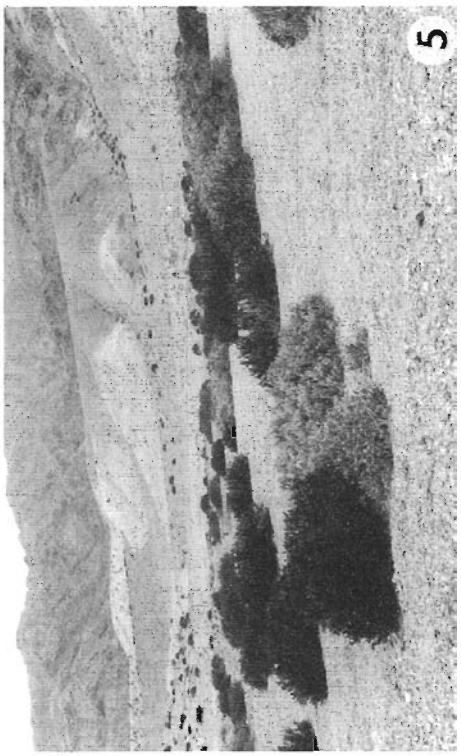
In dry years there are virtually no herbaceous species on these slopes, but in wet years there is an excellent diversity of both annuals and herbaceous perennials. *Argylia radiata* (Bignoniaceae), *Dinemandra ericoides* (Malpighiaceae), *Cistanthe grandiflora* (Portulacaceae), *Cruckshanksia pumila* (Rubiaceae), as well as species of *Adesmia* (Fabaceae), *Spergularia* (Caryophyllaceae), and *Cryptantha* (Boraginaceae) may all be abundant.

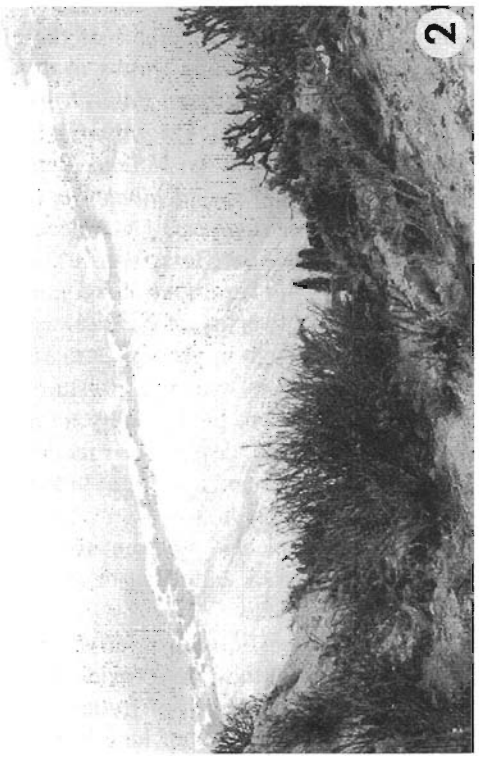
As with the arroyo communities, these bajada communities also seem to be in a state of dynamic equilibrium. A long-term study of seedling establishment on a permanent plot at the lower margin of this bajada slope along the Quebrada de Pan de Azúcar is currently in progress (Rundel and Palma, unpublished data). Here a single year of moderately heavy rain in 1987 was not successful in allowing seedling establishment of the dominant shrub species, *Gypothamnium pinifolium*. Very few seedlings of this species were observed in the first spring following rains, and only a single seedling individual remained alive five years later in the 2000 m^2 area sampled. Three other species, *Nolana mollis*, *Tetragonia macrocarpa*, and *Eremocharis fruticosa* together made up 91% of the surviving seedlings in 1992 despite less than 20% of the mature plants in the same area. This occurrence suggests that *G. pinifolium* has no soil seed pools and requires two years of rain for successful establishment. Thus changing patterns of interannual rainfall may likely produce sharp changes in shrub dominance.

Cactus Plains

Cacti are the overwhelming dominant in these communities which are characterized by conditions of coarse soil texture and geomorphic position which are particularly favorable for the growth of succulents but less favorable for shrubs. There is generally a scattered occurrence of shrub species typical of the bajada communities, but cacti are the clear dominants. Most commonly species of *Copiapoa* dominate with scattered shrubs such as *Gypothamnium pinifo-*







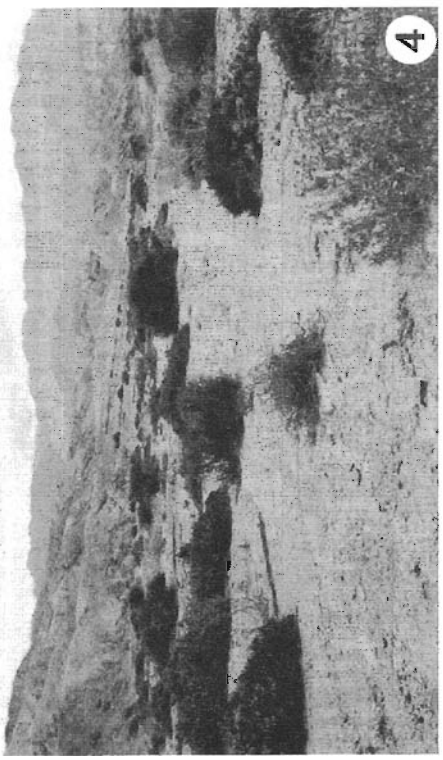


FIG. 2. Fog zone at the edge of the steep coastal escarpment in Pan de Azúcar National Park, with the coastal plain 800 m below. FIG. 3. Rolling plateau atop the coastal hills near Las Lomitas at about 750 m elevation. This is the sector of the park in which guanacos are most commonly encountered. FIG. 4. Arroyo community in the Quebrada de Pan de Azúcar near the eastern margin of Pan de Azúcar National Park with *Nolana mollis*, *Eremocharis fruticosa*, and *Tetragonia maritima* as dominant shrub species. FIG. 5. Bajada community along Quebrada de Pan de Azúcar with *Gypothamnium pinifolium* and *Nolana mollis* as dominant species.

lium, *Tetragonia maritima* and *Heliotropium pycnophyllum*.

Deep, well drained sandy soils collect near the lower margins of some of the major quebradas at Pan de Azúcar, producing relatively flat plains dominated by virtual monocultures of *Copiapoa cinerea* var. *columna-alba*, a remarkable small cactus with stems angled toward the north (Ehleringer *et al.* 1980). These communities are relatively free of any shrub cover and contain remarkable densities of cacti (Figure 6). Good examples of this community can be seen about 3 km from the coast at the junction of Quebrada Agua Salada and Quebrada Pan de Azúcar, and in the northern park near the junctions of Quebrada El Quisco with Quebrada Grande. Measurements by Gulmon *et al.* (1979) at the first of these sites found a mean density of about 20,000 *Copiapoa* ha^{-1} over an area of several hectares. Small geophytic cacti, *Neoporteria esmeraldana*, may be found growing under a thin mantel of quartz sand in these areas (Weisser 1967).

Another remarkable community dominated by single species of *Copiapoa* occurs along broad coastal beach terraces of the park, where large mounds of *C. cinerascens* reach up to a meter or more in diameter and contain dozens of individual cactus heads (Figure 7). This community is particularly evident on the coastal terraces near the southern entrance to the park. Here *C. cinerascens* occurs in densities of up to several thousand individuals or more per hectare, with about 10% of these forming mounds 30 cm or more in diameter. Associated perennial species are *Heliotropium pycnophyllum*, *Frankenia chilensis*, and *Polyachyrus fuscus*.

Two other mound-forming species of *Copiapoa* are present at Pan de Azúcar, *C. serpentisulcata* and *C. longistaminea*. The latter is common near Esmeralda at the northern margin of the park. Both of these may form large mounds up to more than 1 m in diameter and 60 cm in height. Similar cactus dominated coastal terraces occur elsewhere along the coast, most notably from north of Taltal to above Paposo where *Copiapoa cinerea* var. *haseltoniana* is dominant (Rundel and Mahu 1976; Rundel 1976; Mooney *et al.* 1977).

Rocky Slopes

Rocky slopes with poor soil development have very little plant cover at lower elevations. *Gypothamnium pinifolium* is the most typical species in these habitats but other perennials present included the ubiquitous *Tetragonia maritima*, *Nolana crassulifolia* and *Deuterocohnia chrysantha* (Bromeliaceae). The latter species appears to frequently be in very poor health in such sites, and may well be becoming eliminated under current long-term drought conditions.

Rocky slopes in the lower fog zone of the steep western escarpment of the coastal hills contain a much richer assemblage of species, including a variety of herbaceous perennials and semi-woody shrubs. These habitats are not well studied, however.

The Fog Zone

Fog zone communities at Pan de Azúcar National Park are best developed on the steep upper slopes of the coastal escarpment of the Sierra de las Tapias and the sector of Las Lomitas where the effect of the camanchaca is concentrated at elevations of 700-800 m. Canopy cover is commonly 20-30% or more here, with large individuals of *Eulychnia saint-pieana* (Cactaceae), *Euphorbia lactiflua* (Euphorbiaceae), and the shrubby *Echinopsis deserticola* (Cactaceae) as dominants (Figure 8). The former two species reach to 2-3 m in height. *Oxalis gigantea* (Oxalidaceae) and *Puya boliviensis* are locally abundant perennials on rocky edges of the cliffs. Other characteristic woody shrubs in this zone include *Tetragonia maritima*, *Balbisia pedunculares* (Geraniaceae), *Stachys pannosa* (Lamiaceae), *Frankenia chilensis*, *Nolana leptophylla* (Nolanaceae), *Centaurea cachinalensis* (Asteraceae), *Senecio cachinalensis* (Asteraceae), and *Heliotropium taltalense* (Boraginaceae). Mounds of the spiny *Opuntia berteri* are also common.

The species diversity of herbaceous perennials is relatively high in years with rainfall, but less obvious in years with fog moisture alone. Geophytes are present but virtually no annuals occur in the fog zone, despite their moderate diversity on dry slopes and bajadas at lower elevations. Rocky tallus slopes and outcrops within the fog zone may include representatives of species more characteristic of the bajada and dry slopes below the fog zone.

The characteristic high relative humidity and frequent fogs in this zone provide ideal conditions for luxuriant growth of fruticose lichens on the trunks and branches of long-lived woody

species. A vascular epiphyte, *Tillandsia geissei* (Bromeliaceae) is also present, although it is becoming increasingly rare.

Back from the immediate area of the coastal cliffs, the biomass and diversity of plant communities decreases rapidly as the strength of the camanchaca is diffused more broadly. Vascular plants become increasingly restricted to drainage channels and small arroyos where runoff moisture collects. Common species in these open communities back from the escarpment are *Nolana divaricata*, *N. leptophylla*, *Polyachyrus fuscus* and *Adesmia melanocaulos*.

SALINE AND FRESHWATER SPRINGS

As described above, wet soils and standing water are present at a number of springs around Pan de Azúcar National Park (Figure 9). Saline springs are characterized by the presence of *Distichlis spicata*, *Juncus acutus*, *Cressa truxillensis*, *Sarcocornia fruticosa*, *Frankenia chilensis*, and *Ruppia maritima* if sufficient water is present. Freshwater springs have populations of such species as *Polypogon interruptus*, *Paspalum vaginatum*, *Apium panul*, and *Zannichellia palustris*. We have identified 15 vascular plant species associated with springs.

COASTAL DUNES

Scattered areas with sand dunes are present along the coast in the Pan de Azúcar National Park. Frequently these dune communities grade into gentle bajada slopes with sandy soils, providing conditions for mixed growth of bajada and dune species. At least seven species in the park flora have dunes as their characteristic habitat. These include *Skytanthus acutus* (Apocynaceae) *Tiquilia litoralis* (Boraginaceae), *Oenothera coquimbensis* (Onagraceae), and *Euphorbia copiapina* (Euphorbiaceae). Although these communities have not been studied in the park, the floristic composition and community structure of similar dune habitats south of Chañaral have been described (Kohler 1970).

VERTEBRATES

MAMMALS

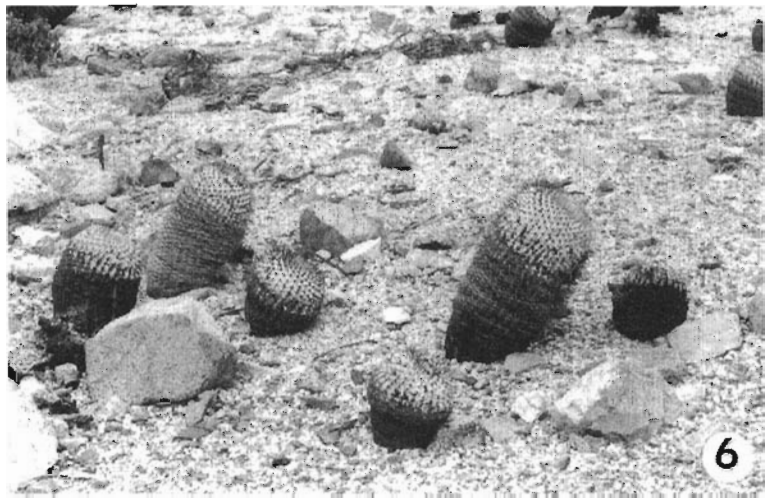
Pan de Azúcar provides an important reserve for a number of significant and endangered species of mammals. The most notable of these in terrestrial environments is the guanaco, *Lama guanicoe*. This species has become seriously endangered in Chile as available habitat has disappeared. Raedeke and Simonetti (1984) estimated a population of at least 80 guanacos within the park, and more recent estimates suggest as many as 200 or more individuals are now present (CONAF 1990). The preferential foods of the guanaco at Pan de Azúcar are *Oxalis gigantea*, *Euphorbia lactiflua* and *Nolana* species among the shrubs, as well as a sporadic use of cacti such as *Copiapoa* and *Eulychnia* (Raedeke and Simonetti, 1984). Ephemeral plants are utilized in years with rain.

Two other large resident mammals of interest are the culpeo fox (*Dusicyon culpaeus*) and the chilla fox (*Dusicyon griseus*) which have an allopatric pattern of ecological distribution. The former species is a characteristic resident of lower elevations and the coastal zone, while the latter species lives at higher elevations in the fog zone (CONAF 1990). Both of these species are widespread in Chile, but included in the Red List of Chilean Vertebrates (Glade 1993) because they are so poorly studied. The puma (*Felis concolor*) is not a resident but an occasional visitor to both the higher elevations and littoral zone of the park.

The fauna of small terrestrial mammals at Pan de Azúcar is very limited, consisting of one marsupial and three rodents. The marsupial representative is the northern mouse-possum (*Marmosa elegans coquimbensis*). This subspecies occurs in the northern four regions of Chile and is classified as rare (Glade 1993). It is an omnivore in food habitats, with arthropods forming a large part of its diet (Mann 1978). It is a nocturnal forager, and lives aboveground in hollows or under shrubs.

Three cricetid rodents are known from the park. These are the long-tailed rice rat (*Oryzmys longicaudatus*), olivaceous akodon (*Akodon olivaceus*), and Darwin's long-eared mouse (*Phyllotis darwini*). All of these are northern subspecies of widespread Chilean species. *Oryzmys longicaudatus* is easily recognized among these by its long tail and diurnal foraging. It nest aboveground and climbs well in shrubs (Mann 1978). *Akodon* and *Phyllotis* are nocturnal and fossorial in behavior. None of these three species is considered rare or endangered.

Two bat species are known from Pan de



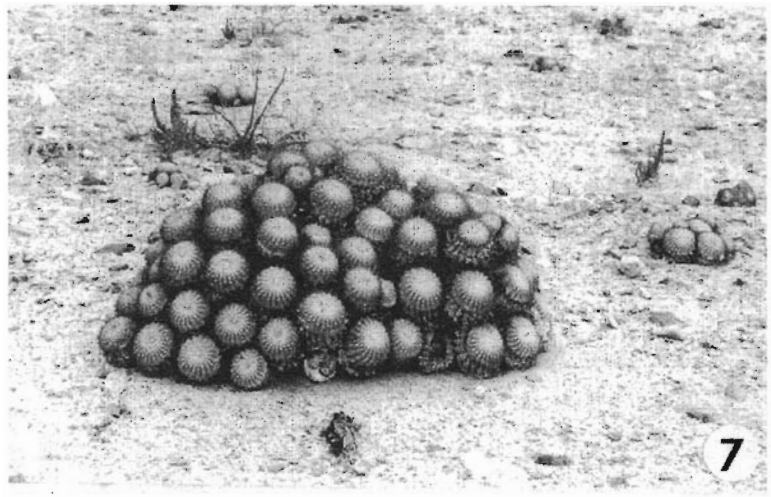


FIG. 6. *Copiapoa cinerea* var. *columna-alba* with its prominent inclination toward the north. FIG. 7. Mound of *Copiapoa cinerescens* on the coastal plain near the southern border of Pan de Azúcar National Park. FIG. 8. Fog zone community at about 800 m elevation in the Las Lomitas sector of Pan de Azúcar National Park, with *Eulychnia saint-pieana* and *Euphorbia lactiflua* as the two tall dominant species. The *Eulychnia* and lower shrubs support a notable abundance of epiphytic fruticose lichens. FIG. 9. Brackish spring at the mouth of the Quebrada las Chilcas. This spring was referred to and illustrated as Cachinal de la Costa by Philippi (1869).

Azúcar. *Myotis atacamensis* is a widespread species and not endangered. The second species is *Desmodus rotundus*, the vampire bat. While its overall range is widespread in Latin America, *D. rotundus* is classified as rare in Chile (Glade 1993), and occurs only from Valparaíso northward. At Pan de Azúcar this species is though to feed largely on blood from marine mammals along the coast (Mann 1978).

The marine mammals represent another important group within the National Park. Isla Pan de Azúcar provides conditions for a resident colony of the southern sea otter (*Lutra felina*). While more than 200 animals live on the island, populations in northern Chile are low compared to southern Chile (Ostfeld *et al.* 1989, Ebensperger and Castilla 1991, 1992), and the southern sea otter is classified overall as vulnerable (Glade 1993). The southern elephant seal (*Mirounga leonina*) is not a resident but an occasional visitor to Isla Pan de Azúcar. It is also classified as vulnerable. The southern fur seal (*Otaria byronia*) is also a resident on the island, but is not considered to be threatened.

While they are permanent residents of the ocean, six species of cetaceans have been observed from the park. These are the bottle-nosed dolphin (*Tursiops nesarnack*), the killer whale (*Orcinus orca*), southern bottle-nosed whale (*Hyperoodon planifrons*), southern right whale dolphin (*Lissodelphis peronii*), Burmeisteris porpoise (*Phocoena spinipinnis*), and long-finned pilot whale (*Globicephala melaena*).

REPTILES AND AMPHIBIANS

Six species of reptiles and one amphibian are residents of Pan de Azúcar National Park (CONAF 1990). Five lizards are present, divided among three families. The geckonid *Garthia gaudichaudi* is small nocturnal species of lower elevations which utilizes the interiors of dead *Copiapoa* as a refuge during the day. Rocky slopes and terraces near the coast are the home of *Callopistes palluma*, a large teid lizard which has suffered from commercial collecting and is considered vulnerable (Glade 1993). Two iguanid lizards, *Liolaemus atacamensis* and *L. platei*, occur further inland in areas of sandy soil. These are fossorial species which utilize burrows under shrubs for cooling. The remaining iguanid lizard is *Tropidurus atacamensis*. This species lives in the infralittoral zone, and apparently consumes marine algae as a major part of its diet. Although this species has not been well studied, it apparently has specialized nasal salt glands to allow it to maintain itself on this unusual diet.

A single snake species, *Philodryas chamisonis*, is present in small numbers in the park. It appears to be restricted to higher elevations in the fog zone. This is also the habitat of *Bufo atacamensis* which is found here at the base of large rocks and fallen trunks of arborescent cacti, as well as around permanent springs at lower elevations. Both of these species are classified as vulnerable in Chile (Glade 1993).

BIRDS

Bird species diversity within Pan de Azúcar National Park is high, with 130 reported species (CONAF 1990). Approximatively 27 of these species appear to breed within the park. Many other of the reported species are regular visitors annually.

Terrestrial habitats in the park are home to a number of subspecies which are endemic to northern Chile. Among these are the white-throated tapaculo (*Scelorchilus albicollis atacamae*) which is a resident, and occasional visitors such as the white-banded mockingbird (*Mimus triurus*). Raptors and their kin are richly represented in the park, with 11 species, six of which are thought to be resident (CONAF 1990). These include the Andean condor (*Vultur gryphus*), the peregrine falcon (*Falco peregrinus*), crested caracara (*Polyborus plancus*), osprey (*Pandion haliaetus*), and red-backed hawk (*Buteo polyosoma*).

Passeriform birds are surprisingly abundant in terrestrial habitats of Pan de Azúcar considering the barren landscape. Ten of the 29 reported species are thought to be residents (CONAF 1990). The dark-faced and spot-billed ground tyrants, *Muscisaxicola macloviana* and *M. maculirostris*, are sympatric during the winter and allopatric during the rest of the year. Other species migrate to the area of the park to spend a portion of each year. For example, the barn swallow (*Hirundo rustica*) migrates from the Northern Hemisphere, while the yellow-rumped siskin (*Carduelis uropygialis*) migrates to the coast in winter.

The marine and pelagic birds of the coastal strip of Pan de Azúcar present a diverse and fascinating group on Isla Pan de Azúcar. Most pro-

minent of these is the Humboldt penguin (*Spheniscus humboldti*) which has been the object of detailed studies. Smaller populations of Magellanic penguins (*S. magellanicus*) are also present. Other significant marine birds here are the Peruvian booby (*Sula variegata*), Chilean brown pelican (*Pelecanus thagus*), Peruvian diving petrel (*Pelecanoides garnottii*), Inca tern (*Larosterna inca*), band-tailed gull (*Larus belcheri*), kelp gull (*Larus dominicanus*), and American oystercatcher (*Haematopus ater*). A number of sea birds migrate here each year from the Northern Hemisphere, including the whimbrel (*Numenius phaeopus*), surfbird (*Aphriza virgata*), ruddy turnstone (*Arenaria interpres*), and sanderling (*Calidris alba*).

ACKNOWLEDGEMENTS

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TABLE 1. Monthly climatic means of temperature and precipitation for Chañaral (26°20' S lat. 70°37' W long.), 20 km south of Pan de Azúcar National Park. Temperature and humidity data are from Hajek and di Castri (1975). Mean monthly precipitation data are from Almeyda (1949) for the period 1926-48.

Month	Mean max. temperature (°C)	Mean min. temperature (°C)	Relative humidity (%)	Precipitation (mm)
January	22.9	15.6	64	0
February	23.2	16.2	64	0
March	22.5	14.8	68	0.4
April	20.3	12.9	71	0.2
May	18.4	9.7	75	1.2
June	16.3	8.8	75	7.7
July	16.3	8.8	75	1.6
August	16.4	9.4	76	4.3
September	16.7	10.2	72	0.4
October	18.1	11.4	70	0.9
November	19.5	13.1	67	0.8
December	21.3	15.1	66	0
Annual	19.3	12.2	70	18

APPENDIX

Checklist of the flora of Pan de Azúcar National Park. Species observed by ourselves or others, but without vouchers in the LOMAFLOR for 25°53' to 26°15'S lat. are indicated with a + symbol. An asterisk indicates an exotic species.

Pteridophyta

+*Cheilanthes mollis* Kunze Herbaceous perennial; dry rocky slopes; reported by Hoffmann (1986).
+*Polypodium espinosae* Weatherby Herbaceous perennial; slopes in fog zone; reported by CONAF (1990).

Gymnospermae

Ephedraceae
+*Ephedra breana* Phil. Stem photosynthetic shrub; dry slopes; reported by Hoffmann (1986).

Monocotyledonae

Amaryllidaceae
+*Hippeastrum laetum* Phil. Geophyte; slopes in the fog zone; reported by Hoffmann (1986).

Bromeliaceae
Deuterocohnia chrysantha (Phil.) Mez Perennial rosette succulent; dry rocky slopes, often in poor condition.
Puya boliviensis Baker Perennial rosette succulent; rocky slopes in the fog zone.
Tillandsia geissei Phil. Epiphyte, most commonly on Euphorbia lactiflua and Eulychnia in the fog zone at the edge of the sea cliffs.

Cyperaceae
+*Eleocharis albibracteata* Nees & Meyen ex Kunth Herbaceous perennial; moist soils around springs; reported by Hoffmann (1986).
+*Scirpus cernuus* Vahl. Herbaceous perennial; moist soils around springs, reported by CONAF (1990).

Iridaceae
Sisyrinchium graminifolium Lindl. Geophyte; slopes in the fog zone.
Tigridia philippiana I.M.Johnst. Geophyte; slopes in the fog zone.

Juncaceae
Juncus acutus L. ssp. *leopoldii* (Parlat.) Snogerup Herbaceous perennial; moist soils around saline springs.

Juncaginaceae
Triglochin striatum Ruiz & Pavón Herbaceous perennial; moist soils around springs; reported by Hoffmann (1986) as *T. palustris*.

Liliaceae
+*Alstroemeria graminae* Phil. Geophyte; dry slopes to lower fog zone; reported by Hoffmann (1986).
Alstroemeria paupercula Phil. Geophyte; slopes in the fog zone.
Fortunatia biflora (Ruiz & Pavón) J.F.Macbr. Geophyte; slopes in the fog zone.
Leucocoryne appendiculata Phil. Geophyte; slopes in the fog zone.

Poaceae
Distichlis spicata (L.) Greene Herbaceous perennial; moist soils around saline springs.
Eragrostis attenuata Hitchc. Herbaceous perennial; slopes in the fog zone.
Festuca australis Nees ex Steud. [=Vulpia australis Blom] Annual; slopes in the fog zone.
Festuca sp. Herbaceous perennial, slopes in the fog zone.
Koeleria trachyantha Phil. [=Raimundochloa trachyantha (Phil.) A.M.Molina]
Herbaceous perennial; slopes in the fog zone.
Nassella pungens Desv. Herbaceous perennial; slopes in the fog zone.
Paspalum vaginatum Sw. Herbaceous perennial; moist soils around springs.
Poa bonariensis (Lam.) Kunth. Herbaceous perennial; slopes in the fog zone.

Polypogon interruptus Kunth. Herbaceous perennial; moist soils around springs.
Stipa plumosa Trin.Herbaceous perennial; dry slopes.
Stipa speciosa Trin. & Rupr. [=*Achnatherum speciosum* (Trin. & Rupr.) Barkworth] Herbaceous perennial; dry slopes.
Stipa tortuosa E.Desv. Herbaceous perennial; dry slopes.

Potamogetonaceae
+*Ruppia maritima* L. Herbaceous perennial; wet areas of standing water around springs; reported by Johnston (1929).
+*Zannichellia palustris* L. Herbaceous perennial; wet areas of standing water around springs; reported by Johnston (1929).

Dicotyledonae

Aizoaceae
Tetragonia angustifolia Barnéoud Shrub; dry flats near the ocean.
Tetragonia macrocarpa Phil. Annual; dry slopes.
Tetragonia maritima Barnéoud Leaf succulent shrub; common in arroyos and on dry and rocky slopes.
Tetragonia microcarpa Phil. Annual; dry slopes and arroyos.
Tetragonia ovata Phil. Annual; dry slopes.

Amaranthaceae
Alternanthera porrigens (Jacq.) Kuntze [=A. junciflora (Remy) I.M.Johnston]. Semi-woody shrub; dry slopes just outside the fog zone.

Apiaceae
Apium panul (Bertero ex DC.) Reiche. Herbaceous perennial; moist soils around springs.
+*Asteriscium chilensis* Cham. & Schltdl. Herbaceous perennial; rocky slopes; not collected in the park, but common both north and south and thus expected.
+*Asteriscium closii* (Kuntze) Mathias & Constance Annual; rocky slopes; not collected in the park, but common both north and south and thus expected.
+*Asteriscium vidali* Phil. Herbaceous perennial; rocky slopes; verified by Mathias and Constance (1962).
Ciclospermum laciniatum (DC.) Constance Annual; rocky slopesin sheltered areas; reported by Philippi from Quebrada Grande.
Domeykoa oppositifolia Phil. Annual; dry hillsides and slopes in the fog zone.
Domeykoa perennis I.M.Johnst. Herbaceous perennial; slopes in the fog zone; endemic to the park.
Eremocharis fruticosa Phil. Shrub; common along arroyos, less frequent on rocky slopes.
+*Gymnophyton foliosum* Phil. Woody shrub; dry flats; not collected in the park, but common both north and south and thus expected.

Apocynaceae
Skytanthus acutus Meyen Semi-woody subshrub; common on sand dunes along the coast.

Asclepiadaceae
+*Cynanchum boerhaviifolium* Hook. & Arn. Perennial vine, rocky slopes; not collected in the park, but common both north and south and thus expected.
Cynanchum viride (Phil.) Reiche Trailing woody subshrub, dry slopes.

Asteraceae
Amblyopappus pusillus Hook. & Arn. Annual; dry slopes.
Baccharis taltalensis I.M.Johnst. Shrub; dry slopes.
Bahia ambrosioides Lag. Semi-woody shrub; dry slopes.
Centaurea atacamensis (Reiche) I.M.Johnst. Shrub; dry slopes.
Centaurea cachinalensis Phil. Shrub; slopes in fog zone.
Chaetanthera glabrata (DC.) F.Meigen Annual/herbaceous perennial; dry slopes.
Chuquiraga ulicina (Hook. & Arn.) Hook. & Arn. Spiny shrub; dry slopes.
Encelia canescens Lam. Shrub; dry slopes.
Gutierrezia taltalensis Phil. Shrub; dry slopes.
Gypothamnium pinifolium Phil. Resinous-leaved shrub; common on dry slopes and bajadas; edges of arroyos.
Haplopappus deserticola Phil. Shrub; dry slopes.
Haplopappus rosulatus Hall Prostrate shrub; slopes in the fog zone
Helenium atacamense Cabrera Annual; dry slopes and disturbed areas.

Hypochaeris grandidentata (Phil.) Reiche Herbaceous perennial; slopes in the fog zone.
Leucheria cumingii Hook. & Arn. Annual; slopes in the fog zone.
+*Moscharia pinnatifida* Ruiz & Pavón Annual; dry slopes, reported by Hoffmann (1986); we have no records of this genus from northern Chile, and thus this report seems doubtful.
Ophryosporus triangularis Meyen Shrub; arroyos and less commonly on rocky slopes.
Oxyphyllum ulicinum Phil. Spiny shrub; arroyos and dry slopes.
Perityle emoryi Torr. Herbaceous perennial to semi-woody subshrub; common on dry slopes and arroyos.
Perityle discoidea (Phil.) I.M.Johnst. Herbaceous perennial; dry slopes.
Polyachyrus cinereus Ricardi & Weldt Perennial herb to subshrub; dry flats and arroyos.
Polyachyrus fuscus (Meyen) Meyen & Walpers Subshrub; dry slopes and flats.
Senecio cachinalensis Phil. Semi-woody subshrub; slopes in fog zone.
Senecio myriophyllus Phil.Semi-woody subshrub; dry slopes.
+*Stevia philippiana* Hieron. Herbaceous perennials; dry hillsides to slopes in the fog zone, reported by Johnston (1929).

Bignoniaceae
Argylia radiata (L.) D.Don. Herbaceous perennial; dry slopes and arroyos.

Boraginaceae
Cryptantha argentea I.M.Johnst. Herbaceous perennial; slopes in the fog zone; endemic to the park.
Cryptantha calycina (Phil.) Reiche Annual; dry slopes.
Cryptantha filaginea (Phil.) Reiche Annual; dry slopes.
Cryptantha parviflora (Phil.) Reiche Annual; dry slopes.
Cryptantha romanii I.M.Johnst. Annual, dry slopes; endemic to the park.
Heliotropium curassavicum L. Semi-woody subshrub; wet soils around springs.
Heliotropium linearifolium Phil. Shrub; Arroyos, less common on dry slopes.
Heliotropium pycnophyllum Phil. Shrub; common on dry slopes.
Heliotropium sclerocarpum Phil. Shrub; rocky slopes near the ocean.
Heliotropium taltalense (Phil.) I.M.Johnst. Shrub; dry slopes, rarely in the fog zone.
Tiquilia litoralis (Phil.) A.T.Richardson Herbaceous perennial; dunes along the coast.

Brassicaceae
Lepidium spathulatum Phil. Herbaceous perennial; slopes in the fog zone.
Mathewsia incana Phil. Semi-woody subshrub; dry slopes.
Menonvillea chilensis (Turcz.) Jackson Herbaceous perennial; dry slopes and flats.
Sisymbrium sagittatum Hook. & Arn. Annual to herbaceous perennial; slopes in the fog zone.
Werdermannia anethifolia (Phil.) I.M.Johnst. Herbaceous perennial; dry slopes.

Cactaceae (following Hoffmann 1989, not currently in LOMAFLOR)
+*Copiapoa cinerea* (Phil.) Britton & Rose var. columna-alba (Ritter) Back. CAM succulent on sandy bajadas and flats near the major arroyos; occasionally with Eulychnia in the fog zone.
+*Copiapoa cinerascens* (Salm-Dyck) Britton & Rose Mound-forming CAM succulent; dry slopes.
+*Copiapoa humilis* (Ritter) Hutchison CAM succulent; geophyte on sandy flats.
+*Copiapoa longistaminea* F.Ritter Mound-forming CAM succulent; dry slopes and coastal plain.
+*Copiapoa marginata* (Salm-Dyck) Britton & Rose CAM succulent; dry slopes.
+*Copiapoa serpentisulcata* F.Ritter Mound-forming CAM succulent; dry slopes and coastal plain.
+*Echinopsis deserticola* (Werderm.) Friedr. & Rowl. Sub-arborescent CAM succulent; slopes in the fog zone.
+*Eriosyce rodentiophila* F.Ritter CAM succulent; dry slopes.
+*Eulychnia saint-pieana* F.Ritter Arborescent CAM succulent; dominant in the fog zone.
+*Neoporteria esmeraldana* (F.Ritter) Donald & Rowley CAM succulent; geophyte in dry sandy soils.
+*Neoporteria intermedia* (Ritter) Donald & Rowley CAM succulent; rocky slopes.
+*Neoporteria taltalensis* Hutchinson CAM succulent; rocky slopes and flats below fog zone.
+*Opuntia berteri* (Colla) A.E.Hoffm. CAM succulent; fog zone and flats.
+*Opuntia tunicata* (Lehman) Link & Otto CAM succulent; rocky slopes.

Caryophyllaceae
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr. Herbaceous perennial; lower fog zone.
Microphyes litoralis Phil. Annual; dunes along the coast.
Paronychia chilensis DC. Trailing herbaceous perennial; slopes in fog zone.
Spergularia arbuscula (Gay) I.M.Johnst. Semi-woody shrub; dry slopes.
Spergularia cremnophila I.M.Johnst. Annual or herbaceous perennial; slopes in the fog zone; endemic to the park.

Spergularia denticulata (Phil.) Phil. Annual or herbaceous perennial; dry slopes and flats.
Spergularia stenocarpa (Phil.) I.M.Johnst. Annual or herbaceous perennial; dry slopes and flats.

Chenopodiaceae
Atriplex clivicola I.M.Johnst. Shrub; arroyos and dry slopes.
Atriplex deserticola Phil. Semi-prostrate shrub; arroyos; reported by Hoffmann (1986).
Atriplex taltalensis I.M.Johnst. Semi-prostrate shrub; perennial; reported by Hoffmann (1986).
Chenopodium petiolare Kunth Semi-woody shrub; saline areas along the coast.
Sarcocornia fruticosa (L.) A.J.Scott Semi-woody shrub; saline areas and springs.
Suaeda divaricata Moq. Semi-woody shrub; saline areas along the coast and Isla Pan de Azúcar, and in wet areas around saline springs.

Convolvulaceae
Convolvulus chilensis Pers. Herbaceous perennial; slopes in the fog zone.
Cressa truxillensis Kunth Herbaceous perennial; moist soils around saline springs.
+*Dichondra sericea* Sw. Herbaceous perennial; slopes in the fog zone;reported by Hoffmann (1986).

Cucurbitaceae
Sicyos baderoa Hook. & Arn. Herbaceous perennial vine; slopes in the fog zone.

Cuscutaceae
Cuscuta purpurata Phil. Herbaceous parasitic vine; dry slopes and bajadas, most commonly on *Gypothamnium pinifolium*; may be conspecific with *C. odorata* Ruiz & Pavón.

Euphorbiaceae
Argythamnia canescens (Phil.) F.Phil. Herbaceous perennial: dry slopes below the fog zone.
Argythamnia cremnophila (I.M.Johnst.) J.Ingram Herbaceous perennial; slopes in the fog zone.
Euphorbia copiapina Phil. Herbaceous perennial with a fleshy root; dunes along the coast.
Euphorbia lactiflua Phil. Succulent stemmed shrub; common in the fog zone.
Euphorbia thinophila Phil. Herbaceous perennial; dry slopes.

Fabaceae
Adesmia latistipula Phil. [=A. eremophila Phil.] Annual to herbaceous perennial; dry slopes.
Adesmia melanocaulos Phil. Spinescent shrub; arroyos and dry slopes; common back from the coast at Las Lomitas.
Adesmia pusilla Phil. Annual; dry slopes.
Astragalus cachinalensis Phil. Herbaceous perennial; slopes in the fog zone.
Astragalus coquimbensis (Hook. & Arn.) Reiche Annual; dry flats and arroyos.
Senna cumingii (Hook. & Arn.) H.S.Irwin & Barneby Shrub; arroyos.
Trifolium polymorphum Poir. Herbaceous perennial; slopes in the fog zone.

Frankeniaceae
Frankenia chilensis K.Presl Semi-woody shrub; arroyos and dry slopes, saline areas.

Geraniaceae
Balbisia peduncularis (Lindl.) D.Don. Shrub; common on slopes in the fog zone.
**Erodium cicutarium* (L.) L'Hér. ex Aiton Annual exotic; disturbed areas, particularly in the fog zone.
+*Geranium* sp. Herbaceous perennial, reported by CONAF (1990).

Lamiaceae
Salvia tubiflora Sm. Semi-woody shrub; slopes in the fog zone
Stachys pannosa Phil. Semi-woody shrub; slopes in the fog zone

Linaceae
Linum cremnophilum I.M.Johnst. Prostrate shrub; slopes in the fog zone; endemic to the park.

Loasaceae
Loasa chilensis (Gay) Urban & Gilg Shrub; dry slopes and arroyos.
Loasa elongata Hook. & Arn. Annual; arroyos and dry slopes.
Loasa fruticosa (Phil.) Urban & Gilg Low shrub; dry inland areas; reported by Hoffmann (1986); we have no seen this species south of Paposo.

Lythrum maritimum Kunth Herbaceous perennial; wet soils around springs.
Pleurophora pungens D. Don. Semi-woody subshrub; dry flats and arroyos.

Malesherbiaceae
Malesherbia humilis Poepp. Annual; dry slopes and flats.

Malpighiaceae
Dinemandra ericoides A.Juss. Herbaceous perennial, rarely a semi-woody shrub; dry slopes and flats.

Malvaceae
Cristaria formosula I.M.Johnst. Annual; arroyos and dunes along the coast.
Cristaria foliosa Phil. Subshrub with a woody base, dry and rocky slopes.
Cristaria fuentesiana I.M.Johnst. Prostrate herbaceous perennial; slopes in the fog zone; endemic to the park.
Cristaria integerrima Phil. Annual to herbaceous perennial; common on dry slopes and in arroyos.
Cristaria viridiluteola Gay Semi-woody subshrub; dunes near the coast.

Nolanaceae
Nolana acuminata (Miers) Miers ex Dunal Annual herb; dry flats and arroyos.
Nolana aplocaryoides (Gaudich.) I.M.Johnst. Annual; abundant, in arroyos, dry flats, and coastal plains in years with significant rain.
+*Nolana crassulifolia* Poepp. Prostrate, succulent-leaved shrub; dry slopes and arroyos.
Nolana divaricata (Lindl.) I.M.Johnst. Shrub; dry flats and arroyos.
Nolana elegans (Phil.) Reiche Annual herb; dry flats and arroyos.
Nolana flaccida (Phil.) I.M.Johnst. Prostrate, succulent-leaved shrub; arroyos.
Nolana incana (Phil.) I.M.Johnst. Prostrate, succulent-leaved shrub; arroyos and dry slopes.
Nolana leptophylla (Miers) I.M.Johnst. Succulent-leaved shrub; dry slopes.
Nolana linearifolia Phil. Herbaceous perennial; slopes in the fog zone.
Nolana mollis (Phil.) I.M.Johnst. Succulent-leaved shrub; dry slopes and arroyos.
Nolana paradoxa Lindl. Herbaceous perennial; arroyos.
Nolana peruviana (Gaudich.) I.M.Johnst. Sprawling succulent-leaved shrub; sandy flats near the ocean and rocky arroyos.
Nolana rostrata (Lindl.) Miers Shrub; sandy flats near the ocean.
Nolana rupicola Gaudich. Annual herb; dry slopes and arroyos.
Nolana salsoloides (Lindl.) I.M.Johnst. Small shrub; arroyos, rarely on dry slopes.
Nolana sedifolia Poepp. Upright or prostrate, succulent-leaved shrub; dry slopes.
Nolana stenophylla I.M.Johnst. Succulent-leaved shrub, arroyo and dry slopes.

Nyctaginaceae
+*Mirabilis elegans* (Choisy) Heimerl Semi-woody subshrub; dry slopes; reported by CONAF (1990).

Onagraceae
Oenothera coquimbensis Gay Annual; arroyos and dunes near the coast.

Oxalidaceae
Oxalis arbuscula Barnéoud Herbaceous perennial; dry slopes at the edge of the fog zone.
Oxalis gigantea Barnéoud Succulent-stemmed shrub; slopes in the fog zone.
Oxalis megalorrhiza Jacq. Herbaceous perennial; rocky slopes both in and below the fog zone.

Phytolacaceae
Anisomeria littoralis (Poepp. & Endl.) Moq. Shrub; slopes in the fog zone.

Piperaceae
Peperomia doellii Phil. Herbaceous perennial; rocky slopes in the lower fog zone.

Plantaginaceae
Plantago litorea Phil. Annual; dry slopes and arroyos.
+*Plantago rancaguae* Steud. Annual; dry slopes and flats; reported by Johnston (1929).

Plumbaginaceae
Limonium plumosum (Phil.) Kuntze [= Bakerolimon plumosum (Phil.) Lincz.]. Herbaceous perennial; coastal flats, especially in saline soils.
Plumbago caerulea Kunth Scandent or spreading shrub; dry arroyos.

Polemoniaceae
Gilia glutinosa Phil. Annual; dry slopes.

Polygonaceae
Chorizanthe deserticola Phil. Annual; dry slopes.

Portulacaceae
Calandrinia (Cistanthe) *cachinalensis* Phil. Annual; dry slopes.
Cistanthe amarantoides (Phil.) Hershk. Herbaceous perennial with succulent leaves; dry slopes or flats and disturbed areas.
Cistanthe calycina (Phil.) Carolin ex Hershk. Annual; dry slopes.
Cistanthe celosiodes (Phil.) Carolin ex Hershk. Annual, dry flats.
Cistanthe grandiflora (Lindl.) Carolin ex Hershk. Herbaceous perennial with succulent leaves; dry slopes.
Portulaca philippii I.M.Johnst. Herbaceous perennial; dry slopes.

Rosaceae
Acaena trifida Ruiz & Pavón Semi-woody subshrub; slopes in the fog zone.

Rubiaceae
Cruckshanksia pumila Clos Annual to herbaceous perennial; dry slopes and rocks areas in the fog zone.
Cruckshanksia tripartita Phil. Annual, dry slopes and flats.

Santalaceae
Quinchamalium carnosum Phil. Hemiparasitic annual; dry slopes.

Scrophulariaceae
Calceolaria paposana Phil. Shrub; slopes in the fog zone.

Solanaceae
+*Lycium deserti* Gay Spinescent shrub; dry slopes and edges of the fog zone reported by Hoffmann (1986).
Lycium minutifolium Remy Shrub; dry slopes and rocky areas.
+*Nicotiana solanifolia* Walp. Shrub; slopes in the fog zone; reported by Hoffmann (1986).
+*Schizanthus laetus* Phil. Annual; dry slopes at edge of fog zone; reported by Hoffmann (1986).
+*Solanum brachyantherum* Phil. Annual, dry slopes and arroyos; reported by Hoffmann (1986).
+*Solanum phyllanthum* Cav. Herbaceous perennial; slopes in the fog zone; reported by Hoffmann (1986).
Solanum remyanum Phil. Semi-woody subshrub; dry slopes below the fog zone.

Tropaeolaceae
Tropaeolum tricolor Sweet Herbaceous perennial vine; slopes in the fog zone.

Valerianaceae
Valeriana atacamensis Borsini Herbaceous perennial; slopes in the fog zone.

Verbenaceae
Verbena (Glandularia) *atacamensis* Reiche Semi-woody subshrub; lower margin of the fog zone.

Violaceae
+*Viola polypoda* Turcz. Annual: dry slopes and arroyos, rarely in dunes; reported by Hoffmann (1986).

Zygophyllaceae
Fagonia chilensis Hook. & Arn. Herbaceous perennial; dry slopes, flats, and arroyos.