REVIEW

Spatiotemporal variation patterns of plants and animals in San Carlos de Apoquindo, central Chile

Patrones de variación espaciotemporal de plantas y animales en San Carlos de Apoquindo, Chile central

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ABSTRACT

I summarize what is known about the mediterranean ecosystem represented in San Carlos de Apoquindo (33° 23' S, 70° 31' W), a rugged area of 835 ha located ca. 20 km east of downtown Santiago on the Andean foothills. This site attracted numerous researchers during 1976-1990 because of its proximity to Santiago and its relatively protected status. I review the literature, and provide unpublished information on this site. A total of 132 literature entries describe the ecology of San Carlos de Apoquindo, in about 30 topics. The shrub and herbaceous vegetation have been well studied, but little is known about the respective seed banks. Among animals, small mammals, rabbits, and avian and mammalian predators are the best investigated, whereas epigean arthropods, amphibians, lizards, snakes, passerine birds, and scavengers of all types are the least studied. Thematically, interactions from plant/climate, to plant/soil, to plant/ herbivore, to herbivore/predator interactions, and to decomposition of animal carcasses, have been addressed. But gross inequalities exist on the thoroughness with which each topic has been researched. The best studied aspects deal with plant/herbivore and herbivore/predator interactions. Up to now, no description existed of soils and climate in the area, which I present in this paper. Taking advantage of the long-term aspect of the research at the site, I highlight temporal variation patterns. And because of the different landscape aspects present at the site, I also highlight data that depict such spatial variability. In general, San Carlos de Apoquindo has contributed greatly to the understanding of ecological processes in central Chile. I call for renewed efforts at studying this site's ecology from an ecosystem perspective.

Key words: mediterranean ecosystem, sclerophyllous vegetation, matorral, animal ecology, animal invaders, spatiotemporal variation, El Niño.

RESUMEN

Resumo lo que se conoce acerca del ecosistema mediterráneo representado en San Carlos de Apoquindo (33º 23' S, 70º 31' O), un área con alto relieve y de 835 ha localizada ca. 20 km al Este del centro de Santiago en la precordillera andina. Este sitio atrajo a numerosos investigadores durante 1976-1990 debido a su proximidad a Santiago y a su condición de relativamente protegido. Reviso la literatura y proveo información no publicada sobre este sitio. Un total de 132 referencias bibliográficas describen la ecología de San Carlos de Apoquindo, en alrededor de 30 tópicos. La vegetación arbustiva y herbácea han sido bien estudiadas, pero poco se sabe acerca de sus respectivos bancos de semillas. Entre los animales, los micromamíferos, conejos, y predadores rapaces y carnívoros son los mejor investigados, en tanto que los artrópodos epígeos, anfibios, lagartijas, culebras, aves paserinas y los carroñeros de todo tipo son los menos estudiados. Temáticamente, se han analizado interacciones planta/clima, planta/suelo, planta/herbívoro y herbívoro/ predador, así como la descomposición de cadáveres animales. Sin embargo, hay desbalances grandes en la profundidad con que se han tratado estos tópicos. Los aspectos mejor estudiados se refieren a interacciones planta/herbívoro y herbívoro/predador. Hasta ahora, no existía descripción detallada de suelos y clima en el área, que aquí presento. Aprovechando el aspecto de largo plazo de la investigación en el sitio, destaco los patrones de variación temporal. Y aprovechando la presencia de diferentes unidades de paisaje en el sitio, también destaco su variabilidad espacial. En general, San Carlos de Apoquindo ha contribuído grandemente al entendimiento de los procesos ecológicos en Chile central. Llamo a realizar esfuerzos renovados para estudiar la ecología de este sitio desde una perspectiva ecosistémica.

Palabras clave: ecosistema mediterráneo, vegetación esclerófila, matorral, ecología animal, animales invasores, variación espaciotemporal, El Niño.

INTRODUCTION

San Carlos de Apoquindo $(33^{\circ} 23' \text{ S}, 70^{\circ} 31' \text{ W})$, also referred to as Los Dominicos (Paynter 1988), is a rugged area of 835 ha located ca. 20 km east of downtown Santiago on the Andean foothills (Fig. 1), with elevations ranging from 1,050 to 1,915 m and slopes of up to 47°. In general, the site consists of a large west-oriented catchment area dissected by three small strictly seasonal creeks. The rocks conforming the area are of volcanic and intrusive types. Geomorphologically, the site is still unstable and broken rocks are frequently carried downhill from the upper slopes, particularly during torrential storms. Sheet and rill erosion is also conspicuous on the steeper slopes.

The lower flat areas (below 1,000 m elevation) were used for agricultural purposes until approximately 1955 and were in a state of early ecological succession, until they were developed for housing and sports facilities in the late eighties. Horse and cow grazing was also common in these lower areas during winter and spring, until the late eighties. The upper parts of the site (above 1,100 m elevation) are still patchily covered by a sclerophyllous vegetation locally known as matorral. Until 1982 there was low-intensity wood-cutting in this upper area, but since then human impact has increased. Grazing by horses has become more common and people are using the area more frequently for horse rides and for picnics. This site attracted numerous researchers during 1976-1990 because it represented a mediterranean scrub (matorral) in close proximity to Santiago, in a relatively protected status. Since then, however, human disturbance has increased strongly.

In the immediate future, a trade-off solution will have to be found, in which the site can still be used for research concomitant with light human use. In this regard, the San Carlos de Apoquindo site could become an example of a multiple purpose (multiple-use) site close to Santiago. To understand the vegetation dynamics and associated fauna in light of this potential use is of great importance. As shown below, this site has contributed enormously to our understanding of ecological processes of flora and fauna components faced with human disturbance, climatic vagaries, and animal invaders. But still more is to be gained if long-term monitoring is continued at the site. In what follows, I summarize all the literature referring to the site, provide unpublished information, and highlight a few of the most salient features that characterize San Carlos de Apoquindo. I end up with a call for renewed efforts at studying this site's ecology from an ecosystem perspective.

LITERATURE REVIEW

A total of 132 literature entries describe varied aspects of the ecology of San Carlos de Apoquindo, in about 30 topics (Table 1). Close to 40 (30 %) references address essentially botanical aspects of the site, the remaining 70 % dealing with animals (Table 1). This bias apparently resulted from botanists preferring to work in less disturbed areas farther from Santiago, such as Fundo Santa Laura (33 °03'S, 71°00'W) near Til-Til. Zoologists, on the other hand, apparently preferred to work closer to home. Among animals, arthropods, amphibians, lizards, snakes, passerine birds, and a variety of scavengers have been little studied, whereas small mammals, rabbits, together with avian and mammalian predators have received a lot of attention. This bias reflects the preferences of the zoologists that worked in the area. Thematically, all sorts of ecological interfaces have been addressed, from plant/climate, to plant/soil, to plant/herbivore, to herbivore/predator interactions, and to decompo-

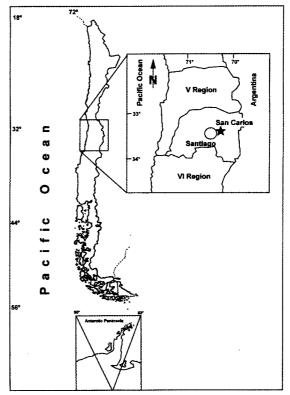


Fig. 1: Location of San Carlos de Apoquindo study site (33° 23' S, 70° 31' W), central Chile. Localización del sitio de estudio denominado San Carlos de Apoquindo (33° 23' S, 70° 31' O), en Chile central.

sition of animal carcasses. But this apparently comprehensive work is misleading. Only one study has been done of each plant/climate, plant/microclimate, plant/soil, and animal decomposition, and the soil seed bank is virtually unknown. Up to now, no description existed of soils and climate in the area. Notably lacking are analyses of the influence of climatic or meteorological factors on animals, as well as an ecosytemic synthesis, which obviously requires filling some of the gaps in the knowledge of ecosytem compartments. I here pinpoint what is well known, and by omission, what is insufficiently known. In presenting different topics, I span the following sequence: climate, soils, habitat types, shrub vegetation, herbaceous vegetation, arthropods, amphibians and reptiles, nonraptorial birds, raptorial birds, mammals, and vertebrate predators.

TABLE 1

Bibliographic references on different ecological aspects of San Carlos de Apoquindo, 1976-2000

Main topic addressed	Literature sources
Vegetation analysis	Armesto & Gutiérrez (1980), Fuentes (1981c, 1990, 1991), Fuentes et al. (1984a), Gutiérrez & Armesto (1978), Hoffmann et al. (1989), Walkowiak et al. (1984)
Vegetation dynamics	Fuentes et al. (1984b, 1986), Martínez & Fuentes (1993), Muñoz & Fuentes (1989), Holmgren et al. (2000)
Vegetation management	Hajek (1981)
Vegetation succession	Armesto & Pickett (1985), Bustamante (1991)
Plant defoliation (experimental)	Poiani & del Pozo (1986), Torres et al. (1980)
Plant microclimate	del Pozo (1985), del Pozo et al. (1989)
Plant morphology	Ginocchio & Montenegro (1989, 1992, 1996), Montenegro & Ginocchio (1993, 1995, 1998)
Plant/climate interaction	Fuentes et al. (1988)
Plant/insect interaction	Aljaro et al. (1984.), Fuentes et al. (1981, 1987), Ginocchio & Montenegro (1994), Martínez et al. (1992), Poiani (1984), Poiani & Fuentes (1985)
Plant/mammal interaction	Fuentes & Simonetti (1982), Fuentes et al. (1983), Gutiérrez & Armesto (1981), Simonetti & Fuentes (1983), Simonetti & Montenegro (1981), Simonetti et al. (1984a)
Plant/plant interaction	Gutiérrez (1977), Fuentes & Gutiérrez (1981), Gutiérrez & Fuentes (1979), Hoffmann et al. (1986)
Plant/soil interaction	Cisternas & Yates (1982)
Lizard ecology	Carothers (1987), Carothers et al. (1997, 1998), Fuentes (1981a, 1981b), Jaksic et al. (1979c, 1980a), Simonetti & Yánez (1984)
Lizards, predation on	Jaksic & Fuentes (1980), Jaksic & Núñez (1979), Jaksic et al. (1982), Medel (1987), Medel et al. (1988, 1990)
Snake ecology	Greene & Jaksic (1992)
Small mammal analysis	Jaksic & Yáñez (1977, 1979a), Simonetti & Maldonado (1988),
6 11 1 11	Yáñez & Jaksic (1977a, 1977b), Yáñez et al. (1979)
Small mammal assemblage	Iriarte et al. (1989a), Jaksic & Yáñez (1978), Jaksic et al. (1981a, 1981c)
Small mammal ecology	Le Boulengé & Fuentes (1978), Yáñez (1976), Yáñez & Jaksic (1978b), Simonetti (1982, 1983, 1986b)
Small mammal predation	Jaksic (1982, 1986), Simonetti (1986a, 1989c)
Small mammal reproduction	Contreras (1977), Rojas et al. (1977)
Rabbit ecology	Jaksic & Fuentes (1988, 1991), Simonetti (1989b)
Rabbits, predation on	Jaksic & Ostfeld (1983), Jaksic & Soriguer (1981), Jaksic & Yáñez (1980a), Jaksic et al. (1979a, 1979b), Simonetti (1989d), Simonetti & Fuentes (1982)
Passerine ecology	Lazo & Anabalón (1991), Lazo et al. (1990)
Raptor behavior	Jiménez (1987), Jiménez & Jaksic (1989, 1991, 1993a), Mendelsohn & Jaksic (1989)
Raptor diet	Jaksic & Yáñez. (1979b), Jaksic et al. (1980b, 1986), Schlatter et al. (1980a, 1980c, 1982), Yáñez & Jaksic (1978a), Yáñez et al. (1978, 1980, 1982)
Raptor ecology	Jiménez (1995), Jiménez & Jaksic (1990)
Raptor niche relationships	Jaksic & Yáñez (1980b), Jaksic et al. (1977), Schlatter et al. (1980b)
Fox diet	Iriarte (1986), Iriarte et al. (1989b), Simonetti (1986c)
Fox niche relationships	Fuentes & Jaksic (1979), Jaksic (1977), Jaksic et al. (1980c), Yáñez & Jaksic (1978c)
Predator assemblage	Jaksic (1980, 1982), Jaksic et al. (1981b), Simonetti (1988, 1989a)
Predator selection of prey	Bozinovic & Medel (1988), Jaksic (1979, 1989), Jiménez & Jaksic (1993b), Pavez et al. (1992)
Animal decomposition	Simonetti et al. (1992)

Referencias bibliográficas sobre distintos aspectos ecológicos de San Carlos de Apoquindo, 1976-2000

CLIMATE

The climate in San Carlos de Apoquindo is mediterranean, with an annual mean of 376.4 mm rainfall, concentrated (65 %) during the winter months from June to August (Table 2). On average, it rains every month of the year, but precipitation is scant from December to March (3 % of the yearly total). Mean temperature is highest from December to March, corresponding to the austral summer, and lowest from June to August, the austral winter. On average, the mean minimum temperature goes 6 °C below the mean temperature, while the maximum mean goes 7 °C higher. The broadest range of temperatures is observed from December to February (16-17 °C between mean maximum and mean minimum temperature), and the narrowest from May to August (9-10 °C). The combination of high temperature and low precipitation occurs from December to March, thus determining a summer drought. Although not quantified, the dominant winds blow up from the valley (from the west) toward the mountains during the day, and from the opposite direction at night. Thermal drafts are observed on equatorial slopes, as the air heats up product of the higher solar radiation received by those slopes, and raises toward the ridgetops. No attempt has been made to detect El Niño/Southern Oscillation signature in the local climate, an overdue task.

SOILS

Essentially two soil types may be recognized in San Carlos de Apoquindo, those found in Equatorial-facing slopes and those in polar-facing slopes. The alluvial fans found in between are a complex mixture of the two fundamental soils in slopes.

Equatorial-facing slopes

Classification according to soil taxonomy: Typic Xeropsanment (prov. class.); according to FAO-Unesco: Cambic Arenosol (prov. class.). Parent material: intermediate volcanic rocks (coarsegrained). General physiography: steep slope valleys in E-W direction. Macrorelief: hilly to mountainous, linear irregular slopes. Rock outcrops: 2-10 %; surface stoniness: 3-5 % (very stony). Slope gradient: $32^\circ = 62$ %. Position on slope: middle slope, about 100 m above valley bottom. Exposure of profile: north. Surface characteristics: moderate brittle surface sealing, no cracking. Water erosion: severe sheet and rill erosion, slight deposition (overwash). Wind erosion: very slight. Ground water influence: absent. Drainage class: somewhat excessively drained.

Profile characteristics. A11 (0-10 cm): Very dark greyish brown to dark brown (10 YR 3/2-3) when moist, dark (greyish) brown (10 YR 4/2-3) when dry, loamy fine sand, weak very thin platy structure, loose (dry), very friable (moist), nonsticky and non-plastic (wet) consistence, many very fine and fine, few medium and coarse continuous tubular pores, many very fine, few fine and medium roots, clear smooth boundary to A12 (below).

A12 (10-40 cm): Very dark greyish brown to dark brown (10 YR 3/2-3) when moist, dark (greyish) brown (10 YR 4/2-3) when dry, slightly stony and slightly gravelly loamy sand, weak, fine to medium subangular blocky structure, soft (dry), very friable (moist), non-sticky and non-plastic (wet) consistence, common very fine and fine, few medium and coarse continuous tubular pores, common very fine and fine, few medium and coarse roots, gradual broken boundary to AC (below).

TABLE 2

Mean monthly precipitation and temperatures in Cerro Calán (33° 23' S, 70° 32' W, 900 m elevation), 1 km west from San Carlos de Apoquindo, 1968-1988

Precipitación mensual media y temperaturas en Cerro Calán (33° 23' S, 70° 32' O, 900 m elevation), 1 km al oeste de San Carlos de Apoquindo, 1968-1988

Parameters	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Precipitation (mm)	1.3	3.2	5.6	15.8	54.8	66.1	111.1	68.2	38.3	20.5	14.4	2.9	376.4
Mean temperature (°C)	21.9	18.4	20.1	16.6	13.2	10.8	10.4	10.9	12.4	15.4	18.1	21.0	15.9
Mean minimum temperature (°C)	13.8	13.5	13.3	9.9	8.3	6.5	6.1	6.0	6.9	8.9	10.6	12.7	9.6
Mean maximum temperature (°C)	30.2	29.9	27.8	23.1	18.1	15.8	15.6	16.2	18.2	22.4	25.1	28.7	22.6

AC (40-60 cm): Dark greyish brown to olive brown (2.5 Y 4/3) when moist, brown (10 YR 5/ 3-4) when dry, slightly stony, gravelly loamy sand, moderately coherent porous massive to weak fine to medium subangular blocky structure, soft (dry), very friable (moist), non-sticky and nonplastic (wet) consistence, common very fine, few fine and medium continuous tubular pores, common very fine, few fine roots, clear smooth boundary to C (below).

C (60-80 cm): Mixed colors of soil (like AC horizon) and rotten rock, strongly coherent massive structure, consisting of gravel and sandy soil material locally. Stones and boulders of various sizes are encountered throughout the profile.

Polar-facing slopes

Classification according to soil taxonomy: Mollic Haploxeralf (prelim. class.); according to FAO-Unesco: Orthic Luvisol (prelim. class.). Parent material: intermediate volcanic rocks. General physiography: steep sloped valleys in E-W direction. Macrorelief: hilly to mountainous, linear irregular slopes. Rock outcrops: less than 2 %; surface stoniness: 3-15 % (very stony). Slope gradient: 31°= 60 %. Position on slope: lower slope, about 15 m above valley bottom. Exposure of profile: south (SEE). Surface characteristics: no surface sealing (granular structure with several cm litter, no crusting nor cracking. Water erosion: moderate sheet erosion, very slight deposition (overwash). Wind erosion: absent. Ground water influence: absent. Drainage class: well drained. Soil fauna: very intense biological activity in upper 20 cm of profile, little activity below 20 cm depth.

Profile characteristics. A11 (0-2 cm): Very dark brown (7.5 YR 2/2) when moist, dark brown (7.5 YR 3-4/2) when dry, slightly stony gravelly clay loam strong very fine and fine granular structure, slightly hard (dry), friable (moist), slightly sticky and slightly plastic (wet) consistence, many very fine to medium exped interstitial pores, few very fine roots, clear smooth boundary to A12 (below).

A12 (2-15 cm): Very dark brown (7.5 YR 2/2) when moist, dark brown (7.5 YR 3-4/2) when dry, slightly stone, gravelly clay loam, mode coarse subangular blocky structure, breaking into strong subangular blocky peds, slightly hard (dry), friable (moist), slightly sticky and slightly plastic (wet) consistence, common very fine and fine, few medium and coarse continuous inped tubular pores, many very fine and fine, few medium and coarse roots, clear smooth boundary to B1t (below).

Blt (15-30 cm): Dark brown (7.5 YR 3/2 when moist, 7.5 YR 3-4/2 when dry) slightly stony gravelly clay loam, moderate coarse subangular blocky structure breaking into strong fine angular blocky peds, broken, thin clay-humus cutans, slightly hard to hard (dry), friable (moist), sticky and plastic (wet) consistence, many very fine, common fine and few coarse continuous inped tubular pores, many very fine, common fine and few medium and coarse roots, gradual smooth boundary to B2t (below).

B2t (30-50 cm): Dark brown (7.5 YR 3/2 when moist, 7.5 YR 3-4/2 when dry) slightly stony gravelly clay, somewhat massive to weak medium subangular blocky structure, broken thin clay-humus cutans, hard (dry), friable (moist), sticky and plastic (wet) consistence, common very fine, few fine to coarse continuous inped tubular pores, common very fine and fine, few medium roots (occasionally very coarse tree roots), gradual smooth boundary to B3t (below).

B3t (50-80 cm): Dark brown (7.5 YR 3/3 both moist and dry) slightly stony gravelly clay, strongly coherent porous massive structure, broken thin clay-humus cutans, hard (dry), friable (moist), sticky and plastic (wet) consistence, common very fine and few fine and medium continuous tubular pores, common very fine and fine, few medium roots (locally very coarse), abrupt broken boundary to R (below).

R (over 80 cm): Hard rock boulders and stones, depth varies between 50 and more than 80 cm.

HABITAT TYPES

In San Carlos de Apoquindo, seven habitat types may be recognized (Table 3): flatlands, ravines, ridgetops, and slopes (east-, west-, polar-, and equatorial-facing). Jiménez & Jaksic (1989) mapped these habitats and calculated their surface areas (slope-corrected) with a digital planimeter from a high-resolution aerial photograph. They also described the vegetation physiognomy of each habitat type with nine linear transects of 20 m each, measuring the cover represented by trees, shrubs, herbs, bare ground, and rocks (Table 3).

Because of its orientation and rugged characteristic, San Carlos de Apoquindo is dominated by ridgetops, equatorial and polar slopes, together accounting for over 60 % of the total area. West slopes follow in representation (ca. 14 %), whereas flatlands, ravines, and east slopes are scarcely represented (Table 3). Elevations range from 1,050 to 1,915 m, and slopes from 0 to 47 degrees. Tree

TABLE 3

Habitat features of San Carlos de Apoquindo. Cover values were obtained in winter 1985

Características del hábitat en San Carlos de Apoquindo. Los valores de cobertura fueron obtenidos en el invierno de 1985

Features	Flatland	Ravine	Ridgetop	Equatorial slope	Polar slope	East slope	West slope
Percent of area	9.5	7.0	18.5	25.7	19.2	6.6	13.5
Elevation (m)	1,050-1,200	1,250-1,350	1,250-1,915	1,100-1,800	1,075-1,575	1,170-1,730	1,200-1,825
Slope (degrees)	7-22	7-41	0-9	28-47	10-41	21-44	20-44
Tree cover (%)	50.9	80.6	1.3	19.9	65.2	4.4	11.5
Shrub cover (%)	12.6	3.9	59.1	26.4	7.9	46.6	50.1
Herb cover (%)	18.7	9.3	13.5	28.2	20.0	0.0	4.4
Bare ground (%)	15.6	5.1	24.7	22.9	6.0	36.1	22.9
Rocky ground (%)	2.2	1.1	1.4	2.6	0.9	12.9	11.1

(or tall shrub) cover is extensive only in flatlands, ravines, and polar slopes, whereas low-shrub cover is predominant in ridgetops, east and west slopes. Herbs (mostly grasses) reach their maximum cover in equatorial slopes. Ridgetops, equatorial, east and west slopes have important areas of bare ground, and the most rocky habitats are on east and west slopes (Table 3).

Shrub vegetation

San Carlos de Apoquindo is covered by sclerophyllous vegetation, which physiognomically may be described as an evergreen scrub, locally know as matorral, and very similar to the chaparral in central and southern California. Although some species and individuals reach tree proportions, the vegetation is best characterized as a shrubland. Shrub cover is dominated by eight shrub species. The best covered areas are the alluvial fans and polar slopes (ca. 70 % cover), with equatorial slopes reaching only half that cover (Table 4). Different shrub species dominate in different landscape aspects: *Colliguaya* odorifera in equatorial slopes, both *Lithrea* caustica and Kageneckia oblonga in polar slopes, and *Quillaja saponaria* in alluvial fans (Table 4).

There is no general phenological description of the shrub vegetation in San Carlos de Apoquindo. But there is a fairly detailed one referring to the flowering and fruiting period of the most common woody shrubs at the site (Table 5). Modal flowering occurs during October and November of each year (Fig. 2), with three species starting flowering as early as in August (*Muehlenbeckia hastulata, Cestrum palqui, Porlieria chilensis*) and one parasitic non-shrubby species finishing flowering as late as in July of the following year (*Tristerix tetrandus*). Twenty-four other species lie in between these dates. Note the special case of *Colliguaya odorifera*, which starts flowering

TABLE 4

Shrub cover in San Carlos de Apoquindo, 1983. Equatorial and polar slopes refer to those that face to the Equator and to the Pole, respectively

Cobertura arbustiva en San Carlos de Apoquindo, 1983. Ladera Ecuatorial y polar se refiere a aquella que mira hacia el Ecuador o al polo, respectivamente

Shrub species	Equatorial slope Absolute (Relative) (%)		Polar slope Absolute (Relative) (%)		Alluvial fan Absolute (Relative) (%)	
Lithrea caustica	9.9	(28.5)	29.4	(42.5)	8.4	(12.1)
Kageneckia oblonga	0.0	(0.0)	20.2	(29.1)	0.0	(0.0)
Colliguaya odorifera	13.0	(37.7)	1.7	(2.5)	4.8	(7.1)
Baccharis rosmarinifolia	3.9	(11.2)	3.9	(5.6)	10.5	(15.2)
Quillaja saponaria	2.7	(7.9)	12.2	(17.6)	37.6	(54.5)
Podanthus mitique	3.4	(9.8)	1.9	(2.7)	0.0	(0.0)
Acacia caven	1.7	(4.9)	0.0	(0.0)	5.6	(8.1)
Azara dentata	0.0	(0.0)	0.0	(0.0)	2.1	(3.0)
Shrub cover (> 1% absolute cover)	34.6	(100.0)	69.3	(100.0)	69.0	(100.0)
Total shrub cover	37.1		75.5	· · ·	69.7	. ,

as early as in May and finishes in October (Table 5). Fruiting is stacked upon flowering, with a mode in March of each year (Fig. 2). Muehlenbeckia hastulata and Tristerix tetrandus are the first to start, in October of any given year, while the last to finish in July of the following year is Cestrum palqui. Twenty-five other species fall in between these dates. Note the exceptional case of the non-shrubby parasite *Tristerix* aphyllus, which starts fruiting in June and finishes in November. Hoffmann et al. (1989) made a comparison of fruit and seed characteristics of shrub woody species in mediterranean-type regions of Chile and California. They found that the abundance of fleshy fruits < 15 mm in diameter (associated to the bird-dispersal syndrome), their size distribution, and the frequency of black fruits was very similar between the evergreen shrublands of Chile and California. Nevertheless, the size distribution and other characteristics of winddispersed seeds were different.

Fuentes et al. (1984) evaluated the seed rain and seed bank of woody species in San Carlos de

Apoquindo. During 1981-1982 they used 40 x 40 cm trays to collect shrub seeds under the canopy of shrubs (n = 20) as well as in exposed areas among shrubs (n = 20). They labelled the seeds collected at these surfaces as seed rain. During May 1982, Fuentes et al. (1984) also took soil samples of 40 x 40 x 1 cm depth to assess the seed bank within the first centimeter of topsoil. They took 40 samples under shrubs and 10 samples in exposed areas. Eight shrub species (all except Schinus polygamus) were found on the surface of exposed areas, and only two in the soil (Table 6). Eight species were identified in the seed bank under shrub cover (all except Schinus polygamus), and only six on the soil surface (all except Muehlenbeckia hastulata and Proustia cuneifolia). A few generalizations may be made with these results: (a) In exposed areas, only a subset of what is in the soil surface is found in the seed bank. (b) The opposite occurs under shrubs. (c) Overall, there are more seeds under shrubs than in exposed areas, except for the wind-dispersed and small-seeded Baccharis spp.

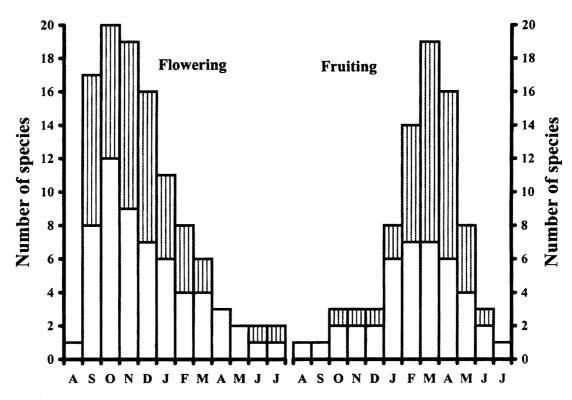


Fig. 2: Reproductive phenology of woody shrub species in San Carlos de Apoquindo. Left panel: Number of species in flower throughout the year. Righ panel: Number of species with ripe fruits throughout the year. In open bars, species with fleshy fruits. Hatched, species with other fruit types.

Fenología reproductiva de las especies arbustivas leñosas en San Carlos de Apoquindo. Panel izquierdo: Número de especies en flor a lo largo del año. Panel derecho: Número de especies con frutos maduros a lo largo del año. En barras blancas, especies con frutos carnosos. En achurado, especies con otros tipos de frutos.

TABLE 5

Flowering and fruiting periods of woody shrub species in San Carlos de Apoquindo, and morphological features of fruits and seeds. Families are arranged alphabetically. Only in the case of *Acacia caven* fruit diameter is expressed as fruit length

Períodos de floración y fructificación de las especies arbustivas leñosas en San Carlos de Apoquindo, y las características morfológicas de frutos y semillas. Las Familias están dispuestas alfabéticamente. Sólo en el caso de *Acacia caven* el diámetro del fruto se expresa como longitud

Woody shrubs	Flowering period	Fruiting period	Fruit type	Fruit color	Fruit diameter (mm)	Number of seeds/fruit	Seed size (mm)
Anacardiaceae							
Lithrea caustica	Oct-Dec	Jan-May	Drupe	Grey-green	61	1	5.9
Schinus polygamus	Oct-Dec	Mar-May	Drupe	Purple-black	54	1	3.9
Berberidaceae			-	-			
Berberis chilensis	Sep-Nov	Jan-Mar	Berry	Violet-blue	52	nd	nd
Cactaceae							
Trichocereus chilensis	Sep-Nov	Jan-Feb	Berry	Yellow-green	365	692	1.9
Celastraceae							
Maytenus boaria	Sep-Dec	Feb-Apr	Capsule	Yellow	6	1-2	4.0
Compositae							
Eupatorium salvia	Sep-Dec	Jan-Feb	Achene	Brown	44	1	1.0
Podanthus mitique	Sep-Dec	Mar-Apr	Achene	Brown	28	1	nd
Gochnata fascicularis	Nov-Feb	Feb-May	Achene	White	41	1	nd
Proustia cuneifolia	Jan-Mar	Feb-May	Achene	White	39	1	1.0
Baccharis sp.	Feb-Mar	Feb-May	Achene	White	23	1	nd
Elaeocarpaceae							
Aristotelia chilensis	Sep-Jan	Jan-Feb	Berry	Purple-black	57	2-4	2.0
Euphorbiaceae							
Colliguaya odorifera	May-Oct	Jan-Feb	Capsule	Light brown	nd	1-3	3.5
Flacourtiaceae							
Azara dentata	Sep-Oct	Jan-Feb	Berry	Pale orange	52	nd	2.4
Azara petiolaris	Sep-Oct	Mar-Apr	Berry	Grey-green	63	4-6	1.5
Leguminosae							
Acacia caven	Sep-Oct	Mar-Jun	Indehiscent legume	Dark brown	739	15-28	6.4
Psoralea glandulosa	Sep-Feb	Feb-Apr	Legume	Light brown	65	1	4.5
Loranthaceae							
Tristerix aphyllus	Oct-May	Jun-Nov	Spurious berry	Pale orange	86	1	7.2
Tristerix tetrandus	Jan-Jul	Oct-Dec	Spurious berry	Yellow-white	89	1	7.3
Myrtaceae							
Myrceugenia chequen	Oct-Apr	Mar-Apr	Berry	Redish-black	65	3-4	3.0
Polygonaceae							
Muehlenbeckia hastulata	Aug-Jan	Oct-Dec	Nut	Yellow-white	5	1	nd
Rhamnaceae							
Trevoa trinervis	Sep-Oct	Dec-Jan	Drupe	Green	54	1	3.8
Talguenea quinquinervis	Oct-Nov	Mar-Apr	Nut	Light brown	42	1	4.0
Colletia spinosa	Nov-Dec	Dec-Feb	Drupe	Brown	45	3	1.8
Rosaceae							
Kageneckia oblonga	Sep-Dec	Mar-Apr	Folicle	Light brown	268	50-70	10.3
Quillaja saponaria	Nov-Jan	Jan-Apr	Folicle	Light brown	224	50-70	10.3
Solanaceae							
Cestrum palqui	Aug-Mar	Feb-Jul	Berry	Purple-black	10	8-10	nd
Solanum tomatillo	Sep-Jan	Feb-May	Berry	Red	69	15-18	nd
Zygophyllaceae							
Porlieria chilensis	Aug-Sep	Feb-Mar	Capsule	Dark violet	15	1-4	8.9

Herbaceous vegetation

Most herb species in the open areas of San Carlos de Apoquindo are invasive European grasses (Rojas et al. 1977), with native herbs essentially concentrated under shrubs. Consequently, the presence of herb species was evaluated under the canopy of two shrub species/forms on equatorialand polar-facing slopes, and in open space. Shrub forms were: erect branches versus prostate branches (reaching down to the ground). The presence and frequency of herbaceous plants depended strongly on slope aspect and on the presence/absence of shrubs.

TABLE 6

Seed rain and seed bank of woody shrubs in San Carlos de Apoquindo, 1981-1982

Shrub species	Dispersal	Expo	osed	Under shrubs		
	-	Surface (n = 20)	Soil (n = 10)	Surface (n = 20)	Soil (n = 40)	
Azara dentata	Birds	0.3	0.0	90.0	64.9	
Baccharis sp.	Wind	102.5	0.0	14.8	0.4	
Colliguaya odorifera	Self	5.0	1.5	13.5	6.9	
Lithrea caustica	Birds	1.3	4.5	3.0	6.4	
Muehlenbeckia hastulata	Birds	0.3	0.0	0.0	1.5	
Proustia cuneifolia	Wind	1.3	0.0	0.0	3.3	
Quillaja saponaria	Wind	0.3	0.0	4.0	18.4	
Schinus polygamus	Birds?	0.0	0.0	1.5	0.0	
Trevoa trinervis	Birds?	0.5	0.0	0.0	0.5	

Lluvia de semillas y banco de semillas de arbustos leñosos en San Carlos de Apoquindo, 1981-1982

In equatorial slopes, at least six annuals and four perennials were identified, but were never found all together. Four herb species each were identified under the canopy of *Lithrea caustica*, either erect or prostate (Table 7). Under *Colliguaya odorifera*, either erect or prostate, six or five species were identified, respectively. And six species were identified in the open, where there were no shrubs present (Table 7). In polar slopes, at least four annuals and two perennials were identified: three to one species under *Lithrea caustica*, four to three under *Kageneckia oblonga*, and two in open

spaces (Table 7). In general, there were more herb species under shrubs in equatorial than in polar slopes. It is curious that there were more herb species in open spaces of equatorial slopes than in open spaces of polar slopes, which are more mesic. A cautionary note should be introduced here: herb presence and growth is strongly dependent on the rainfall previous to plant sampling. Therefore, results from a single year of sampling should be viewed conservatively.

Holmgren et al. (2000) showed that in exposed areas of San Carlos de Apôquindo, the herb layer

TABLE 7

Distribution of herbaceous plants in San Carlos de Apoquindo, 1983. Results are expressed as percentage frequency per species, n = 9 samples

Distribución de plantas herbáceas en San Carlos de Apoquindo, 1983. Los results se expresan como porcentaje de frecuencia por especie, n = 9 muestras

Equatorial slope	Туре	Lithrea	caustica	Colligua	va odorifera	Exposed
1 1	7 1	Erect	Prostate	Erect	Prostate	•
Chaetanthera flabellata	Annual	0.0	0.0	0.0	0.0	22.2
Erodium cicutarium	Annual	0.0	0.0	11.1	0.0	33.3
Helenium aromaticum	Annual	22.2	0.0	22.2	11.1	33.3
Madia sp.	Annual	44.4	22.2	44.4	44.4	11.1
Moscharia pinnatifida	Annual	0.0	0.0	0.0	0.0	11.1
Stellaria cuspidata	Annual	22.2	11.1	0.0	11.1	0.0
Gnaphalium sp.	Perennial	33.3	22.2	33.3	0.0	33.3
Oxalis lineata	Perennial	0.0	0.0	0.0	22.2	0.0
Phacelia secunda	Perennial	0.0	0.0	22.2	22.2	0.0
Senecio officinalis	Perennial	0.0	11.1	, 11.1	0.0	0.0
Polar slope	Туре	Lithrea	caustica	Colliguay	a odorifera	Exposed
•		Erect	Prostate	Erect	Prostate	-
Madia sp.	Annual	0.0	0.0	11.3	0.0	0.0
Moscharia pinnatifida	Annual	22.2	0.0	0.0	11.1	0.0
Oxalis sp.	Annual	22.2	0.0	0.0	11.1	0.0
Stellaria cuspidata	Annual	0.0	0.0	11.1	0.0	0.0
Pasithea coerulea	Perennial	44.4	0.0	22.2	11.1	11.1
Solenomelus officinalis	Perennial	0.0	11.1	11.1	0.0	33.3

was dominated by introduced herbs which tended to have a prostate growth form (Table 8). Interestingly, there was a temporal component determining the presence or absence of some species (two species were recorded only in 1989, three only in 1990, and eight in both years), which Holmgren et al. (2000) could not attribute to any specific factor.

ARTHROPODS

There is no list of arthropods present in San Carlos de Apoquindo. The only quantitative information available on this faunal component is hidden in a paper on the microhabitat use by small mammals at the site (Simonetti 1989c). This author sampled terrestrial (epigean) arthropods larger than 5 mm body length with 1 m² quadrats placed randomly in two microhabitat types (under shrubs and in the open) during spring 1984 and summer 1985. Insects and arachnids were classified to ordinal level, and some interesting patterns emerged (Table 9). Coleopterans dominated numerically in the two microhabitats during the two seasons, except in the open during summer 1985, when 100 % of the arthropod fauna was represented by hemipterans, likely an anomaly. Overall, lepidopteran larvae and pupae together with hemipterans were the second most numerous components. Except for a high representation of spiders during summer 1985 under shrubs, arachnids were never abundant. It is clear that arthropod abundance was higher in spring than in summer in both microhabitats, and that abundance was always higher under shrubs, regardless of season (Table 9). It should be kept in mind that all data refer to terrestrial (epigean) arthropods. There is no information whatsoever on foliage arthropods, nor on soil arthropods.

AMPHIBIANS AND REPTILES

Only the toad *Bufo chilensis* has been detected in San Carlos de Apoquindo, in congruence with the seasonal character of streams and few pounded areas. Nevertheless, no exhaustive search for amphibians has been conducted at the site, and no study has been made of *Bufo chilensis* to learn how it copes with the relatively arid environment afforded by the site. This would be a worthwhile effort.

The five lizard species present in San Carlos de Apoquindo, and their respective weights are reported in Table 10. Despite intense ecological activity at the site, few studies has been conducted on lizard ecology there. An exception is the work of Medel et al. (1990). They studied the correlates of predation on three syntopic Liolaemus species in a 0.82 ha site during two periods: January to March 1986 and October 1986 to January 1987. They color-marked lizards during the first period, measuring them, determining their abundance and microhabitat use, and assessing the state of their tail (intact or damaged). During the second period, Medel et al. (1990) recaptured marked lizards and reassessed their tail. Knowing how many were initially marked, they were able to estimate the survivorship of the lizards. Results are in Table 11.

TABLE 8

Herbaceous species in exposed areas of San Carlos de Apoquindo, 1989-90. Listing is in approximate decreasing cover, + = present, - = absent

Herb species	Family	Origin	Growth habit	1989	1990
Bromus berterianus	Poaceae	Native	Erect	+	+
Lophocloa cristata	Poaceae	Introduced	Erect	+	+
Erodium cicutarium	Geraniaceae	Introduced	Prostate	+	+
Medicago polymorpha	Leguminosae	Introduced	Prostate	+	+
Trifolium glomeratum	Leguminosae	Introduced	Prostate	+	• +
Amsinckia hispida	Boraginaceae	Native	Erect	+	+
Clarkia tenella	Onagraceae	Native	Erect	+	+
Madia chilensis	Asteraceae	Native	Erect	+	+
Vulpia bromoides	Poaceae	Introduced	Erect	+	-
Facelis retusa	Asteraceae	Introduced	Erect	+	-
Capsella bursa-pastoris	Brassicaceae	Introduced	Erect	-	+
Erodium moschatum	Geraniaceae	Introduced	Prostate	-	+
Deschampsia sp.	Poaceae	Native	Erect	-	+

Especies herbáceas en áreas expuestas de San Carlos de Apoquindo, 1989-90. La lista sigue un orden aproximadamente decreciente en cobertura, + = presente, - = ausente

TABLE 9

Arthropod composition (%) and abundance in two microhabitat types (in the open and under shrubs) in San Carlos de Apoquindo, 1984-1985

Composición (%) y abundancia de artrópodos en dos tipos de microhábitat (expuesto y bajo arbustos) en San Carlos de Apoquindo, 1984-1985

Arthropod orders	Under	shrubs	Ex	posed
•	Spring 1984	Summer 1985	Spring 1984	Summer 1985
Insects				
Coleoptera adults	27.9	27.7	48.4	0.0
Coleoptera larvae	4.4	16.7	0.0	0.0
Hemiptera	22.1	0.0	6.5	100.0
Homoptera	1.5	0.0	16.1	0.0
Lepidoptera larvae	33.8	0.0	25.8	0.0
Lepidoptera pupae	0.0	5.6	0.0	0.0
Orthoptera	2.9	16.7	3.2	0.0
Unidentified	1.5	5.6	0.0	0.0
Arachnids				
Araneae	4.4	22.1	0.0	0.0
Scorpionida	1.5	5.6	0.0	0.0
Total	100.0	100.0	100.0	100.0
Number $m^{-2} \pm 2SE(n)$	3.2 ± 0.4 (21)	1.5 ± 0.3 (12)	1.0 ± 0.2 (31)	0.1 ± 0.1 (10)

Liolaemus fuscus was the smallest, most abundant, and it used ground and rocks. Liolaemus monticola was the largest, least abundant, and the one lizard that used rocks most frequently. Liolaemus lemniscatus was intermediate in size, intermediate in abundance, and the only lizard that used the ground extensively (Table 11). Both L. fuscus and L. monticola survived well into the second study period (ca. 35 %) and had relatively low frequency of damaged tails (ca. 53 %). In contrast, Liolaemus lemniscatus survived at about half the rate of its congeners, and had a slightly

TABLE 10

Lizard species in San Carlos de Apoquindo, 1973-1979. Values given are weight and ranking by relative abundance (1 = highest abundance)

Especies de lagartijas en San Carlos de Apoquindo, 1973-1979. Se muestra peso y ordenación por abundancia relativa (1 = abundancia mayor)

Species	Weight (g), $\overline{x} \pm 2SE(n)$	Abundance rank (1973-79)
Liolaemus lemniscatus	2.5 ± 0.5 (11)	2
Liolaemus fuscus	2.5 ± 0.0 (1)	3
Liolaemus monticola	5.3 ± 1.2 (14)	1
Liolaemus tenuis	4.7 ± 0.7 (3)	4
Callopistes palluma	82.3 ± 18.2 (6)	5

higher frequency of damaged tails. Local predators perhaps keyed on this species because of its more terrestrial habit, and perhaps even reduced its abundance. It should be interesting to have detailed data on the lizards consumed by local predators, in order to test these hypotheses.

NON-RAPTORIAL BIRDS

Twenty-nine non-raptorial terrestrial species are rather common in San Carlos de Apoquindo (Table 12). Twenty-two are passerines (76 %), most of them residents. Among passerines, the most common food habits are represented by primarily insectivores (15 species) and granivores (five species). One species of each a folivore and a primarily frugivore are found at the site. The nonpasserine species are represented by four granivores, two nectarivores, and one insectivore (Table 12). The suite of species represented at San Carlos de Apoquindo is typical of relatively undisturbed evergreen shrublands anywhere in central Chile. It should be noted that the quail Callipepla californica is an invader from California, which now thrives in matorral areas of central Chile.

Only a couple of ecological studies have been conducted on the local passerine fauna. Lazo et al. (1990) quantified the number of nests, their composition in terms of nesting species identity, and the trophic structure (percentage of insectivorous, granivorous and omnivorous birds rep-

TABLE 11

Body length ($\bar{x} \pm 2SE$, n in parentheses), abundance, microhabitat use, survivorship, and frequency of tail damage, in three *Liolaemus* species in San Carlos de Apoquindo, 1986-1987

Longitud corporal ($\bar{x} \pm 2EE$, n en paréntesis), abundancia, uso de microhábitat, sobrevivencia, y frecuencia de daño en la cola, en tres especies de *Liolaemus* en San Carlos de Apoquindo, 1986-1987

Species	L. fuscus	L. lemniscatus	L. monticola
Snout-vent length (mm)	44.3 ± 0.7 (133)	45.1 ± 0.9 (57)	55.5 ± 1.6 (28)
Relative abundance (%)	59.5 (144)	23.6 (57)	16.9 (41)
Ground: rock use (%)	5.9:94.1 (291)	29.8:70.2 (158)	0.3:99.7 (333)
Frequency of survivorship (%)	32 (57)	19 (21)	37 (27)
Frequency of damaged tail (%)	53 (57)	57 (21)	52 (27)

resented as nesters) in an assemblage of ten passerine species. The study was conducted over two different years (1987 and 1990) in the same 1.7ha site in San Carlos de Apoquindo. Between these two years, human disturbance increased markedly in regard to visitation rates, shrub thinning and cutting, humus extraction from underneath shrubs, and because of the establishment of a recreation area. During 1990, Lazo et al. (1990) also studied a 1.7-ha plot located 0.8 km away from the disturbed site, and considered it a "control" for changes observed in the "experimental" site (i.e., that subjected to an increase in human disturbance). They found that, in comparison to 1987, the following trends obtained in the "experimental" site during 1990: a halving of the number of active nests; the disappearance (as nesters) of four of the ten original species; and the appearance of a new one (Table 13). More specifically, the most dramatic changes involved the disappearance as nesters of two insectivorous species (Leptasthenura aegithaloides and Asthenes humicola), previously among the most abundant; their replacement by another insectivore (Troglodytes aedon) previously absent; a doubling in nesting by a granivore (Diuca diuca); and a seven-fold increase in the nesting of an omnivore (Mimus thenca; see Table 13). In contrast, during 1990 the "control" plot demonstrated the same features observed during 1987 in the "experimental" plot.

Lazo et al. (1990) offered the following explanations for the changes observed: (a) Shrub thinning, cutting, and removal of topsoil, all reduced the abundance of insects associated to the flowering and leaf-shedding, and thus impacted negatively on the insectivorous birds. (b) The establishment of a recreational area was accompanied by an increase in litter, particularly of cans, which were readily used by *Troglodytes aedon* for nesting. (c) Shrub cutting allowed the colonization of the vacated areas by grasses, thus increasing seed availability, and thus favoring granivorous species. Lazo et al. (1990) noted that some subtle effects may have operated as well. For instance, the lack of an increase among the granivorous Zonotrichia capensis, despite increased seed availability, may be owing to the cutting of shrubs preferred by this species as nesting structures (those shrubs < 2-m high). All of these explanations deserve to be tested. This work illuminates on what may be expected from increased human use of other evergreen shrubland areas.

RAPTORIAL BIRDS

There has been rather intense study of the raptor fauna in San Carlos de Apoquindo over two distinct periods: 1973-1979 and 1984-1989 (Table 14). Comparing the residence status of raptors between these two periods, there is some temporal variation in the composition of the raptor assemblage. Disregarding occasional or seasonal visitors, there were nine resident raptors during the years 1973-1979. During 1984-1989, three species became residents in the area (Falco peregrinus, Phalcoboenus megalopterus and Glaucidium nanum), and one ceased to reside year-round (Elanus leucurus). Because raptors are large and generally conspicuous by sight or voice, assessing their residence status gives some indication of changes that may have have occurred in the study area. But specifically why three species are now more common than before, and one is apparently disappearing, requires more study. This is a worthwhile enterprise.

Jiménez & Jaksic (1989) made behavioral observations of the eagle Geranoaetus melanoleucus from the top of a hill (1,266 m elevation) near the center of San Carlos de Apoquindo. For each eagle they recorded activity type, duration, and habitat beneath the bird. Observations were made in spring (1 August - 30 October 1984), summer (1 November 1984- 31 January 1985), autumn (1 February - 30 April 1985), and winter (1 May - 31 July 1985). Clearly, *G. melanoleucus* used the habitat in a non-homogeneous manner, spending most of its time on equatorial and west slopes, and on ridgetops (Table 15). This is likely because this eagle takes advantage of wind drafts that blow from the west, and of thermal updrafts that are generated on the equatorial slopes and ridgetops. The east slope, which does not receive much wind, was used chiefly during winter. In sum, there is spatial variation in habitat use, but superimposed on this there is also temporal variation, as seen by the varying percentages of use throughout the year.

Simultaneous observations were also made by Jiménez & Jaksic (1991, 1993a) of two hawks

TABLE 12

Common non-raptorial birds in San Carlos de Apoquindo, their weight, food habits and residence, 1973-1979

Aves no-rapaces comunes en San Carlos de Apoquindo, su peso, hábitos alimentarios y residencia, 1973-1979

Species	Weight (g) $\bar{x} \pm 2SE(n)$	Food habits	Residence
Tinamidae			
Nothoprocta perdicaria	160.0 ± 0.0 (1)	Granivore/Insectivore	Resident
Phasianidae			
Callipepla californica	64.0 ± 0.0 (1)	Granivore	Resident
Columbidae			
Zenaida auriculata	137.0 ± 0.0 (1)	Granivore	Resident
Columbina picui	45.7 ± 1.97 (5)	Granivore	Resident
Throchilidae			
Sephanoides sephaniodes	$5.8 \pm 0.01 (127)$	Nectarivore/Insectivore	Winter visitor
Patagona gigas	18.2 ± 1.15 (3)	Nectarivore/Insectivore	Summer visitor
Picidae			
Colaptes pitius	100.0 ± 0.0 (1)	Insectivore	Resident
Furnariidae			
Upucerthia dumetaria	44.1 ± 0.84 (12)	Insectivore	Winter visitor
Leptasthenura aegithaloides	9.2 ± 0.25 (41)	Insectivore	Resident
Asthenes humicola	$22.5 \pm 0.19(57)$	Insectivore	Resident
Asthenes pyrholeuca	21.8 ± 0.0 (1)	Insectivore	Winter visitor
Rhinocryptidae	. ,		
Pteroptochos megapodius	119.0 ± 0.0 (1)	Insectivore/Granivore	Resident
Scelorchilus albicollis	60.0 ± 0.0 (1)	Insectivore/Granivore	Resident
Tyrannidae			
Agriornis livida	$99.2 \pm 0.0 (1)$	Insectivore/Carnivore	Resident
Pyrope pyrope	35.8 ± 4.74 (5)	Insectivore/Frugivore	Resident
Elaenia albiceps	17.0 ± 0.0 (1)	Insectivore/Frugivore	Summer visitor
Anairetes parulus	6.2 ± 0.09 (113)	Insectivore/Frugivore	Resident
Phytotomidae			
Phytotoma rara	47.8 ± 0.87 (9)	Folivore	Resident
Hirudinidae			
Tachycineta leucopyga	14.9 ± 0.0 (1)	Insectivore	Winter visitor
Troglodytidae			
Troglodytes aedon	10.4 ± 0.21 (75)	Insectivore	Resident
Mimidae			
Mimus thenca	66.0 ± 0.0 (1)	Insectivore/Herbivore	Resident
Turdidae	00.0 = 0.0 (1)		100100110
Turdus falcklandi	86.8 ± 5.10 (4)	Frugivore/Insectivore	Resident
Icteridae	30.0 = 5.10 (1)	1 ugi toto insecutore	
Curaeus curaeus	90.0 ± 0.0 (1)	Insectivore/Herbivore	Resident
Sturnella loyca	112.6 ± 0.0 (1)	Insectivore/Herbivore	Resident
Fringillidae	112.0 ± 0.0 (1)		Resident
Diuca diuca	36.8 ± 1.18 (21)	Granivore/Insectivore	Resident
Phrygilus gayi	20.5 ± 0.0 (1)	Granivore/Insectivore	Winter visitor
Phrygilus fruticeti	20.5 ± 0.0 (1) 37.6 ± 2.65 (7)	Granivore/Insectivore	Resident
Phrygilus alaudinus	22.7 ± 0.40 (64)	Granivore/Insectivore	Resident
Zonotrichia capensis	21.5 ± 0.15 (411)	Granivore/Insectivore	Resident
Number of common species	29	Grantvore/motorvore	Restuent

TABLE 13

Major changes observed in the bird nesting assemblage in San Carlos de Apoquindo, 1987-1990

Cambios mayores observados en el ensamble nidificante en San Carlos de Apoquindo, 1987-1990

Characteristic	1987	1990
Human disurbance	Baseline	Higher
Number of active nests	Baseline	0.5 x Baseline
Number of nesting species	10	7
Leptasthenura_aegithaloides (insectivore)	Abundant	Absent
Asthenes humicola (insectivore)	Abundant	Absent
Troglodytes aedon (insectivore)	Absent	Abundant
Zonotrichia capensis (granivore)	Baseline	= Baseline
Diuca diuca (granivore)	Baseline	2 x Baseline
Mimus thenca (omnivore)	Baseline	7 x Baseline

sympatric with the eagle (Table 16). During spring, G. melanoleucus spent ca. 60 % of its time on equatorial and west slopes, whereas the hawk B. polyosoma spent its time chiefly on ridgetops (> 75 %), and the hawk P. unicinctus spent ca. 70 % of its time on equatorial slopes and ravines (Table 16). Clearly, these three raptors used landscape aspects differently. It may be because they chose to hunt in specific habitat types, or that they avoided each other and thus partitioned habitat. Thus, there is demonstrable spatial variation in habitat use by the different species studied. And

TABLE 14

Raptor species (Falconiformes and Strigiformes) in San Carlos de Apoquindo, 1973-1979 and 1984-1989. Key to species' abundance: Abundant = > 5 individuals detected (seen or heard) daily. Common = 1-5 detected daily. Frequent = 1 detected weekly. Scarce = 1 detected monthly. Rare = < 5 detected yearly

Especies de rapaces (Falconiformes y Strigiformes) en San Carlos de Apoquindo, 1973-1979 y 1984-1989. Clave
para abundancia de especies: Abundant = > 5 individuos detectados (vistos o escuchados) diariamente. Common =
1-5 detectados diariamente. Frequent = 1 detectado semanalmente. Scarce = 1 detectado mensualmente.
Rare = < 5 detectado anualmente

Species	Years 1973-1979	Years 1984-1989
Cathartidae		
Coragyps atratus	Not present	Occasional visitor (Rare)
Vultur gryphus	Occasional visitor	Regular visitor (Common)
Accipitridae		-
Accipiter chilensis	Not present	Occasional visitor (Rare)
Buteo albigula	Not present	Spring-Fall migrant (Scarce)
Buteo polyosoma	All-year resident	All-year resident (Common)
Circus cinereus	Not present	Occasional visitor (Rare)
Elanus leucurus	All-year resident	Occasional visitor (Scarce)
Geranoaetus melanoleucus	All-year resident	All-year resident (Common)
Parabuteo unicinctus	All-year resident	All-year resident (Common)
Falconidae		•
Falco femoralis	Not present	Occasional visitor (Rare)
Falco peregrinus	Occasional visitor	All-year resident (Frequent)
Falco sparverius	All-year resident	All-year resident (Common)
Milvago chimango	All-year resident	All-year resident (Abundant)
Phalcoboenus megalopterus	Not present	Regular visitor (Frequent)
Tytonidae	-	
Tyto alba	All-year resident	All-year resident (Frequent)
Strigidae		
Asio flammeus	Not present	Occasional visitor (Rare)
Athene cunicularia	All-year resident	All-year resident (Scarce)
Bubo magellanicus	All-year resident	All-year resident (Frequent)
Glaucidium nanum	Occasional visitor	All-year resident (Common)

490

TABLE 15

Absolute (min) and relative (%) time spent by the eagle Geranoaetus melanoleucus in seven habitat types of San Carlos de Apoquindo, during four biological seasons, 1984-1985. Time/day = mean per observation day ± 2 SE (days observed)

Tiempo absoluto (min) y relativo (%) usado por el águila *Geranoaetus melanoleucus* en siete tipos de hábitat de San Carlos de Apoquindo, durante cuatro estaciones biológicas,1984-1985. Time/day = media por día de observación ± 2 EE (días observados)

Activity (% time)	Spring 1984	Summer 1984-85	Fall 1985	Winter 1985
Flatland	0.1	1.1	0.7	0.1
Ravine	6.6	9.2	3.0	1.4
Ridgetop	25.1	29.1	29.6	14.1
Equatorial slope	37.2	30.4	34.4	27.9
Polar slope	2.7	10.8	2.0	3.1
East slope	5.9	8.0	11.9	24.9
West slope	22.4	11.4	18.4	28.5
Time/day (min)	$170.0 \pm 58.3 (15)$	$72.9 \pm 23.2 (12)$	99.8 ± 38.9 (6)	255.7 ± 167.6 (6)

there is also temporal variation, as exemplified in Table 15, above.

MAMMALS

There are no large native mammals in San Carlos de Apoquindo. Perhaps the guanaco Lama guanicoe was present in the past, but currently the largest mammals are two carnivores, the fox *Pseudalopex culpaeus* and the grison *Galictis* cuja. They are dealt with in the predator section, below. Introduced European hares (Lepus europaeus) are not abundant in the site, and native cururos (Spalacopus cyanus) are localized and scarce. The most common small-mammal residents in San Carlos de Apoquindo are six native rodents, one marsupial, and one introduced rabbit (Table 17). Iriarte et al. (1989a) showed that all mammals except the rabbit, can be captured with medium-sized Sherman traps, and that large-sized Tomahawk traps are capable of capturing rabbits, but only when they are young. These authors placed traps in sparse and dense habitat patches, and thus were able to determine which microhabitat was more frequented by each species (Table 17). They also equipped traps with a watch, and thus were able to time the mammals' activity periods (Table 17). Only the large rodent Abrocoma bennetti used sparse scrub exclusively, while four small rodents and the marsupial used dense scrub exclusively. The rodent Octodon degus and the rabbit Oryctolagus cuniculus used both sparse and dense scrub (Table 17). Two

TABLE 16

Absolute (min) and relative (%) time spent by the eagle *Geranoaetus melanoleucus*, and the hawks *Buteo polyosoma* and *Parabuteo unicinctus* in seven habitat types of San Carlos de Apoquindo, during Spring 1984. Time/day = mean per observation day ± 2SE (days observed)

Tiempo absoluto (min) y relativo (%) usado por el águila *Geranoaetus melanoleucus*, y por los halcones *Buteo* polyosoma y Parabuteo unicinctus en siete tipos de hábitat de San Carlos de Apoquindo, durante primavera 1984. Time/day = media por día de observación ± 2EE (días observados)

Activity (% time)	Geranoaetus melanoleucus	Buteo polyosoma	Parabuteo unicinctus
Flatland	0.1	0.2	0.4
Ravine	6.6	1.5	32.8
Ridgetop	25.1	75.7	16.6
Equatorial slope	37.2	16.8	38.2
Polar slope	2.7	0.0	2.1
East slope	5.9	0.9	0.0
West slope	22.4	4.9	9.9
Time/day (min)	$170.0 \pm 58.3 (15)$	$47.0 \pm 28.8(14)$	$24.1 \pm 10.6 (12)$

TABLE 17

Weight, microhabitat use, and activity period of small mammals in San Carlos de Apoquindo, 1983-1984

Peso, uso de microhábitat, y período de actividad de micromamíferos en San Carlos de A	Apoquindo, 1983-1984
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Species	Weight (g), $\bar{x} \pm 2SE(n)$	Microhabitat	Activity
Abrocomidae		· · · · ·	
Abrocoma bennetti	230.9 ± 35.63 (15)	Sparse scrub	Nocturnal
Cricetidae		-	
Akodon longipilis	62.5 ± 3.13 (20)	Dense scrub	Nocturnal
Akodon olivaceus	43.6 ± 2.36 (18)	Dense scrub	Nocturnal/Crepuscular
Oryzomys longicaudatus	36.3 ± 2.16 (55)	Dense scrub	Nocturnal/Crepuscular
Phyllotis darwini	61.5 ± 3.10 (120)	Dense scrub	Nocturnal/Crepuscular
Octodontidae			-
Octodon degus	183.7 ± 8.81 (91)	Sparse & dense	Diurnal/Crepuscular
Didelphidae		-	*
Thylamys elegans	30.3 ± 3.02 (28)	Dense scrub	Nocturnal/Crepuscular
Leporidae			-
Oryctolagus cuniculus (j)	740.0 ± 123.00 (4)	Sparse & dense	Diurnal/Crepuscular

rodents (Abrocoma bennetti and Akodon longipilis) were exclusive nocturnal, one rodent (Octodon degus) and the rabbit (Oryctolagus cuniculus) were diurnal/crepuscular, and the remaining three rodents and the marsupial were nocturnal/crepuscular (Table 17).

Jiménez & Jaksic (1989) used traps to estimate the abundance of small mammals in each habitat type described in Table 3. During 14 consecutive days and 14 intervening nights, from 20 July to 2 August 1985, they trapped small mammals on the four mountain slopes, at the summit, and at a ravine. All six trapping grids had a 7 by 7 configuration with one trap per station (49 traps per grid), alternating one Sherman live with one Victor kill trap over both rows and columns, with stations separated by 7 m. For the flatland, they used information provided by Iriarte et al. (1989a), who trapped small mammals directly to the west of Jiménez & Jaksic's (1989) observation post. The rodent Phyllotis darwini and the marsupial Thylamys elegans were the most abundant species, particularly in ravines, polar slopes, and flatlands (Table 18). The third most abundant species was the rodent Octodon degus, scarce everywhere except in east and west slopes. The least abundant species was the rodent Abrocoma bennetti, trapped only on east slopes. The introduced European rabbit (Oryctolagus cuniculus) was also present at the site, but the traps used were not adequate for its capture. Jiménez & Jaksic (1989) observed rabbits to be most abundant in east and west slopes. Overall, equatorial and west slopes, and ridgetops had lower mammalian densities than other areas (accounting for about 5, 10, and 4 % of the total mammals cap-

TABLE 18

Abundance (ind ha⁻¹) of small mammals in seven habitat types of San Carlos de Apoquindo, during winter 1985

Abundancia (ind ha⁻¹) de micromamíferos en siete tipos de hábitat de San Carlos de Apoquindo, durante invierno 1985

Habitat types	Octodon degus	Akodon olivaceus	Akodon longipilis	Oryzomys longicaudus	Phyllotis darwini	Thylamys elegans	Abrocoma bennetti	a Total abundance
Flatland	4.1	12.0	4.1	24.2	20.2	12.0	0.0	76.6
Ravine	0.0	2.9	11.7	2.9	41.1	23.5	0.0	82.1
Ridgetop	0.0	4.0	0.0	2.0	6.0	4.0	0.0	16.0
Equatorial slope	2.0	0.0	2.0	8.0	6.0	2.0	0.0	20.0
Polar slope	4.1	2.0	16.3	6.1	26.5	14.3	0.0	69.3
East slope	33.3	2.0	3.9	0.0	19.6	9.8	2.0	70.6
West slope	17.6	1.9	1.9	0.0	9.8	7.8	0.0	39.0

tured, Table 18). Mammals were more abundant in ravines, flatlands, east and polar slopes (accounting for about 22, 21, 19, and 19 % of the total mammals captured, Table 18).

Spatial variation has been demonstrated also at the microscale: that represented by the mosaic of individual shrubs placed on the grass-covered matrix. Simonetti (1986a, 1989c) used two grids each with a 10 by 5 configuration and with stations separated 10 m, each equipped with a single Sherman trap. He operated these grids from August 1984 to February 1985. Shrub:grass cover was approximately 55:45 in the two sampling areas, and because Simonetti (1986a, 1989c) used relative trapping success in these two microhabitat states, his results are comparable throughout. He found that the five most common species sampled (accounting for 92.5 % of all individuals) were consistently captured by traps placed under shrubs (Table 19). That is, all five species rarely (< 11.4 %) ventured into the open matrix, and only in dark nights. During bright nights, not a single individual of any species was ever captured in the open. Although the explanation is complex, food availability was higher, and predation risk was lower, under shrubs (Simonetti 1986a, 1989c). But the main point here is that small mammals seem able to not only discriminate landscape aspects, but also to fine-tune their microhabitat selection within a given landscape.

Apart from spatial variation, there is also temporal variation in species abundance at a single habitat type in San Carlos de Apoquindo. Iriarte et al. (1989a) live-trapped small mammals during 1983 and 1984 in a flat area directly west of the observation post used by Jiménez & Jaksic (1989). They set a grid consisting of 99 Sherman traps in an 11 by 9 configuration, with 7 m separating rows and 5 m separating columns (total grid area = 0.35 ha, including outer boundary strips equal to 3.5 and 2.5 m, respectively). This grid was operated for 5 consecutive days each month from May 1983 to October 1984. Iriarte et al. (1989a) found that abundance fluctuated 2.7x overall, and that individual species varied their densities from as low as two-fold to as high as infinite (Table 20). Infinite, because species such as the rodent Abrocoma bennetti and the marsupial Thylamys elegans were completely absent from the study plot for entire seasons. Thus, there was a strong temporal component in small mammal abundance, for all species.

On a longer time scale, there have been five El Niño periods during recent years (1972-1973, 1982-1983, 1986-1987, 1991-1992, and 1997-1998). Trapping at San Carlos de Apoquindo has coincided with only one of these, that reported by Iriarte et al. (1989a, see Table 20). Unfortunately, there is no information from the years preceding El Niño 1982-1983, but it is clear that densities were higher during winter and spring of 1983 (55-74 ind ha⁻¹) than they were in 1984 (31-39 ind ha⁻¹, respectively). Determining the influence of El Niño on small mammal densities is another worthwhile endeavor that requires sustained monitoring.

TABLE 19

Percentage of captures of small mammals in two microhabitat types (in the open and under shrubs), and with two contrasting illumination regimes at nighttime, in San Carlos de Apoquindo, 1984-1985

Porcentaje de captures de micromamíferos en dos tipos de microhábitats (expuesto y bajo arbustos), y con dos regímenes contrastantes de iluminación durante la noche, en San Carlos de Apoquindo, 1984-1985

Species	Nightlight	ν	Vinter 1984	S	Summer 1985		
		Exposed	Exposed Shrub		Exposed	Shrub	n
Akodon longipilis	Dark	6.3	93.7	16	0.0	100.0	3
	Bright	0.0	100.0	2	0.0	0.0	0
Akodon olivaceus	Dark	4.3	95.7	23	0.0	100.0	27
	Bright	0.0	100.0	1	0.0	100.0	7
Thylamys elegans	Dark	8.3	91.7	12	0.0	100.0	7
	Bright	0.0	100.0	2	0.0	100.0	1
Oryzomys longicaudatus	Dark	11.4	88.6	89	6.7	93.3	30
	Bright	0.0	100.0	15	0.0	100.0	3
Phyllotis darwini	Dark	6.7	93.3	15	0.0	0.0	0
-	Bright	0.0	100.0	3	0.0	0.0	0

TABLE 20

Abundance (ind ha⁻¹) of small mammals captured each season in San Carlos de Apoquindo, 1983-1984

Abundancia (ind ha	 de micromamíferos 	capturados cada	estación en San	Carlos de A	Apoquindo, 1983-1984
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Species	Winter 83	Spring 83	Summer 84	Autumn 84	Winter 84	Spring 84	Variation
Abrocoma bennetti	0.0	0.0	8.6	0.0	0.0	0.0	Infinite
Akodon longipilis	2.9	3.8	7.6	2.9	4.8	5.7	2.6x
Akodon olivaceus	2.9	1.0	12.4	3.8	2.9	1.9	12.4x
Thylamys elegans	3.8	4.8	10.5	11.4	1.9	0.0	Infinite
Octodon degus	11.4	7.6	15.2	16.2	3.8	2.9	5.6x
Oryzomys longicaudatus	11.4	25.7	3.8	6.7	9.5	14.3	6.8x
Phyllotis darwini	22.9	31.4	27.6	21.0	16.2	6.7	4.7x
Abundance (ind ha ⁻¹)	55.2	74.3	85.7	61.9	39.0	31.4	2.7x

TABLE 21

Predator species (Falconiformes, Strigiformes, mammalian carnivores, and snakes) in San Carlos de Apoquindo, their weight and residence, 1973-1989 (see Table 14 for further details on raptors)

Especies de predadores (Falconiformes, Strigiformes, mamíferos carnívoros y serpientes) en San Carlos de Apoquindo, su peso y residencia, 1973-1989 (véase Tabla 14 para mayores detalles sobre rapaces)

Species	Weight (g), $\overline{x} \pm 2SE(n)$	Residence
Cathartidae		
Coragyps atratus	No data	Occasional
Vultur gryphus	No data	All-year
Accipitridae		
Accipiter chilensis	875.0 ± 50.0 (2)	Occasional
Buteo albigula	No data	Occasional
Buteo polyosoma	975.0 ± 0.0 (1)	All-year
Circus cinereus	No data	Occasional
Elanus leucurus	302.2 ± 32.2 (3)	Occasional
Geranoaetus melanoleucus	$2,738.3 \pm 1371.6$ (3)	All-year
Parabuteo unicinctus	875.8 ± 40.6 (6)	All-year
Falconidae		-
Falco femoralis	No data	Occasional
Falco peregrinus	No data	All-year
Falco sparverius	$115.8 \pm 4.1 \ (18)$	All-year
Milvago chimango	295.8 ± 11.7 (29)	All-year
Phalcoboenus megalopterus	No data	All-year
Tytonidae		
Tyto alba	306.5 ± 21.6 (8)	All-year
Strigidae		
Asio flammeus	No data	Occasional
Athene cunicularia	247.0 ± 21.8 (3)	All-year
Bubo magellanicus	$1,227.2 \pm 196.5$ (6)	All-year
Glaucidium nanum	$67.6 \pm 7.7 (5)$	All-year
Mustelidae		•
Galictis cuja	600.0 ± 0.0 (1)	All-year
Canidae		-
Pseudalopex culpaeus	$7,366.7 \pm 1,387.2$ (3)	All-year
Colubridae		-
Philodryas chamissonis	96.3 ± 24.4 (50)	All-year
Number of resident species	• •	15

AVIAN, MAMMALIAN, AND REPTILIAN PREDATORS

Eight diurnal raptors (Falconiformes), four nocturnal raptors (Strigiformes), two carnivores (Carnivora), and one snake (Serpentes), reside continuously in San Carlos de Apoquindo (Table 21). Other seven raptor species are occasionally sighted at the site. This is quite a diverse assemblage of predators. Over several years, it has been possible to synthetize the diets of most of the resident predators in San Carlos de Apoquindo (Jaksic et al. 1981b, see Table 22). Eleven sympatric predators prey on seven major prey categories. The four hawks and eagles (*Buteo polyosoma, Elanus leucurus, Geranoaetus melanoleucus, Parabuteo unicinctus*) prey exclusively on vertebrates, chiefly on small mammals, but the two falcons

TABLE 22

Food habits of predators in San Carlos de Apoquindo, 1973-1979. Data are percentages of total diet. Key to predators' names: B. pol = Buteo polyosoma (Accipitridae); E. leu = Elanus leucurus; F. spa = Falco sparverius; G. mel = Geranoaetus melanoleucus; M. chi = Milvago chimango; P. uni = Parabuteo unicinctus ; A. cun = Athene cunicularia; B. mag = Bubo magellanicus; T. alb = Tyto alba; P. cha = Philodryas chamissonis; P. cul = Pseudalopex culpaeus

Hábitos alimentarios de los predadores en San Carlos de Apoquindo, 1973-1979. Los datos son porcentajes de la dieta total. Clave para los nombres de los predadores, arriba

Species	B. pol	E. leu	F. spa	G. mel	M. chi	P. uni	A. cun	B. mag	T. alb	P. cha	P. cul
Mammals											
Abrocoma bennetti	12.0	0.0	0.0	7.6	0.0	12.8	0.3	22.8	18.5	0.0	11.6
Akodon longipilis	0.0	10.0	0.0	0.0	0.0	1.2	0.8	20.7	4.8	0.0	0.0
Akodon olivaceus	2.6	34.4	1.1	0.0	0.0	1.2	3.6	1.1	6.0	4.4	4.1
Thylamys elegans	1.0	0.0	0.0	0.0	0.0	0.0	0.4	4.4	6.7	0.0	0.0
Octodon degus	57.6	8.6	1.8	57.7	0.0	64.5	3.3	0.0	12.0	0.0	41.2
Oryctolagus cuniculus	6.1	0.0	0.0	18.8	0.0	1.2	0.1	19.6	0.0	4.4	19.7
Oryzomys longicaudatus	1.8	37.1	2.4	0.6	0.1	0.0	3.0	5.4	16.4	0.0	0.0
Phyllotis darwini	14.3	1.3	0.0	2.9	0.0	7.0	4.3	5.4	32.7	0.0	5.3
Spalacopus cyanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Unidentified	1.0	6.6	5.8	7.1	1.4	5.1	1.7	6.5	0.7	8.7	7.8
Birds											
Passeriformes	3.3	2.0	12.7	1.2	0.7	1.8	1.0	14.1	2.0	13.0	5.6
Reptiles											
Liolaemus spp.	0.3	0.0	.8.2	0.6	1.9	3.4	tr*	0.0	0.0	69.5	0.0
Philodryas chamissonis	0.0	0.0	1.1	3.5	0.0	1.8	0.0	0.0	0.0	0.0	4.7
Insects											
Coleoptera	0.0	0.0	28.6	0.0	48.3	0.0	74.0	0.0	0.0	0.0	0.0
Dermaptera	0.0	0.0	0.0 °	0.0	0.3	0.0	tr*	0.0	0.0	0.0	0.0
Diptera	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	0.0	0.0	0.0	0.0	0.2	0.0	tr*	0.0	0.0	0.0	0.0
Hymenoptera	0.0	0.0	0.0	0.0	0.7	0.0	0.1	0.0	0.0	0.0	0.0
Lepidoptera	0.0	0.0	7.7	0.0	10.0	0.0	2.8	0.0	0.0	0.0	0.0
Orthoptera	0.0	0.0	18.0	0.0	24.0	0.0	3.2	0.0	0.0	0.0	0.0
Unidentified	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arachnids											
Aranea	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.0	0.0
Scorpionida	0.0	0.0	0.2	0.0	0.3	0.0	1.1	0.0	0.0	0.0	0.0
Chilopods											
Unidentified	0.0	0.0	1.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Oligochaets											
Unidentified	0.0	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.0
Subtotal vertebrates	100.0	100.0	33.1	100.0	4.1	100.0	18.5	100.0	100.0	100.0	100.0
Subtotal invertebrates	0.0	0.0	66.9	0.0	95.9	0.0	81.5	0.0	0.0	0.0	0.0
Total prey (n)	391	151	378	164	1068	172	2909	92	729	23	319

tr = trace = < 0.1%

(Falco sparverius and Milvago chimango) prey heavily on invertebrates. Among owls, Bubo magellanicus and Tyto alba prey exclusively on vertebrates, but Athene cunicularia takes mostly invertebrates. The snake Philodryas chamissonis preys extensively on lizards, but it also takes birds and mammals. The fox Pseudalopex culpaeus preys chiefly on mammals. Among native prey species, the rodents Octodon degus and Phyllotis darwini are heavily preyed by most predators. The introduced rabbit Oryctolagus cuniculus never accounted for more than 20 % of the diet of any predator, but the situation seems to have changed more recently (see below).

Iriarte et al. (1989b) studied the seasonal diet of the fox Pseudalopex culpaeus as evaluated from fresh feces that were collected simultaneously with the trapping sessions conducted May 1983-October 1984 by Iriarte et al. (1989a). They collected fox feces inside the trapping grid and within a radius of 200 m (thus totaling an area of 6.6 ha). In 18 months they collected 202 feces, the contents of which were identified and classified in four seasons (Table 23). The three most preved mammals were the rabbit Oryctolagus cuniculus, and the large rodents Octodon degus and Abrocoma bennetti, accounting from 65 to 85 % of the fox diet by numbers. Of course, because these three mammals were the largest in the area, the biomass they supplied to foxes was larger than that indicated by their numbers. Some local small mammals were not preyed at all -despite being captured in traps-specifically the rodents Akodon longipilis, Akodon olivaceus, and Oryzomys

longicaudatus, and the marsupial Thylamys elegans. Their small size may render them unattractive to the foxes. Birds were rarely preyed on, but snakes were rather common in the fox diet, specially during autumn and winter. Plant matter (mostly fruits) and insects were consumed throughout the year, but with fluctuations (Table 23). The main point driven here is that despite the small area where fox feces were collected, presumably produced by a couple of individuals, some strong temporal components were detected in the diet. And a peripheral point may be noteworthy: rabbit consumption was very high (23-47 %) in comparison to previous data, which never surpassed 20 % (see Table 22). This point is elaborated below.

Temporal fluctuations in predator diet in San Carlos de Apoquindo are not only short-term (seasonal), but also manifest in longer time scales. There have been long-term shifts in the diet of some local predators. The fox Pseudalopex culpaeus more than doubled its consumption of the introduced rabbit Oryctolagus cuniculus over 8 years, and the same did the eagle Geranoaetus melanoleucus over 13 years (Simonetti 1986, Pavéz et al. 1992, see Table 24). These results are interesting because, noting that rabbits behaved as if they had no predators, Jaksic et al. (1979a) proposed that lack of adaptation to hunt for this introduced prey determined the low consumption of rabbits by local predators. Clearly, that behavioral adaptation developed over less than a decade. It should be interesting to conduct more dietary studies of local predators, to determine if

TABLE 23

Seasonal diet of the fox Pseudalopex culpaeus in San Carlos de Apoquindo, 1983-1984

Prey items	Winter 1983 & 1984	Spring 1983 & 1984	Summer 1984	Autumn 1984
Mammals				
Abrocoma bennetti	12.1	12.5	26.7	15.0
Octodon degus	31.8	29.2	24.4	26.7
Phyllotis darwini	1.5	0.0	2.2	5.0
Unidentified	7.6	9.7	11.1	11.7
Oryctolagus cuniculus	40.9	47.2	33.3	23.3
Birds				
Eggs	0.0	0.0	0.0	3.3
Unidentified	0.0	1.4	0.0	1.7
Reptiles				
Liolaemus sp.	0.0	0.0	0.0	0.0
Philodryas chamissonis	6.1	0.0	2.2	13.3
Total prey	66	72	45	60
Total feces	54	60	41	47
Feces with plants (%)	11.1	15.0	22.0	19.1
Feces with insects (%)	3.7	15.0	9.8	4.3

Dieta estacional del zorro Pseudalopex culpaeus en San Carlos de Apoquindo, 1983-1984

TABLE 24

Changes in the consumption of rabbits (*Oryctolagus cuniculus*) by predators (the fox *Pseudalopex culpaeus* and the eagle *Geranoaetus melanoleucus*) in San Carlos de Apoquindo, 1976-1984 and 1973-1988, respectively

Cambios en el consumo de conejos (Oryctolagus cuniculus) por predadores (el zorro Pseudalopex culpaeus y el águila Geranoaetus melanoleucus) en San Carlos de Apoquindo, 1976-1984 y 1973-1988, respectivamente

Predators	Previous consumption	Later consumption Year 1984	
Pseudalopex_culpaeus	Year 1976		
Small mammals	70.0 %	52.0 %	
Oryctolagus cuniculus	19.7 %	48.0 %	
Other vertebrates	10.3 %	0.0~%	
Geranoaetus melanoleucus	Years 1973-1974	Years 1987-1988	
Small mammals	75.9 %	34.3 %	
Oryctolagus cuniculus	18.8 %	43.9 %	
Other vertebrates	5.3 %	14.0 %	
Insects	0.0~%	7.8 %	

rabbit consumption has continued to increase or has reached a plateau.

CONCLUSIONS

There is a rather broad but patchy picture of ecological interactions taking place in San Carlos de Apoquindo. Some interfaces between consumers are sharply focused, and they provide inspiration for further hypothesis testing. This is the case of herbivore/predator interactions, and perhaps also of plant/herbivore interactions, although there is evident room for improvement. And it is also obvious that the soil compartment is inadequately known, same as is the interface with the vegetation compartment. In addition, there is a lack of studies relating climate forcing (El Niño), and both vegetation and animal dynamics. Decomposition processes (including litter and carcasses) are pathetically unstudied. Most of these maladies ensue from not having made efforts to monitor this ecosystem continuously over time. Despite this, it is clear that a sustained effort resulted in a steady number of publications and theses from 1976 to 1990 (15 years). But thereafter the output declined markedly over the last decade (Table 25). There is no mystery as to the cause: researchers were discouraged from entering San Carlos de Apoquindo by a clueless administration. And researchers themselves became discouraged by the rampant human disturbance affecting the site. But with more controlled access, a more enlightened administration, and the funding from the Faculty of Biological Sciences of the Catholic University of Chile, it has been possible to erect a new research facility at the site. Researchers are now being enticed to not lay awaste the intellectual principal afforded by more

TABLE 25

Published number of papers (including book chapters) and theses (including Bachelor, Master, and Doctoral degrees) based on field work in San Carlos de Apoquindo, 1976-2000

Artículos publicados (incluyendo capítulos de libro) y tesis (incluyendo Licenciatura, Magister y Doctorado) basados en trabajo de terreno en San Carlos de Apoquindo, 1976-2000

Year Papers		Theses	Theses' authors			
1976-1980	36	4	Contreras (1977), Gutiérrez (1977), Jaksic (1977), Yáñez (1976)			
1981-1985	31	3	Jaksic (1982), Poiani (1984), del Pozo (1985)			
1986-1990	32	5	Carothers (1987), Iriarte (1986), Jiménez (1987), Medel (1987), Simonetti (1986)			
1991-1995	16	0	None			
1996-2000	5	0	None			
Total (25 years)	120	12				

than two decades of hard work. Let us hope that San Carlos de Apoquindo will again become the lightening rod of ecological research in central Chile. And this time, from an ecosystem perspective.

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