HABITAT ASSOCIATION PATTERNS OF FOREST AND STEPPE BIRDS OF NORTHERN PATAGONIA, ARGENTINA

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ABSTRACT.—I censused birds across a moisture gradient in northern Patagonia, Argentina, in the vicinity of Bariloche. Over a 60-km distance, the 12 sites ranged from grassland at lower elevations to upland climax *Nothofagus* forests of the eastern Andes. Here, I correlated bird abundance and diversities with various vegetation measures. Using all sites, bird diversities and abundances were positively correlated with various foliage measures. When grasslands were excluded, however, an inverse relationship was found: birds were more diverse and abundant in the lower stature shrub communities than in complex forests. Multiple regression analyses of this apparently paradoxical situation indicated that certain species of plants probably had important effects on community structure.

As a habitat in a region becomes more complex, the bird community in that habitat usually becomes more complex as well (e.g., MacArthur and MacArthur 1961, Willson 1974). In southern Argentina, however, Vuilleumier (1972) concluded that the southern beech (*Nothofagus*) forests had a less complex avifauna than nearby, simpler, scrub areas. In order to describe the avifauna, its habitat associations, and to test this seemingly paradoxical situation, I sampled the avifauna and vegetation associations of the region in the spring of 1980. In this paper, I describe the vegetation types, the bird species associated with each type, and their interrelationships.

After the pioneering work of MacArthur and MacArthur (1961), many studies have confirmed their initial finding that, for terrestrial communities, the number of bird species, as well as their diversity, are strongly positively correlated with aspects of the structural complexity of vegetation (e.g., MacArthur 1964, Recher 1969, Karr and Roth 1971, Pearson and Ralph 1978). That is, the more complex the structure or composition of the vegetation, the more likely it is that the habitat will contain more bird species (higher richness) or more even abundances of the species (evenness). This relationship is usually interpreted as evidence for the underlying dependence of birds upon their habitat, and thus, lends some degree of predictability.

Exceptions to this pattern should be of interest because of what they may reveal about the pattern itself or the systems it attempts to summarize. Thus, it is of interest that Vuilleumier (1972) regarded the northern Patagonian forest bird communities of southern Argentina as such an exception. Although his data were few, they indicated that more species of birds inhabited the structurally simpler scrub-steppe habitats than the more complex, nearby, dense beech forests. Vuilleumier also thought that bird species diversity was higher in the scrub-steppe habitat. A re-calculation (Church 1974) of his data, however, showed that Vuilleumier's diversity values (H') in the two habitats were essentially identical (dense forest-1.993; scrub-steppe forest-1.837). One other study has suggested that bird species diversity was unrelated to vegetation complexity (Howell 1971). This study, although intensive, had samples drawn from very few study sites.

The avifauna of Patagonia is relatively little described, at least in terms of population numbers. My study is the first detailed quantification of these birds and their habitat associations. Such data are important because most ecological generalizations are based on northern hemisphere temperate communities. Comparative data from other areas can provide information on the applicability of these generalizations.

METHODS

STUDY SITES

In the region of my study (eastward from the crest of the Andes in southern Argentina), annual rainfall diminished from more than 2,000 mm to 200 mm over about a 50-km area (De Fina 1972). The vegetative growth pattern reflected this moisture gradient. Although there was some effect of elevation and temperature on the vegetation, De Fina considered it comparatively small. Owing to a varied topography, the habitat types were somewhat patchy in this region, with each "patch" occupying several hundred or more hectares. Habitats became uniform only where the more or less continuous grassland steppe was reached at about 200 mm annual rainfall.

In the region of this moisture gradient, I



FIGURE 1. Map of study locations in northern Patagonia, Argentina. The letters refer to the locations described in Methods.

selected 12 sites (Fig. 1) at which to census birds and measure vegetation. I made no attempt to select any certain habitat type; rather, at any given site, I used the largest area of reasonably contiguous, similar vegetation (summarized in Table 2), with a minimum size of approximately 25 ha. Census stations at each site were at least 100 m from what I judged to be the edge of another habitat type. The only exception to these last two rules was the Sedgescrub Site (see below), which was only about 5 ha, and several of its stations were within 25 m of the edge. The vegetation data that I gathered, based on an index to foliage density, were subjected to a cluster analysis procedure (SAS 1979), which confirmed the vegetation (structural) similarity of the stations at each site. That is, the great majority of the census stations at a site were more similar to each other than to stations at other sites. The rainfall at the twelve sites was extrapolated from the data in De Fina (1972) from measurements higher and lower in the altitudinal gradients. The location of the sites on Figures 1 to 4 are indicated by the letter following their names below.

Grassland sites. Bunchgrass Grassland (A) – 42 km north-northeast of Bariloche, on open, windswept hills, 2 km south of Arroyo Corral. The vegetation was less than 0.5 m tall, and consisted of primarily bunchgrass (*Festuca* sp.) and a small prickly shrub, *Mulinum spinosum*. I estimate that annual rainfall was probably 300-500 mm.

Cactus Grassland (B)—a mixed grass-scrub area within 1 km south of Laguna Blanca, an alkaline lake 20 km southeast of Zapala, Neuquén. The vegetation was mostly less than 1.5 m tall, and consisted of primarily bunchgrass, a small cactus, and two small shrubs (less than 0.5 m tall), one being *Acaena ovalifolia*. Rainfall was probably 200–400 mm annually.

Herbaceous Grassland (C)-73 km north of Bariloche and 4 km east-northeast of Caleufú, Neuquén, 0.5 km to the south of Río Caleufú. It resembled the Cactus Grassland Site, with similar rainfall, but had less bunchgrass and more *Mulinum* and herbs.

Scrub-cedar sites. Scrub-sedge (D)—an oasis of shrubs in a swale surrounded by grassland, on low hills near the Bunchgrass Grassland Site at Arroyo Corral and with similar rainfall. The area of this patch was about 5 ha. The vegetation was a mixture of grassland, with barberry (*Berberis* sp.) 1–2 m high and a small (2–3 m high) tree, probably *Maytenus boaria*.

Scrub-beech (É)-4 km east-southeast of Bariloche, and 0.5 to 1.5 km south of the southern base of Cerro Otto. The vegetation consisted of several shrub species, mostly 2-3 m in height. Nothofagus antarcticus was the most common shrub, occasionally reaching 5 m in height. Diostea juncea, Berberis spp., and Lomatia hirsuta were less common. This was the "Nothofagus steppe" of Vuilleumier (1972). Rainfall was probably 500-700 mm.

Sparse Cedar Forest (F)-3.5 km southeast of the junction of the Río Cuyín Manzano and the Río Traful, and 6 km east-southeast of Confluencia, Neuquén. The cedar (*Austrocedrus chilensis*), often 5–8 m high, was the most abundant plant, followed by shrubs of the genera *Diostea, Lomatia,* and *Berberis.* Rainfall was probably 400–600 mm.

Dense Cedar Forest (G)-2.5 km northeast of Confluencia, at the junction of Río Limay and Río Traful, Neuquén. Similar to the preceding site in rainfall, its vegetation differed largely in having a higher density of cedar.

Southern beech forest sites. Beech (dombeyi-no bamboo) Forest (H)-1.5 km northeast of the preceding site in a rather steepsided canyon, it had an overstory 10-30 m high, of primarily Nothofagus dombeyi and Austrocedrus. The understory was Berberis and Ribes magellanicus. The rainfall was probably between 750 and 1,000 mm.

Beech (pumilio-no bamboo) Forest (I)-1.5 km east-southeast of the summit of Cerro Otto, and 5 km west-southwest of Bariloche. The trees were primarily Nothofagus pumilio 20-30 m high, with an understory of Ribes magellanicus, Berberis pierceii, and Lomatia, with almost no bamboo (Chusquea spp.) understory. This was the "Nothofagus dombeyi" (sic) forest of Builleumier (1972). Rainfall was probably between 800-1,200 mm annually.

Dense Beech (*dombeyi*-bamboo) Forest (J)-a mixture of mature Nothofagus dombeyi 20-30 m high and small amounts of Austrocedrus, within 200 m of the east shore of Lago Escondido on the Llao Llao Peninsula, and 26 km west-northwest of Bariloche. The understory was a dense, almost impenetrable, mass of bamboo. Rainfall was probably 1,500–2,000 mm annually.

Beech (antarctica-dombeyi-bamboo) Forest (K)-at Ruca Malén, near the northwest end of Lago Correntos, and 19 km northnorthwest of Villa la Angostura. It was a mixed forest, 10-30 m high, and consisted of primarily Nothofagus dombeyi and some N. antarctica, with a Berberis and Chusquea understory. Except for the addition of N. antarctica, the forest resembled that of the previous site, with rainfall probably 1,500-2,000 mm.

Beech (*pumilio-dombeyi* – bamboo) Forest (L)—a beech forest 8 km east-southeast of the summit of Mt. Tronador, within 1 km of Río Castaño Overo. It was similar to the Llao Llao Peninsula site, but had an almost equal mixture of *Nothofagus dombeyi* and *N. pumilio*. Rainfall was probably about 2,000–2,500 mm.

CENSUS PROCEDURES

I censused birds in the three grassland sites by using variable distance strip censuses (Emlen 1971), which I believe are the most appropriate for habitat of such low stature. Each segment that was 0.1 km long was tallied separately. I measured the vegetation at the end of every fifth (0.5-km) segment. At sites of taller stature, I censused the birds by using a variable distance station count (Reynolds et al. 1980), with stations 100 m apart on a line through the habitat. Vegetation was measured at each station. I believe that any differences that resulted from comparing data by using the two different census methods are minimal and do not affect species richness or diversity calculations.

I censused birds on about 75% of the mornings between 7 November and 10 December 1980. This was in the spring, when singing bird activity was at its height. Before beginning censusing, I spent more than a week becoming familiar with all the songs and calls of birds in the areas. During non-census periods, I continually observed birds and spent a great deal of time confirming the identities of birds that were singing and calling. On each morning, I began within 30 min of dawn and continued either for 2-3 h or until wind interfered with my hearing the birds. I usually censused between seven and 12 stations or segments per morning, spending 10 min at each station or on each segment. Each site was usually censused within a 3- to 5-day period.

Using the statistics derived from Ramsey and Scott (1979), I calculated the "Effective Detection Distance" (EDD) for each bird species for all sites combined. Using this distance to estimate the area that I surveyed for each species, I then estimated the density from the number seen at each site. I felt justified in combining data from sites because I found no significant (t-test; P < 0.05) difference between the EDD for the same species in different habitats. I determined this from an examination of the six species that occurred in more than one of the three major non-grassland habitat types with more than 25 individuals in each of at least two habitats. In none of these species did the average EDD differ between habitats. This is consistent with the studies summarized by Dawson (1981:13). Those species that occurred so sparsely that no meaningful EDD could be calculated were assigned EDDs of birds with similar habits. This assignment had little effect upon diversity (H')calculations, since rare species contribute little to the diversity measure. Although wide-ranging species, such as raptors, do not meet most of the assumptions of the census methods, because they are relatively rare, they also contribute almost nothing to diversity calculations.

Diversity was derived from the standard H'method (MacArthur and MacArthur 1961) for each of my sites. The percent used in the diversity calculation was the percent that each species contributed to the total density at each site. Because of the criticism that some investigators have applied to variable distance census methods (e.g., Dawson 1981), I also used the number of individuals that I actually saw or heard at each site as the basis of my diversity calculations. The subsequent results, however, did not differ noticeably, except that correlations with habitat variables were almost invariably slightly higher using the density figures. This indicates that the somewhat arbitrary assignment of EDDs probably had little effect upon the data. Although the number of stations that I censused at each site varied, and therefore resulted in potentially more species at sites with more effort, these rare species contributed little to the H' calculations. I therefore combined all observations at a site for the H'calculation. I calculated bird species richness (BSR) by calculating the mean of the number of species that I saw at each station in each site.

English and scientific names of birds are taken from Humphrey et al. (1970), Johnson (1967), and Olrog (1959), in that order of priority. Scientific names not contained in the text are given in Appendix 1.

VEGETATION MEASURES

Vegetation was quantified by a method originated by MacArthur and MacArthur (1961) and used extensively by Ohmart and his colleagues (e.g., Rice et al. 1983; Anderson,

Ohmart, and Rice 1983). The validity of the method as a quick and accurate index to vegetation density is well established (Anderson, Ohmart, and Hunter 1983). At each station, I estimated as accurately as possible the distance at which a 1-m² board would, on the average, be 50% obscured by foliage at various heights, combining all compass directions. These heights were 0-0.1, 0.5, 1, 2, 5, 10, 20, 30, 40, and 50 m. If the distance was greater than 200 m, no data were taken at that height. At each height, I estimated the percent that each plant species or growth form (Table 2) contributed to the foliage. The distance can be translated into foliage density, by species, at each height by use of the following derivation of Mac-Arthur and MacArthur's (1961) formula:

$$k=\frac{0.69315}{D}\,,$$

where k is the estimate of foliage leaf area (m²/m³), D is the distance to the imaginary board, and 0.69315 is \log_{e^2} .

In the analyses below, I used the total amount of foliage surface area to calculate the abundance of each plant species. This number was the total leaf surface area, derived from the calculation in method (2) below in determining Foliage Species Diversity.

Foliage Species Diversity. This was calculated from the volume of each species or growth form, either: (1) proportional to the foliage area (m^2/m^3) that each species or growth form occupies, weighted by the height of that span; or (2) a span measurement, with each height measurement contributing equally, regardless of the area that the estimate sampled. Although (2) has been used by other investigators, I wished to see if (1) might be a better predictor, as it estimates the total leaf surface area of vegetation.

At each site, I discriminated between plant species whenever possible, but many of the plants were recorded as "shrub A," "shrub B," and so forth. Species diversity was calculated on this basis. For Table 2, however, and for comparisons between sites, these were combined into such categories as "grass, sp." and "shrub, sp."

Foliage Height Diversity. This measurement was calculated from the percent of the total foliage area of all species of plants contributed by each level in a similar fashion to the species diversity measure with either: (1) proportional diversity, with each estimate at each level contributing proportionally to the area it samples; or (2) interval diversity, with each level contributing equally. The latter is the method that MacArthur and MacArthur (1961) used.

Comparison of bird and plant communities. I compared bird communities as a whole with

various aspects of the plant community, by using the average of each variable at each of the 12 sites. For these and other analyses, I used a simple correlation analysis, as well as stepwise multiple regression analyses. This latter technique adds independent variables to the one that was most correlated with the dependent variable. As it adds a variable, it determines the "maximum r^2 improvement" (Hocking 1976, SAS 1979) or the highest percent of the variation of the dependent variable explained by two or more independent variables. Thus, a model with an r^2 of 0.95 explained 95% of the variation. Surprisingly, no vegetation variables were highly intercorrelated with any others; therefore, all were included in the analyses.

RESULTS

BIRD CENSUSES

My results represent data taken at 275 stations, and within the limitations of the method (see papers referenced in Ralph and Scott 1981:x), I feel that they fairly approximate the actual populations present. The data (Table 1), expressed in individuals per 10 ha, should not be construed to be as precise as this figure. Rather, these figures are for comparative purposes only.

I recorded 50 species at all the sites combined. The most common was the White-crested Elaenia (*Elaenia albiceps*), a small tyrannid that gleans foliage as well as catches flying insects. It was absent only in the grassland sites. The House Wren (*Troglodytes aedon*) was next in abundance, followed by the Thorn-tailed Rayadito (*Aphrastura spinicauda*) and the Green-backed Firecrown (*Sephanoides sephanoides*), a small hummingbird.

VEGETATION MEASURES

The five beech forest sites had much higher total leaf area (57–120 $m^2/100 m^3$) than the other sites (Table 2). The cedar and scrub areas ranged from 16 to 37 $m^2/100 m^3$, and the grass-lands between 3 and 7 $m^2/100 m^3$.

No consistent pattern was found in Foliage Species Diversity (FSD; Table 2), either with the proportional or the interval method. Foliage Height Diversity (FHD) was more predictable, however, with the taller, more complex forests generally having, as expected, higher values than the scrub or grassland habitats.

COMPARISON OF COMMUNITY DIVERSITIES AND ABUNDANCES

All sites. The number of bird species and the density of birds increased as FHD (by two

measures) increased at each site (all P < 0.01; Table 3). FSD, total leaf area, and average canopy height were not significantly correlated with any of the bird measures, and BSD was not correlated with any of the plant measures. In a stepwise multiple regression analysis, the best predictor of the bird variables was always proportional FHD. Adding a second variable to these models markedly improved the percent of the variation explained. Adding total leaf area to FHD improved both prediction of bird species richness ($r^2 = 0.88$; P < 0.0001) and total density ($r^2 = 0.74$; P < 0.01). BSD was best explained by adding average canopy height to proportional FHD ($r^2 = 0.62$; P < 0.05).

All of these relationships were positive, as many other workers have found in many communities. Inspection of the correlations derived (e.g., Fig. 2), however, shows that these results were largely due to the low diversity and abundance of both birds and plants at the grassland sites.

Non-grassland sites. Analyses that excluded grassland sites, conversely, showed that BSD decreased as vegetation measures increased (Table 3). This is the paradoxical situation that Vuilleumier (1972) inferred from his observations, which did not include data from grassland habitats.

A predictive model using stepwise regression analysis, even with three vegetation variables, failed to predict either bird species richness (BSR; $r^2 = 0.45$; P = 0.36) or estimated total density ($r^2 = 0.12$; P = 0.68). BSD was best predicted, however, by a combination of average leaf area and interval FSD ($r^2 = 0.91$; P < 0.001).

The cause of these apparently paradoxical correlations can best be seen in an example (Fig. 2). If grassland sites are excluded from a comparison of BSD and proportional FHD, the relationship is inverse: BSD declines as FHD increases.

Thus, birds reach their greatest abundances and diversities at intermediate densities and diversities of foliage and plant species. A further example of this pattern is bird species diversity as compared to total leaf area (Fig. 3).

An interesting pattern emerges when comparing the bird species richness with either average canopy height (not shown) or average leaf area (Fig. 4). A regression line, drawn separately on either the beech forests or the combined scrub-cedar sites, shows a significant negative correlation. That is, in the more complex habitats, the number of species declined. When these very different habitats were combined, however, this relationship disappeared.

Because of this persistent difference between grassland and non-grassland sites, many of the

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TABLE 1. Results of bird census with calculations of density (Den.) in birds per 10 ha, numbers of individuals (Ind.) of each species that were seen at each location, and summary statistics. A plus (+) indicates less than 0.5 birds per 10 ha.

			Grassla	nds				Scrub				
	Bunchg	rass	Cactu	s	Herbace	ous	Sedge	<u> </u>	Beech			
Species	Den.	Ind.	Den.	Ind.	Den.	Ind.	Den.	Ind.	Den.	Ind.		
Buff-necked Ibis	-	_	_	~	_	-	1	6		~		
Ashy-headed Goose	_	_	-	~	+	4	-	-	+	2		
Andean Condor	_		-	_	-	_	-	-	+	1		
Black Vulture		-	-	-	-	-	+	1	—	-		
Turkey Vulture	_		_	_	-	-	_	_	_	_		
Red-backed Hawk	-		+	1	-	-	+	1	-	_		
Cinereous Harrier		-	-	_	-	_	+	2	-	-		
Chimango Caracara	~	~	-	-	+	1	+	3	+	1		
American Kestrel	-	_	-	~	_	_	+	1	_	_		
California Quail	_	_		-	2	8	9	38	4	19		
Southern Lapwing	-	_	-	—	1	2	2	16	-	_		
Eared Dove	+	1	-	-	+	1	+	3	+	2		
Austral Parakeet	-	-	—	_	-		—	_	-	_		
Band-winged Nightjar	_	_	+	1	-	_	_	_	_	_		
Green-backed Firecrown	_	_	_	~	-	_	1	1	1	1		
Magellanic Woodpecker			—	_	-	-	—	-	_	_		
Austral Flicker			-	_	-	_		_	2	16		
Striped Woodpecker	_	_		-	_	_	_	-		_		
Short-billed Miner	—	_	+	1	-	-	_	_		_		
Rulous-banded Miner	_	_		_	_	_	1	2		_		
Scale-throated Earthcreeper	_	_	+	3	_	_	_	—	+	2		
Thorn-tailed Rayadito	_	_	-	_	-	_	~	-		12		
Lesser Canastero	_	_	I	3	-	-	30	40	9	13		
Austral Canastero	_	_		_	I	1	16	11	8	0		
White-throated Treerunner	_	_	_	-	_	_	_	_	+	1		
Huet-nuet Charac	—	_	_	_	-	-	_	_	~	-		
	_	_	~		_	_	_	~	+	3		
Creat Shrika Tarrant	_	_	-	_	_	_	-	- -	_	_		
Great Shrike Tyrant		_	-	_	_	~~	4	0	_	_		
Charlete	—	_	1	0	_	_	_	-	_	_		
Eira aved Diveon	_		т	2	_	1	_	_	2	0		
Spot billed Ground Tyrant	_	_	1	0	т 5	10	_		5	,		
Cinnamon bellied Ground Tyrant		_	1	1	5	10		_		_		
Tuffed Tit Tyrant	-			_	_		7	7	10	11		
White crested Flaenia	_	_			_	_	3	, 1	66	102		
Rufous-tailed Plantcutter	_	_	_	_	_	_	2	16	- UU	102		
Rue and White Swallow	_	_	_	_	+	1	_	-	1	1		
House Wren	_	_	_	_	<u> </u>	_	30	38	19	27		
Austral Thrush	-	-	_		1	2	ğ	28	í	- 4		
Hellmayr's Pipit	1	2	_	_	_	_	í	4	_	_		
Austral Blackbird	_	_	_	_	_	_	ī	3	_	_		
Greater Red-breasted Meadowlark	_	_		_	_	_	5	41	·	_		
Patagonian Sierra Finch	_	_	_	_	_	-	_	_	11	33		
Grev-headed Sierra Finch	_	_	_	_	~		1	2	_	_		
Mourning Sierra Finch	_	_	_	_	_		2	5	_	_		
Plumbeous Sierra Finch	_	_	-	_	_	_		_	_	_		
Rufous-collared Sparrow	_	_	6	41	1	3	_	-	19	51		
Black-chinned Siskin	_	_	_	_	_	_	1	2	12	36		
Common Diuca Finch	_	_	~	-	9	18	24	36	1	2		
Total density	1	3	10	70	21	52	158	323	167	346		
Number of species	2	÷	10	. 🗸	12		26		23	2.0		
Number of stations censused	14		60		21		22		25			
Diversity (density)	0.0	6365	1.4	4632	1.1	7522	2.3	3556	2.0)726		
Diversity (individual)	1.0	0986	1.4	1393	1.9	9647	2.6	6447	2.3	3469		
Average no. species/stations	0.1	2	0.7	7	1.0	0	7.7	7	6.	7		

TABLE 1. Extended.

	_								Beech f	orests			=		
		Cedar for	ests			No bam	boo	<u> </u>			Bamboo/a	ombeyi			
Sp	arse	In d	Dens	Tend -	pumil	lio Ind	dombe	yi Ind	Dens	Jed -	antarc	tica	pumi.	lio	Total
Den.		Ind.	Den.	Ina.	Den.	Ind.	Den.	Ino.	Den.	Ind.	Den.	Ind.	Den.	ina.	Total
			-	—	_	_	_	-	-	_	-	_	-	-	6
		_	-	-	—	_	_	-	+	1	-	-		-	7
	_	_	+	1	_	_	-	_	_	_	_	_		_	2
	_	_	+	6		_	_	_			_	_	_	_	6
	+	1	+	2	1	4	_	_	_	_	+	1	-	-	10
			-	_	_	_	-	-	-	-	-	-	_	_	2
	—	_	-	-	_	-	-	-	-	_	_	-	-	-	4
	1	15	- 5	- 16			_	_	_	_	_	_	_	_	06
		-		- 10	~	_	_	_	_	_	_	_	_	_	18
			_	_	_	_	_	_	_	_	_	_	_	_	7
	-	—	-	-	_	_	-	-	+	3	+	3	1	4	10
	-	-	_	_	-	_	-	-	_	_	-	-	_		1
	_	_	4	3	8	8	_	_	41	33	48	/0	35	20	136
	_	_	_	_	+	4	_	_	+	2	+	2	_	_	21
	_	_	_	_	1	7	_	_	_	_	_	_	+	1	8
	-	-	_	-	-	_	_	-	-	_	_	-	_	_	1
	-	-	_	—		_	_	-	_		_	_	-	-	2
	_	_	- 2	-	30	52	- 15	- 7		48	37	80	20	28	210
	17	13	11	11	- 50	52	- 15	_		40	52	- 80	- 29	20	86
	7	3	9	5	_	_	_	_		_	_	_	_	_	26
	-	-	_	_	3	10	1	1	3	9	4	17	4	7	45
	-	_	_	-	2	9	1	2	6	3	1	. 3	4	14	31
	+	3	_	-	1	19	_	_	2 +	22	3	00 11	2	13	128
	т —		_	_	т —		_	_		_	-		- -	_	6
	_	_		_	_	_	-	-	_	_	_	_	-	_	8
	-	-	-	_	-	-	-	-	—	-	-		_		2
	-	-	+	1	1	4	_	-	—	-	1	4	7	13	32
	_		_	_	_	_	_	_	_	_	_	_	_	_	19
	27	15	13	10	_	_	_		_	_	3	5	_	_	48
	31	25	13	14	84	130	41	18	70	87	47	106	72	63	549
	-		+	1		_	_	-	-	-	_	_	_	_	18
			2	- 20	2	7	20	-	$\overline{\alpha}$	20	3	14	2	3	26
	27	20	30 4	38	49	۱/ و	20	8 2	20 +	30	11	23 4	50	41	290
	_	_	_	_	_	_	_	_	_	_	-	_	_	-	6
	1	1	_	_	_	—	_	_	-	_	3	14	2	3	21
	-	_	_	_		_	_	_	_	_	_	_	_	-	41
	2	3	5	11	15	43	7	6	10	23	4	18	12	19	156
	_		_	_	_		_	_	_	_	_	_	_	_	5
	_	_	1	1	_	_	2	2	_	_	_	_	-	_	3
	-	_	_	_	-	_	-	-	-	_	1	2	-		97
	10	16	9	19	11	33	1	1	+	1	1	6	1	1	115
	-	-	-	_		—	-	—		-	-	-	-	_	56
1	29	119	112	152	210	414	91	47	189	265	163	449	220	233	2,473
	13		1/		1/		9 7		15		19		15		275
	1.9	360	2.	1750	1.	7680	1.5	5328	1.0	6316	1.	8595	1.1	8325	215
	2.1	573	2.	3919	2.	1603	1.7	7822	1.9	9584	2.	2526	2.	2102	
	5.7	7	4.	7	7.0	0	4.4	ţ	6.0	0	6.	2	7.	8	

		- - (Beech forests		
Canadian	-	Grasslands		Sc	rub	Cedar	forests	No b	amboo		3amboo/dombey	1
species	Bunchgrass	Cactus	Herbaceous	Sedge	Beech	Sparse	Dense	pumilio	dombeyi	Dense	antarcticus	pumilio
Berberis spp.	I	I	1	9.30	2.54	1.94	0.51	3.90	1.66	4 53	767	6 37
Diostea juncea	I	I	I	I	5.21	4.06	11.78	I	1		è I	
Chusquea spp.	I	I	I	I	I	I	ł	0.08	I	46.85	26 56	14 88
Austrocearus chilensis	ł	I	I	I	1	7.38	14.16	1	22.36	3.76	0.01	00.1
Desjonatinea spinosa	ļ	I	I	I	I	I	I	I	I	1	0 71	0.75
Urass spp.	1.75	0.75	0.54	2.84	0.10	I	1.02	ł	I	1	0.04	
Heros spp.	0.19	0.04	0.97	0.33	0.52	1.78	5.44	1.32	I	0.61	0.66	2 64
Lomana nirsuta	1	Ι	I	I	1.78	2.59	2.04	I	1	I	, ;	
Mulinum spinosum	2.04	0.85	1.12	0.14	ł	1	I	I	I	ł		I
Notholagus antarctica	I	I	1	I	11.08	0.35	ł	I	I		- 0 26	1
Notholagus dombeyi	1	I	I	I	I	I	0.03	I	72.00	62.35	26.17	18 36
Nothojagus pumilio	I	ł	I	I	ł	I	ļ	57.35	I	1	1	14.08
E MUOUNTIUM COCCINEUM	I	1	I	I	١	0.11	0.20	I	I	1	I	
Acaena ovalifolia	I	1.31	I	0.18	0.59	I	I	0.05	1.18	ł	0.13	
Kibes mageilanicus	I	I	I	ł	I	ł	1	2.95	6.61	1.24	0.18	I
onrue spp.	I	4.09	I	3.06	1.55	i	2.16	0.11	0.25	0.39	0.13	۱
lotal	3.98	7.04	2.63	15.86	23.37	18.21	37.34	65.77	104.05	119.22	71.41	56.57
Average height	0.1	0.2	0.1	5.0	2.1	4.8	7.8	21.7	31.4	33.7	253	20.0
Spp. diversity (vol.)	0.5958	1.0778	0.7832	0.9292	1.0947	1.2003	1.1160	0.4566	0.8161	0.8180	0.9725	1 3759
Spp. urversity (level)	0.2928	1.0892	0.7832	0.8161	1.0798	1.2526	1.0592	1.0315	1.2190	0.7196	0.8785	1.2317
Fol ht direction	0.000	0.0858	0.0000	1.2398	0.9861	1.2931	1.2834	1.5020	1.6824	1.8446	1.7296	1.6977
roi. ut. urver. (IIIt.) Number of complet	0.000	c//0.0	0.0000	0.9385	0.8814	1.0896	0.8721	1.5957	1.8437	1.3176	1.2357	1.3200
TAULON OF SALIPTICS	12	10	1/	17	25	13	17	24	7	19	36	14

TABLE 2. Estimates of the leaf surface area $(m^2/100 m^3)$ by species or growth form, as calculated from the average of each station's value.

TABLE 3.	Comparison	of community	y diversities and	abundances.
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		Foliage surface	Foliage speci	es diversity	Foliage height	diversity
Bird variables	Canopy height	area	Proportional	Interval	Proportional	Interval
All locations	(n = 12)					
Average no. species Bird species diversity Average density	+0.48 +0.03 +0.58*	+0.45 +0.03 +0.55	+0.29 +0.47 +0.21	+0.36 +0.39 +0.29	+0.85*** +0.47 +0.86***	+0.79** +0.37 +0.78**
No grasslands	(n = 9)					
Average no. species Bird species diversity Average density	-0.22 -0.86** +0.16*	-0.34 -0.86** +0.08	+0.08 +0.34 -0.09	$-0.22 \\ -0.17 \\ -0.27$	-0.10 -0.76* +0.24	-0.22 -0.87** +0.03

P <: * = 0.05; ** = 0.01; *** = 0.001.

results below are divided into analyses of all sites, and all sites except the grasslands.

BIRD SPECIES RICHNESS (BSR) VS. INDIVIDUAL PLANT SPECIES

BSR was negatively correlated with the leaf surface area of *Mulinum*, a common grassland plant (r = -0.86; P < 0.001), and positively correlated with foliage area of *Berberis* (r = 0.78; P < 0.01). A stepwise regression using both species explained 89% of the variation in BSR (P < 0.0001). Addition of other plants added less than 3% to the model.

Excluding the grassland sites, foliage of *Berberis* was a good correlate of BSR (r = 0.75; P < 0.05). Increasing BSR in the non-grassland sites, however, was also correlated with decreasing foliage of the cedar, *Austrocedrus* (r = -0.88; P < 0.01). The "best" stepwise regression of three variables included *Austrocedrus*, *Nothofagus antarcticus*, and a small herb (*Acaena*; $r^2 = 0.93$; P < 0.01). Adding further variables increased the percent variation explained by less than 4%.

BIRD SPECIES DIVERSITY (BSD) VS. INDIVIDUAL PLANT SPECIES

The only plant species that had a significant correlation with BSD was Mulinum (r =



FIGURE 2. Bird species diversity (from density) vs. proportional foliage height diversity from three habitat types in northern Patagonia, Argentina. The letters refer to the locations described in Methods.

-0.78; P < 0.01). In a stepwise regression, foliage of *Mulinum* and all *Nothofagus* combined explained 86% (P < 0.001) of the variation in BSD. Additional plants explained only about 4.5% more of the variation.

Excluding grasslands, increased BSD was correlated with increasing foliage of all shrub species combined (r = 0.84; P < 0.01), grasses (r = 0.78; P < 0.05), and with decreasing Nothofagus foliage area (r = -0.90; P < 0.0001). A stepwise regression with the best two variables chose Nothofagus and all shrubs ($r^2 = 0.95$; P < 0.0001). Addition of another species or group increased the variation explained by less than 3%.

ESTIMATED TOTAL BIRD DENSITY VS. INDIVIDUAL PLANT SPECIES

Greater leaf surface area of a grassland plant, Mulinum, was correlated with decreasing bird density of all species combined (r = -0.73;P < 0.01), reflecting the depauperate nature of the grassland bird community. A stepwise regression added another negative vegetation component to Mulinum, that of cedar, resulting in a significant model $(r^2 = 0.80; P < 0.001)$. In addition, increasing Berberis was correlated (r = 0.73; P < 0.01) with increasing bird density.

Among the non-grassland sites, increasing bird density was correlated with decreasing *Austrocedrus* (r = -0.84; P < 0.01). This was the only significant correlation and, since there were 17 plant variables, could be expected by chance alone. The best three-variable, stepwise model used *Austrocedrus*, herb cover, and *Nothofagus pumilio* for a model ($r^2 = 0.85$; P < 0.01). Adding an additional plant variable explained less than 2% additional variation.

PREDICTING BIRD OCCURRENCE BY INDIVIDUAL PLANT SPECIES

To see if the variation in the density of common birds was related to leaf area of the various plant species, I used the 27 bird species with at least 10 individuals at all sites com-



FIGURE 3. Bird species diversity compared with the total leaf area from three habitats in northern Patagonia, Argentina. Letters refer to locations described in the Methods.



FIGURE 4. Average number of species per station for each location in three habitat types in northern Patagonia, Argentina, as compared to average leaf areas of all plant species combined. Letters refer to locations described in Methods.

bined (Table 4). I found 24 (89%) of these significantly correlated with foliage surface area of at least one plant species. Surprisingly, an increase in the surface area of most plants was significantly correlated with an increase in the bird count. If chance had been operating to any significant degree, I would have expected many more negative relationships.

Seven birds were positively correlated with grasses, and many of these were open-grassland foragers. Some, however, reached their peak densities in the scrub-sedge habitat. Two other species were negatively correlated. Nine birds were positively correlated with Notho*fagus*, either with one of the species, or by combining all Nothofagus species. Most of these species forage commonly in Nothofagus. Bam-

TABLE 4. Summary of correlations between species or growth forms of plants and species of birds and the best plant variables used in constructing a two-variable stepwise regression model. Numbers in the table are simple correlation coefficients.^a r^2 is the percent of the variation explained by the model.

Species	n	Berberis	Diostea	Chusquea	Austro- cedrus	Desfontainea	Grass sp.	Herbs sp.
Red-backed Hawk	10	_	_	_	_	_	_	_
California Quail	96	_	_	_	_	_	0.65+	_
Southern Lapwing	18	0.40	_	_	_	_	0.89++++	_
Austral Parakeet	10	_	_	_	_	_	_	_
Green-backed Firecrown	136	0.64+		0.91++++	—	0.68+	_	+0.11
Austral Flicker	21	_	-	_	_	-0.04		_
Thorn-tailed Rayadito	219	-	_	0.73+	_	_	_	_
Lesser Canastero	86	_	_	-	_	_	0.76++	_
Austral Canastero	26	_	_	_	—	_	0.71	_
White-throated Treerunner	45	_	_	0.72++	—		_	_
Huet-huet	31	_	_	_	—	—	_	_
Chucao	128	0.72++	_	0.87+++	_	0.78++	-	-
Magellanic Babbler	20	0.63+	-	0.58+	_	0.77++	_	_
Fire-eyed Diucon	32	_		_	_	_	_	-
Spot-billed Ground-Tyrant	19	_	_	_	_	_	_	
Tufted Tit Tyrant	48	—	−(0.57)°	-	-			
White-crested Elaenia	549	_	_	_	_	-	-0.62+	_
Rufous-tailed Plantcutter	18	_	-	-	-	-	-0.91++++	
Greater Red-breasted Meadowlark	41	_			_		0.90++++	-
House Wren	296	_	-	_	—	_	_	_
Austral Thrush	61		-	-	_	_	0.81++	—
Austral Blackbird	21	0.83+++	_	—	_	0.88^{+++}	-	_
Blue and White Swallow	26	0.67+	-	—	_	0.76++	—	_
Patagonian Sierra Finch	156	—	—	—	_	-0.02	—	_
Rufous-collared Sparrow	97	_	-	_	_	_		_
Black-chinned Siskin	115	—	0.66+	—	_		-	_
Common Diuca Finch	56	-	_	-	-	—	0.86+++	-

* Their significance level is indicated to the right of each number (P < : * = 0.05; ** = 0.01; *** = 0.001; **** = 0.0001). Italic numbers are those variables that contributed to a two-variable model (correlation values are given for those variables that were not significantly correlated, but contributed to a model). * Although all *Notholague* species combined were the best correlated, the two species separately contributed best to a two-variable model. * Although positively correlated (P = 0.053), the information it contributed to the predictive model was negative. * *Mulinum* alone was the only combination of variables that would significantly predict the species' abundance.

boo (*Chusquea*) was positively correlated only with a rhinocryptid, the Chucao (*Scelorchilus rubecula*), and the Green-backed Firecrown. Abundances of three other birds were correlated with bamboo, but it was not selected in stepwise models, possibly reflecting only an ancillary role in organization of the bird community. Some shrub species were also involved in models or correlations. Their roles as a substrate for feeding or as food themselves are unknown. Most important were *Mulinum*, with mostly negative associations, *Lomatia* and *Berberis* with all positive associations, and *Desfontainea* with mostly positive associations.

A few other plants were fairly common and in more than one site, but were not well correlated with any bird species. These were the cedar (*Austrocedrus*), a currant (*Ribes magellanicus*), and a shrub (*Diostea juncea*). Of these, the lack of association with *Austrocedrus* was most surprising, as it is a major component of some ecosystems.

DISCUSSION

My major finding is the first well-documented negative correlation of vegetation abundance

with bird abundance. Specifically, in the nongrassland sites, as foliage height diversity, average canopy height, and average leaf surface area all increased, bird species diversity decreased (Table 3).

The explanation of this paradoxical situation probably lies in the specific habitat relationships of each of the bird species to each plant species. My analyses show that the principal correlates and predictors of the abundances of individual bird species were the abundances of certain plant taxa, namely: positive correlations of *Berberis*, grass, *Chusquea*, Nothofagus dombevi, N. pumilio, Desfontainea, and Lomatia; and a negative correlation with Mulinum. All of these, with the exception of Lomatia, are plants of either the grassland or the beech forests. Those plants most common (Table 2) in the intermediate scrub and cedar forest sites, such as Austrocedrus, Embothrium, and Diostea, were all rather unimportant as predictors or correlates of bird species abundances (Table 4).

I found no real indication that bird species diversity was related in any simple fashion to plant species diversity. The sites with higher plant diversity values were distributed irreg-

TABLE 4. Extended.

Lomatia	Mulinum	N. antarctica	N. dombeyi	N. pumilio	Nothofagus (all)	Embothrium	Acaena	Ribes	Shrub sp.	r ²	
	_	_		0.70+	0.21	_	_	_	_	0.88	++++
0.51		_	_	_	_	_	_	_	-	0.79	++
_	_		_	_	—		_	_	-	0.84	+++
_	_		-	—	—	_	_	-	-	0.34	n.s.
_	_	-	0.82++	—	0.71+	_	_		-	0.86	++++
-	_	0.64+	-	-	—		-	_	-	0.96	++++
_	—	-	0.75++	+0.43	0.92+++ь	—	-	_	-	0.89	++++
_	-0.24	-	—	—	-	_	—	-		0.78	++
0.51	_	—	—	—	—		-	—		0.88	++++
_	_	_	0.70+	-	0.87++++	—	_	0.43	-	0.81	+++
-	-	—	_	_	—	—	_		-	0.24	n.s.
_	_	_	0.74++	+0.22	0.83+++	_	_	_		0.88	++++
-		-	-	-	_			_	-0.45	0.68	++
-	_	-		_	-	_	_	—		0.18	n.s.
-	0.59+	—	-		_	_	-	—	-	0.37	n.s.ª
0.79++	-	-		_	_	0.63+	-	_	-	0.69	++
	-0.69^{+}	-	—	_	0.77++	—	-	_	-	0.73	++
	-0.10	-	—	_	_	_	_	-		0.94	++++
	-0.08	_	-	_	_	_	_	—		0.91	++++
-	-0.74^{++}	-0.21	_	_	_	_	-	—	-	0.82	++
	-0.28	_	—	_	—	-	-	_		0.90	++++
	_	-	-	_	_	-	-	—		0.87	+++
-	-		_	0.51	0.71++	_	-		_	0.92	++++
-	-0.65+	-	-	0.59+	0.67+	_		0.61+	—	0.61	+
0.57	—	—	-	_	_	_	0.65+	—	-	0.68	++
0.79++	-	-	—	0.42	-	-		_	—	0.98	++++
_	_		_	-	_	-0.17	-	-	-	0.76	++

ularly through the habitats (Table 2). Although some of these higher plant values were in the scrub-cedar habitats, this was, by no means, always the case. The highest bird species diversity and (generally) richness occurred in habitats that were intermediate in vegetation measures such as total foliage area and foliage height diversity. This indicates that these habitats are either unique in themselves, or they possess some attribute(s) that causes them to be rich in bird species. Their intermediate stature and foliage height diversities argue against any uniqueness, at least in their vegetation structure.

Rather, it seems possible that their high bird species diversity (as well as possibly richness) can be attributed to their intermediate position in the moisture gradient between the widespread steppe habitats of southern South America, and the unique and isolated Nothofagus forest of the Andes, as suggested by Rabinovich and Rapoport (1975:146). The scrub-cedar habitat has elements of both steppe and beech forests. Twelve of the 27 bird species that were common in my census (Table 4) were positively related to plant species found in the beech forests, such as Nothofagus itself, Chusquea, and Ribes, as well as others. Many of these bird species are probably adapted to the beech forests, as many do not commonly occur outside of them (Vuilleumier 1967), although they can be found in some of the scrub-cedar habitats. Similarly, the birds adapted to the widespread steppe habitats can live in the transitional cedar forest habitats. These intermediate habitats are not common in this region: they occur only where the elevational and rainfall gradients intersect appropriately. One might be tempted to ascribe this richness to the "edge" effect, the mixture of two diverse habitats. It is more than this, however; some plant species are generally restricted to this habitat type (e.g., Lomatia and Diostea-Table 2). Therefore, floristically and faunistically, the scrub-cedar habitat is a mixture of steppe and beech forest, containing not only substantial elements of each, but also unique elements of its own. This combination might assure species richness and diversity.

This explanation, however, contradicts the prediction that bird species diversity, especially the evenness component, would be higher in the structurally complex beech forests, even if they are somewhat poor in bird species. One might expect that those fewer species should be about equal in abundance (the evenness component of diversity), compensating for the lower richness.

The beech forests of the Andes are, however, under three constraints that might lower their

stability and presumably their diversity. The most important is the isolation of these forests from others. The Nothofagus and Araucaria forests of the Andes of Argentina and Chile are separated from other forests by about 2,000 km of steppe and desert. This might lead to relatively small populations which are more prone to local extinction, with resultant low diversity. The second factor is the relative harshness of the climate. These forests have a more persistent snow cover in the winter than do the steppe habitats at lower elevations. This climatic factor may add to the risk of local extinction and unstable bird populations, when coupled with the forests' isolation, the possible "island" effect, and low colonization rates. Finally, the abundance of bamboo (Chusquea spp.) in the understory of many of the beech forests (Table 2) may play a role. The large leaf surface area of bamboo, coupled with what I observed to be its apparent low use by insects (possibly due to its relative unpalatability), may produce lower food densities for foraging birds than is normal in taller forests such as these.

An interesting test of the role of bamboo will come with its blooming (it blooms only once about every 40+ years) and subsequent superabundance of seeds. This may happen in the next few years (O. P. Pearson, pers. comm.). I predict that, during the year of extensive bloom and seed set of this important component of many of the beech forests, the number of bird species using the forest will increase. This may also result in an increase of bird species diversities.

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APPENDIX 1. List of species whose scientific names do not appear in the text.

Buff-necked Ibis Ashy-headed Goose Andean Condor Black Vulture Turkey Vulture Red-backed Hawk Cinereous Harrier Chimango Caracara American Kestrel California Quail Southern Lapwing Eared Dove Austral Parakeet Band-winged Nightjar Magellanic Woodpecker Austral Flicker Striped Woodpecker Short-billed Miner Rufous-banded Miner Scale-throated Earthcreeper Lesser Canastero Austral Canastero White-throated Treerunner Huet-huet Magellanic Babbler Great Shrike Tyrant Grey-bellied Shrike Tyrant Chorlote Fire-eyed Diucon Spot-billed Ground-Tyrant Cinnamon-bellied Ground-Tyrant Tufted Tit Tyrant Rufous-tailed Plantcutter Blue and White Swallow Austral Thrush Hellmayr's Pipit Austral Blackbird Greater Red-breasted Meadowlark Patagonian Sierra Finch Gray-hooded Sierra Finch Mourning Sierra Finch Plumbeous Sierra Finch Rufous-collared Sparrow Black-chinned Siskin Common Diuca Finch

Theristicus caudatus Chloephaga poliocephala Vultur gryphus Coragyps atratus Cathartes aura Buteo polvosoma Circus cinereus Milvago chimango Falco sparverius Lophortyx californica Vanellus chilensis Zenaida auriculata Enicognathus ferrugineus Caprimulgus longirostris Campephilus magellanicus Colaptes pitius Dendrocopus lignarius Geositta antarctica Geositta rufipennis Upucerthia dumetaria Asthenes pyrrholeuca Asthenes anthoides Pygarrhichas albogularis Pteroptochos tarnii Scytalopus magellanicus Agriornis livida Agriornis microptera Pseudoseisura gutturalis Pyrope pyrope Muscisaxicola maculirostris Muscisaxicola capistrata Anaerates parulus Phytotoma rara Notiochelidon cyanoleuca Turdus falcklandii Anthus hellmavri Curaeus curaeus Pezites militaris

Phrygilus patagonicus Phrygilus gayi Phrygilus fruticeti Phrygilus unicolor Zonotrichia capensis Spinus barbatus Diuca diuca