

FOREST BIRDS OF PATAGONIA: ECOLOGICAL GEOGRAPHY, SPECIATION, ENDEMISM, AND FAUNAL HISTORY

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ABSTRACT. The beech (*Nothofagus*) forests of Patagonia (southern South America) are isolated from other South American forests by 1100 (Andean forests of northwestern Argentina) to 1400 (lowland forests of southern Brazil) km of nonforest vegetation (including matorral, steppe, monte, espinal, pampa grassland, chaco woodland). This isolation makes the *Nothofagus* forest biome an island-like biota. Its avifauna includes 46 species of 40 genera, in 21 families of breeding landbirds. The patterns of ecological, elevational, and latitudinal distribution of these forest-inhabiting species of birds suggest that they have a wide habitat-niche, a pattern characteristic of truly insular taxa. Isolate formation has taken place in populations of a few species living on outlying islands but has led to insular speciation in three cases only, in the genera *Aphrastura*, *Anairetes*, and *Sephanoides*. The majority of forest species show no geographical variation on the continent. Only two cases of actual or potential continental speciation were detected, in the genera *Pteroptochos* and *Scytalopus*. Both are centered on the valley of the Rio Bío-Bío (central Chile), which may act as a barrier to gene flow. Several forest-dwelling allospecies are members of superspecies including one or more other allospecies that occupy forest or nonforest vegetation elsewhere in South America or in North America. Endemism is high in the Patagonian forest avifauna; about 41 percent of the species and allospecies, and 10 percent of the genera, are restricted in their distribution to the *Nothofagus* forest region. Levels of endemism were analyzed taking into account three different classifications of these birds, in order to assess the effects of changes in taxonomic practice on our evaluation of endemism. Levels of endemism in Patagonian forest birds (inhabiting a habitat island) are intermediate between the lower levels found in Tasmanian forest birds (a continental island) and the high levels found in New Zealand forest birds (an oceanic island group). Endemism in Patagonian forest birds is concentrated among the species that belong to families now distributed in South America, or to families that have been attributed to old autochthonous faunal elements (especially the Furnariidae and the Rhinocryptidae). The implications of these findings are discussed in terms of the Cenozoic history of the Patagonian forest region. The cycles of glaciation and deglaciation of the Pleistocene have played an important role in the development of the present avifauna. Niche shifts have been a biologically significant element in the evolution of several forest birds whose ancestors probably came from open vegetation farther north in the Andes or east in the lowlands of southern South America. The present fauna is a mixture of old relicts and of several strata of more or less recent immigrants.

RESUMEN. Los bosques de hayas (*Nothofagus*) de Patagonia (la porción más austral de Sudamérica) están aislados de otros bosques sudamericanos por 1.100 km (bosques andinos del noroeste argentino) hasta 1.400 km (bosques de galerías del sur de Brazil) por vegetación no boscosa (incluyendo matorral, estepa, monte, espinal, pampas y monte chaqueño). Esta aislación convierte a los bosques de *Nothofagus* en una biota de tipo insular. Su avifauna incluye 46 especies en 40 géneros, en 21 familias de aves terrestres anidadoras. Los modelos de distribución ecológica, altitudinal y latitudinal de las especies habitantes de estos bosques sugieren que poseen un amplio nicho-habitat, situación característica de taxa verdaderamente insulares. Se ha producido diferenciación ("isolate formation") en poblaciones de pocas especies que viven en islas periféricas, pero se ha producido especiación insular en sólo tres casos, en los géneros *Aphrastura*, *Anairetes* y *Sephanoides*. La mayoría de las especies de bosque no presentan diferenciación geográfica en el continente. Sólo dos casos de especiación actual o potencial han sido detectados en situaciones continentales: en los géneros *Pteroptochos* y *Scytalopus*. Ambos están centrados en el valle del río Bío-Bío (región central de Chile), que puede actuar como barrera para el flujo genético. Varias allospecies de habitats boscosos son miembros de superspecies las cuales incluyen una o más allospecies que ocupan vegetación boscosa y no boscosa en otros sitios en

América del Sur y del Norte. El nivel de endemismo en Patagonia es alto, alrededor del 41 por ciento de las especies y alloespecies y el 10 por ciento de los géneros tienen su distribución restringida a los bosques de *Nothofagus* de la región. Los niveles de endemismo se analizaron tomando en consideración 3 diferentes clasificaciones para estas aves, de manera de prever los efectos de cambios en la práctica taxonómica en nuestro evaluación de endemismo. Los niveles de endemismo en las aves de los bosques patagónicos (habitando un habitat insular) son intermedios entre los niveles bajos que se encuentran en las aves de bosques de Tasmania (una isla continental) y los niveles altos de las aves de los bosques de Nueva Zelandia (un grupo de islas oceánicas). El endemismo en las especies de aves del bosque patagónico se concentra alrededor de especies pertenecientes a familias actualmente distribuidas en Sudamérica o familias que han estado atribuidas a elementos faunísticos autóctonos muy antiguos ("old autochthonous") (especialmente los Furnariidae y los Rhinocryptidae). Las implicaciones producto de estos hallazgos son discutidas en relación con la historia del cenozoico de los bosques de la región patagónica. Los ciclos de avance y retroceso de los glaciares durante el Pleistoceno han jugado un papel importante en el desarrollo de la avifauna actual. El cambio de nichos ha sido un elemento biológico significativo en la evolución de varias aves de bosques cuyos antecesores provienen probablemente de la vegetación de campo abierto más al norte en los Andes o en las llanuras orientales del sur de Sudamérica. La fauna actual es una mezcla de los vestigios antiguos y de inmigrantes mas o menos recientes de varios estratos.

Patagonia is defined as the southern part of temperate South America, approximately south of a line running southeast across the continent from the mouth of the Rio Maule in Chile to the mouth of the Rio Colorado in Argentina (see Aubert de la Rüe 1959). The two main vegetation formations of Patagonia are forests dominated by southern beeches (*Nothofagus*, Fagaceae) and semi-desertic steppes. The mountainous western side of the continent, a thin ribbon more than 2000 km long but only 100 to 200 km wide, is covered with forests, while steppes stretch across the much wider upland and lowland areas east of the Andes to the shores of the Atlantic Ocean. A very narrow ecotone separates these formations along the eastern foothills of the Andes. The floras of forest and steppe differ sharply from one another in taxonomic composition and physiognomy. Their climates are also dramatically different.

The *Nothofagus* forests of Patagonia are approximately 1100 km from the nearest montane forests in northwestern Argentina and 1400 km from the nearest lowland forests in southern Brazil, northeastern Argentina, and Paraguay (Fig. 1). The intermediate areas have a dry to arid climate (Knoch 1930; Sorge 1930) and are covered with nonforest vegetation, including pampa grassland, semi-desert scrub, monte, matorral, espinal, and savanna (Cabrera 1953; Schmithüsen 1956; Hueck and Seibert 1972; Solbrig 1976). The presence of an island of forest vegetation at the southern tip of South America immediately suggests a series of questions: Does the composition of the avifauna of Patagonian forests reflect the isolation of their environment? Is this fauna related to the faunas of distant forests elsewhere or to steppe faunas nearby? To what extent is this fauna tied ecologically to the forest environment? What are the ecological and evolutionary consequences of the ecological isolation? What is the history of this fauna? In an effort to answer these questions, I describe in this paper the composition of the Patagonian forest avifauna, discuss the ecological preferences of these birds, analyze their speciation, and examine their levels of endemism and their distribution patterns.

Similar questions have attracted the attention of biologists ever since Darwin visited Patagonia. One fact, especially, has whetted the curiosity of biogeographers. Forests dominated by *Nothofagus* are found in other parts of the southern hemisphere besides South America: Tasmania, Australia, New Zealand, New Caledonia, and New Guinea. Biotic relationships among the plants (Skottsberg 1910, 1916, 1960; Couper 1960; Godley 1960; Cranwell 1963, 1964; Schmithüsen 1964; Cerceau-Larrival 1968; Raven and Axelrod 1972, 1974, 1975) and animals (Simpson 1940, 1966; Darlington 1957, 1960, 1965; Brundin 1965, 1966; Rapoport 1968, 1971; Reig 1968; Hoffstetter 1970; Keast 1972) of these disjunct areas have been discussed in many papers.

Whereas several arthropod taxa found in Patagonian forests show clearcut affinities with those of New Zealand, Tasmania or Australia (Kuschel 1960; Brundin 1965, 1966; Darlington 1965), this is not the case for the birds. Fifteen species of the passerine suborder Tyranni (5 species of Furnariidae, 5 Rhinocryptidae, 4 Tyrannidae, and 1 Phytotomidae) comprise 33 percent of the 46 land bird species. Mayr (1964) classified the Furnariidae and Rhinocryptidae

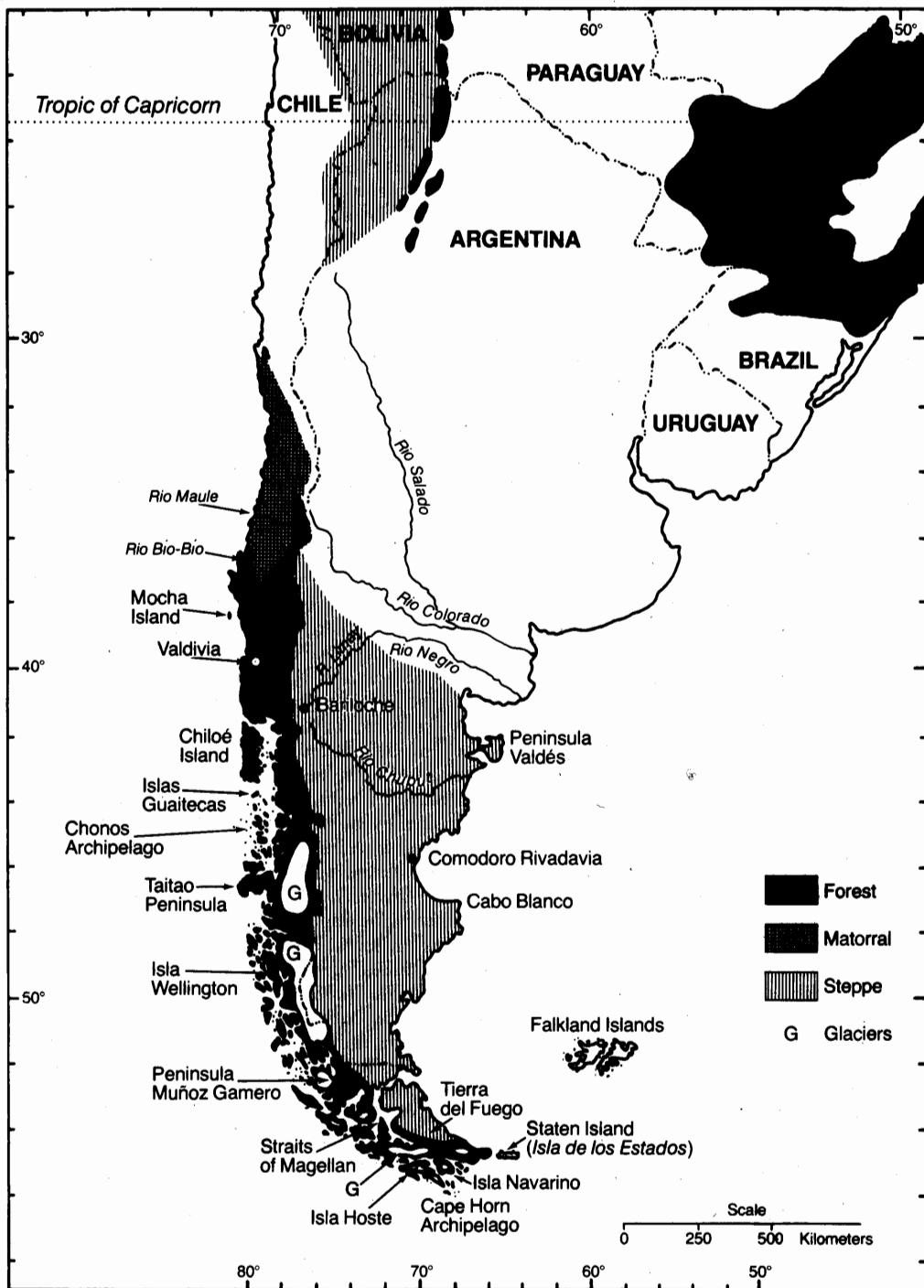


FIG. 1. Schematic map showing location of Patagonian forests in southwestern South America, of Andean montane forests in northwestern Argentina, and of lowland forests in southern Brazil. Puna steppes of Bolivia, Argentina, and Chile are disjunct from Patagonian steppes of Argentina. Other nonforest vegetation types (only matorral identified on map) occur between the three forested areas.

as "Primarily South American," and the Tyrannidae as "Expanding South American." Cracraft (1973), however, considered the suborder Tyranni to be "Southern Hemisphere" rather than "South American." More recently, Feduccia and Olson (1982) suggested that the family Rhinocryptidae is related to the Menurae of Australia. Whether these taxa are primarily South American in origin or have broader southern hemisphere affinities are clearly problems for further research. The discovery of a late Eocene or early Oligocene marsupial (Polydolopidae) on Seymour Island, Antarctic Peninsula, does suggest the possibility of exchange between Australia and South America via Antarctica (Woodburne and Zinsmeister 1983). Other bird taxa living in Patagonian forests (*Accipiter*, *Columba*, *Strix*, *Colaptes*, *Picoides*, *Troglodytes*, Icteridae, and Emberizidae) have Pan-American or Old World affinities.

The relative complexity of the affinities of the birds of Patagonian forests suggests that the development of this avifauna was more complicated than just an influx of immigrants from northerly latitudes, as suggested by Darlington (1957, 1960, 1965). This view needs revision, as does also the conclusion of Hershkovitz (1969:58) that "the extensive beech-conifer forest of southern Chile, bordered by sea on one side and by scrub steppes on the other side, has no proper fauna" of mammals (see data in Baker 1967). On the basis of data from amphibians, birds, reptiles, and mammals, Müller (1973) considered the Patagonian forest region to be a dispersal center. Birds (Vuilleumier 1967a), amphibians (Vuilleumier 1968; Formas 1979), and perhaps mammals (Vuilleumier, unpubl. data) seem to have had rather similar patterns of biogeographic evolution in Patagonian forests, but apparently reptiles did not (Formas 1979).

MATERIALS AND METHODS

Only the landbirds are considered in this paper. All marine birds, as well as the following freshwater birds occurring in or around Patagonian forests, were excluded: grebes (Podicipedidae), herons (Ardeidae), cormorants (Phalacrocoracidae), swans and ducks (Anatidae), rails and coots (Rallidae), gulls (Laridae), oystercatchers (Haematopodidae), snipes (Scolopacidae), and plovers (Charadriidae, except *Vanellus [chilensis] chilensis*).

There are 89 genera and 138 species of land birds in Patagonia (Appendix I), as I define this region. Of these, 40 genera and 46 species are considered to live in Patagonian forests (marked F and B in Appendix I; Appendix II). The decision to classify a given species as a forest bird was based on personal field experience and literature reports. Besides the 46 species accepted as forest birds, 11 others occur locally along (or even in) *Nothofagus* forests, especially clearings, but were excluded from the list because they breed in open country either in the Andes above timberline or east of the Andes: *Falco sparverius*, *Zenaida auriculata*, *Tyto alba*, *Upucerthia dumetaria*, *Cinclodes oustaleti*, *Leptasthenura aegithaloides*, *Cistothorus platensis*, *Mimus thenca*, *Mimus patagonicus*, *Molothrus bonariensis*, and *Diuca diuca*. In contrast, I included as forest birds several species that are found in steppes and open woodlands but that also commonly occur and breed along forest edges, in forest openings, or in parkland within the forest region. These are *Theristicus caudatus*, *Vultur gryphus*, *Coragyps atratus*, *Buteo [albicaudatus] polyosoma*, *Polyborus chimango*, *Vanellus [chilensis] chilensis*, *Cinclodes [fuscus] fuscus*, *Notiochelidon cyanoleuca*, and *Zonotrichia capensis*. Finally, I included *Ceryle [alcyon] torquata* and *Cinclodes patagonicus*, which inhabit stream and lake shores, but are widespread within the forest region. My definition of a forest bird is, thus, broader than that of Moreau (1966:81-82), who did not include as forest birds species that occur in clearings. Some ornithologists may disagree with my decision to include as forest birds several species that occur essentially in open habitats. Excluding these would reduce the number of species considered, but would probably increase the proportion of ecologically restricted or endemic taxa. If I have erred, I have done so on the "generous" side and, thus, have not biased the list "in favor" of forest taxa.

In Appendix II I have summarized the information obtained from my examination of museum skins and from the literature, on geographic variation, species limits, and taxonomic relationships for each species of forest bird; the nomenclature followed in this paper is also indicated. I used the superspecies concept and its formalization by means of brackets (Amadon 1966). I adopted Mayr's (1959) concept of population structure of species in the study of speciation.

Information on geographical and ecological distribution comes from my personal field work in and around *Nothofagus* forests of Argentina and Chile between February and April 1965 (Vuilleumier 1967b, 1972, and unpubl. data), supplemented by the literature (Crawshay 1907;

Pässler 1922; Peters 1923b; Wetmore 1926a, 1926b; Reynolds 1932, 1934, 1935; Radboone 1935; Morrison 1940; Trimble 1943; Behn 1947; Olrog 1948, 1950; Ripley 1950; Krieg 1951; Goodall et al. 1951, 1957, 1964; Philippi et al. 1954; Cawkell and Hamilton 1961; Horváth and Topál 1963; Bernath 1965; Johnson 1965, 1967, 1972; Johansen 1966; Short 1969a, 1969b, 1970a, 1970b, 1971, 1972, 1982; Humphrey et al. 1970; Keith 1970; Texera 1972; Forshaw and Cooper 1973; Araya et al. 1974; Schlatter 1976; Parmelee and MacDonald 1975; Jehl and Rumboll 1976; Venegas 1976, 1981, 1982a, 1982b; Sielfeld 1977; Contreras et al. 1980; Yáñez et al. 1982).

For the measurement of faunal resemblance I used Simpson's (1960:301) index no. 2:

$$\frac{\text{number of taxa common to both faunas}}{\text{total taxa in smaller fauna}} \times 100$$

since in most cases one fauna is richer than the other.

NOTHOFAGUS FORESTS OF PATAGONIA

Although these forests grow entirely at temperate latitudes, they are tall and luxuriant, and resemble tropical or subtropical rainforests in their evergreenness, structure (trees, epiphytes), and physiognomy. Reynolds (1935:66) described the vegetation found near the southernmost localities where forest grows, in the Cape Horn area, at ca. 56°S: "In sheltered places, such as the proximity of a lake at the northern side of Freycinet, precipitous ravines are submerged by evergreen forest of tropical aspect. So thick is the canopy that a chaos of decay exists in the semi-darkness prevailing beneath, and a small maidenhair fern combines with a deep layer of spongy moss to cover everything."

The resemblance to tropical rainforests does not extend to the taxonomic composition of the flora, however. As a result, some botanists have called the southern Patagonian forests "subantarctic" (Young 1972). Patagonian forests are floristically related to forests in New Zealand or Tasmania (Godley 1960), but some floral elements occur also in other South American forests (southern Brazil, Smith 1962; Andes, Hueck 1966).

Nothofagus forests stretch along the Andes from about 35°S south to Tierra del Fuego (Isla Grande) and the islands and islets of the Cape Horn Archipelago at about 56°S (Fig. 1). A few forest fragments are found north of 35°S; the northernmost, the Fray Jorge and Talinay woodlands at about 30°S, contain genera of plants with southern affinities (Muñoz and Pisano 1947; Schmithüsen 1956) but lack *Nothofagus*. Between 31° and 35°S, the patches of forest and woodland are still composed chiefly of trees belonging to genera other than *Nothofagus*. Only from about 36°S southward is *Nothofagus* the common or dominant taxon.

The northernmost species appears to be *Nothofagus obliqua*, found at middle elevations along the Chilean Andes in the Provinces of Santiago and Aconcagua. It associates with *N. procera* farther south, where both deciduous species comprise lowland forests which occur mostly south to the provinces of Valdivia, Osorno, and Llanquihue (Chile) along the western slope of the Andes, and in Neuquén Province (Argentina) along the eastern slope. Moving up into the Andes, these two species are progressively replaced altitudinally by *N. antarctica* and *N. pumilio* (both deciduous), which become more and more shrubby toward timberline. Timberline is found as high as 1800 to 2000 m in the northern *Nothofagus* forests.

In the Valdivian region, between 39° to 40°S and 44° to 45°S, forests are generally luxuriant and resemble tropical rainforests. On the whole, the forests are tallest and most humid in Chilean territory because of the influence of the moisture-carrying westerly winds. The forests decrease in density and floral diversity from west to east along a gradient of decreasing rainfall that corresponds to the lessened maritime influence of winds from the Pacific coast across the Andes and down to the eastern Andean foothills. The forests also decrease in diversity along a north to south gradient of increasing yearly temperature fluctuations.

Valdivian forests are dominated by *Nothofagus dombeyi*, an evergreen species found with the conifers *Saxegothea conspicua* (Podocarpaceae), *Fitzroya cupressoides* (Cupressaceae), *Pilgerodendron uviferum* (Cupressaceae), and *Podocarpus nubigena* (Podocarpaceae). Another conifer, *Araucaria araucana* (Araucariaceae) grows between 37° and 40°S on Andean slopes from about 1000 to 1600 meters. Together with *N. dombeyi*, it forms a montane forest belt. *Nothofagus pumilio* and *N. antarctica* are found up to 1800 m or even higher. A schematic representation of an elevational vegetation sequence on the west slope of the Andes at 41°S can be found in Heusser (1981: fig. 2).

South of 41°S the altitude of timberline decreases (Godley 1960). Between 47° to 48°S and

TABLE 1
FAUNAL RESEMBLANCE AMONG AVIFAUNAS¹

	<i>Nothofagus</i> forest	Patagonian nonforest	Andean forest	Puna	Californian coastal forest
<i>Nothofagus</i> forest	—	53	30	45	30
Patagonian nonforest	43	—	11	81	16
Andean forest	15	4	—	12	18
Puna	33	50	5	—	14
Californian coastal forest	11	9	7	7	—

¹ Values given are index 2 of Simpson (1960:301), in percent. Values to right of diagonal = generic level resemblance. Values to left = specific and superspecific level resemblance.

51° to 52°S two extensive ice caps (Fig. 1) reduce the area available for forests, which are only found in a thin band along the Andes. Furthermore, the southwestern fringe of the area, including many of the outlying islands, is covered in part with an open vegetation called Magellanic moorland (Godley 1960; Moore 1979). Forests occur again in large and more continuous tracts south of about 52°S.

The southernmost forests, often called Magellanic or Subantarctic (Young 1972), do not have the species diversity and height of Valdivian forests, and consist mostly of deciduous *Nothofagus pumilio* and *N. antarctica*, and evergreen *N. betuloides*. The boundary between the rich evergreen Valdivian rainforest and the poorer, largely deciduous Subantarctic forest lies between 46° and 48°S. However, the southernmost forests do not differ much in aspect from the Valdivian rainforests (Darwin 1906:199–200; Reynolds 1935).

In southern South America the Andes do not form an uninterrupted high mountain chain as they do farther north. Consequently, the forests do not occur in two separate tracts along the eastern and western slopes, respectively. Rather, the southern Andes can be visualized as a long series of mountain peaks and hills. Treeless alpine vegetation occurs on their tops whereas extensive forests clothe their slopes with little interruption from east to west across numerous relatively low passes.

More information on the vegetation of Patagonian forests can be found in Dusén (1903–1906), Reiche (1907), Skottsberg (1910, 1916), Hauman-Merck (1913), Ljungner (1939), Kallela (1941), Cabrera (1953), Schmithüsen (1956, 1960), Auer (1958), Thomasson (1959), Godley (1960), Dimitri (1962), Ward (1965), Hueck (1966), Eskuche (1968), Pisano (1974, 1977, 1981), Fernández (1976), Veblen et al. (1977, 1980, 1981), Tomaselli (1981), and Veblen (1982). Ecological descriptions were published by Kuschel (1960), di Castri (1968), and Formas (1979).

AFFINITIES OF THE PATAGONIAN FOREST AVIFAUNA

Faunal resemblance.—The Patagonian forest avifauna is closest geographically to the fauna living in the ecologically dissimilar Patagonian steppes. It is, thus, of interest to investigate faunal resemblances between these two avifaunas. Because the *Nothofagus* forests are distributed along the Andes, it is reasonable to inquire whether their avifauna resembles the fauna of other Andean forests, the montane forests much farther north in northwestern Argentina (Fig. 1). Similarly, because the Patagonian steppe has many taxa in common with the high Andean puna farther north, one wonders about resemblances between Patagonian forest and puna faunas. Finally, in view of the well-known resemblances between Pacific North American and Pacific South American biota (Constance 1963) one wonders whether the avifaunas of Patagonian forests and equivalent forests in Pacific North America resemble each other (for mammals, see Baker 1967).

Faunal resemblances (Table 1) were determined on the basis of species lists in Appendices I, III, IV, and V. Both specific (and allospecific) and generic levels of faunal resemblances were considered.

At the generic level, the *Nothofagus* forest avifauna is about equally similar to the neighboring (Fig. 1) Patagonian nonforest fauna (53%) and to the very distant puna fauna (45%). This is not unexpected in view of the high generic level resemblance (81%) between Patagonian nonforest and puna avifaunas. The *Nothofagus* forest fauna shares 30 percent of its genera with the fauna of Andean forests (distant) as it does also with the fauna of Californian forests

TABLE 2
NUMBERS OF GENERA AND SPECIES IN VARIOUS AVIFAUNAS

Avifauna	No. of		Species : genus ratio
	Genera	Species	
Patagonian forest	40	46	1.15
Patagonian nonforest	70	110	1.57
Andean forest	65	79	1.22
Puna	52	98	1.88
California forest	49	57	1.16
			Mean = 1.40
			Mean without puna = 1.28

(very distant). This is not surprising in view of the fact that Andean and Californian forests share 18 percent of their genera.

At the specific level the indices of similarity are, of course, lower, but the same patterns obtain, at least in part. The resemblance between Patagonian nonforest and puna avifaunas (50%) is reflected in the 43 percent resemblance between Patagonian forest and Patagonian nonforest avifaunas, as well as the 33 percent resemblance between Patagonian forest and puna avifaunas. The Patagonian forest fauna is much less similar to either the Andean forest fauna (15%) or the Californian forest fauna (11%).

Conclusions.—The Patagonian forest avifauna is mixed, sharing elements with Patagonian nonforest and puna avifaunas, and with Andean and North American forest avifaunas. Interestingly, the Patagonian forest avifauna is more closely related to nonforest than to other forest avifaunas.

Among the five faunas discussed, the Patagonian forest avifauna is the poorest in numbers of genera and species (Table 2). Its generic and specific diversities are most comparable to those of the Californian forest fauna. The Patagonian nonforest fauna is the richest, but also occupies the largest area, about three times that of Patagonian forests. The difference in faunal diversity is correlated with area (110 vs. 46 species, or a 2.4:1 ratio; if the 20 species common to Patagonian nonforest and forest faunas are excluded, the ratio is 90 vs. 26 species, or about 3.5:1). The discrepancy between the Andean forest fauna and the Patagonian forest fauna (79 vs. 46 species, or a 1.7:1 ratio) is also of interest because the area of Andean forests is less than half that of Patagonian forests (Fig. 1). Part of the richness in taxa of Argentine Andean forests can be attributed to the presence of a large reservoir of taxa in the rich tropical montane forests of the Peruvian and Bolivian Andes. Finally, the puna avifauna of the southern altiplano, occupying an area about half that of Patagonian nonforest, is only slightly poorer in number of species than the Patagonian steppe avifauna (98 vs. 110) but has proportionately more genera. The 1.88 species : genus ratio in the puna is the highest of all five faunas. This strongly suggests that speciation within the puna has played a role in species enrichment (Vuilleumier 1969, 1980; Vuilleumier and Simberloff 1980), whereas that phenomenon has been either negligible or of lesser importance in the other faunas. In conclusion it appears that both Patagonian faunas are depauperate. They are located at the temperate southern tip of South America and are rather distant from the rich potential sources of taxa at more tropical latitudes. Species numbers show clearly that Patagonian forests constitute a habitat island.

ECOLOGICAL GEOGRAPHY OF THE PATAGONIAN FOREST AVIFAUNA

Habitat preferences.—The 46 species exhibit varying degrees of ecological dependence on forest vegetation. Some species are rather strictly limited to dense forest and do not venture into more open types of vegetation. Other species, however, occur in forest as well as in other vegetation types, such as matorral (scrublands). Furthermore, some species appear to be restricted to forest during the breeding season, migrating north out of the Patagonian forest region, and into more open vegetation, during the southern hemisphere winter (Appendices I, II).

Most species (about 75%) occur in several different kinds of forest during the breeding season, and as many as 30 (65%) even enter the shrublands around the periphery of the forest region. Fewer than half also inhabit the steppe or semi-desert scrub (19 or 41%). The greatest

TABLE 3
 ECOLOGICAL DISTRIBUTION OF LAND BIRDS OF PATAGONIAN FORESTS

Species or allospecies	Vegetation type										
	Rain forest	Meso-phytic forest	Mon-tane forest	Park-land	Open-ings within forest	Forest/steppe ecotone	Shrub-lands (matorral)	Steppe or semi-desert scrub	Alpine scrub	Streams and lake shores	Moor-land
<i>Theristicus caudatus</i>	—	—	—	—	X	X	X	X	—	X	X
<i>Cathartes aura</i>	?	X	X	X	X	X	X	X	—	—	—
<i>Coragyps atratus</i>	—	X	—	X	X	X	X	X	—	—	—
<i>Vultur gryphus</i>	—	X	X	X	X	X	X	X	X	—	—
<i>Accipiter [bicolor]</i>											
<i>bicolor</i>	X	X	X	X	X	X	—	—	—	—	—
<i>Buteo [albicaudatus]</i>											
<i>polyosoma</i>	—	X	X	X	X	X	X	X	X	—	—
<i>B. [jamaicensis]</i>											
<i>ventralis</i>	?	X	—	X	X	X	—	—	—	—	—
<i>Geranoaetus melano-</i>											
<i>leucus</i>	X	X	X	X	X	X	X	X	X	—	—
<i>Polyborus chimango</i>	—	—	—	X	X	X	X	X	—	X	X
<i>P. [megalopterus] albogu-</i>											
<i>laris</i>	?	X	X	X	X	X	X	?	?	—	—
<i>P. plancus</i>	—	—	—	X	X	X	X	X	—	—	—
<i>Vanellus [chilensis]</i>											
<i>chilensis</i>	—	—	—	X	X	—	—	X	—	X	X
<i>Columba [fasciata]</i>											
<i>araucana</i>	X	X	—	X	X	?	—	—	—	—	—
<i>Enicognathus ferru-</i>											
<i>gineus</i>	X	X	X	X	X	X	X	—	—	—	—
<i>E. leptorhynchus</i>	—	X	—	X	X	X	—	—	—	—	—
<i>Bubo [bubo] virginianus</i>	?	X	X	X	X	X	X	X	—	—	—
<i>Glaucidium [brasilianum]</i>											
<i>nanum</i>	?	X	X	X	X	X	X	—	—	—	—
<i>Strix rufipes</i>	X	X	—	X	X	X	—	—	—	—	—
<i>Sephanoides sephani-</i>											
<i>odes</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Ceryle [alcyon] torquata</i>	—	—	—	—	X	—	—	—	—	X	—
<i>Picoides [mixtus]</i>											
<i>lignarius</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Colaptes pitius</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Campephilus magellani-</i>											
<i>cus</i>	X	X	X	X	—	—	—	—	—	—	—
<i>Cinclodes patagonicus</i>	—	—	—	—	X	X	—	—	—	X	—
<i>C. [fuscus] fuscus</i>	—	—	—	—	X	X	X	X	X	X	X
<i>Sylviothorhynchus</i>											
<i>desmursii</i>	?	X	—	X	X	—	X	—	—	—	—
<i>Aphrastura [spini-</i>											
<i>cauda</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Pygarrhichas albogu-</i>											
<i>laris</i>	X	X	X	X	—	—	—	—	—	—	—
<i>Pteroptochos [tarnii]</i>											
<i>tarnii</i>	X	X	X	X	—	—	—	—	—	—	—
<i>P. [tarnii] castaneus</i>	X	X	X	X	—	—	—	—	—	—	—
<i>Scelorchilus [rubecula]</i>											
<i>rubecula</i>	X	X	X	X	—	—	—	—	—	—	—
<i>Eugralla paradoxa</i>	X	X	—	X	—	—	—	—	—	—	—
<i>Scytalopus magellanicus</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Elaenia albiceps</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Anairetes parulus</i>	—	—	—	X	X	X	X	X	—	—	—
<i>Ochthoeca parvirostris</i>	X	X	X	X	—	—	—	—	—	—	—
<i>Xolmis pyrope</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Phytotoma rara</i>	—	—	—	X	X	X	X	X	—	—	—
<i>Notiochelidon cyanoleuca</i>	—	—	—	X	X	X	X	X	X	X	X
<i>Tachycineta [leucorrhoa]</i>											
<i>leucopyga</i>	X	X	X	X	X	X	—	—	—	X	—

TABLE 3
CONTINUED

Species or allospecies	Vegetation type										
	Rain forest	Meso-phytic forest	Mon-tane forest	Park-land	Open-ings within forest	Forest/steppe ecotone	Shrub-lands (matorral)	Steppe or semi-desert scrub	Alpine scrub	Streams and lake shores	Moor-land
<i>Troglodytes aedon</i>	x	x	x	x	x	x	x	x	—	—	—
<i>Turdus falcklandii</i>	x	x	x	x	x	x	x	?	—	—	—
<i>Curaeus curaeus</i>	x	x	—	x	x	x	x	?	—	—	—
<i>Phrygilus [gayi] pata-gonicus</i>	x	x	x	x	x	x	?	—	—	—	—
<i>Zonotrichia capensis</i>	—	—	—	x	x	x	x	x	?	—	—
<i>Carduelis [barbata] barbata</i>	x	x	x	x	x	x	x	—	—	—	—
Totals (N = 46 species)	25–31	35	27	42	39	35–36	29–30	16–19	5–7	8	5

diversity is found in parklands and openings within the forest (39–42 species, or 85–91%; Table 3). In pure forest, the greatest diversity seems to be found in mesophytic forests (35 species or 76%, vs. 31 or 67% in rainforest, and 27 or 59% in montane forest). These results confirm what I described previously (Vuilleumier 1972), that dense rainforest has a somewhat less diverse avifauna than mesophytic forest (see Pearson and Pearson 1982, for a comparable analysis in mammals). As a whole, Patagonian forest birds appear to show little specialization to different forest types; they are found in most kinds of forest.

Elevational distribution.—All 46 species in the northern part of the Patagonian forests occur up to about 1000 meters; nearly 80 percent are found up to 1500, but only about 40 percent up to 2000 meters (Table 4). Most species (60%) thus occupy a broad elevational range, and only a few (40%) appear to fail to reach subalpine forests. The data, however, are still limited. Further field work may well show that more species occur in the 1500 to 2000 meter range. Patagonian forest species are clearly tolerant of a wide range of conditions along elevational gradients.

Latitudinal distribution.—The center of diversity of the 46 species during the breeding season (44–45 species, or 96–98%) occurs between latitudes 35°S and 44°S, an area that corresponds in part to the Valdivian rainforest (Table 5). Farther north, the number of species decreases rather abruptly but is still high (80% to latitude 33°S). Farther south, species numbers decrease progressively, south of 44°S: 87 percent at 44–47°S, 85 percent at 47–50°S, 78 percent at 50–53°S, and 74 percent at 53–56°S. It is interesting that the substantial reduction in forest area due to ice-caps (Fig. 1) and moorlands between about 47°S and 52°S seems to result in only a small decrease in bird species diversity. Furthermore, the poorer Magellanic or Subantarctic forests of higher latitudes still harbor 74 percent or more of the total species diversity. Birds appear to be relatively evenly distributed along the north–south eco-climatic gradient.

Conclusions.—Patagonian forest birds are rather widely distributed over forest types, as well as elevationally and latitudinally (Tables 3, 4, 5). This sort of broad niche-distribution is the one usually found in island birds (Blondel 1979). Cody (1970) noted that Chilean birds as a whole, not just Patagonian forest birds, have the following insular characteristics, (1) high within-habitat diversity (i.e., “individuals are more equitably distributed among species”), (2) extremely low species turnover between habitats in the same latitudinal zone, and (3) limited occupation of areas by bird species, which are replaced by others only with major shifts in vegetation or latitude. Kikkawa (1974) compared feeding and foraging niches of birds in *Nothofagus* forests of Patagonia, Tasmania, New Zealand, Australia, and New Guinea. He described some similarities, as well as differences, in the patterns of resource exploitation, but did not discuss the problem of niche width associated with the various degrees of insularity shown in these faunas. The problem of niche width in birds of Patagonian forests (a habitat island) is worth further investigation.

SPECIATION PHENOMENA IN PATAGONIAN FOREST BIRDS

The species: genus ratio is low (1.15) in Patagonian forest birds (Table 2). Of 40 genera, only 5 (*Buteo*, *Polyborus*, *Enicognathus*, *Cinclodes*, and *Pteroptochos*) or 12.5 percent have more than one species in the *Nothofagus* forest region. Speciation, therefore, does not seem

TABLE 4
ELEVATIONAL DISTRIBUTIONS OF BIRDS IN NORTHERN PATAGONIAN FORESTS BETWEEN 37°S
AND 43°S¹

Species or allospecies	Elevation (meters)			
	0-500	500-1000	1000-1500	1500-2000
<i>Theristicus caudatus</i>	x	x	x	—
<i>Cathartes aura</i>	x	x	—	—
<i>Coragyps atratus</i>	x	x	x	—
<i>Vultur gryphus</i>	—	x	x	x
<i>Accipiter [bicolor] bicolor</i>	x	x	—	—
<i>Buteo [albicaudatus] polyosoma</i>	x	x	x	x
<i>B. [jamaicensis] ventralis</i>	x	x	—	—
<i>Geranoaetus melanoleucus</i>	x	x	x	x
<i>Polyborus chimango</i>	x	x	x	—
<i>P. [megalopterus] albogularis</i>	x	x	x	—
<i>P. plancus</i>	x	x	x	—
<i>Vanellus [chilensis] chilensis</i>	x	x	x	—
<i>Columba [fasciata] araucana</i>	x	x	—	—
<i>Enicognathus ferrugineus</i>	x	x	x	x
<i>E. leptorhynchus</i>	x	x	—	—
<i>Bubo [bubo] virginianus</i>	x	x	x	x
<i>Glaucidium [brasilianum] nanum</i>	x	x	x	—
<i>Strix rufipes</i>	x	x	—	—
<i>Sephanoides sephaniodes</i>	x	x	x	x
<i>Ceryle [alcyon] torquata</i>	x	x	—	—
<i>Picoides [mixtus] lignarius</i>	x	x	x	—
<i>Colaptes pitiis</i>	x	x	x	—
<i>Campephilus magellanicus</i>	x	x	x	x
<i>Cinclodes patagonicus</i>	x	x	x	—
<i>C. [fuscus] fuscus</i>	x	x	x	x
<i>Sylviorthorhynchus desmursii</i>	x	x	—	—
<i>Aphrastura [spinicauca] spinicauda</i>	x	x	x	x
<i>Pygarrhichas albogularis</i>	x	x	x	x
<i>Pteroptochos [tarnii] tarnii</i>	x	x	x	—
<i>P. [tarnii] castaneus</i>	x	x	x	—
<i>Scelorchilus [rubecula] rubecula</i>	x	x	x	—
<i>Eugralla paradoxa</i>	x	x	—	—
<i>Scytalopus magellanicus</i>	x	x	x	x
<i>Elaenia albiceps</i>	x	x	x	x
<i>Anairetes parulus</i>	x	x	—	—
<i>Ochthoeca parvirostris</i>	x	x	x	—
<i>Xolmis pyrope</i>	x	x	x	—
<i>Phytotoma rara</i>	x	x	x	—
<i>Notiochelidon cyanoleuca</i>	x	x	x	x
<i>Tachycineta [leucorrhoa] leucopyga</i>	x	x	x	x
<i>Troglodytes aedon</i>	x	x	x	x
<i>Turdus falcklandii</i>	x	x	x	x
<i>Curaeus curaeus</i>	x	x	x	—
<i>Phrygilus [gayi] patagonicus</i>	x	x	x	x
<i>Zonotrichia capensis</i>	x	x	x	—
<i>Carduelis [barbata] barbata</i>	x	x	x	x
Totals (N = 46 species)	45	46	36	18

¹ Breeding range only.

to be—or to have been—very active in Patagonian forests. It is necessary, nevertheless, to analyze speciation phenomena in detail to determine the possible reasons for the lack of active species formation. The analysis will be done in terms of isolate formation, superspecies, and old speciation patterns (Table 6).

POPULATION STRUCTURE AND ISOLATE FORMATION

As Mayr (1959) pointed out, population structure is of great interest from the speciation viewpoint, when the species is broken down into morphologically (and genetically) differen-

TABLE 5
LATITUDINAL DISTRIBUTIONS OF THE BREEDING RANGES OF PATAGONIAN FOREST BIRDS

Species or allospecies	Degrees S							
	33-35	35-38	38-41	41-44	44-47	47-50	50-53	53-56
<i>Theristicus caudatus</i>	x	x	x	x	x	x	x	x
<i>Cathartes aura</i>	x	x	x	x	x	x	x	x
<i>Coragyps atratus</i>	x	x	x	x	—	—	—	—
<i>Vultur gryphus</i>	x	x	x	x	x	x	x	x
<i>Accipiter [bicolor] bicolor</i>	x	x	x	x	x	x	x	x
<i>Buteo [albicaudatus] polyosoma</i>	x	x	x	x	x	x	x	x
<i>B. [jamaicensis] ventralis</i>	—	x	x	x	x	x	x	x
<i>Geranoaetus melanoleucus</i>	x	x	x	x	x	x	x	x
<i>Polyborus chimango</i>	x	x	x	x	x	x	x	x
<i>P. [megalopterus] albogularis</i>	—	x	x	x	x	x	x	x
<i>P. plancus</i>	x	x	x	x	x	x	x	x
<i>Vanellus [chilensis] chilensis</i>	x	x	x	x	x	x	x	x
<i>Columba [fasciata] araucana</i>	—	x	x	x	x	—	—	—
<i>Enicognathus ferrugineus</i>	—	x	x	x	x	x	x	x
<i>E. leptorhynchus</i>	x	x	x	x	—	—	—	—
<i>Bubo [bubo] virginianus</i>	x	x	x	x	x	x	x	x
<i>Glauucidium [brasilianum] nanum</i>	x	x	x	x	x	x	x	x
<i>Strix rufipes</i>	x	x	x	x	x	x	x	x
<i>Sephanoides sephaniodes</i>	x	x	x	x	x	x	x	x
<i>Ceryle [alcyon] torquata</i>	x	x	x	x	x	x	x	x
<i>Picoides [mixtus] lignarius</i>	x	x	x	x	x	x	x	—
<i>Colaptes pitius</i>	x	x	x	x	x	x	x	—
<i>Campephilus magellanicus</i>	—	x	x	x	x	x	x	x
<i>Cinclodes patagonicus</i>	x	x	x	x	x	x	x	x
<i>C. [fuscus] fuscus</i>	x	x	x	x	x	x	x	x
<i>Sylviorthorhynchus desmursii</i>	x	x	x	x	x	x	—	—
<i>Aphrastura [spinicauda] spinicauda</i>	x	x	x	x	x	x	x	x
<i>Pygarrhichas albogularis</i>	x	x	x	x	x	x	x	x
<i>Pteroptochos [tarnii] tarnii</i>	x	x	—	—	—	—	—	—
<i>P. [tarnii] castaneus</i>	—	—	x	x	x	x	—	—
<i>Scelorchilus [rubecula] rubecula</i>	x	x	x	x	x	x	—	—
<i>Eugralla paradoxa</i>	—	x	x	x	—	—	—	—
<i>Scytalopus magellanicus</i>	x	x	x	x	x	x	x	x
<i>Elaenia albiceps</i>	x	x	x	x	x	x	x	x
<i>Anairetes parulus</i>	x	x	x	x	x	x	—	—
<i>Ochthoeca parvirostris</i>	—	—	x	x	x	x	x	x
<i>Xolmis pyrope</i>	x	x	x	x	x	x	x	x
<i>Phytotoma rara</i>	x	x	x	x	x	x	—	—
<i>Notiochelidon cyanoleuca</i>	x	x	x	x	x	x	x	x
<i>Tachycineta [leucorrhoa] leucopyga</i>	x	x	x	x	x	x	x	x
<i>Troglodytes aedon</i>	x	x	x	x	x	x	x	x
<i>Turdus falcklandii</i>	x	x	x	x	x	x	x	x
<i>Curaeus curaeus</i>	x	x	x	x	x	x	x	x
<i>Phrygilus [gayi] patagonicus</i>	—	x	x	x	x	x	x	x
<i>Zonotrichia capensis</i>	x	x	x	x	x	x	x	x
<i>Carduelis [barbata] barbata</i>	x	x	x	x	x	x	x	x
Totals (N = 46 species)	37	44	45	45	40	39	36	34

tiated and geographically (and ecologically) isolated populations. Each isolate constitutes a potential or incipient species. I analyze this phenomenon separately for the continental and for the insular populations of forest species (Table 6).

Mainland populations.—Thirty-six of the 46 forest species (78%) show no geographical variation in the continental part of their ranges (however, some of these species also range beyond the forest belt and vary geographically outside of it). Of the 10 species (22%) that show geographical variation, nine (20%) vary gradually or perhaps clinally. Trends of geographical variation include a north to south increase in size (as measured by wing-length or bill-length) and a parallel north to south increase in the intensity or "saturation" of pigmen-

TABLE 6
POPULATION STRUCTURE AND SPECIATION PHENOMENA OF LAND BIRDS OF PATAGONIAN FORESTS¹

Species or allospecies	Geographical variation				Belongs to a superspecies
	Within mainland populations		Differentiation of island from mainland populations		
	Slight to moderate	Marked	Slight to moderate	Marked	
<i>Theristicus caudatus</i>	—	—	—	—	—
<i>Cathartes aura</i>	(<i>falklandica</i> , <i>jota</i>)	—	—	—	—
<i>Coragyps atratus</i>	—	—	—	—	—
<i>Vultur gryphus</i>	—	—	—	—	—
<i>Accipiter [bicolor] bicolor</i>	—	—	—	—	x
<i>Buteo [albicaudatus] polyo-</i> <i>soma</i>	—	—	—	x	x
<i>B. [jamaicensis] ventralis</i>	—	—	—	—	x
<i>Geranoaetus melanoleucus</i>	—	—	—	—	—
<i>Polyborus chimango</i>	(<i>temucoensis</i> , <i>chimango</i>)	—	x	—	(ex-superspecies with <i>P. chimachima</i>)
<i>P. [megalopterus] albogu-</i> <i>laris</i>	—	—	—	—	x
<i>P. plancus</i>	—	—	—	—	—
<i>Vanellus [chilensis]</i> <i>chilensis</i>	—	—	—	—	x
<i>Columba [fasciata]</i> <i>araucana</i>	—	—	—	—	x
<i>Enicognathus ferrugineus</i>	(<i>ferrugineus</i> , <i>minor</i>)	—	—	—	—
<i>E. leptorhynchus</i>	—	—	—	—	—
<i>Bubo [bubo] virginianus</i>	—	—	—	—	x
<i>Glaucidium [brasilianum]</i> <i>nanum</i>	(<i>nanum</i> , <i>vafrum</i>)	—	—	—	x
<i>Strix rufipes</i>	—	—	x	—	—
<i>Sephanoides sephaniodes</i>	—	—	—	—	—
<i>Ceryle [alcyon] torquata</i>	—	—	—	—	x
<i>Picoides [mixtus] lignarius</i>	—	—	—	—	x
<i>Colaptes pitiuis</i>	(<i>cachinnans</i> , <i>pitiuis</i>)	—	x	—	(ex-superspecies with <i>C.</i> <i>rupicola</i> , <i>C. campestris</i>) (ex-superspecies with <i>C. leucopogon</i>)
<i>Campephilus magellanicus</i>	—	—	—	—	—
<i>Cinclodes patagonicus</i>	(<i>chilensis</i> , <i>patagonicus</i>)	—	—	—	—
<i>C. [fuscus] fuscus</i>	—	—	—	—	x
<i>Sylviorthorhynchus</i> <i>desmursii</i>	—	—	—	—	—
<i>Aphrastura [spinicauda]</i> <i>spinicauda</i>	—	—	x	x	x
<i>Pygarrhichas albogularis</i>	—	—	—	—	—
<i>Pteroptochos [tarnii] tarnii</i>	—	—	—	—	(ex-superspecies with <i>P. megapodius</i>)
<i>P. [tarnii] castaneus</i>	—	—	—	—	—
<i>Scelorchilus [rubecula]</i> <i>rubecula</i>	—	—	x	—	x
<i>Eugralla paradoxa</i>	—	—	—	—	—
<i>Scytalopus magellanicus</i>	—	(<i>magellanicus</i> , <i>fuscus</i>)	—	—	—
<i>Elaenia albiceps</i>	—	—	—	—	(ex-superspecies with <i>E. parvirostris</i>) (x?)
<i>Anairetes parulus</i>	(<i>lippus</i> , <i>patagonicus</i>)	—	—	—	—
<i>Ochthoeca parvirostris</i>	—	—	—	—	—

TABLE 6
CONTINUED

Species or allospecies	Geographical variation				Belongs to a superspecies
	Within mainland populations		Differentiation of island from mainland populations		
	Slight to moderate	Marked	Slight to moderate	Marked	
<i>Xolmis pyrope</i>	—	—	x	—	—
<i>Phytotoma rara</i>	—	—	—	—	(ex-superspecies with <i>P. rutila</i> , <i>P. raimondii</i>)
<i>Notiochelidon cyanoleuca</i>	—	—	—	—	—
<i>Tachycineta [leucorroha] leucopyga</i>	—	—	—	—	x
<i>Troglodytes aedon</i>	—	—	—	x	—
<i>Turdus falcklandii</i> (magellanicus, pembrotoni)	—	—	x	—	—
<i>Curaeus curaeus</i>	—	—	x	—	—
<i>Phrygilus [gayi] patagonicus</i>	—	—	—	—	x
<i>Zonotrichia capensis</i> (australis, chilensis)	—	—	—	—	—
<i>Carduelis [barbata] barbata</i>	—	—	—	—	x
Totals (N = 46 species)	9	1	8	3	18
(%)	20%	2%	17%	7%	39%

¹ For detailed treatment see Appendix II.

tation (or increase in barrings giving a darker tone to the general coloration). In all of the nine latter species geographical variation has been recognized by taxonomists who have described subspecies (Table 6). That very few species vary geographically was confirmed by Texera (1972), who stated that only three of a total of 122 land bird species in Magallanes Province (Chile) had subspecies; unfortunately, he did not list them.

In only one forest species, *Scytalopus magellanicus*, are the ranges of the continental populations disjunct. This species has two well-marked subspecies, one (*magellanicus*) south, and the other (*fuscus*) north of the Río Bío-Bío. It is at present unclear whether the Bío-Bío river valley does indeed separate these forms or whether they actually overlap. Differences in morphology are said to parallel differences in vocalizations (Goodall et al. 1957; Johnson 1967). This species merits detailed field investigation.

Insular populations.—Forty of the 46 species have populations living on one or more of the islands, such as the distant Juan Fernández and Falkland Islands, and the closer Mocha, Chiloé, Guaitecas, Navarino, Hoste, and Cape Horn Islands, lying off southern South America (Fig. 1). Eleven of the 40 species (27.5%) have morphologically differentiated insular populations (Table 6). Eight species have slightly to moderately differentiated isolates (subspecies have been described for seven of these species), and three species have markedly differentiated subspecies (Table 7). In three additional species the insular isolate has clearly reached species or allospecies status (Table 7). Two of the three well-marked insular subspecies are from distant islands (Juan Fernández, Falklands), and all three cases of completed speciation involve the distant Juan Fernández archipelago.

One of the three species-level insular isolates, *Aphrastura [spinicauda] masafuerae*, is clearly an allospecies of the mainland taxon. A second, *Anairetes fernandezianus*, is related to a mainland taxon, but it is not clear to which one of two possible species (*A. reguloides* or *A. parulus*). The third (*Sephanoides fernandensis*) is sympatric with its mainland relative on one island, thus showing an instance of double invasion.

In conclusion, the probability of isolate formation seems to be extremely low in continental populations (1 of 46 species or 2%) but markedly higher in island populations (12 of 40 species, or 30%, including all instances in Table 7). If all isolates, rather than species, are counted then the probability is about 15 in 40 species or 37.5%. Bird species living in Patagonian forests can form morphologically differentiated isolates, as is shown by the insular populations of some of them. The fact that virtually no isolates occur within the continental forest belt

TABLE 7
INSULAR ISOLATES AMONG LANDBIRDS OF PATAGONIAN FORESTS

Species or allospecies on mainland	Insular subspecies or allospecies	Islands
A. Slightly to moderately differentiated isolates (subspecies)		
<i>Polyborus chimango</i>	<i>fuegiensis</i>	Isla Grande (Tierra del Fuego)
<i>Strix rufipes</i>	<i>sanborni</i>	Chiloé
<i>Colaptes pitiús</i>	none named	Chiloé and Guaitecas
<i>Aphrastura [spinicauda] spinicauda</i>	<i>bullocki</i>	Mocha
<i>Scelorchilus [rubecula] rubecula</i>	<i>mochae</i>	Mocha
<i>Xolmis pyrope</i>	<i>fortis</i>	Chiloé
<i>Turdus falcklandii</i>	<i>falcklandii</i>	Falklands
<i>Curaeus curaeus</i>	<i>reynoldsi</i>	Tierra del Fuego, Cape Horn Archipelago, Navarino, Hoste
	<i>recurvirostris</i>	Isla Riesco
B. Markedly differentiated isolates (subspecies)		
<i>Buteo [albicaudatus] polyosoma</i>	<i>exsul</i>	Juán Fernández
<i>Aphrastura [spinicauda] spinicauda</i>	<i>fulva</i>	Chiloé
<i>Troglodytes aedon</i>	<i>cobbi</i>	Falklands
C. Insular isolates with species status		
<i>Aphrastura [spinicauda] spinicauda</i>	[s.] <i>masafuerae</i>	Másafuera (Juán Fernández)
<i>Anairetes [parulus] [reguloides]</i>	<i>fernandezianus</i>	Másafuera (Juán Fernández)
<i>Sephanoides sephaniodes</i>	<i>fernandensis</i>	Juán Fernández (sympatric on Másafuera with <i>S. sephaniodes</i> ; double invasion)

suggests either that the continental area is so uniform geographically that a considerable amount of gene flow occurs within the species living in it, or that selection pressures from this uniform environment produce much phenetic uniformity, or both. Of course, former isolates may have gone extinct. Another possible reason for the virtual absence of isolate formation within the continental Patagonian forest region is that the present area of forest resulted from a late Pleistocene event (see Discussion and Conclusions).

SUPERSPECIES PHENOMENA

Superspecies with all allospecies within the forest region.—Eighteen of the 46 (39%) Patagonian forest species are members (allospecies) of superspecies, but only one of these superspecies occurs strictly within the forest region (Table 6). Its allospecies are the tapaculos, *Pterotochus [tarnii] tarnii* and *P. [tarnii] castaneus*, which, in the absence of detailed field work, seem to be isolated by the Rio Bío-Bío (Behn 1944).

Superspecies with one allospecies in Patagonian forest and one or more allospecies outside the forest.—Fifteen of 40 forest genera (37.5%) and 16 of 46 forest species (34.8%) exhibit this pattern (Table 8). In all of these cases it is reasonably certain that the allospecies involved have reached or are close to reaching species status (Appendix II).

Distributionally, the most interesting superspecies are those nine (20%) in which the allospecies found in *Nothofagus* forests is restricted (or virtually restricted) to it. Ecologically, these superspecies can be classified into two categories. In the first, one allospecies is found in *Nothofagus* forests, while the other or others occur in nonforest vegetation elsewhere. Superspecies included are *Polyborus [megalopterus]*, *Picoides [mixtus]*, *Scelorchilus [rubecula]*, *Tachycineta [leucorrhoea]*, and *Phrygilus [gayi]*. *Polyborus*, *Scelorchilus*, and *Phrygilus* are essentially Andean superspecies, whereas the other two (*Picoides*, *Tachycineta*) are southern South American.

In the second category all allospecies are found in forests or woodlands; included are *Buteo [jamaicensis]*, *Columba [fasciata]*, *Aphrastura [spinicauda]*, and *Carduelis [barbata]*. *Columba* and *Carduelis* are essentially Andean, whereas the other two are southern South American (*Aphrastura*), or cosmopolitan (*Buteo*).

Ex-superspecies.—In the "ex-superspecies" category (Table 6) I include pairs or triplets of

TABLE 8
SUPERSPECIES WITH REPRESENTATIVES AMONG LAND BIRDS OF PATAGONIAN FORESTS¹

Genus	Allopecies in Patagonian forests	Allopecies outside Patagonian forests (habitat and range)
<i>Accipiter</i>	<i>bicolor</i>	<i>cooperi</i> (woodlands, North America), <i>gundlachi</i> (woodlands, Cuba)
<i>Buteo</i>	<i>polyosoma</i>	<i>poecilochrous</i> (puna, high Andes), <i>albicaudatus</i> (open country, N and NE South America), <i>galapagoensis</i> (open country, Galapagos)
<i>Buteo</i>	<i>ventralis</i> *	<i>buteo</i> (woodlands, Palearctic), <i>oreophilus</i> (woodlands, Africa), <i>jamaicensis</i> (woodlands, North America)
<i>Polyborus</i>	<i>albogularis</i> *	<i>carunculatus</i> (páramo, high Andes), <i>megalopterus</i> (puna, high Andes)
<i>Vanellus</i>	<i>chilensis</i>	<i>resplendens</i> (puna, high Andes)
<i>Columba</i>	<i>araucana</i> *	<i>fasciata</i> (woodlands, western North America; forests, Andes), <i>caribaea</i> (forests, West Indies)
<i>Bubo</i>	<i>virginianus</i>	<i>bubo</i> (various habitats, Palearctic), <i>africanus</i> (various habitats, Africa)
<i>Glauclidium</i>	<i>nanum</i>	<i>jardirii</i> (forests, high Andes), <i>brasilianum</i> (woodlands, forests, Central and South America)
<i>Ceryle</i>	<i>torquata</i>	<i>alcyon</i> (North America), <i>lugubris</i> (Asia), <i>maxima</i> (Africa)
<i>Picoides</i>	<i>lignarius</i> *	<i>mixtus</i> (woodlands, southcentral South America)
<i>Cinclodes</i>	<i>fuscus</i>	<i>pabsti</i> (open areas, southern Brazil), <i>?comechingonus</i> (open areas, Córdoba, Argentina)
<i>Aphrastura</i>	<i>spinaucada</i> *	<i>masafuerae</i> (forests, Juan Fernández Islands)
<i>Schelorchilus</i>	<i>rubecula</i> *	<i>albicollis</i> (matorral, central Chile)
<i>Tachycineta</i>	<i>leucopyga</i> *	<i>leucorrhoea</i> (open habitats, southern South America)
<i>Phrygilus</i>	<i>patagonicus</i> *	<i>gayi</i> (puna, Andes and steppes, Patagonia), <i>atriceps</i> (puna, high Andes), <i>chloronotus</i> (puna, high Andes)
<i>Carduelis</i>	<i>barbata</i> *	<i>magellanica</i> (various habitats, incl. woodlands, Andes, and southern South America)

¹ * indicates superspecies with *Nothofagus* allopecies restricted to this region.

obviously related species that are either largely sympatric or else allopatric but too divergent morphologically to be grouped as a superspecies (e.g., *Polyborus chimango* and *P. chimachima*, see Vuilleumier 1970; Olson 1976). All exhibit southern South American and Andean patterns of distribution.

Conclusions.—Only one superspecies has been detected wholly within the Patagonian forest region (genus *Pteroptochos*); there is a similar pattern of variation, but at the subspecies level, in the genus *Scytalopus*. In both cases the apparent barrier is the Río Bío-Bío. All other cases of superspecies or ex-superspecies involve one Patagonian forest allopecies or species and one or more non-Patagonian allopecies or species. There appear to be different ecological and distributional patterns of allospecific variation, including forest-forest and forest-nonforest, and Andean and southern South American. The barriers (if any) that separate the various allopecies at present are far from clear. Each one of these cases deserves careful study, especially those involving forest-nonforest pairs (or triplets) of allopecies, because this ecological pattern strongly implies an important niche shift during speciation (Vuilleumier, unpubl. data).

LONG-COMPLETED SPECIATION

Only one genus of 40 (2.5%) shows a case of long-completed speciation. In the parrot genus *Enicognathus* the two species (*ferrugineus* and *leptorhynchus*) are widely sympatric. The extent of morphological similarity between these two species (the only ones in the genus, Peters and Blake 1948) makes it likely that they are derived from a common ancestor. The extent of sympatry, however, does not allow one to infer speciation history. It is, therefore, not possible to tell whether the splitting of the original *Enicognathus* stock took place within the forest, with subsequent development of sympatry there, or whether the two species achieved sympatry as a result of a double invasion of the *Nothofagus* region from some other region.

TABLE 9
LEVELS OF ENDEMISM IN PATAGONIAN FOREST BIRDS ACCORDING TO DIFFERENT TAXONOMIC TREATMENTS

Level of endemism	Treatment ¹		
	Hellmayr	Philippi	This paper
<i>A. Subspecific and specific levels</i>			
No. of non-endemic species without endemic subspecies	18 (40%)	19 (41%)	22 (48%)
No. of non-endemic species with endemic subspecies	5 (11%)	6 (13%)	5 (11%)
No. of endemic species or allospecies	22 (49%)	21 (46%)	19 (41%)
Total species	45 (100%)	46 (100%)	46 (100%)
<i>B. Generic level</i>			
No. of endemic genera	8 (19%)	7 (17%)	4 (10%)
Total genera	43	42	40

¹ Data for Hellmayr in Appendix VI. Data for Philippi in Appendix VII. Data for treatment in this paper in Appendix VIII.

ENDEMISM IN PATAGONIAN FOREST BIRDS

I define an endemic taxon here as a taxon (of any rank) living exclusively in the Patagonian forest region of southern South America. The 46 species of forest birds can be assigned to one of the following categories:

Non-endemic species without endemic subspecies.—These species live in *Nothofagus* forests as well as elsewhere. Their populations inside Patagonian forests are not differentiated at the subspecies level from subspecies living elsewhere. An example is *Bubo virginianus magellanicus*, a species widespread in North and South America and a subspecies widespread in the Andes and southern South America (Traylor 1958).

Non-endemic species with endemic subspecies.—These species live inside and outside Patagonian forests, but the subspecies inhabiting the forest region is restricted to that region. An example is *Accipiter bicolor chilensis*. The species is widespread in South America, but the subspecies is restricted to Patagonian forests (Stresemann and Amadon 1979).

Endemic species.—These are species that are restricted to Patagonian forests. An example is *Campephilus magellanicus* (Short 1970b).

Endemic genus.—Genera whose species are found only in the Patagonian forests are considered to be endemic, for example *Pygarrhichas* (Vaurie 1980).

In order to determine the influence of different taxonomic points of view on the perceived levels of endemism, I calculated levels of endemism (Table 9) based on the taxonomic treatments of Hellmayr (1932; Appendix VI), Philippi (1964; Appendix VII), and the one adopted in this paper (Appendices II, VIII).

As our knowledge of systematic affinities between species, geographical variation within species, and intergeneric relationships has progressed from Hellmayr's days to the present, our concepts of species and genus have been modified. As a result, we have: (1) an increased number of non-endemic species without endemic subspecies, (2) a concomitant decreased number of endemic species, and (3) a decreased number of endemic genera. Important as these changes may be in single instances, they do not appreciably modify the structure of endemism in the Patagonian forest fauna (Table 9). The important point is, thus, that the Patagonian forest avifauna has 40–48 percent non-endemic species, 11–13 percent endemic subspecies, and 41–49 percent endemic species. Several of the endemic species belong to endemic genera (10–19%). Different taxonomic interpretations of the taxa in the fauna do not influence markedly the results of an analysis of endemism.

In order to place these levels of endemism in a broader perspective, I analyzed endemism in forest birds of Patagonia, Tasmania, and New Zealand (Table 10; Appendices VIII, IX, X).

Tasmania is a continental or landbridge island that has only been separated from Australia for about 12,000 years (Ridpath and Moreau 1966; Thomas 1974). Endemism should be relatively low, either because isolation is recent and has allowed little time for allopatric speciation, or because isolation is incomplete and allows gene flow to prevent or retard

TABLE 10
COMPARISON OF ENDEMISM IN FOREST BIRDS OF TASMANIA, PATAGONIA, AND NEW ZEALAND¹

Level of endemism	Tasmania	Patagonia	New Zealand
<i>A. Subspecific and specific level</i>			
No. of non-endemic species without endemic subspecies	36 (55%)	22 (48%)	3 (9.5%)
No. of non-endemic species with endemic subspecies	16 (25%)	5 (11%)	2 (6%)
No. of endemic species or allospecies	13 (20%)	19 (41%)	27 (84.5%)
Total species	65 (100%)	46 (100%)	32 (100%)
<i>B. Generic level</i>			
No. of endemic genera	2 (4%)	4 (10%)	16 (67%)
Total genera	47	40	24

¹ Tasmania = a continental or landbridge island; Patagonia = an ecological island; New Zealand = an oceanic island.

speciation; both factors could have played roles in the differentiation of the Tasmanian avifauna (see also Thomas 1974:350–356). The two oceanic islands forming New Zealand have been isolated from other land masses for about 50 million years (Fleming 1979). Endemism in them should, therefore, be very high. The Patagonian forest region is isolated from other forests in South America at present by more than 1000 km of nonforest vegetation. It may have been an ecological island for about 10 million years (Vuilleumier 1967a). It may, thus, be supposed to be intermediate in its degree of isolation between continental Tasmania and oceanic New Zealand. Levels of endemism in Patagonian forests may be expected to be intermediate, and this is what the data show (Table 10). Tasmania (least isolated) has the most species; New Zealand (most isolated) has the fewest species. Tasmanian forests have far more (80%) non-endemic species (with or without endemic subspecies) than either Patagonian (59%) or New Zealand forests (15.5%). But New Zealand forests have about twice (84.5%) as many endemic species as Patagonian forests (41%), and about four times as many endemic species as Tasmanian forests (20%). Finally, generic endemism is very high in New Zealand (67%) as compared to Patagonia (10%) or Tasmania (4%).

GEOGRAPHICAL DISTRIBUTION OF PATAGONIAN FOREST BIRDS

To gain insight into the geographical origins of the taxa living in Patagonian forests today one can analyze the present distribution of species and genera (Tables 11, 12). The majority of species and allospecies (19, 41.3%) are endemics; smaller numbers of species have southern South American (8, 17.4%), Andean (8, 17.4%), widespread South American (6, 13%), or Pan-American (5, 10.9%) distributions. (No species or allospecies has a Cosmopolitan distribution.) This suggests that the origins of the fauna are, potentially, quite diverse, although the great majority of species and allospecies (41, 89.1%) are South American.

An analysis of genera shows that half (20) belong in the pooled category Pan-American plus Cosmopolitan (Table 12). Other, smaller numbers of genera are distributed in various ways in South America (50% of the genera are South American by pooling all these categories).

In summary, the great majority of Patagonian forest species are South American (89%), the rest are Pan-American. Half the genera are South American, 20 percent are Pan-American, and a rather high percentage (30%) are Cosmopolitan. Only 15 percent of both genera and species are Andean. This mixture of geographical distribution patterns could lead one to conclude that the *Nothofagus* avifauna is composed of autochthonous elements (old or young) and of others that are immigrants (again, more or less recent).

CORRELATION BETWEEN ENDEMISM AND GEOGRAPHICAL DISTRIBUTION

Von Ihering (1927), Mayr (1946, 1964), and Cracraft (1973) speculated on the geographical origins of South American birds. Von Ihering (1927:433) called Archinotis a "large continent, which has for the most part disappeared," and supposed that "in the Cretaceous and in the beginning of the Tertiary it connected Patagonia with Australia and New Zealand." He assumed that "unusual families of birds in South America which cannot be ascribed to later immigration, must have come from Archinotis." Among these birds, he included the tracheo-

TABLE 11
GEOGRAPHICAL DISTRIBUTION OF SPECIES AND ALLOSPECIES OF LAND BIRDS OF PATAGONIAN FORESTS

Species or allospecies	Endemic	Southern South American	Andean	Widespread South American	Pan-American	Cosmopolitan
<i>Theristicus caudatus</i>	—	—	—	x	—	—
<i>Cathartes aura</i>	—	—	—	—	x	—
<i>Coragyps atratus</i>	—	—	—	—	x	—
<i>Vultur gryphus</i>	—	—	x	—	—	—
<i>Accipiter [bicolor] bicolor</i>	(endemic subspecies <i>chilensis</i>)	—	—	x	—	—
<i>Buteo [albicaudatus] polyosoma</i>	—	—	x	—	—	—
<i>B. [jamaicensis] ventralis</i>	x	—	—	—	—	—
<i>Geranoaetus melanoleucus</i>	—	—	x	—	—	—
<i>Polyborus chimango</i>	(endemic subspecies <i>temucoensis</i> and <i>fuegiensis</i>)	x	—	—	—	—
<i>P. [megalopterus] albogularis</i>	x	—	—	—	—	—
<i>P. plancus</i>	—	—	—	—	x	—
<i>Vanellus [chilensis] chilensis</i>	—	—	—	x	—	—
<i>Columba [fasciata] araucana</i>	x	—	—	—	—	—
<i>Enicognathus ferrugineus</i>	x	—	—	—	—	—
<i>E. leptorhynchus</i>	x	—	—	—	—	—
<i>Bubo [bubo] virginianus</i>	—	—	—	—	x	—
<i>Glaucidium [brasilianum] nanum</i>	(endemic subspecies <i>nanum</i> and <i>vaftrum</i>)	—	x	—	—	—
<i>Strix rufipes</i>	(endemic subspecies <i>rufipes</i> and <i>sanborni</i>)	x	—	—	—	—
<i>Sephanoides sephaniodes</i>	—	x	—	—	—	—
<i>Ceryle [alcyon] torquata</i>	(endemic subspecies <i>stellata</i>)	—	—	x	—	—
<i>Picoides [mixtus] lignarius</i>	—	x	—	—	—	—
<i>Colaptes pitius</i>	—	x	—	—	—	—
<i>Campephilus magellanicus</i>	x	—	—	—	—	—
<i>Cinclodes patagonicus</i>	—	—	x	—	—	—
<i>C. [fuscus] fuscus</i>	—	—	x	—	—	—
<i>Sylviorhynchus desmursii</i>	x	—	—	—	—	—
<i>Aphrastura [spinicauda] spinicauda</i>	x	—	—	—	—	—
<i>Pygarrhichas albogularis</i>	x	—	—	—	—	—
<i>Pterotochos [tarnii] tarnii</i>	x	—	—	—	—	—
<i>P. [tarnii] castaneus</i>	x	—	—	—	—	—
<i>Scelorchilus [rubecula] rubecula</i>	x	—	—	—	—	—
<i>Eugralla paradoxa</i>	x	—	—	—	—	—
<i>Scytalopus magellanicus</i>	—	—	x	—	—	—
<i>Elaenia albiceps</i>	—	x	—	—	—	—
<i>Anairetes parulus</i>	—	—	x	—	—	—
<i>Ochthoeca parvirostris</i>	x	—	—	—	—	—
<i>Xolmis pyrope</i>	x	—	—	—	—	—
<i>Phytotoma rara</i>	—	x	—	—	—	—
<i>Notiochelidon cyanoleuca</i>	—	—	—	x	—	—
<i>Tachycineta [leucorrhoa] leucopyga</i>	x	—	—	—	—	—
<i>Troglodytes aedon</i>	—	—	—	—	x	—
<i>Turdus falcklandii</i>	—	x	—	—	—	—
<i>Curaeus curaeus</i>	x	—	—	—	—	—
<i>Phrygilus [gayi] patagonicus</i>	x	—	—	—	—	—
<i>Zonotrichia capensis</i>	—	—	—	x	—	—
<i>Carduelis [barbata] barbata</i>	x	—	—	—	—	—
Totals (N = 46 species)	19	8	8	6	5	0
(%)	(41.3)	(17.4)	(17.4)	(13.0)	(10.9)	(0)

TABLE 12
GEOGRAPHICAL DISTRIBUTION OF GENERA OF LAND BIRDS OF PATAGONIAN FORESTS

Genus	Endemic	Southern South American	Andean	Widespread South American	Pan-American	Cosmopolitan
<i>Theristicus</i>	—	—	—	x	—	—
<i>Cathartes</i>	—	—	—	—	x	—
<i>Coragyps</i>	—	—	—	—	x	—
<i>Vultur</i>	—	—	—	—	x	—
<i>Accipiter</i>	—	—	—	—	—	x
<i>Buteo</i>	—	—	—	—	—	x
<i>Geranoaetus</i>	—	—	x	—	—	—
<i>Polyborus</i>	—	—	—	—	x	—
<i>Vanellus</i>	—	—	—	—	—	x
<i>Columba</i>	—	—	—	—	—	x
<i>Enicognathus</i>	x	—	—	—	—	—
<i>Bubo</i>	—	—	—	—	—	x
<i>Glaucidium</i>	—	—	—	—	—	x
<i>Strix</i>	—	—	—	—	—	x
<i>Sephanoides</i>	—	x	—	—	—	—
<i>Ceryle</i>	—	—	—	—	—	x
<i>Picooides</i>	—	—	—	—	—	x
<i>Colaptes</i>	—	—	—	—	x	—
<i>Campephilus</i>	—	—	—	—	x	—
<i>Cinclodes</i>	—	—	x	—	—	—
<i>Sylviorhynchus</i>	x	—	—	—	—	—
<i>Aphrastura</i>	—	x	—	—	—	—
<i>Pygarrhichas</i>	x	—	—	—	—	—
<i>Pteroptichos</i>	—	x	—	—	—	—
<i>Scelorchilus</i>	—	x	—	—	—	—
<i>Eugralla</i>	x	—	—	—	—	—
<i>Scytalopus</i>	—	—	x	—	—	—
<i>Elaenia</i>	—	—	—	x	—	—
<i>Anairetes</i>	—	—	x	—	—	—
<i>Ochthoeca</i>	—	—	x	—	—	—
<i>Xolmis</i>	—	—	—	x	—	—
<i>Phytotoma</i>	—	—	—	x	—	—
<i>Notiochelidon</i>	—	—	—	x	—	—
<i>Tachycineta</i>	—	—	—	—	x	—
<i>Troglodytes</i>	—	—	—	—	—	x
<i>Turdus</i>	—	—	—	—	—	x
<i>Curaeus</i>	—	x	—	—	—	—
<i>Phrygilus</i>	—	—	x	—	—	—
<i>Zonotrichia</i>	—	—	—	—	x	—
<i>Carduelis</i>	—	—	—	—	—	x
Totals (N = 40 genera)	4	5	6	5	8	12
(%)	(10)	(12.5)	(15)	(12.5)	(20)	(30)

phone Passeres, which “survive only in South America” but “must, however, have had a wider distribution in earlier times which could have only extended across Archinotis” (p. 439).

Mayr (1946) classified the faunas of the Americas in terms of faunal elements (1946: fig. 2), thus following Dunn’s (1922, 1931) analysis of reptiles. Mayr’s (1946) South American Element included three families of tracheophones now living in Patagonian forests, the Furnariidae, Rhinocryptidae, and Phytotomidae. In Mayr’s (1946:25) opinion, “there can be no doubt about their South American origin.”

Using somewhat different criteria in his 1964 paper Mayr classified the American faunas into faunal elements once again. He wrote (1964:283) that “The South American origin of the Suboscines can hardly be questioned.” He included the Furnariidae and the Rhinocryptidae among the Primary South American families.

Cracraft (1973) re-evaluated these faunal elements on the basis of advances in our knowledge of plate tectonics and avian systematics, and provided a modified classification. He placed the Furnariidae, Rhinocryptidae, Phytotomidae, together with other families, such as other members of the Tyranni, in the Southern Hemisphere Element, which "includes those families with probable Southern affinities and which lack close relationships to taxa in the north" (p. 519). Cracraft (1973:519) stated that the Southern Hemisphere Element "contains birds that may have evolved in South America proper, but [whose] ancestors are considered to have had a broader distribution on southern lands." Cracraft (1973) thus reverted to the much earlier thinking of von Ihering (1927).

If the South American Element of Mayr (1946, 1964) or the Southern Hemisphere Element of Cracraft (1973) indeed represents an old autochthonous group of taxa, then their representatives in the now ecologically isolated forests of Patagonia, which are as much southern hemisphere as Neotropical in their floristic affinities, should be the ones with the greatest amount of differentiation as judged by their specific- or generic-level endemism.

I categorized the species of Patagonian forest birds as non-endemic, or endemic (Table 13). I also considered endemic genera. I then analyzed endemism in terms of the present geographical distribution of families (Table 13A), Mayr's (1946) faunal elements (Table 13B), and Cracraft's (1973) faunal elements (Table 13C). Because of the small number of families involved, I pooled Old World and North American elements (as Mayr did in his 1964 paper), and pooled Unanalyzed and Pantropical (= Cosmopolitan Tropical) because most Unanalyzed taxa are also Cosmopolitan or virtually so.

The majority of birds that now have a predominantly South American distribution are endemic species (Table 13A; 7 of 11 species, or 64%, are endemic; 3 of 4 genera, or 75%, are endemic). The majority of birds that are members of Mayr's South American Element are endemic (Table 13B; 10 of 17 species, or 59%; 3 of 4 genera, or 75%). Finally, the majority of birds in Cracraft's Southern Hemisphere Element are endemic (Table 13C; 12 of 18 species, or 67%; 4 genera, or 100%). Note that no Patagonian forest species belongs to his South American Element.

The majority of non-endemic species belong to Cosmopolitan families (Table 13A; 17 of 27, or 63%). Many non-endemic species belong to Old World and North American families (Table 13B; 11 of 27, or 41%), or to Northern Element families (30%). Nevertheless 9 of 19 endemic species or allospecies (47%, Table 13A) belong to Cosmopolitan families, 4 of them (21%) are members of Mayr's Old World and North American Element (Table 13B), and 3 of them (16%) are members of Cracraft's Northern Element (Table 13C).

In conclusion, endemism is clearly concentrated in families that are considered to be old and autochthonous (whether ultimately of South American or Southern Hemisphere origin). Of the 19 endemic species and allospecies, seven are shared among the three categories of South American distribution (Table 13A), South American Element (Table 13B), and Southern Hemisphere Element (Table 13C): *Sylviorthorhynchus desmursii*, *Aphrastura [spiniicauda] spinicauda*, *Pygarrichas albogularis*, *Pteroptochos [tarnii] castaneus*, *P. [t.] tarnii*, *Scelorchilus [rubecula] rubecula*, and *Eugralla paradoxa*. The first three are Furnariidae of uncertain affinities (Vaurie 1980); the others are Rhinocryptidae (claimed by Feduccia and Olson 1982, to be related to the *Menurae* of Australia). Three of the five endemic genera, *Sylviorthorhynchus*, *Pygarrichas* and *Eugralla*, are similarly shared. The first two of these genera are probably the most differentiated taxa of the Patagonian forest fauna today.

DISCUSSION AND CONCLUSIONS

CHARACTERISTICS OF PATAGONIAN FOREST BIRDS

The 46 species of land birds breeding in Patagonian forests show four main characteristics.

(1) They resemble more, as a faunal assemblage, the avifaunas of the Patagonian steppes and of the high Andean puna than the avifauna of montane Andean forests, but they also show some resemblance to the avifauna of coastal forests in western North America. The *Nothofagus* avifauna can, thus, be termed Andean and southern South American with North American affinities.

(2) Most species living in *Nothofagus* forests range widely across habitat types and have a broad elevational and latitudinal range. The species may, thus, have wide habitat-niches, a phenomenon characteristic of insular birds.

TABLE 13
ENDEMISM AND GEOGRAPHICAL DISTRIBUTION OF LAND BIRDS OF PATAGONIAN FORESTS

	Numbers of			
	Non-endemic species	Endemic species and allospecies	Total species	Endemic genera
A. Present geographical distribution of families¹				
Cosmopolitan	17	9	26	1
Pan-American	6	3	9	0
Tropical American and temperate South American (essentially South American)	4	7	11	3
Totals	27	19	46	4
B. Mayr's (1946) faunal elements²				
Old World and North American	11	4	15	0
South American	7	10	17	3
Unanalyzed and Pantropical	9	5	14	1
Totals	27	19	46	4
C. Cracraft's (1973) faunal elements³				
Northern Element	8	3	11	0
South American Element	—	—	—	—
Southern Hemisphere Element	6	12	18	4
Unanalyzed Element	13	4	17	0
Totals	27	19	46	4

¹ Cosmopolitan families: Threskiornithidae, Accipitridae, Falconidae, Charadriidae, Strigidae, Columbidae, Psittacidae, Alcedinidae, Picidae, Hirundinidae, Troglodytidae, Turdidae, Emberizidae, Carduelidae. Pan-American families: Cathartidae, Trochilidae, Tyrannidae, Icteridae. South American families: Furnariidae, Rhinocryptidae, Phytotomidae.

² Old World and North American Element: Cathartidae, Columbidae, Strigidae, Alcedinidae, Hirundinidae, Troglodytidae, Turdidae, Emberizidae, Carduelidae. South American Element: Trochilidae, Furnariidae, Rhinocryptidae, Tyrannidae, Phytotomidae, Icteridae. Unanalyzed Element and Pantropical: Threskiornithidae, Accipitridae, Falconidae, Charadriidae, Psittacidae, Picidae.

³ Northern Element: Cathartidae, Trochilidae, Alcedinidae, Troglodytidae, Turdidae, Emberizidae, Carduelidae, Icteridae. Southern Hemisphere Element: Columbidae, Psittacidae, Furnariidae, Rhinocryptidae, Tyrannidae, Phytotomidae. Unanalyzed Element: Threskiornithidae, Accipitridae, Falconidae, Charadriidae, Strigidae, Picidae, Hirundinidae.

(3) Active or recent speciation within the *Nothofagus* forest region is limited to one instance of isolation within a species (*Scytalopus magellanicus*) and one case of isolation within a superspecies (*Pteroptochos [tarnii]*), both occurring across the Rio Bio-Bio, an area also noted as a barrier for plants (Simpson 1973, 1979). A pair of now largely sympatric parrots (*Enicognathus ferrugineus* and *E. leptorhynchus*) probably represents a case of older speciation within the forest region. Thus, intra-forest speciation is relatively unimportant, although the potential for differentiation in geographical isolation does exist in the fauna, as shown by several instances of insular isolates (on Mocha, Chiloé, the Guaitecas, the Juan Fernández, and other islands). In contrast, speciation involving one allospecies in the *Nothofagus* forest area and one or more allospecies in other areas in South or in North America (and even in the Old World) is frequent and involves 16 of 46 species (35%). In nine instances (29%) one allospecies is endemic to the Patagonian forest region, and one or more other allospecies occur elsewhere (southern South America, Andes, or North America). Speciation appears to involve niche shifts, as exemplified in the genus *Phrygilus*. All species in this genus occur in nonforest habitat, except *P. patagonicus*, an allospecies of the *gayi* superspecies living in *Nothofagus* forests. The three other members of the *gayi* superspecies live in Patagonian steppes or in high Andean scrub. "Invasion" of the forest area from steppes has thus been followed by species-level differentiation.

(4) Levels of endemism of Patagonian forest birds are intermediate between those of Tasmanian and New Zealand forest birds, thus conforming to the insular nature of their environment. Several taxa of endemics are without obvious taxonomic affinities with other genera of South American birds. They include *Sylviorthorhynchus* and *Pygarrhichas* (Furnariidae). Little doubt exists that these taxa are among the "primitive" Furnarioidea that belong to old groups, either Primarily South American (Mayr 1964), or Southern Hemisphere (Cracraft 1973) in origin.

RECONSTRUCTING THE HISTORY OF PATAGONIAN FOREST BIRDS

A possible model (scenario) for the evolution of the Patagonian forest fauna, taking into account the characteristics of Patagonian forest birds described above, might involve four stages.

(1) In the early to middle Cenozoic existed an autochthonous fauna of which only a few relicts survive today. These are *Enicognathus* (Psittacidae), *Sylviorthorhynchus*, *Aphrastura*, *Pygarrichas* (Furnariidae), *Pteroptochos*, *Scelorchilus*, and *Eugralla* (Rhinocryptidae).

(2) During the middle to late Cenozoic, stocks present in the Andes or southern South America (or widespread in South America) invaded Patagonian forests where they left representatives, which are now relatively differentiated taxonomically from other members of their genera. Examples of these old South American immigrants are *Colaptes pitius*, *Campophilus magellanicus*, and *Ochthoeca parvirostris*. The mechanism of invasion and differentiation is unknown.

(3) During the Pleistocene, other South American or North American stocks penetrated the *Nothofagus* forests and left isolates that are now allospecific members of superspecies. These younger immigrants include *Buteo [jamaicensis] ventralis*, *Polyborus [megalopterus] albogularis*, *Columba [fasciata] araucana*, *Picoides [mixtus] lignarius*, *Tachycineta [leucorroha] leucopyga*, and *Phrygilus [gavi] patagonicus*.

(4) The process of invasion is still active and involves most of the remaining species (newcomers). An example is *Accipiter [bicolor]*, with the subspecies *chilensis* in Patagonian forests.

For the four faunal components postulated above, the lack of intraforest speciation (except in *Enicognathus*) is explained if the very large area covered with forest today represents a southward expansion in the late Pleistocene of forest that was restricted to a small area north of the huge ice caps during the latest glacial maximum. If the old endemics are also the birds confined to (or commoner in) dense rainforest, whereas the younger non-endemics are commoner in other, more marginal or peripheral kinds of forest, a continental analog to Wilson's (1961) taxon cycle in insular faunas might have taken place in *Nothofagus* forest birds. Preliminary results (Vuilleumier 1972) suggested that this kind of forest occupancy might be correct. Hence, "older elements of the forest fauna . . . might be distributed throughout forest types, but in higher densities in rain forest, so that later colonists . . . were prevented from attaining higher densities there through competition" (Vuilleumier 1972:270). Interestingly, a parallel can be made with the avifauna of New Zealand forests studied by Kikkawa (1966) and Williams (1981). Cody (1970:459), however, suggested that both the earlier residents and later arrivals "occupy many habitat types." The solution of this problem will necessitate further field work. Pearson and Pearson (1982) studied the mammal fauna of Patagonian forests and reached conclusions somewhat similar to mine (Vuilleumier 1972).

POSSIBLE HISTORY OF PATAGONIAN FORESTS AND ITS RELEVANCE TO THE HISTORY OF THE FOREST AVIFAUNA

Previous studies.—A few years ago, I (Vuilleumier 1967a) hypothesized that the low speciation and high endemism in forest-inhabiting landbirds could be explained if their evolution had been phyletic during a rather long period of the Cenozoic. Simpson (1973) analyzed the distribution and differentiation patterns of Compositae of the genus *Perezia* and found that some taxa in this genus have evolutionary features compatible with the hypothesis of a phyletic mode.

Humphrey and Péfaur (1979) reconstructed the species diversity of birds on several outlying islands on the basis of predictions from equilibrium biogeography. They assumed that some islands (Isla Grande de Tierra del Fuego, Los Estados, Hoste, and Wollaston in the Cape Horn Archipelago) had been fully glaciated during the last major advance of the Patagonian ice cap (Llanquihue Glaciation, about 13,000 years BP) and that their avian populations had been eliminated. As a contrast, they studied the bird diversity of several unglaciated or partially glaciated islands (Mocha, Chiloé, Guaitecas). They concluded that species numbers were: (1) above equilibrium for two partially glaciated land-bridge islands (Chiloé, Guaitecas), (2) at equilibrium for an unglaciated island (Mocha), and (3) at equilibrium for the four glaciated islands. Humphrey and Péfaur (1979) included in their species lists all birds except the seabirds (Procellariiformes and Sphenisciformes). Thus, their conclusions may not apply entirely to the forest avifauna as defined in this paper.

In the remainder of this section I review the information available on past climates and environments in Patagonia and relate it to the possible history of the forest avifauna.

Cenozoic history of Patagonia.—To my knowledge no student with a thorough grasp of stratigraphy, fossil floras, and fossil faunas has attempted to write a synthetic review of the rich literature on fossil vertebrates, fossil plants, geology, and glaciology of Patagonia. In the meantime I present below a summary based upon the reviews of geology by Groeber (1936) and Harrington (1962), and of vertebrate fossil communities by Pascual and Odreman Rivas (1971), together with evidence from fossil plants (Berry 1937a, b; Gerth 1941; Couper 1960; Cranwell 1963, 1964; Cerceau-Larrival 1968; Menéndez 1971; Moore 1978).

At times during the early Cenozoic (Eocene), what is now covered with forest was under seawater. Marine transgressions occurred again in the Oligocene and Miocene. Between periods of transgression and volcanic activity, continental sedimentation occurred. The continental areas of Patagonia were warm and moist in the early Tertiary. Since the Andes were still low, humid air from the Pacific probably influenced the climate much farther east than it does today. Phases of orogeny took place during the Tertiary, but it is only from the Pliocene onward that the Andean uplift was well-marked, leading eventually to the present Patagonian geography and, in part, vegetation and climate.

The Patagonian climate during much of the period from the Eocene to the Pliocene must have been more benign and more moist than it is today. Vegetation included forests and woodlands, as shown by plant remains that belong either to the same taxa that occur in Patagonia today or their precursors, as well as a variety of more or less open types of landscape, including savannas and grassy steppes. The mammalian fossil assemblages appear to have included preponderantly open-country forms at times, and at other times, a mixture including forest or woodland forms. Other assemblages suggest the presence of marshes and ponds under warm temperate or even subtropical conditions.

Thus, Patagonia has had forest and nonforest vegetation formations. These vegetation types must have varied in location and area at various times, forming either a mosaic or zones, the extents and the patterns of which depended in part on the relation between sea (transgressions) and land (volcanic activity) in the first half of the Tertiary. No doubt exists that at times the forest extended considerably farther east than it does today. The primeval forest avifauna of the first half of the Tertiary, whatever its taxonomic composition may have been, lived partially where it is found today and partially where steppes now occur. The restriction of forests to western (Andean) Patagonia is a phenomenon associated with the desertification of eastern Patagonia and is largely correlated with the late Tertiary uplift phases of the Andes. This orogeny created a sharp moisture gradient along the eastern Andean slopes, starting some time in the Pliocene. One can, therefore, postulate that the remaining taxa of the old forest avifauna are relict in their geographical distribution, just as their habitat is.

In the late Cenozoic the climatic deterioration led to intense episodes of glaciation. Glaciation began about 3.5 million years ago in Patagonia and continued in numerous cycles of glacial advance and retreat until about 11,000 years BP, although some minor advances took place more recently still, for example 4600 to 4200 years BP and even 2700 to 2000 years BP. The onset of aridity in eastern Patagonia thus coincided not only with the uplift of the Andes but also with severe deterioration of the climate in the late Pliocene. These climatic changes began to influence the mammalian faunas as early as the Friasian (Miocene). Some of the warm elements of the mammalian fauna disappeared from Patagonia between the Friasian and the Chasicuan (Pliocene), although others persisted longer. If the primeval forest avifauna was tropical or subtropical, such a climatic deterioration was probably felt at the same time as it was for mammals elsewhere in Patagonia. One may suppose that several forest taxa of birds either became extinct or moved out of the present range of the forest. Others still might have adapted to the changing conditions and survived.

The Pleistocene of Patagonia has been extensively studied geologically, glaciologically, climatologically, and palynologically (Caldenius 1932; Auer 1946, 1958, 1960, 1970; Brügger 1948, 1950; Flint 1959; Heusser 1960, 1961, 1966, 1974, 1981, 1982; Polanski 1965; Mercer 1972, 1976; Mercer et al. 1975; Heusser and Flint 1977; Paskoff 1977; Heusser and Streeter 1980; Heusser et al. 1981; Markgraf 1980, 1983; Porter 1981; Markgraf and Bradbury 1982). The effects of Pleistocene events have been studied from a biological point of view by Báez and Scillato Yané (1979), Formas (1979), B. S. Vuilleumier (1971) and Simpson (1979). The review is based on this literature.

Characteristically, during a glacial advance, the ice cap occupied the western coast of Pat-



FIG. 2. Schematic map showing location of late Wisconsin (17,000 to 21,000 BP) ice margins in southern South America, simplified and slightly modified from Hollin and Schilling (1981). Estimated area of late Wisconsin Patagonian ice-cap about 478,000 km²; today about 19,500 km².

agonia and the adjacent Andean backbone, and extended some distance eastward into the steppe area. Depending on the severity of the episode, some or all of the outlying islands were covered with ice (e.g., Fig. 2; Auer 1960; B. S. Vuilleumier 1971; Hollin and Schilling 1981). Isostatic lowering of sea level during a glacial period extended the continental margin considerably eastward (see reconstruction in B. S. Vuilleumier 1971). The Falkland Islands had cirque glaciers (Clapperton and Sugden 1976) and, insofar as present evidence shows, no trees during the late Pleistocene (Barrow 1978). Thus, although largely free of ice and occupying an area slightly larger than that occupied today, they probably could not have served as a refugium for forest birds.

In a reconstruction of the avifaunal history at the level of resolution attempted here, whether some of the outlying islands were glaciated or not during some glacial advances is not very important. It is likely that all southernmost islands were covered with ice during at least one episode of glacial expansion. Chiloé, somewhat farther north, apparently remained partially ice free. Markgraf (pers. comm.) suggested that forest elements survived locally in Tierra del Fuego, even though they were perhaps very restricted in their area. If forest refugia existed on one or more of the islands, they were apparently not large enough and/or of sufficient duration to have produced species level isolates among the birds. Within the continental area, however, the valley of the Bío-Bío River, which now apparently serves to isolate subspecies of *Scytalopus magellanicus*, and allospecies of the *Pteroptochos [tarnii]* superspecies, probably acted as a barrier during a glacial episode (Simpson 1973, 1979). The barrier is now near the northern limit of the *Nothofagus* forest region (Fig. 1). This location suggests that its main effects were felt in the past, when the forest belt was displaced northward.

One of the most important aspects of the Pleistocene history of forested Patagonia is the repetition of phases of glaciation and deglaciation, because they resulted in several episodes of retreat northward and of later re-advance southward of the forest vegetation along the Andean axis. Simpson (1973, 1979; see also B. S. Vuilleumier 1971) published a diagram showing the latitudinal contraction of vegetation northward during a glacial advance, as compared to the present (interglacial) distribution. During glacial maxima, the forest vegetation probably retreated northward to the area corresponding roughly to the mediterranean zone of Chile, today covered with matorral (Fig. 1), and was restricted to the western slopes of the Andes because mountain glaciers covered the crests (Fig. 2). Nevertheless, as pointed out by Markgraf (pers. comm.), some forest elements persisted in the far south during glacial maxima, so that not all plant movements involved constriction during glaciation, and recolonization after deglaciation. The latest southward re-advance of forest took place shortly after the last main advance of the ice cap about 13,000 years BP. Forest probably occupied its present area about 11,000 years BP (but see Heusser 1983), but shrank again somewhat during re-advances of glaciers on two or more occasions since that time. The repetition of cycles of forest retreat and re-expansion closely following the repetition of glaciation and deglaciation would not have been conducive to allopatric speciation because the forest area probably was not fragmented into blocks that could hold isolates or incipient species. Also, if small forest refugia existed (Markgraf, pers. comm.), they were probably too small either to support viable populations of some species, or they did not last long enough for the isolate within to become differentiated. Thus, the Pleistocene did not lead to repeated episodes of speciation in forest birds in Patagonia, as it did in puna birds of the high Andes (Vuilleumier 1969; B. S. Vuilleumier 1971; Vuilleumier and Simberloff 1980).

Old stocks of forest birds that did not become extinct as a consequence of the climatic deterioration in the Pliocene-Pleistocene may well have become extinct during the episodes of forest shrinkage of the Pleistocene, thus leading to a considerable impoverishment of the fauna. The surviving stocks did not multiply by allopatric speciation (possible exception *Enicognathus*). Faunal enrichment did occur, however, as is clearly evidenced in patterns of speciation involving forest and nonforest allospecies today (e.g., *Phrygilus [gayi]* superspecies). Steppe-inhabiting stocks were evidently able to adapt to the forest, most likely during periods of forest reduction corresponding to glacial advances. A stock that was in some way preadapted to the forest/steppe ecotone and that found itself "caught" along the edge of the forest as the latter shrank either adapted to forest conditions in the refuge area or became extinct. Vanzolini and Williams (1981) published a model (the vanishing refuge) to help account for speciation of forest forms that became adapted to open vegetation formations during dry-wet cycles in Amazonia. The reverse situation probably occurred in Patagonia: adaptation of steppe forms

to forest and their subsequent speciation. The role of ecotones is very important in this scenario of speciation involving such marked niche shifts (Vuilleumier, unpubl. data).

ACKNOWLEDGMENTS

I thank E. Mayr, the late E. Eisenmann, the late B. Patterson, E. E. Williams, K. F. Koopman, O. A. Reig, and B. B. Simpson for help during this work. Very helpful comments were made on the manuscript by A. Keast, O. Pearson, M. Foster, V. Markgraf, and an anonymous referee. I am grateful to R. A. Paynter, Jr. (Museum of Comparative Zoology, Harvard), V. Aellen (Museum d'Histoire Naturelle, Geneva), the late R. A. Philippi B. (Museo Nacional de Historia Natural, Santiago), and the late F. Behn (Concepción) for permitting me to work in the collections in their care. For hospitality and assistance during field work, I thank the late F. Behn and M. A. Ricardi. Field work in Patagonia was made possible by grants from the National Science Foundation to the Department of Biology, Harvard University (Evolutionary Biology Fund), from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and from the Society of Sigma Xi. No synthetic paper on Patagonian birds could be attempted without the basic work of J. L. Peters, A. Wetmore, C. E. Hellmayr, C. C. Olog, J. D. Goodall, A. W. Johnson, F. Behn, and R. A. Philippi B. All students of southern South American birds owe them much. V. Morales drew the illustrations. I am grateful to J. Drobnick and M. Ardagna for typing the manuscript.

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