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FIELD STUDY OF ALLOPATRY, SYMPATRY, PARAPATRY, AND REPRODUCTIVE ISOLATION IN STEPPE BIRDS OF PATAGONIA

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Resumen. La vegetación estépica o subdesértica de Patagonia (América del Sur desde 36 °S hasta 56 °S) representa el 70 % de la superficie total de la región (1.140.000 kilómetros cuadrados). Esta zona, con una población humana escasa sirve sin embargo para una industria ovejera extensiva. De las aproximadamente 90 especies de aves terrestres que anidan en estepas patagónicas, unas 70 apartenecen a un gremio ecológico de especies que buscan su alimentación en el suelo o cerca del suelo en la vegetación baja, herbácea o arbustiva. Aunque la fauna esta empoberecida, se encuentran varios casos de distribución que sugieren patrones de especiación local, incluyendo ejemplos de especies alopátricas o parcialmente simpátricas, y ejemplos de aislamiento reproductivo post-especiacional que merecen investigación detallada. Durante una transecta desde el Oceano Atlántico hasta la zona pre-Andina en la Provincia del Chubut, Argentina, en Noviembre de 1991, se estudiaron de manera preliminar problemas de alopatria, simpatria, y aislamiento reproductivo en una muestra de 26 especies (en 14 generos: *Eudromia*, *Tinamotis*, *Thinocorus*, *Geositta*, *Upucerthia*, *Eremobius*, *Asthenes*, *Leptasthenura*, *Agriornis*, *Muscisaxicola*, *Mimus*, *Anthus*, *Sicalis*, y *Phrygilus*), representando el 30 % de las especies terrestres anidando en estepas de Patagonia. Las interacciones entre varias especies congenéricas (o afines) estan discutidas en términos de diferencias o semejanzas al nivel ecológico al nivel etológico, y en términos de territorialidad interespecífica. Investigaciones futuras deberán averiguar si los patrones descritos en este artículo pueden estar verificados por medio de trabajos a largo plazo. Parece claro que fenómenos eco-evolutivos acerca de problemas especiacionales y distribucionales en el extremo sur del continente Sudamericano merecen más amplia investigación.

Abstract. The steppe or semi-desert vegetation (shrubsteppe) of Patagonia (southern South America between 36 °S and 56 °S) covers about 70 % of the total area of this region (1,140,000 square kilometers). Although this zone has a sparse human population, it is used extensively to raise sheep. Of the 90-odd species of landbirds that breed in Patagonian steppes, about 70 belong to the ground or near-ground foraging guild. In spite of the low species diversity in the Patagonian steppe avifauna, speciation appears to have been active in that region in the past, as revealed by the occurrence of several distribution patterns among congeneric or closely related species, which suggests that these patterns are the results of local speciation. These cases include instances of allopatry, partial sympatry, and reproductive isolation. During a transect from the Atlantic coast westward to the foothills of the Andes in Chubut Province, Argentina, in November 1991, preliminary field studies were carried out on a sample of 26 species (in 14 genera: *Eudromia*, *Tinamotis*, *Thinocorus*, *Geositta*, *Upucerthia*, *Eremobius*, *Asthenes*, *Leptasthenura*, *Agriornis*, *Muscisaxicola*, *Mimus*, *Anthus*, *Sicalis*, and *Phrygilus*), representing about 30 % of the species breeding in Patagonian steppes. Interspecific interactions (including differences or similarities in habitat preferences and behavioral traits) were studied in order to better understand patterns of eco-geographic overlap versus non-overlap. Preliminary conclusions about the modalities of reproductive isolation suggest a number of questions for future, long-term research on the details of the speciational history of Patagonian birds. *Accepted 3 July 1992.*

Key words: Steppes, Patagonia, Chubut, Argentina, landbirds, allopatry, sympatry, reproductive isolation, biogeography.

INTRODUCTION

The vegetation of most of Patagonia (southern South America; defined *in* Vuilleumier 1985, 1991a) consists of dry shrubsteppes on vast plateaus, which often stretch, gray-green in color, from one end of the horizon to the other (Fig. 1). Perhaps as much as 800,000 km² of Patagonia's 1,140,000 km², or about 70%, is covered with steppes. A very sparse human population uses these steppes to raise sheep. Steppe habitats extend for hundreds of kilometers, from the shores of the Atlantic Ocean in the east all the way to beech (*Nothofagus*) forests at the foothills of the Andes in the west (map in Hueck & Seibert 1972). Here and there, however, the relative monotony of this arid landscape is broken by spectacular cliffs of colorful rocks or huge screes (Fig. 2), by shallow lagoons, extensive salt flats, and green and shady manmade oases (chacras) where willows (*Salix*) and poplars (*Populus*) grow along some river valleys (Fig. 3) and where various crops are cultivated on the irrigated valley floor.

In spite of their relative structural and botanical uniformity the steppes of Patagonia have a very interesting avifauna. First, although it is depauperate and includes only about 90 species of breeding landbirds, it is taxonomically varied. Especially remarkable is the guild (cf. Root 1967) of species foraging on the ground or in low shrubs near the ground and eating seeds and/or small invertebrates. This guild has about 70 species in eleven families: Rheidae (rheas), Tinamidae (tinamous), Charadriidae (plovers), Thinocoridae (seedsnipe), Furnariidae (ovenbirds), Rhinocryptidae (tapaculos), Tyrannidae (flycatchers), Mimidae (mockingbirds), Motacillidae (pipits), Icteridae (meadowlarks), and Emberizidae (finch-like birds). Secondly, members of this guild are not only speciose, but they are also numerically dominant at many sites (especially Furnariidae, Tyrannidae, and Emberizidae). Thirdly, in several avian groups, geographical and ecological overlaps between similar species suggest that the physiognomically simple steppe habitats of Patagonia can sustain a rather com-

FIG. 1. Very open, dry shrubsteppe on soft, sandy substrate near Piedra Parada, Chubut, looking westward toward the snow-capped peaks of the Andes. Vegetation is "Patagonian Steppes and Semideserts, Subandean and Western Sector," No. 64 in Hueck & Seibert (1972). Photo F. Vuilleumier, November 1991.

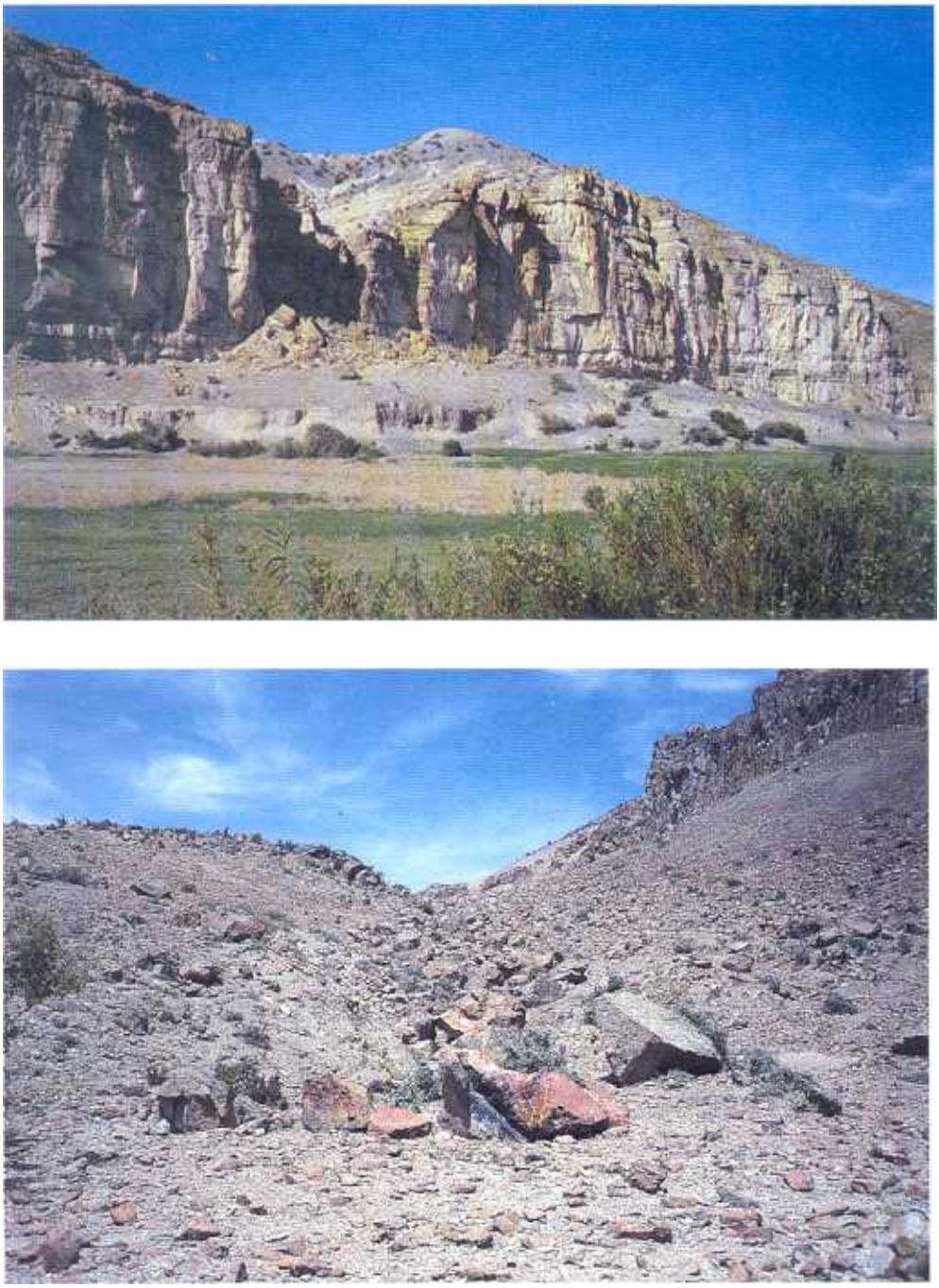

FIG. 2. Top: cliffs in the Chubut river valley a few km west of Paso del Sapo, Chubut; valley floor in foreground, Chubut River behind photographer. Bottom: scree of large rocks and boulders, Chubut river valley a few km west of Piedra Parada, Chubut; Chubut river behind photographer. Photos F. Vuilleumier, November 1991.

plex ecological assembly of birds. Fourth, in a few of these groups, the species concerned are either congeners or members of closely related genera. Finally, several cases of sympatry or parapatry occur between species that appear to be reproductively isolated and to have speciated either in Patagonia or in neighboring regions (Vuilleumier 1991a, 1991b).

To the biogeographer the steppe avifauna of Patagonia poses an ecological challenge in terms of niche segregation and interspecific competition (proximate factors of community structuring), and an evolutionary challenge in terms of the spatio-temporal origins of the parapatric or sympatric situations observed today (ultimate factors of speciation). Community structure has usually been studied by ecologists who have analyzed the factors (climate, vegetation, interspecific competition) thought to be responsible for overlaps between or among species of birds in given vegetation types. For example, Wiens & Rotenberry (1980) and Rotenberry & Wiens (1980) described avian communities in the grasslands and shrubsteppes of North America, environments that are equivalent to some of the steppes of Patagonia.

Speciation has usually been studied by evolutionists interested in patterns of differentiation detectable between sister species. Rarely have patterns of allopatry/sympatry between or among species been studied in an entire avifauna, in an attempt to combine an analysis of proximate (ecological) and of ultimate (evolutionary) factors.

In this paper, I examine the ecological question of overlaps versus non-overlaps and assess the evolutionary problem of reproductive isolation in several congeneric or closely related pairs of species occurring in north-central Patagonia, in an attempt to document patterns of overlaps in a substantial portion of the Patagonian landbird fauna. The 26 species discussed below constitute about 30% of the breeding landbird fauna of Patagonian steppes (total about 90 species).

In two recently published surveys of speciation phenomena in Patagonian landbirds, I concluded that this region showed many instances of various stages in the speciation process (Vuilleumier 1991a, 1991b). I suggested that an analysis of the nature of secondary overlaps (including parapatry) was necessary before significant progress could be made in our understanding of avian evolution in that region. Among specific questions that need answers I included (Vuilleumier 1991a: 25): (1) "How do the species behave toward each other in areas of secondary overlap?", (2) "Is interspecific territoriality common?", and (3) "What is the nature of reproductive isolation in parapatric zones?"

Gochfeld (1978) studied habitat selection between two species of *Mimus* in northeastern Patagonia and interspecific territoriality between two species of *Sturnella* (1979) at the northern edge of the Patagonian region. These two papers appear to be the only ones focusing on the problem investigated here, although Maclean (1969) mentioned habitat differences between species of *Thinocorus* and Short (1968) studied sympatry in *Sturnella* north of Patagonia. Gochfeld (pers. comm.) also studied *Phrygilus* and *Anthus*, but unfortunately did not publish his results. Papers such as those by Durnford (1877, 1878), Peters (1923), Wetmore (1926a, 1926b), and Fjeldså (1988), and the book by Fjeldså & Krabbe (1990) all give valuable information on the distribution of many Patagonian bird species, but are of little use in elucidating patterns of overlap and reproductive isolation, because these authors were not working on these problems. Cody (1970) discussed a series of patterns of overlaps among congeneric species of Chilean birds, including ground birds like *Muscisaxicola*. His paper explored some of the questions of interest here, but because he worked west of the Andes and in the Andes themselves, and not in Patagonian steppes east of these mountains, his results may not be directly applicable. Thus, fresh field work is necessary. Evolutionary questions posed by allopatry or sympatry can be approached by field work carried out at two out of several levels of biogeographic perception (Blondel & Choisy 1983): local (biotope in Blondel & Choisy 1983) and regional.

On a local geographical scale, my ongoing field work in Chilean Patagonia and northwestern Tierra del Fuego on the genera *Phrygilus* and *Geositta* (Vuilleumier 1991a: 14—18, 21—22, and unpublished) has been directed at one instance of parapatry (*Phrygilus*) and one of secondary overlap (*Geositta*). In order to study problems of overlaps on a regional scale, I carried out a transect in November 1991 in Chubut, across the

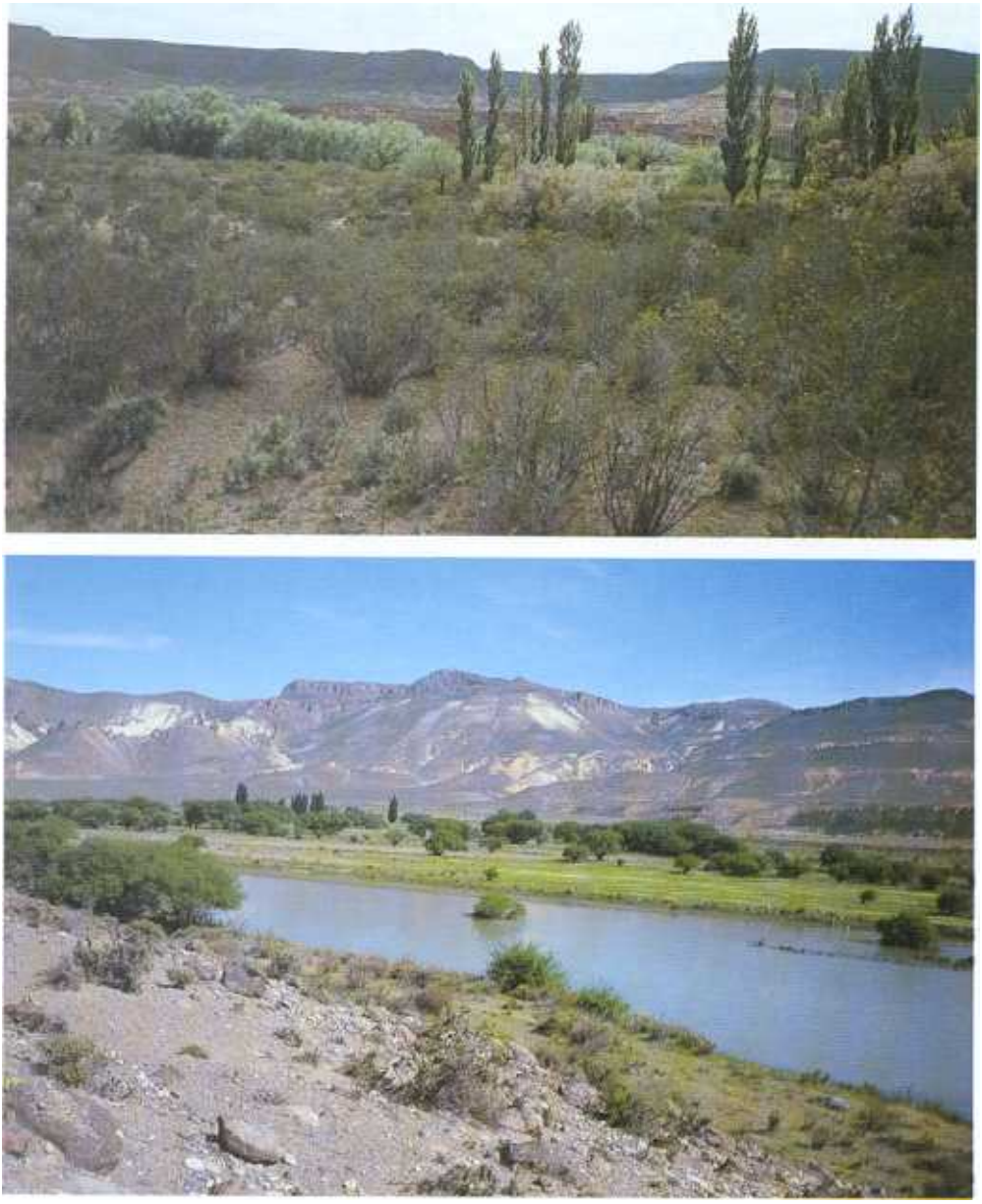

FIG. 3. Top: abrupt transition between shrubsteppe (foreground) and dense riverine vegetation of willows (*Salix*) and poplars (*Populus*) along Arroyo Telsen, a few km west of Telsen, Chubut. Bottom: open, overgrazed, grassy riverine vegetation with groves of willows (*Salix*) and poplars (*Populus*) along the Río Chubut, a few km west of Paso del Sapo, Chubut. Photos F. Vuilleumier, November 1991.

steppes of north-central Patagonia from the Atlantic Ocean to the Andean foothills. During this trip I focused my attention on several groups of ground or bush inhabiting birds presenting evolutionary problems and gathered information on distribution, habitat selection, relative abundance, and interspecific interactions of the different species involved. In this paper I report field observations concerning species in the genera *Eudromia* and *Tinamotis* (Tinamidae); *Thinocorus* (Thinocoridae); *Geositta*, *Upucerthia*, *Eremobius*, *Asthenes*, and *Leptasthenura* (Furnariidae); *Agriornis* and *Muscisaxicola* (Tyrannidae); *Mimus* (Mimidae); *Anthus* (Motacillidae); and *Sicalis* and *Phrygilus* (Emberizidae). A few observations I made in 1965 near Bariloche (Río Negro Province) are also cited. This field work is part of a long-term research program on the biogeography, ecology, and evolution of the avifauna of Patagonia (Vuilleumier 1967a, 1967b, 1972, 1985, 1991a, 1991b).

MATERIAL AND METHODS

Transect

Field observations were made in the austral spring, between 5 November and 18 November 1991 in Chubut Province, Argentina, along a transect from the Atlantic Ocean at Península Valdés and Cabo Dos Bahías westward to Esquel at the foot of the Andes, between about 42 °S and 45 °S and 64 °W and 71 °W. Fig. 4 shows the localization of the transect (dotted line) and indicates the routes and the main localities along them. From Trelew to Puerto Madryn I followed route 3. From Puerto Madryn to Península Valdés I followed routes 2, 47, and 52. From Puerto Madryn to Esquel I followed route 4 to Telsen, Gan-Gan, Gastre, and El Molle, then route 13 to Paso del Sapo, and route 12 to Gualjaina and Esquel. From Esquel, I went back to the Atlantic coast following routes 40 and 25 to Las Chapas, then route 31 to Uzcudún and routes 3 and 30 to the Camarones/Cabo Dos Bahías/Puerto Melo area. I returned to Trelew via routes 30, 3, and 9 through Gaimán.

Locality names on Fig. 4 are taken from the undated map "Provincia del Chubut," published in Buenos Aires by the Automóvil Club Argentino (ACA). This map has a scale of 1:1 000 000 (map of entire territory of Chubut Province), and 1:400 000 (insets for Península Valdés/Madryn/Trelew/Rawson area, and for El Bolsón/Esquel area). Two other maps that are widely used and available in Argentina have either incomplete road localizations, or incomplete locality names, or both, at least in the transect area. They are the Esso/Exxon road map ("Mapa carretero República Argentina," 1986, Esso S.A. Petrolera Argentina, scale 1:4 000 000) and the undated map, "República Argentina: Red Caminera Principal," published by the ACA, scale 1:4 000 000. Of the two, the ACA map is the better one as far as roads and place names go. Note that the Times Atlas, Eight Comprehensive Edition, 1990, includes several of the localities mentioned in this paper on Plate 121, scale 1:5 000 000.

Field observations

The target taxa of birds selected for analysis of allopatry versus sympatry and reproductive isolation were observed at about 20 study sites chosen to represent the range of steppe habitats as well as other vegetation and landscape types, as described below. At each site, a period of from 1—8 hours (average about 3 hours) was spent observing birds and noting the following: habitat preference, relative abundance, territorial behavior, nesting behavior, foraging behavior, vocal behavior, and interspecific behavioral interactions, if any. No birds could be collected. During the study period the weather was generally good, with sunny skies, little or no cloud cover, good to excellent visibility, mild temperatures reaching about 25 °C by midday or early afternoon, and little wind; rain and thunderstorms were encountered only on the high basaltic plateaus between Telsen and Gan-Gan. Locally (near Puerto Madryn and Sierra Chata; and near the intersection of routes 3 and 30 south of Uzcudún) ash clouds from Cerro Hudson in Chile at about 46 °S impeded the visibility slightly. Volcano Hudson (identified in Fig. 4) erupted in August 1991 and produced vast volumes of fine ash, much of which was deposited not only near the Chilean border but also all the way to the Atlantic Ocean as far west as the ports of Puerto Deseado and San Julián (see N.C. Nash, New York Times, Monday, October 21, 1991, pp. A1 and A6).

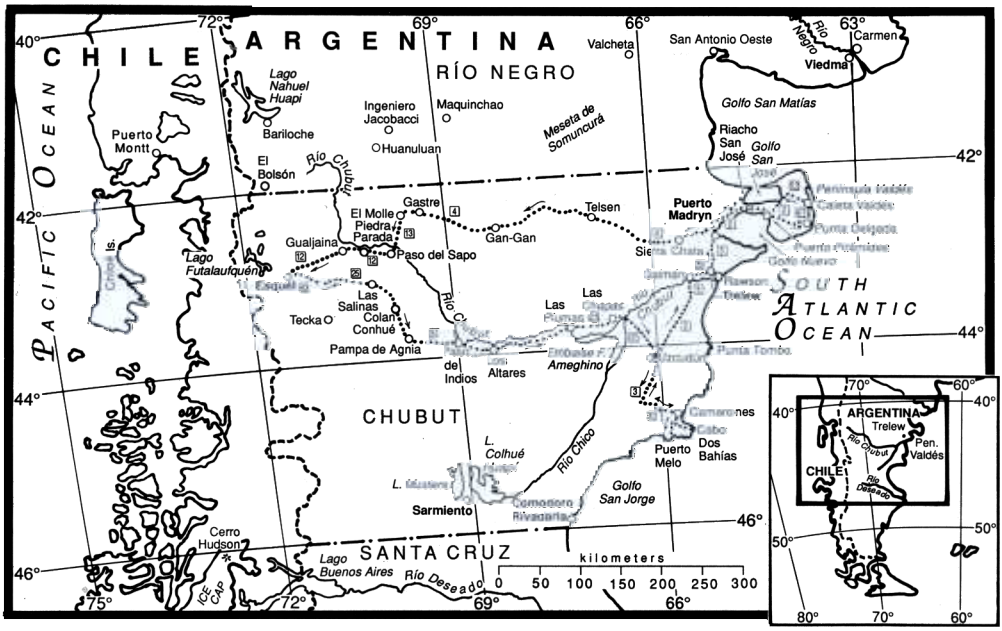

FIG. 4. Schematic map of Chubut Province, Argentina, showing the transect route (dotted line) followed in November 1991. The numbers along the route are the road numbers (see text). The main localities mentioned in the text are indicated.

Vegetation

Shrubsteppes composed of low, spaced out bushes (many of them thorny) are the dominant vegetation throughout the transect. In most areas, the ground is bare and made up of relatively fine material, often including wind- and sand-polished pebbles. In the central part of the transect, especially between Telsen and Gastre, outcrops of basaltic rocks are prominent. According to Hueck and Seibert (1972: 43, 51—53), the main vegetation formations from east to west along the transect are: (1) Monte-Shrubsteppe ("Monte-Strauchsteppe" or "Estepa arbustiva de Monte;" no. 51), including *Larrea*, *Prosopis*, *Cassia*, *and Chuquiraga*, and (2) Patagonian Steppes and Semideserts ("Patagonische Steppen und Halbwüsten" or "Estepas y semidesiertos patagónicos;" central sector no. 66, San Jorge sector no. 67, and subandean and western sector no. 64). Physiognomically important plants in nos. 64, 66, and 67 include *Berberis*, *Senecio*, *Chuquiraga*, *Verbena*, and *Mulinum spinosum* (the last especially abundant in the western sector).

In the Península Valdés area and near Puerto Madryn, the steppe vegetation grows locally on sand dunes near the ocean (Fig. 5). Areas of grassy steppes were seen near Punta Delgada on Península Valdés (Fig. 6) and near Colan Conhué (no illustration). At scattered localities, substantial man-made oases with relatively dense groves of willows (*Salix humboldtiana*) and poplars (*Populus* sp.), and with locally extensive riverine marshy vegetation were encountered, notably on Península Valdés, in the Telsen area (Arroyo Telsen, Fig. 3, top), near Paso del Sapo (Río Chubut Valley, Fig. 3, bottom), near Gualjaina, along the Río Chubut below the F. Ameghino Dam, and in the Gaimán area (Río Chubut). A very narrow, often discontinuous, band of willows and other riverine vegetation lies along the banks of the Río Chubut between Piedra Parada and Paso del Sapo, between Paso de Indios and Las Chapas, and in the Gaimán-Trelew area. In most of these areas, the green riverine oases extend just a few meters away from the Río or Arroyo and abruptly make way to arid shrubsteppe (Fig. 3, top).

Figs. 7 and 8 illustrate several types of steppe vegetation along the transect from the base of Península Valdés westward to the Gastre area

FIG. 5. Top: low, open shrubsteppe growing on sand dunes at the top of coastal cliffs, Puerto Pirámides, Chubut. Bottom: low, open shrubsteppe growing on coastal dunes and on top of low cliffs, a few km north of Puerto Madryn, Chubut. Photos F. Vuilleumier, November 1991.

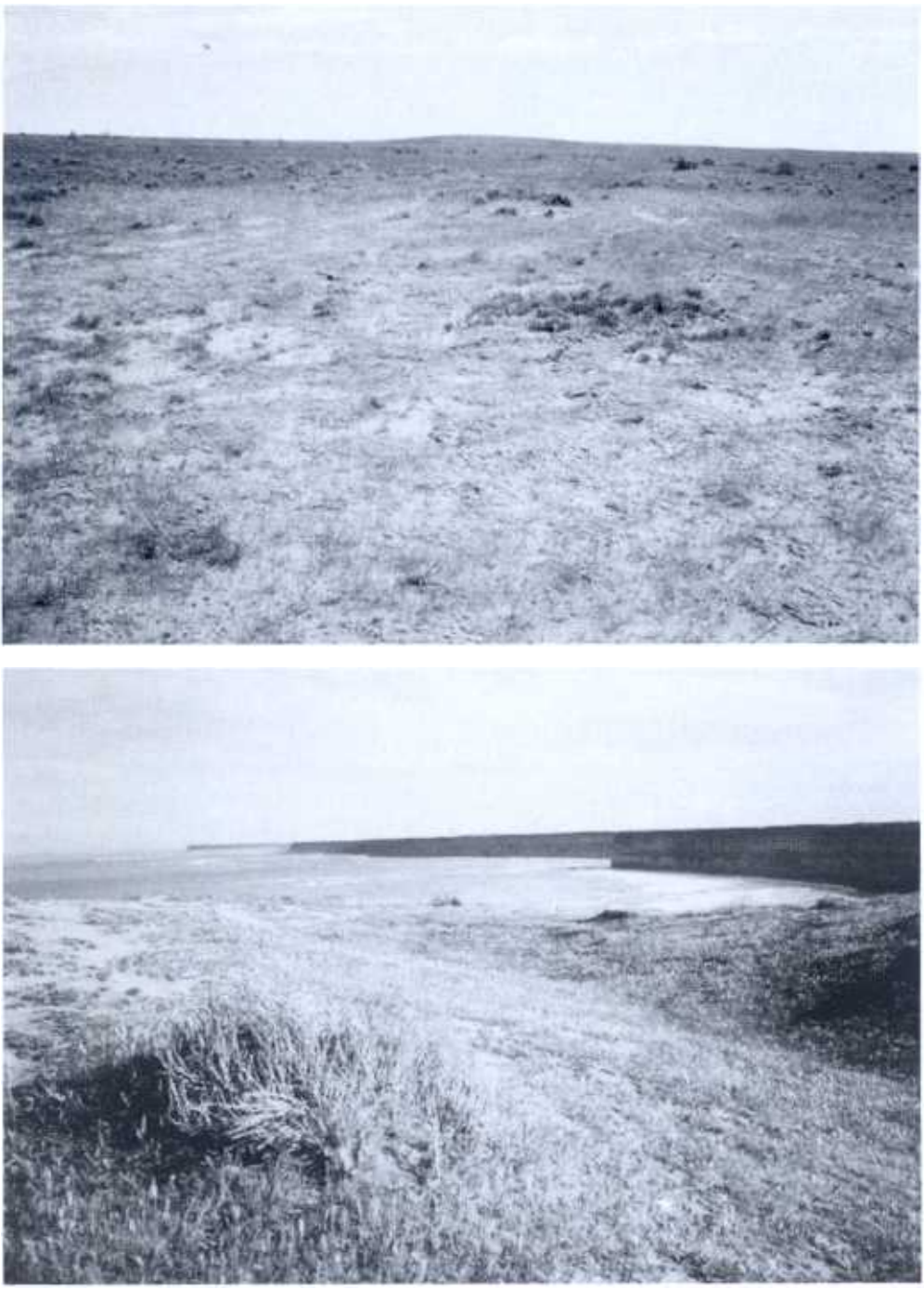

FIG. 6. Top: very open steppe of low grasses interspersed with tiny shrubs, Punta Delgada, Chubut. Bottom: low, grassy steppe at the top of coastal cliffs, Punta Delgada, Chubut. Photos F. Vuilleumier, November 1991.

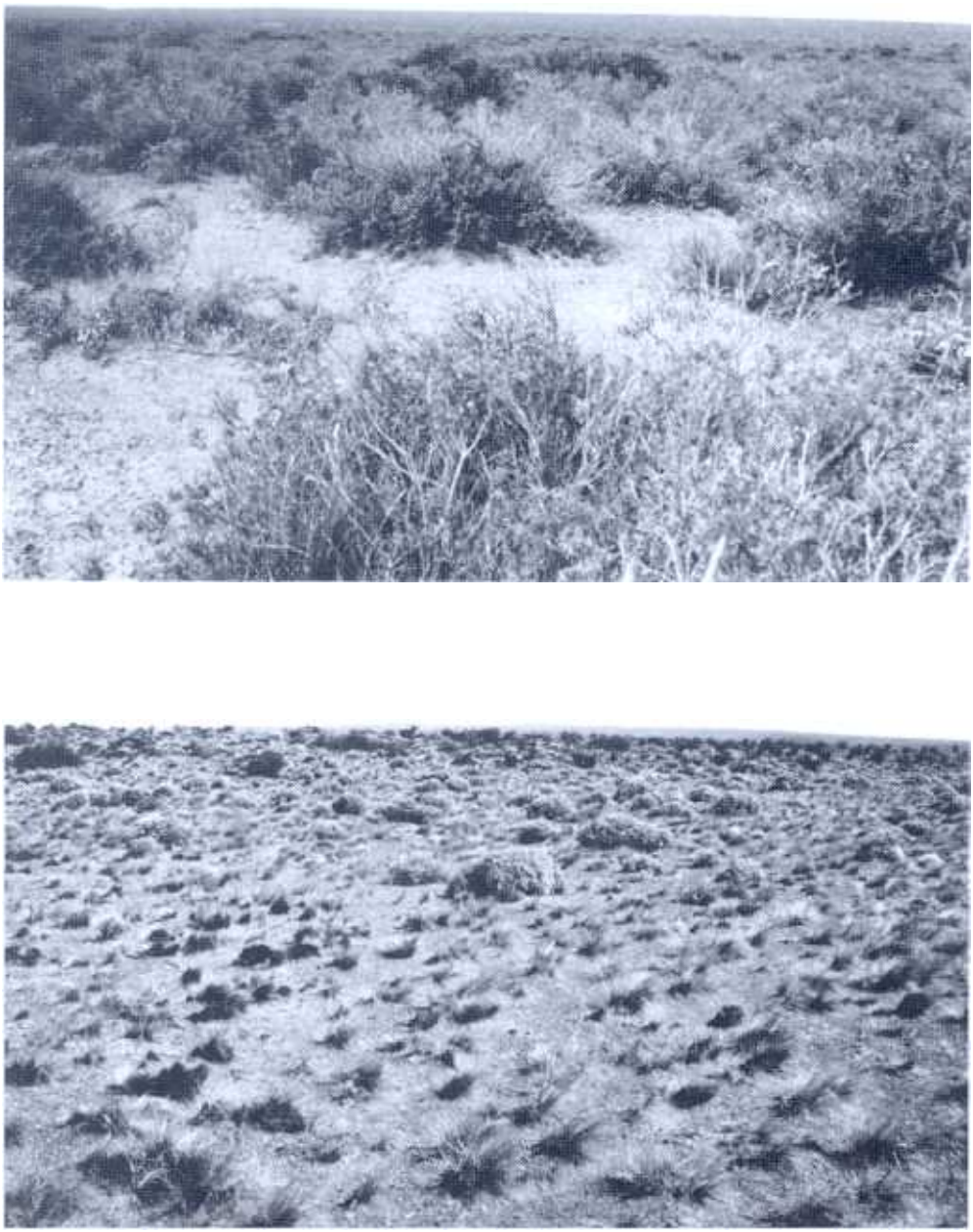

FIG. 7. Top: relatively dense shrubsteppe at the base of Península Valdés, a few km west of Puerto Pirámides, Chubut; note absence of grass cover. Bottom: very open, low steppe on soft pebbly soil with grazed, hard grass tussocks in flat area of foreground and low shrubs on ridges of background, about 30 km east of Gan-Gan, Chubut. Photos F. Vuilleumier, November 1991.

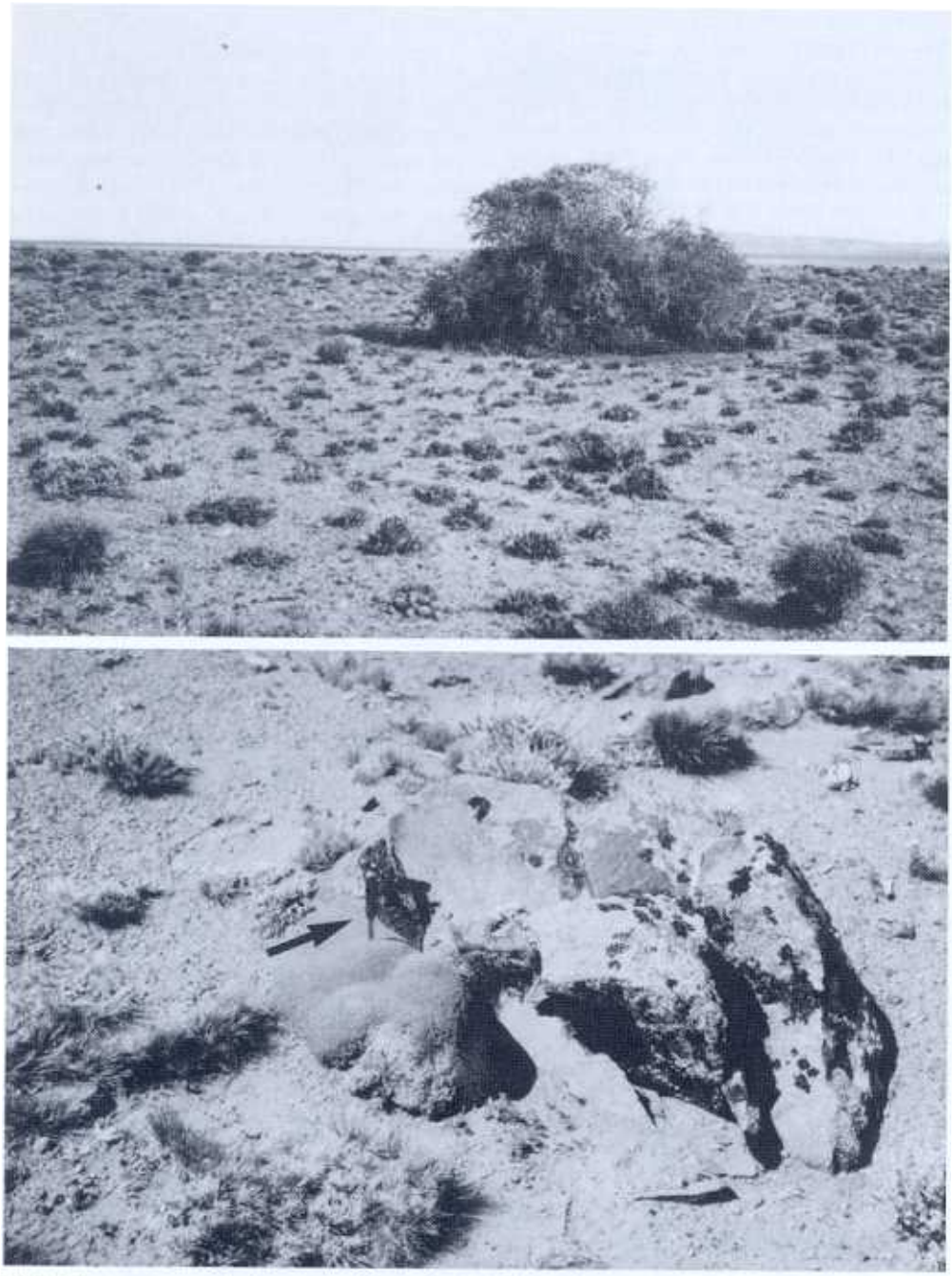

FIG. 8. Top: very open shrubsteppe in wide, flat basin (alkaline lake in left background); lone tree in middle ground has an active nest of *Buteo polyosoma*; near El Molle, Chubut. Bottom: close-up view of open, grassy steppe with small tussocks and hard cushion plants in area of basaltic outcrops; handle of knife in cushion plant (arrow) is 9 cm long; a few km west of Gastre, about 1300 m, Chubut. Photos F. Vuilleumier, November 1991.

(and Fig. 1 shows the vegetation toward Esquel). West of Esquel toward the Chilean border, Andean valleys receive more and more rainfall, and have, first relatively dry and open *Austrocedrus* woodlands and then mesic to very humid beech (*Nothofagus*) forests. The avifauna of Patagonian beech forests has been treated elsewhere (Vuilleumier 1967a, 1967b, 1972, 1985, Vuilleumier & Kikkawa 1991) and was not studied during this transect.

RESULTS

In this section, observations on overlaps, nonoverlaps, and reproductive isolation are presented for each pair (or triplet) of species studied in the field. For convenience, the order and nomenclature of birds follow Meyer de Schauensee (1982).

Eudromia and *Tinamotis* (Tinamidae)

Eudromia elegans and *Tinamotis ingoufi* are the only tinamous that I observed along the transect. Even though they are not congeneric and did not originate from the same speciation event, I include a discussion of their distribution here because of their similarity in size and color, as well as in habitat preference. Their respective distributions, in Patagonia at least, appear to be dependent on their interactions.

Eudromia elegans was seen (isolated, or up to three birds together) and heard commonly in steppes from Península Valdés to the Telsen area, and after an absence in the Gan-Gan area, heard again near Gastre at about 1200 m, near Paso del Sapo, and near Gualjaina. It was not seen or heard from there on to Esquel, or along the road from Esquel to Los Altares in the Chubut valley, but was noted again in steppes between the F. Ameghino Dam and Uzcudún, and was seen commonly in the steppes of the Camarones/Puerto Melo/Cabo Dos Bahías coastal area (see Fig. 9). In spite of its relative abundance, *E. elegans* was not as common as Wetmore (1926b: 32) reported from western Neuquén, where, he states, "it was not rare to see 30 or 40, or even 100, all adults, banded together" in 1920. The species may be rarer today than 70 years ago (see Appendix 1 about *Nothura*). Fig. 9 shows locality records of *E. elegans* in Río Negro according to Peters (1923), Wetmore (1926a, b), and Bettinelli & Chebez (1986). Fig. 10 illustrates the characteristic habitats of *E. elegans*.

FIG. 9. Distribution of *Eudromia elegans* (black dots) and *Tinamotis ingoufi* (black triangles) along the transect route; additional localities in Río Negro from the literature (see text).

FIG. 10. Two views of characteristic shrubsteppe habitat of *Eudromia elegans*. Top: a few km west of Puerto Pirámides, Chubut. Bottom: a few km west of Punta Delgada, Chubut. Photos F. Vuilleumier, November 1991.

FIG. 11. Two views of shrubsteppe habitat of *Tinamotis ingoufi*; note very open nature of vegetation. Top: about 30 km east of Gan-Gan, altitude about 1100 m, Chubut. Bottom: about 10 km west of Gan-Gan, altitude about 1050 m, Chubut. Photos F. Vuilleumier, November 1991.

Tinamotis ingoufi was noted at only three localities (Fig. 9): (1) along route 4 about 30 km E of Gan-Gan at 1100 m, (2) along route 4 about 10 km W of Gan-Gan at 1050 m, and (3) about 25 km W of Gan-Gan at 1050 m along a private ranch road off route 4. The three sites are similar to each other in that they have open steppe with low and spaced out shrubs growing on sandy or pebbly soil, with hard cushion plants and sparse tufts of coarse, sheep-grazed tussock grass interspersed here and there (Figs. 11 and 12). These sites differ from one another in that the first one is located on a vast basaltic plateau, whereas the other two are somewhat different geologically, the soil being composed of pebbles and rocks of sedimentary, rather than volcanic, material. Peters (1923: 287) reported a specimen of *T. ingoufi* from Huanuluan, where *E. elegans* "occurred sparingly in a few localities" (p. 286).

Thus *Eudromia* and *Tinamotis* were both found in steppes, but *Tinamotis* occurred only at higher elevations in the central part of the transect, whereas *Eudromia* was found all the way from sea level to a high elevation near 1200 m. Only one species was recorded (seen or heard) at any one site (Fig. 9). Although actual habitat

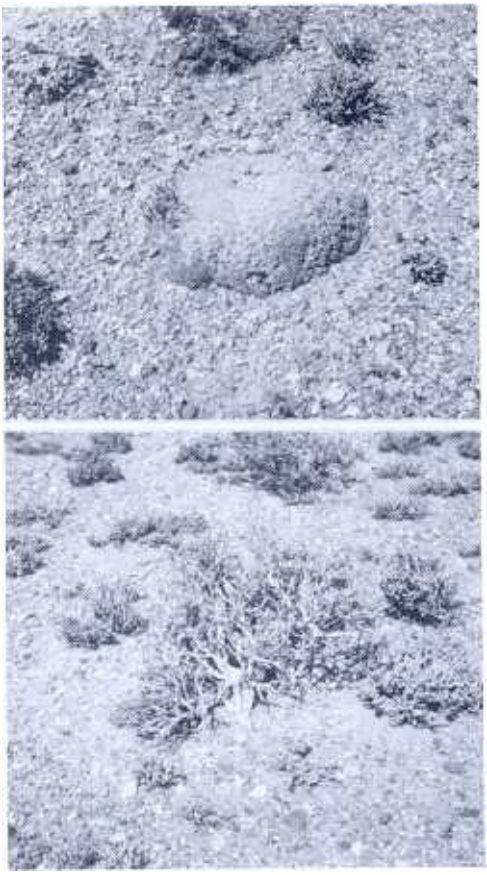

FIG. 12. Two close-up views of the habitat of *Tinamotis ingoufi* about 25 km west of Gan-Gan, altitude about 1050 m, Chubut. Top: sparse shrubs and a hard cushion plant (center, diameter about 25 cm) on pebbly ground. Bottom: sparse woody shrubs on pebbly ground. Photos F. Vuilleumier, November 1991.

overlap should be expected (see Peters 1923, cited above, and range description in Olrog 1979), I did not observe it. These two species are very similar and may exclude each other mutually. The crest of *Eudromia* is lacking in *Tinamotis*, but otherwise both species are large tinamous with similar head and neck patterns and with long necks which they raise vertically in similar ways to observe their surroundings. Both species are fond of foraging on dirt roads. The flute-like, two or three syllabic, whistled calls of *Eudromia elegans* remind me of the calls of certain Andean *Grallaria* spp., but also of the louder, whistled, and more melancholy *kiewla* of *Tinamotis ingoufi*. Wetmore (1926b: 31) described the call of *E. elegans* as "a low mournful whistle given slowly" and compared it to the call of *Rhynchotus rufescens*. One slight behavioral difference between *Eudromia* and *Tinamotis* is that, when alarmed, *Eudromia* keeps its raised neck slightly curved, whereas *Tinamotis* maintains its neck quite straight, with the head held at a right angle, periscope-like. When startled, *Eudromia* flies off easily, but *Tinamotis* runs and disappears, simply melting away in the low vegetation.

My observations of the habitat of *Tinamotis ingoufi* do not seem to match those published by Fjeldså & Krabbe (1990: 64), who wrote that it occurs in "grassland steppes, in sheltered valleys with patches of dense, low brush (*Berberis*, *Pernetyia* [sic], *Verbena*)," and "mainly at 200—800 m in sheltered valleys between the barren and windy plateaus of Arg. Patagonia from w Río Negro to Sta. Cruz . . ." Fjeldså (1988: 87) had written earlier: "Southern Patagonia is inhabited by the Elegant Crested Tinamou (*Eudromias* [sic] *elegans*) and the Patagonian Tinamou (*Tinamotis ingoufi*), which are both restricted to brush and shrub in sheltered valleys, and avoid the windswept plateaus."

My observations suggest that *Tinamotis ingoufi* occurs on these plateaus and that it is replaced by *Eudromia elegans* in lower areas or sheltered valleys. In fact, the distribution map in Fjeldså & Krabbe (1990: 63) shows a gap in the distribution of *Eudromia elegans* in Río Negro — Chubut, precisely where high elevation basaltic plateaus are located and where *Tinamotis ingoufi* occurs.

Clearly the geographical and ecological distribution of these tinamous in Patagonia requires more field work before it can be understood. An attempt should be made to locate a site where *Eudromia elegans* and *Tinamotis ingoufi* occur near each other and where their habitat preferences, foraging habits (including food items), and direct or indirect interactions (including competition) could be quantified. The various mechanisms that keep them separate in areas of contact or overlap need to be studied.

Thinocorus (Thinocoridae)

Notwithstanding some differences in size and color, the two species of the genus *Thinocorus* are

very similar to each other and are likely to have evolved from a common ancestor through a single vicariant event. The apparent extent of overlap between these species makes it difficult to infer the nature and localization of that vicariant event, however. Descriptions or maps of the geographic distribution of *T. rumicivorus* and *T. orbignyianus* (e.g., Meyer de Schauensee 1982, Fjeldså & Krabbe 1990) suggest a very extensive zone of overlap between them. Actually, the two species of *Thinocorus* seem to have only partially overlapping distributions and may in fact be largely allopatric.

Maclean (1969: 35) thus wrote of *T. rumicivorus* that "in Patagonia . . . it occurs far inland on the open steppe," and of *T. orbignyianus* that it "seldom descends below 700 meters except in the extreme southern part of its range" (i.e., Patagonia). Elsewhere, Maclean (1969: 37) stated that "just as the Least Seedsnipe [*T. rumicivorus*] is essentially a bird of the lowlands, the Gray-breasted Seedsnipe [*T. orbignyianus*] is a bird of the mountains." And further: "in the southernmost part of its range the Gray-breasted is still more a bird of higher elevations than the Least (Crawshay 1907) although the inhabitants of Argentine Patagonia assured me that in winter the Gray-breasted is common on the pampa" (p. 37).

In my experience *Thinocorus orbignyianus* lives in mountain valleys and slopes and is usually relatively scarce wherever it occurs, whereas *T. rumicivorus* lives in open plains where it can be extremely abundant. Thus, in a transect I carried out through the steppes of Chilean Patagonia at about 52 °S, from Morro Chico westward to Gallegos Chico, O'Higgins, Kimiri Aike, and Punta Dungeness on February 27 and 28, 1987 and on March 1, 1987, I saw only one *Thinocorus orbignyianus* but thousands of *T. rumicivorus*.

During the present transect in Chubut Province, *Thinocorus* spp. were encountered at 12 sites: 1 pair *rumicivorus* at Caleta Valdés, 1 pair *rumicivorus* 30 km E of Gan-Gan, 1 ♂ *rumicivorus* 35 km E of Gan-Gan, 1 pair *rumicivorus* about 25 km W of Gan-Gan, song *orbignyianus* about 40 km E of Gastre, song *orbignyianus* near Gastre, 1 pair *orbignyianus* with 3 downy chicks

FIG. 13. Distribution of *Thinocorus rumicivorus* (black dots) and *T. orbignyianus* (black triangles) along transect route; additional localities in Río Negro for these two species from the literature and personal observations (see text).

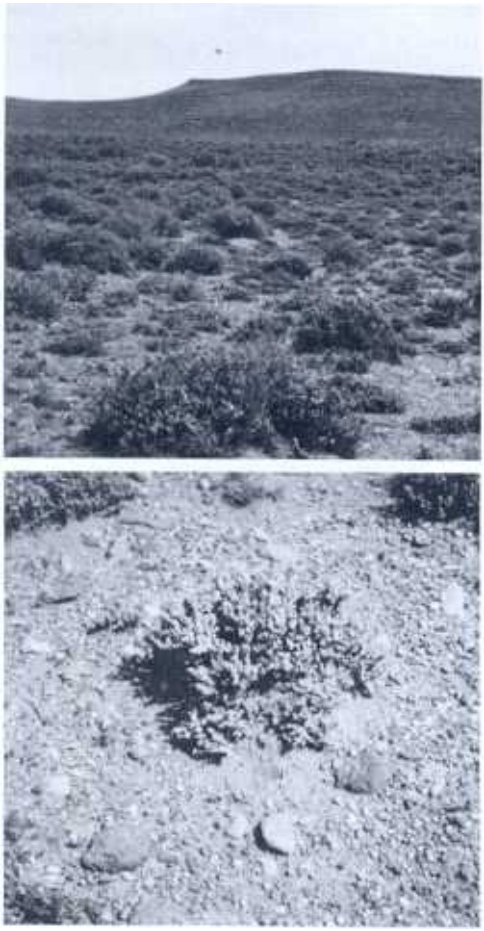

FIG. 14. Top: habitat of *Thinocorus rumicivorus* about 25 km west of Gan-Gan, altitude about 1050 m, Chubut. Bottom: close-up view of habitat of *T. rumicivorus* at same locality; low shrub (*Verbena* sp.) in center is about 30 cm in diameter and 15 cm tall. Photos F. Vuilleumier, November 1991.

about 30 km W of Gualjaina, 1 pair *rumicivorus* near Puerto Melo, 1 pair *rumicivorus* near Cabo Dos Bahías, 1 + 2 + 4 birds at 3 sites along route 30, between Camarones and the intersection of route 30 with route 3.

These records, mapped on Fig. 13, suggest, first that *Thinocorus* is patchily distributed, and second that the two species do not overlap geographically. *Thinocorus orbignyianus* seems confined to the central area of plateaus and higher mountains (habitat similar to that in Fig. 17), whereas *T. rumicivorus* occurs mostly in the lower eastern part of the study area (habitat illustrated in Fig. 14). The distribution pattern of *Thinocorus* spp. is somewhat similar to that of the tinamous *Eudromia elegans* and *Tinamotis ingoufi*.

Durnford (1877, 1878) mentioned only *Thinocorus rumicivorus*, which he called "common" (1877) or "abundant" (1878). In his 1877 paper, he wrote that *T. rumicivorus* was "seen most frequently on the higher stony plateaux, but occasionally in the valley." Peters (1923: 292) found *T. orbignyianus* to be "a characteristic resident of the western portion of the Plain of Patagonia." He observed it "only in the vicinity of Huanuluan, almost invariably up among the higher gullies and ravines which cut back into the table-lands or head far up on El Escorial." Of *T. rumicivorus*, Peters (1923: 293) wrote that it was "a common resident in the western part of Río Negro" but that "unlike its larger relative, *T. orbignyianus* (sic), it does not frequent the rocky gullies and ravines, but is found on the gravelly plains and sandy valleys." Peters (1923: 293) reported an adult female "taken seven miles east of Bariloche on February 13." I have seen *T. rumicivorus* in the Pampa de Nahuel Huapí near Bariloche on 11 February 1965. Wetmore (1926a) reported specimens of *T. rumicivorus* from Arroyo Seco (Río Negro, near Valcheta, Fig. 13), and of *T. orbignyianus* from Huanuluan and Arroyo Anecon Grande (both in Río Negro, the two localities being about 20 miles from each other; Fig. 13). In his 1926b paper, Wetmore stated that he "encountered the small seed snipe on its breeding grounds on the closely grazed slopes of an open valley in which there was a tiny stream and occasional little seeps or spring holes" at Zapala, Neuquén.

In the transect area, *Thinocorus rumicivorus* would therefore appear to occur from the coast westward to the Andean foothills, in suitable habitats at relatively low elevations, whereas *T. orbignyianus* would seem to be restricted to the higher altitude plateaus of the central area. The apparent broad geographical overlap one sees on published maps (e.g., Fjeldså & Krabbe 1990) does not seem to be accompanied by an equivalent ecological overlap, and the two species may in fact not breed side by side. In an earlier paper (Vuilleumier 1991b: 329) I classified the situation

in *Thinocorus* as a zone of parapatry with a narrow but long overlap zone along the Andean foothills. There is apparently no published information on the interactions of these closely related species in areas of overlap or parapatry, and no statement based on actual field data can be made at this time about reproductive isolating mechanisms. One may speculate, however, that the color differences in male plumage, especially the presence (*T. rumicivorus*) or absence (*T. orbignyianus*) of a black bar between the throat and the breast, combined with overall size differences and differences in vocalizations, act, together with the habitat differences mentioned above, as isolating mechanisms. A field study of these mechanisms would be very rewarding.

Geositta (Furnariidae)

The two species of *Geositta* (*rufipennis* and *cunicularia*) encountered along the transect are not very closely related to each other (Vuilleumier 1967, Vaurie 1980). *G. rufipennis* seems to be isolated within the genus and *G. cunicularia* seems to be related to high Andean *G. punensis* and southern Patagonian *G. antarctica*. I nevertheless discuss the distribution of these two species along the transect to illustrate differences in habitat preference and patchiness.

Geositta rufipennis was observed only once, 2 birds (paired?) in a scree of huge boulders with almost no vegetation along route 12 at 530 m in the Chubut River Valley near Piedra Parada about 75 km W of Paso del Sapo (Fig. 15, Fig. 16, top). Peters (1923: 312) collected the species in rocky habitats near Huanuluan and Maquinchao (Río Negro). Wetmore (1926a: 438) reported *G. rufipennis* from Río Negro (Arroyo Cumallo) and Chubut (Maitén). In his 1926b paper, Wetmore saw *G. rufipennis* "among low brush on rocky slopes" near Mendoza. Olrog (1979: 166) stated that *G. rufipennis* occurred "possibly" in Chubut and Santa Cruz.

Geositta cunicularia was noted on 9 occasions, 6 of them in Península Valdés, where the species was locally abundant, especially in the Punta Delgada area, in very open, low grassy and scrubby steppes on sandy and dune-like substrates (Fig. 16, bottom). I did not see *G. cunicularia* at the base of the Península in denser and taller shrubsteppe with no or very little grass. In spite

FIG. 15. Distribution of *Geositta cunicularia* (black dots) and *G. rufipennis* (black triangles) along the transect route; additional localities in Río Negro for these two species from the literature and unpublished personal observations (see text).

FIG. 16. Top: area of sympatry between *Geositta cunicularia* (habitat: open riverside vegetation in left middle ground) and *G. rufipennis* (habitat: rocky scree in foreground) along the Chubut river near Piedra Parada, Chubut. Bottom: shrubsteppe with low grass, habitat of *G. cunicularia* a few km west of Punta Delgada, Chubut. Photos F. Vuilleumier, November 1991.

of active search, I did not encounter *G. cunicularia* along the rest of the transect, with three exceptions: (1) 2 birds at about 1300 m, about 30 km E of Gastre, in an open, sandy valley with low bushy steppe on hills and grassy slopes (Fig. 17); these birds emitted the "*wittu-wittu-wittu*" vocalization characteristically heard in Tierra del Fuego; (2) 1 bird in a damp, grassy area near a small pond and open and dry steppe near Piedra Parada at 530 m (bird not heard); (3) 1—2 birds ("*wittu*" call type) in a damp meadow along the edge of an artificial pond about 20 km SE of Colan Conhué at about 800 m.

FIG. 17. Habitat of *Geositta cunicularia* ("*wittu*" vocalization type) about 30 km east of Gastre, altitude about 1300 m, Chubut; the birds occurred in the very open grassy area at the edge of the small lagoon in the middle ground. Photo F. Vuilleumier, November 1991.

My observations strongly suggest that *G. cunicularia* is patchily distributed and is absent from large areas of north-central Patagonia covered with pure shrubsteppe, whether at relatively low altitudes near the coast or higher up on the basaltic plateaus, but that it occurs only in areas with very open, grazed, grassy steppe on soft sandy soil (perhaps only in areas with *Ctenomys* colonies, as in Tierra del Fuego). Fig. 15 illustrates this distribution. Furthermore, it seems that two populations, with two distinguishable song types, occur in the transect area: the trill (followed by repeated notes) in the Península Valdés, and the "*wittu*" vocalization locally inland.

It is of interest to point out that Durnford (1878) did not find *Geositta cunicularia* to be common in the Chubut Valley, but that Peters (1923: 312) found that species "very common" in Río Negro. (Unfortunately, Peters did not give any locality data for *G. cunicularia*.) Of the several specimens cited by Wetmore (1926a: 438), only the one from Guaguel Niyeu, Río Negro, November 14, 1911 is mapped on Fig. 15. The other birds are from late summer or winter and could be migrants from elsewhere. Wetmore (1926b: 244) stated that "near Zapala [Neuquén] the miner frequented sandy areas along the slopes of little valleys."

Habitat co-occupancy was not noted between the two species of *Geositta*, which live in very

different environments (see also Peters 1923: 312, who stated that *G. rufipennis* "is invariably found in rocky situations, whereas *G. c. cunicularia* frequents the dry, sandy plains"). Records of *G. rufipennis* and *G. cunicularia* from the Bariloche area on Fig. 15 represent my own field observations made in 1965. I observed *rufipennis* in rocky areas and *cunicularia* in open steppes.

In southern Patagonia and Tierra del Fuego where *Geositta cunicularia* and *G. antarctica* overlap and even breed side by side locally, I have obtained no evidence of interbreeding. *G. cunicularia* and *G. antarctica* are very similar to each other morphologically but differ in voice. One can thus suppose that reproductive isolation is primarily achieved through differences in vocalizations. Because of substantial differences in morphology, reproductive isolation between *Geositta cunicularia* and *G. rufipennis* is more likely to be due to their external appearance than their vocalizations, if one reasons by analogy with the situation between similar-looking *G. cunicularia* and *G. antarctica*, although the voices of *cunicularia* and *rufipennis* are quite different. Overlaps between species of the genus *Geositta*, irrespective of the taxonomic relationship of these species, have not been studied in detail in the field and are worth investigating. The two *Geositta* species encountered along the transect are largely segregated by habitat, whereas the two species in Tierra del Fuego coexist in the same habitat. These two pairs of species represent the extremes observed in the genus: most other species pairs found together or near each other exhibit at least some difference in habitat preference.

Upucerthia and *Eremobius* (Furnariidae)

Three species of earthcreepers were observed along the transect, *Upucerthia ruficauda*, *U. dumetaria*, and *Eremobius phoenicurus*. The two species of *Upucerthia* are not each others' closest relatives (Vaurie 1980). The monotypic *Eremobius*, although very similar morphologically to some species of *Upucerthia*, like *ruficauda* and *andaecola*, does differ from them in its nest site and nest structure. As in the case of *Geositta* above, overlaps in this group of furnariids are dis-

FIG. 18. Distribution of *Eremobius phoenicurus* (black dots), *Upucerthia dumetaria* (black triangles), and *U. ruficauda* (star) along the transect route; additional localities in Río Negro for *E. phoenicurus* and *U. dumetaria* from the literature and unpublished personal observations (see text).

FIG. 19. Two views of the habitat of *Upucerthia dumetaria*. Top: open steppe on rocky (basaltic) ground a few km west of Telsen, Chubut; birds were displaying from the top of the shrubs in the left background. Bottom: unused roadside gravel pit a few km west of Punta Delgada, Chubut; a pair was breeding in a hole (arrow) near the top of the cut just below the shrub off the center of the picture (see Fig. 20). Photos F. Vuilleumier, November 1991.

FIG. 20. Nesting hole of *Upucerthia dumetaria* a few km west of Punta Delgada, Chubut (see Fig. 19, bottom for site location). Photo F. Vuilleumier, November 1991.

cussed here because interspecific interactions might influence their distribution patterns.

Upucerthia ruficauda was seen only once, about 30 km W of Paso del Sapo in the Chubut River Valley at an elevation of 480 m (Fig. 18). The single bird was actively foraging for food at the foot of a vertical, 50 m high cliff, at the edge of the valley (Fig. 21, bottom). It searched for larvae in the semi-soft ground, at the base of small stones. One large prey item (probably a beetle larva) was killed with repeated blows of the bill, then the bird flew to the top of a rock to finish the kill and start eating his prize, before disappearing out of sight. Neither Peters (1923) nor Wetmore (1926a, 1926b) mentioned *Upucerthia ruficauda* from northern Patagonia. Olrog (1979: 169) gave its distribution and habitat as follows: "Arenales pedregrosos entre 3500 y 4000 m de altura en los cerros de Jujuy, Salta, Catamarca y Tucumán y después por el oeste sucesivamente más bajo, hasta el sur de Chubut."

Of the two other species, *Upucerthia dumetaria* was observed regularly from the Península Valdés (where two different pairs were feeding young in nests in holes in road-side ditches on 8 and 9 November; Fig. 19, bottom, and Fig. 20) all the way to the steppes west of Gualjaina. It occurred in a variety of habitats, including scrubby, open steppes on basaltic plateaus (Fig. 19, top), fairly dense shrubsteppe on level, pebbly areas, low grass-scrub steppe in sandy areas, and denser shrubsteppe on coastal plateaus. Peters (1923: 312—313) cited the species from San Antonio ("in the bushes growing close to the edge of the saltmarsh"), from west-central Río Negro ("on the plains, up the ravines and gullies, but always among the bushes"), and from the Lake Nahuel Huapí area (one record from near the beach of the lake). Wetmore (1926a: 439) listed only one breeding season specimen from west-central Río Negro (juvenile male). Wetmore (1926b: 249—250) found the species near General

Roca (Río Negro) "among the heaviest growths of *Atriplex* and other shrubs in the lowland flood plain of the Rio Negro" and near Zapala (Neuquén) "in heavy tracts of thorny brush in an arroyo leading toward the lowlands." Wetmore (1926b: 250) aptly mentioned the "thrasherlike [*Toxostoma*, Mimidae] appearance of *U. dumetaria* in bill shape and habits.

Eremobius was observed in the same areas and habitats as *Upucerthia dumetaria*, from Península Valdés to near Gastre (5 observations), from sea level (but not in the open steppes on dunes and sandy soil near Punta Delgada) to about 1300 m (Fig. 18). Several nests were seen (Fig. 21, top), but those I opened up turned out to be inactive. Peters (1923: 314) called *Eremobius phoenicurus* "a common resident in arid northwestern Patagonia" (Huanuluan/Maquinchao area). Wetmore (1926a: 440) mentioned two specimens from San Antonio and Paja Alta (near Valcheta), both in eastern Río Negro. Wetmore (1926b: 253) found *Eremobius* near Zapala (Neuquén) "amid patches of low thorny brush that grew on the slopes of rolling hills, where the soil was composed of sand and stones." He compared the species to "long-tailed wrens" but found them more terrestrial.

My observations suggest that habitat sharing is common between two of the three earthcreepers (*Upucerthia dumetaria* and *Eremobius phoenicurus*). Along the transect, these two species were characteristically found in similar shrubsteppes on open stony ground with little or no grass tussocks. Durnford (1878) called *Upucerthia dumetaria* and *Eremobius phoenicurus* "common . . . throughout our journey".

Sympatry and habitat co-occupancy among these two earthcreepers could be achieved because of differences in size and in bill shape. *Eremobius phoenicurus* is relatively small and has a long, thin, and slightly decurved bill. *Upucerthia dumetaria* is larger and has a longer, thicker, and more decurved bill. Their nests also differ. *Eremobius* makes large stick nests in shrubs (Fig. 21, top). On the other hand, *Upucerthia dumetaria* makes its nest at the bottom of holes in small cliffs or banks (Fig. 19, bottom; Fig. 20).

In the field, *Eremobius phoenicurus* and *Upucerthia ruficauda* appear quite similar in color, pattern, bill size and shape, and in the way they cock their tail up at an angle. In this case, reproductive isolation between these birds would be achieved chiefly through their substantial differences in habitat preference. *Eremobius phoenicurus* and *Upucerthia dumetaria*, on the other hand, are quite different from each other in both morphology and vocalization.

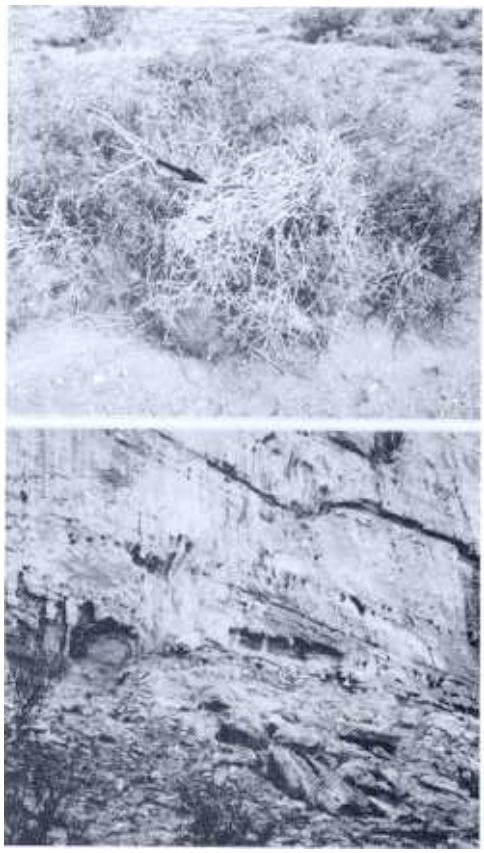

FIG 21. Top: large stick nest of *Eremobius phoenicurus* in a low shrub, open shrubsteppe about 10 km west of Gan-Gan, Chubut (arrow points to 9 cm long Swiss knife on top of nest). Bottom: habitat of *Upucerthia ruficauda* a few km west of Paso del Sapo, Chubut; the bird was foraging on the rocky ground at the bottom of the cliff among the sparse shrubs in the left foreground. Photos F. Vuilleumier, November 1991.

Leptasthenura (Furnariidae)

The two species of *Leptasthenura* (*L. platensis* and *L. aegithaloides*) observed along the transect are probably sister species (Wetmore 1926b: 256;

Fjeldså 1991: 349) that have evolved from a common ancestor, although the vicariance event responsible for this speciation event is unknown. Although largely allopatric, these two near-sibling species seem to overlap in steppes of northeastern Patagonia and in parts of the Monte and Espinal vegetation types (Hueck & Seibert, 1972) of eastern and central Argentina.

Leptasthenura platensis was identified on 7 November at Riacho San José, base of Península Valdés, on 8 November in Península Valdés about 5 km W of Puerto Piramides, 11 November in the Telsen area, and 14 November about 5 km W of Paso del Sapo (Figs. 22 and 23). *L. platensis* was not recorded from Chubut by Durnford (1877), or from Río Negro by Peters (1923), Wetmore (1926a), or Bettinelli & Chebez (1986), or from Neuquén by Wetmore (1926b). My observations seem to extend the range of *L. platensis* to parts of Chubut, although Meyer de Schauensee (1982: 207) states "Argentina to Chubut," and Olrog (1963: 214 and 1979: 175) indicates "hasta el norte de Chubut." It is unfortunate that Fjeldså & Krabbe (1990) did not include *L. platensis* in their book. This species, which is very similar to *L. aegithaloides*, does occur in part of the area they cover. Users of the book working in Patagonia will not be aware of the potential occurrence of *L. platensis* there. The distribution of *Leptasthenura* spp. may not be as well known as previously believed. For example, I discovered a hitherto unknown breeding population of *L. aegithaloides* in Chilean Tierra del Fuego (specimens collected in 1985 and 1987).

L. aegithaloides was observed at two localities in Península Valdés (about 20 km W of P. Pirámides; near Caleta Valdés), near Puerto Madryn, near Gan-Gan, a few kilometers west of Paso del Sapo (nesting; parents were actively feeding nestlings at a nest in a hole in a cliff, 14 November, see Fig. 24; a few km west of area with *L. platensis*), between Gualjaina and Esquel, between Colan Conhué and Pampa de Agnia, and at Cabo Dos Bahías. Peters (1923: 315, 316) found *L. aegithaloides* a "common resident" and collected it at San Antonio, Huanuluan/Maquinchao and Bariloche. Wetmore (1926a: 441) re-

FIG. 22. Distribution of *Leptasthenura platensis* (black dots) and *L. aegithaloides* (black triangles) along the transect route; additional localities for *L. aegithaloides* in Río Negro from the literature and unpublished personal observations (see text).

FIG. 23. Dense shrubsteppe habitat of *Leptasthenura platensis* a few km east of Puerto Pirámides, Chubut. Photo F. Vuilleumier, November 1991.

ported two winter specimens from near Valcheta, Río Negro. In 1965, I found this species common in a variety of brushy habitats near Bariloche (Fig. 22).

Wetmore (1926b: 256) encountered *L. platensis* in La Pampa Province (Argentina) and Uruguay "in trees of the densest foliage . . . where they clambered like titmice in a leisurely manner through the dense growth of limbs." Of *L. aegithaloides*, Wetmore (1926b: 257) stated that it was "distinguished from *L. platensis* by somewhat more bushy crest, darker coloration [Chilean population], and grayish white on the inner webs of the retrices." Patagonian populations, however, are paler and look more like *L. platensis* in color. In Río Negro, Wetmore (1926b: 257) found *L. aegithaloides* "in the tops of thick bushes in a region where the atriplex and other growth typical of alkaline flats was tall and dense." Wetmore (1926b: 256—257) gave the voice of *L. platensis* as "a faint *tsee-ee-ee*" and that of *L. aegithaloides* as "a low buzzing trill."

Fig. 22 shows that, according to my observations, these two species of *Leptasthenura* are potentially sympatric. Even though observed near each other in two areas (Península Valdés and near Paso del Sapo) I did not actually see them side by side. Thus, I have no first-hand information on interspecific interactions in sympatry. In the future, specimens should be collected at localities where these two species either occur

FIG. 24. Top: habitat of *Leptasthenura aegithaloides* a few km west of Paso del Sapo in the Río Chubut Valley; birds were foraging among the shrubs in the middle distance as well as at the foot of the tall cliff in the left of the photograph. Bottom: breeding habitat of *L. aegithaloides* a few km west of Paso del Sapo in the Río Chubut Valley; arrow indicates nest location in hole in cliff; the two parents were actively feeding nestlings (nest was too high to check age and number of nestlings). Photos F. Vuilleumier, November 1991.

together or near each other in order to fully document their occurrence.

If *L. platensis* and *L. aegithaloides* live together in the same shrubsteppe habitat, study of their reproductive isolation should be extremely interesting because they are very similar to each other morphologically and perhaps also vocally. Four specimens of *L. aegithaloides* (AMNH

818454, 817073, 826140, 818455) that I collected in Tierra del Fuego in 1985 and 1987 weigh respectively 9.0, 9.1, 9.3, and 9.5 grams. Two specimens of *L. platensis* (AMNH 779562, 779584) collected in Entre Rios weigh respectively 9.8 and 10.4 grams. *L. platensis* may therefore be a little heavier than *L. aegithaloides*. Plumage differences between these two species include the presence of a crest in *L. platensis* (absent in *aegithaloides*), less heavily streaked crown in *platensis* (heavily marked with buffy in *aegithaloides*), paler and buffier tail feathers in *platensis* (darker and grayer in *aegithaloides*), and streaked throat in *platensis* (in *aegithaloides* the throat is either unstreaked or less streaked). These differences are fairly well-marked on study skins but much less so when observing birds in the field. If vocalizations are similar, then such morphological differences as presence/absence of a crest, poorly marked versus well marked crown, and streaked versus unstreaked throat might be characters used as isolating mechanisms.

Asthenes (Furnariidae)

The two species of *Asthenes* observed along the transect, *patagonica* and *pyrrholeuca*, may belong to two different species groups (Vuilleumier 1967), and are thus probably not very closely related to each other (see also Vaurie 1980). In the field, however, they look very similar and often behave in similar fashion. It is thus reasonable to expect that, if found together, they may interact and hence influence their respective distributions.

Asthenes patagonica was seen at the base of Península Valdés (adult flushed from a nest that I did not open, 7 November), Península Valdés (near Puerto Piramides), Sierra Chata, W of Sierra Chata (nest building), about 10 km W of Telsen (inactive nest), and about 30 km W of Paso del Sapo (Fig. 25). Peters (1923: 316) stated that he "found [this species] only at San Antonio where a male and a female were taken on August 18." He did not describe its habitat. Wetmore (1926a: 442) similarly mentioned two specimens from San Antonio without specifying their habitat. In his 1926b paper, Wetmore stated (p. 271) that *A. patagonica* "was found in the semiarid region that bordered the Rio Negro, where it frequented the denser, taller stands of *Atriplex* and other shrubs that grew in the river bottom or

FIG. 25. Distribution of *Asthenes patagonica* (black dots) and *Asthenes pyrrholeuca* (black triangles) along the transect route; additional localities in Río Negro for these two species from the literature and unpublished personal observations (see text).

occurred more sparingly in the smaller, more scattered growth that clothed the gravel hills above the flood plain." Fig. 26 (bottom) illustrates the habitat of *A. patagonica*.

Asthenes pyrrholeuca was observed at Riacho San José (base of Península Valdés, nest with three eggs, 7 November), about 60 km E of Telsen, near Telsen, at two localities in the Paso del Sapo area, and one locality between Gualjaina and Esquel (Fig. 25). Peters (1923: 317) wrote that "this was the common spiney-tail of the Huanuluan-Maquinchao region, always found in the thicker and denser growths of bushes." Wetmore (1926a: 442) listed two specimens from western Chubut, "both in barred juvenal plumage," from 4 February and 3 March. He (1926b: 270) stated that "in places, as near the coast at Bahia Blanca, these birds were abundant and formed the dominant element among passerine species." *A. pyrrholeuca* is listed from Chipauquil, Meseta de Somuncurá, by Bettinelli & Chebez (1986).

Actual sympatry and habitat co-occupancy was detected between the two species of *Asthenes* at only one locality (about 30 km west of Paso del Sapo). At this site, the vegetation ranged from riverine willows along the Río Chubut to overgrazed meadows with scattered *Berberis* bushes and to open scrub at the foot of a cliff. *Asthenes patagonica* and *A. pyrrholeuca* both occurred in the drier vegetation near the base of the cliff, but *A. pyrrholeuca* was also found in the *Berberis* bushes and the riverine willows (Fig. 26, top). At that site, *A. pyrrholeuca* thus occurred in a broader range of habitats, and may have preferred denser vegetation types near the river. This difference may help explain why I did not observe *A. patagonica* and *A. pyrrholeuca* together more often. Olrog (1979: 179–180) stated that *A. pyrrholeuca* occurred generally near water courses, and that *A. patagonica* was found in arid scrub.

Morphologically *A. patagonica* is shorter tailed and appears slightly plumper than *A. pyrrholeuca*. *A. patagonica* appears at times to be pale or more sandy in color, whereas *A. pyrrholeuca* is more mouse-brown. In some individuals of *A. pyrrholeuca* the tail is very long. Both species emit trills. *A. pyrrholeuca* has characteristic call notes that can be transcribed as "*huit*" or "*twit*," either isolated or repeated. The nests of

FIG. 26. Top: habitat of *Asthenes pyrrholeuca* in a riverine grove of willows a few km west of Paso del Sapo along the Chubut River, Chubut. Bottom: habitat of *Asthenes patagonica* in dense shrubsteppe a few km east of Puerto Pirámides, Chubut; note large stick nest in shrub in center of photograph. Photos F. Vuilleumier, November 1991.

the two species differ. The one nest of *A. pyrrholeuca* I saw was in a 70 cm tall shrub; it was spherical, about 25 cm in diameter, with a side opening. For a description of a nest of *A. pyrrholeuca* see Wetmore (1926b: 270–271). I found several nests of *Asthenes patagonica*, usually very visible and voluminous, placed near the top of thorny bushes (Fig. 26, bottom). They were elliptical, at least about 45 cm long and 25 cm wide in the center with an entrance tunnel sometimes as long as 15 to 20 cm or more. Wetmore (1926b:

272) described a similarly-shaped nest of *A. patagonica*.

The differences between these two species of *Asthenes* (morphology, voice, nest structure) could easily explain their reproductive isolation. In this pair of species, as well as in other sympatric pairs of *Asthenes* elsewhere, no study of interspecific interactions exists. Because these species are common in northern Patagonia, and their nests are very easy to find, it would be relatively easy to investigate such interactions through detailed field study.

Agriornis (Tyrannidae)

Speciation in flycatchers of the genus *Agriornis* was discussed previously (Vuilleumier 1971), but problems of interspecific interactions or reproductive isolation were not treated in that paper, and sympatry was discussed in one paragraph only. Three of the five species of *Agriornis* (*montana*, *microptera*, and *murina*) were seen along the transect (Fig. 27).

Agriornis montana was observed only once on 13 November at about 1300 m near Gastre in a valley with mixed vegetation including very open grazed grassland and shrubbery near basaltic rocks (Fig. 28). The Bariloche records in Fig. 27 are from observations I made in 1965. Wetmore (1926a: 446) reported birds from near Cholila (Chubut) and one 60 miles W of Valcheta (Río Negro). Wetmore (1926b: 297) collected *A. montana* near Mendoza "on the ground or on low bushes near streams." He also stated (1926b: 297) that *A. montana* "did not differ in actions from *striata* [= *microptera*] or *livida*, but [was] readily distinguished by the white in the tail."

Agriornis microptera was seen at the same locality as *A. montana*, foraging on the ground in a patch of grassy steppe (Fig. 28), as well as at two localities in Península Valdés in shrubby steppe on sandy soil between Punta Delgada and Caleta Valdés (Fig. 29, top), near Puerto Madryn in shrubsteppe (foraging on the ground and on a gravel road), and near Puerto Melo in scrub similar to that near Puerto Madryn. Display flights were seen near Puerto Madryn and Punta Delgada (Península Valdés). The displaying bird flies up to about 100 m above the ground, then alternates between upward flights with active

FIG. 27. Distribution of *Agriornis microptera* (black dots), *A. murina* (black triangles) and *A. montana* (stars) along the transect route; additional localities for *A. murina* and *A. montana* in Río Negro and Chubut from the literature and unpublished personal observations (see text).

FIG. 28. Locality where *Agriornis microptera* and *A. montana* occurred side by side a few km west of Gastre at about 1300 m, Chubut; *A. microptera* foraged on the ground in the low grassy steppe at the edge of the dry pool in the background, whereas *A. montana* foraged from the dense shrubbery and perched on the basaltic rocks in the foreground. Photos F. Vuilleumier, November 1991.

FIG. 29. Top: shrubsteppe habitat of *Agriornis microptera* on sandy soil near Punta Delgada, Chubut. Bottom: shrubsteppe habitat of *A. murina* at the top of coastal cliffs near Caleta Valdés, Chubut. Note structural similarity of habitats of two species. Photos F. Vuilleumier, November 1991.

wing flaps and downglides with closed wings, in relatively rapid sequence. The performance appeared to be silent. Wetmore (1926a: 446) reports three specimens from near Valcheta, Río Negro, where *A. murina* was also collected. In his 1926b paper (p. 296), Wetmore reported finding *A. microptera* in Río Negro "in a region of arid gravel hills covered with an open growth of low brush."

Agriornis murina was seen only twice, one bird near Caleta Valdés in relatively dense coastal shrubsteppe on 9 November, and one bird at Cabo Dos Bahías in similar, but more open coastal steppe on 17 November (Fig. 27). In both cases the birds disappeared after a short period of observation and could not be found again. Peters (1923: 320) collected one *A. murina* in coastal Río Negro on 18 August, but did not find it elsewhere; Wetmore (1926a: 447) reported two *A. murina* from coastal Río Negro, and one from near Valcheta, further inland in Río Negro, and (1926b: 301) other specimens from near General Roca, Río Negro (Fig. 27). The first nest of that species was found by Nores and Salvador (1990) in Catamarca, a locality extending the breeding range by about 1200 km northward.

Although seen within a short distance of each other (a few km) I did not observe *A. microptera* and *A. murina* together in Península Valdés. *A. microptera* was seen in more open habitat than *A. murina*. Near Gastre, *A. microptera* and *A. montana* were observed within 200 m of each other. *A. microptera* was foraging on the ground in a grazed meadow, whereas *A. montana* foraged in an area of boulders surrounded by thorny shrub at the edge of the meadow, and did not fly toward the meadow (Fig. 28). Study of interactions among *Agriornis* spp. would be very interesting but are likely to be difficult to carry out because of the relative shyness and scarcity of these tyrants.

Muscisaxicola (Tyrannidae)

Speciation patterns in the genus *Muscisaxicola* were described in a previous publication (Vuilleumier 1971). The two species observed along the transect, *M. capistrata* and *M. maculirostris*, were placed in two different species groups in that paper. *Muscisaxicola capistrata* was observed on three occasions: one pair near Gastre at about 1300 m, an isolated bird between Paso del Sapo and Piedra Parada, and an isolated bird about 30 km NE of Esquel (Fig. 30, and Fig. 31, top). Peters (1923: 323) found that species "rather uncommon" in the Huanuluan area, but did not indicate its breeding habitat. Wetmore (1926a: 450) cited a September specimen from the Valcheta area, but did not mention the species in his other paper (1926b).

By contrast, *M. maculirostris* was abundant along the transect, from near Telsen all the way to the Gualjaina area. Along the coast I did not observe it on Península Valdés but found it near Puerto Melo (Fig. 30). Locally it was common, and at any one locality, up to 3—6 birds could be either seen or heard simultaneously during their flight songs (well described by Peters 1925: 323). The flight song sounds like "*pssip*" from a distance (like the calls of *Motacilla flava*) ["*pe-chee*" in Peters 1923: 323], but closer by, the vocalization is more complex in structure: "*tsit-tsit-tsit-tsitsitsipirisih.*" I found *M. maculirostris* in several habitats, including low open shrubsteppe on flat stony ground, shrubsteppe of the high basaltic plateaus (Fig. 31, bottom), in rocky screes at the edge of escarpments, in arid plains with very sparse vegetation, and in low scrub near the coast. Wetmore (1926b: 306) stated that *M. maculirostris* "seen on their breeding grounds were found among low bushes on sandy or gravelly hillsides." Fjeldså & Krabbe (1990: 508) wrote that *M. maculirostris* "has a broad habitat preference, but is always close to vertical rocks, banks or walls." However, in several areas along the transect, I found *M. maculirostris* to be abundant in flat, uniform shrubsteppe with no rocks, banks or walls (e.g., between Telsen and Gan-Gan, see Fig. 32). After *Zonotrichia capensis* and *Lessonia rufa*, *M. maculirostris* was probably the third most common and widespread passerine species along the transect. Interestingly, Durnford (1878: 395) found *M. maculirostris* to be uncommon, but Peters (1923: 323) qualified it as "a fairly common resident in western Río Negro" (Huanuluan area).

FIG. 30. Distribution of *Muscisaxicola maculirostris* (black dots) and *M. capistrata* (black triangles) along the transect route; additional localities in Río Negro from the literature (see text).

FIG. 31. Left: habitat of *Muscisaxicola capistrata* a few km west of Gastre at about 1300 m, Chubut; the birds foraged in the open steppe area on sandy soil of the foreground. Right: dense shrubsteppe habitat of *M. maculirostris* a few km west of Telsen, Chubut. Photos F. Vuilleumier, November 1991.

FIG. 32. Two views of flat shrubsteppe where *Muscisaxicola maculirostris* occurred at high densities, between Telsen and Gan-Gan, Chubut. Photos F. Vuilleumier, November 1991.

In the Meseta de Somuncurá, Bettinelli & Chebez (1986) reported *M. capistrata* at Laguna Blanca and *M. maculirostris* at Cerro Corona Chico. Because their observations are from the second half of February, it is possible that these birds were already migrants, rather than breeding.

Mimus (Mimidae)

Two species of mockingbirds occur in the transect area, *Mimus patagonicus* and *M. triurus*. *M. patagonicus* is closely related to *M. saturninus* (map in Short 1975: 290), and *M. triurus* to *M. dorsalis* (Short 1975: 290—291). *Mimus triurus* was observed at only two localities, one or two birds about 15 km west of Puerto Madryn along route 4 on 5 and 10 November, and one individual about 65 km west of Puerto Madryn along route 4 on 10 November (Fig. 33). Both observations were made in shrubsteppe growing on rather flat ground. By contrast, *Mimus patagonicus* was observed at many localities along the transect, from coastal areas in the Península Valdés region (including: family with one fledgling on 7 November at Riacho San José; family with one adult and two fledglings on 9 November) to the Telsen area, but not between Telsen and Gan-Gan. It was seen again W of Gan-Gan to the Esquel region, and in coastal areas near Camarones. Habitats where I found *M. patagonicus* varied from arid steppe with sparse and low thorny shrubs growing on bare soil to moist, man-made oases with fairly dense groves of willows growing along arroyos and the Río Chubut.

At the two localities where both *M. triurus* and *M. patagonicus* were observed together (Fig. 34), individuals of the two species were seen a few meters from each other, singing from the top of adjacent shrubs. In one case, I even saw one bird of each species singing from the top of the same shrub. I never saw individuals of *M. triurus* pay any attention to individuals of *M. patagonicus*, no matter how close they were to each other.

Seen next to each other, the two species of *Mimus* look different. *M. patagonicus* appears somewhat larger and coarser-plumaged, with a longer bill, whereas *M. triurus* appears more slender, with a smaller and thinner bill and a longer tail. Furthermore, the large areas of white in the wings and tail of *M. triurus* are quite conspicuous, especially in flight, and also when the bird

FIG. 33. Distribution of *Mimus patagonicus* (black dots) and two localities of overlap between *M. patagonicus* and *M. triurus* (stars) along the transect route (see text).

is perched. The songs of these two species are quite similar, but that of *M. triurus* may be more melodious and more varied, with rich liquid trills and gurgling sounds. At times, the song of *M. triurus* reminded me of phrases of *Alauda arvensis* or of *Acrocephalus schoenobaenus*; at other times, it seemed that the bird imitated some of the trills emitted by *Geositta cunicularia* (interestingly, since there were none nearby). Wetmore (1926b: 351) indicated that *M. triurus* frequently mimicked the Vermilion Flycatcher (*Pyrocephalus rubinus*).

Durnford (1877: 31) wrote that *Mimus patagonicus* was "not uncommon," but did not mention *M. triurus*. Peters (1923: 328) did not mention *M. triurus* from Río Negro. He found *M. patagonicus* "abundant" along the coast but "rather uncommon" in the Huanuluan-Maquinchao area. Wetmore (1926a: 455) reported two specimens of *M. patagonicus* from eastern Río Negro, but did not list *M. triurus*. Wetmore (1926b: 350—353) cited *M. triurus* "in fair numbers" from General Roca (Río Negro) and *M. patagonicus* from General Roca (Río Negro), Challaco (Neuquén), but not Zapala (Neuquén) (Fig. 33). According to Wetmore (1926b: 351), *M. triurus*'s song "strongly resembles that of *Mimus polyglottos*, and is accompanied frequently by aerial gyrations, in which the birds spring into the air and support themselves with slow beats of the widely open wings, that, with the spread tail, display their contrasted markings to the utmost." Wetmore (1926b: 353) found *M. patagonicus* "common in growths of atriplex (*Atriplex lampa* and *A. crenatifolia*), creosote bush, and greasewoods on the flood plain of the Rio Negro, near General Roca, and proved to be a true desert form since it spread out through the arid, gravel hills north of the railroad, where water was wholly lacking." He described the song as "similar to that of *M. triurus*, though the performers were less flamboyant in actions during delivery." Boswall and Prytherch (1972) mention only *M. patagonicus* from Punta Tombo, coastal Chubut.

Gochfeld (1978) described the sympatry between *M. triurus* and *M. patagonicus*, which he studied in northeastern Chubut, eastern Río Negro, and southern Buenos Aires Provinces. Gochfeld (1978: 64—65) concluded as follows: "At the Bahia Blanca study area there was no evidence that the territories of the two species overlapped, but there was also no evidence of interspecific aggression." And further: "The present study has shown that where they are sympatric the Patagonian and White-banded Mockingbirds have different habitat preferences or tolerances. The former was found in both desert scrub and monte, while the latter was essentially absent from desert scrub areas."

FIG. 34. Habitat where *Mimus patagonicus* and *M. triurus* were found sympatricly west of Sierra Chata, Chubut; the other locality where these two species were found together, near Puerto Madryn has very similar vegetation. Photo F. Vuilleumier, November 1991.

It thus appears that the two species of *Mimus* coexist with overlapping territories in a rather narrow zone of geographical overlap in north-central and northern Patagonia. Gochfeld's (1978) pioneering work deserves to be pursued further.

Anthus (Motacillidae)

Three species of pipits (*Anthus furcatus*, *A. hellmayri*, and *A. correndera*) occur in the transect area. Durnford (1877: 32) mentioned only *A. correndera*, stating that it was "common throughout the valley [of the Río Chubut] and on the hills where there was any grass." Wetmore (1926a: 456) only reported *A. correndera*, from eastern Río Negro, but Bettinelli & Chebez (1986) cited *A. hellmayri* (but no other species) from the Meseta de Somuncurá. Wetmore (1926b: 360—361) did not cite *A. furcatus* from Río Negro, but found *A. correndera* at Zapala (Neuquén). He did not cite *A. hellmayri*. Peters (1923: 329) stated: "Two species of pipits very closely resembling each other in the field, occur in Argentina;

nearly all field-observers confuse the two and I must plead guilty to the same error." He collected only 2 *Anthus furcatus* but "over twenty" *A. correndera* at Huanuluan. Peters (1923: 330) also stated that "the possibility of the occurrence of *Anthus hellmayri dabbenei* Hellmayr (Hornero, 1921, 2, p. 191. Río Traful, Gob. de Neuquén) in extreme western Río Negro should also be considered."

I saw pipits at only two localities along the transect (Fig. 35) at Punta Delgada near sea level on Península Valdés on 8 and 9 November, and near Las Salinas, about 90 km east of Esquel along route 25, at 650 m on 15 November. No other suitable-looking habitats yielded pipits, very surprisingly.

At Punta Delgada, pipits were found in grassy steppes (Fig. 36) and were abundant in flat areas with a very sparse growth of short grass (Fig. 36, bottom). All the birds that I saw well were *A. furcatus*. Many birds emitted flight songs that can be transcribed by "*tzi-ti-tititiriri*" and sharp calls by "*whitt*" or "*pitt*," or else "*dzipp*" or "*dzitt*" (somewhat reminiscent of calls of *Motacilla flava*). Wetmore (1926b: 361) found that in Buenos Aires Province, *A. furcatus* was "common over rolling, open country covered with low tufts of grass."

Near Las Salinas, several pairs of pipits were seen in grassy meadows and very low scrub. All of them were *Anthus correndera*. I heard no flight songs; calls I heard can be transcribed as "*tziht*," "*twit*," or "*tziht*."

My observations thus add little information about the distribution and relationships of pipits in north-central Patagonia, other than to suggest that these birds may be patchily distributed and localized, and that they may overlap only little. Wetmore (1926b: 361), however, stated that *Anthus furcatus* "was locally common in some of the areas visited, and though closely similar to *A. c. correndera*, with which it was often associated, was readily told by its grayer, less distinctly streaked dorsal surface, and by the fact that in walking it did not tilt the tail." In Uruguay, Wetmore (1926b: 361) found *A. furcatus* and *A. correndera* breeding side by side (specimens collected). The latest published color plates of pipits (by Fjeldså *in* Fjeldså & Krabbe 1990; and by Tudor *in* Ridgely & Tudor 1989) are unfortu-

FIG. 35. Distribution of *Anthus furcatus* (black dot) and *A. correndera* (black triangle) along the transect route; additional localities in Río Negro from the literature (see text).

nately not sufficient for accurate field identification of these very difficult birds that look and sound very similar. Furthermore, the texts in these two books are not very informative either, insofar as field identification goes. Extreme caution is therefore advised for observers who want to identify pipits in the field in Patagonia. What is needed to clarify problems of identification and hence distribution and speciation is a research program including the collection of adequate series of specimens, tape recordings of vocalizations and playback experiments.

Sicalis (Emberizidae)

In an earlier paper (Vuilleumier 1991b: 329), I suggested that the allopatric distribution of *S. lebruni* (Patagonia) and *S. olivascens* (high Andes further north) could be due to competition with *S. auriventris*, which occurs in the intervening area. I was not able to verify this statement during the transect in Chubut because I did not see *auriventris*. However, I observed *S. lebruni* and *S. luteola* and found them to occupy very different habitats.

Sicalis lebruni was seen in the Punta Delgada-Caleta Valdés area of Península Valdés, where it is abundant and breeds in holes along road cuts (Fig. 37). *S. luteola* was observed in man-made oases (Telsen, along Arroyo Telsen; and various localities in the Chubut Valley, especially near Los Altares), where it is abundant and occurs in tall grass and dense riverine vegetation of weedy plants (Fig. 37). Fig. 38 illustrates the habitats of *S. lebruni* and *S. luteola* along the transect. Wetmore (1926b: 403) described the habitat and behavior of *S. luteola*, but not those of *S. lebruni*.

Peters (1923: 331—332) found 3 species of *Sicalis* in the Huanuluan-Maquinchao area: *S. luteola*, *S. auriventris*, and *S. lebruni*, although only the last one was "fairly common". Wetmore (1926a: 458) cited specimens of *S. luteola* from Bariloche and of *S. lebruni* from near Lake Nahuel Huapí (western Río Negro), records which suggest some geographic, if not ecological overlap, between these two species (Fig. 38).

The distribution of *Sicalis lebruni* and *S. luteola* in northern Patagonia appears to be patchy, each species preferring a different habitat. In places where these habitats occur side by side, one should expect parapatry. It would be worthwhile investigating such parapatric contacts in the future.

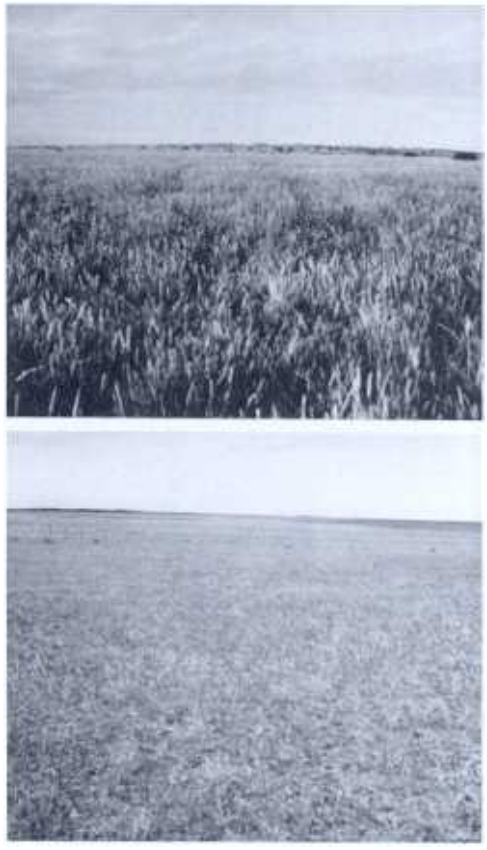

FIG. 36. Two views of habitat of *Anthus furcatus* near Punta Delgada, Chubut. Top: dense grassland. Bottom: very open steppe with low and sparse grass cover. Note that habitat of *A. correndera* near Las Salinas (not illustrated) was very similar to the bottom photograph. Photos F. Vuilleumier, November 1991.

Phrygilus (Emberizidae)

Wetmore (1926b: 405) has discussed the affinities within *Phrygilus*. *Phrygilus fruticeti* and *P. carbonarius* are probably closely related to each other. Both were seen along the transect (Fig. 39). Of the two, *P. fruticeti* was the more common and the more widespread. In some areas it was abundant (between Puerto Madryn and Telsen along route 4, for instance). I did not find it in Península Valdés. *P. fruticeti* was found in open steppes on pebbly or rocky ground, with sparse to relatively dense thorny shrubs. More densely vegetated areas had more birds, reaching a density of about one singer per hectare. *Phrygilus carbonari-*

FIG. 37. Distribution of *Sicalis lebruni* (black dots) and *S. luteola* (black triangles) along the transect route; additional localities in Río Negro from the literature (see text).

FIG. 38. Top: shrubsteppe on dunes, habitat of *Sicalis lebruni* at Punta Delgada, Chubut. Bottom: dense riverine weedy vegetation, habitat of *S. luteola* at Arroyo Telsen, a few km west of Telsen, Chubut. Photos F. Vuilleumier, November 1991.

us was seen at only five localities: near Puerto Madryn, near Sierra Chata, near Telsen, near Las Chapas, and near Uzcudún, always in habitat cooccupancy with *P. fruticeti*.

At two of these five localities I was able to observe the interactions between *P. fruticeti* and *P. carbonarius*. At the first locality (near Sierra Chata, Fig. 40, top) I thought that they had interspecific territoriality, but at the second (near Telsen, Fig. 40, bottom), I noted that these two species had overlapping territories, and that displaying males did not pay any attention to each other. At these two localities, where shrubs were relatively high and abundant, *P. fruticeti* outnumbered *P. carbonarius* about 75 to 1.

Although both *P. fruticeti* and *P. carbonarius* have similar display flights, they differ in some respects. First, their vocalizations are distinct. The song of *P. carbonarius* is pipit-like, a buzzy series of notes that can be transcribed as "*wheezy-wheezy-wheezy-wheezy-wheezy*," each sound a clearly demarcated two-syllable "*whee-zee*," repeated quickly about 5—9 times during the parachuting sequence, which lasts no more than 2—3 seconds. There is much individual variation, however, and some birds have a more trill-like

FIG. 39. Distribution of *Phrygilus fruticeti* (black dots) and five localities of overlap between *P. fruticeti* and *P. carbonarius* (stars) along the transect route (see text).

song, "*pzii-pzee-pzee-pzee-pzee.*" By contrast, *P. fruticeti* has a shorter, more nasal song, with a blackbird-quality to it. Wetmore (1926b: 406) wrote very aptly that "males were singing a song that sounded like the effort of some icterid." The singer of *P. carbonarius* can fly up from a perch right within the vegetation, and return to a perch out of sight of the observer, whereas many *P. fruticeti* remain well in sight. The down flight in *P. carbonarius* is parachute-like, tail spread out, banking from side to side. *P. fruticeti*'s down-flight is more butterfly-like and less a simple parachuting descent, as in *P. carbonarius*.

Phrygilus carbonarius was not mentioned by Durnford (1877, 1878), Peters (1923), or Bettinelli & Chebez (1986). Wetmore (1926a: 460) cited only an immature specimen from Nahuel Niyeu, eastern Río Negro (5 July 1911, a winter date). Wetmore (1926b: 406—407) recorded *P. fruticeti* at Zapala (Neuquén) and General Roca (Río Negro), and *P. carbonarius* near Bahía Blanca (Buenos Aires) and Victorica (La Pampa). Hence the literature is of no help in providing data on the details of the overlap between these two species in Patagonia. Because these two species are easy to observe at the localities where I

FIG. 40. Two views of shrubsteppes where *Phrygilus fruticeti* and *P. carbonarius* were sympatric. Top: near Sierra Chata, Chubut. Bottom: west of Telsen, Chubut. Photos F. Vuilleumier, November 1991.

saw them, it should be possible to quantify their habitat preferences, feeding habits, breeding behavior, and interspecific interactions. The visibility of males during their display flights should enable one to map their territories precisely and hence to ascertain whether their territories do indeed overlap, as my observations near Telsen seem to suggest.

DISCUSSION

The data presented in this paper are preliminary in nature, since they are based on a survey of a large area of north-central Patagonia. Nevertheless, these observations allow me to make several comments about patterns of habitat overlap or non-overlap in situations of allopatry, sympatry, and parapatry, and make some speculations about factors of reproductive isolation in about 30% of the breeding landbird fauna of Patagonia.

Before discussing these patterns, however, I wish to point out that several other groups of congeners that I expected to study in the field were not encountered, thus suggesting the possibility of either changes in distribution patterns since visits by earlier observers, or man-induced modifications of the habitats in the last 50—100 years. I discuss these (apparent) absences in Appendix 1.

Interactions of various sympatric congeners have been discussed for the Chilean avifauna by Cody (1970), who analyzed some of the groups of ground or bush inhabiting birds reported upon in this paper, including *Geositta*, *Muscisaxicola*, *Sicalis*, and *Phrygilus*. Cody (1970) studied especially altitudinal replacements in the Andes. In Patagonian steppes, however, which lack the altitudinal dimension present in the Andes farther west, species replacements and/or overlaps take place largely latitudinally, rather than altitudinally. Hence Cody's (1970) conclusions may not apply to the area I visited.

The data presented in this report show two classes of distribution patterns. In some cases the species pairs or triplets studied were largely allopatric, whereas in other cases I found evidence of sympatry or parapatry. Superimposed on this pattern of geographic distribution of non-overlap versus overlap are patterns of similarities or differences of habitat preferences.

Allopatric situations. Allopatric is used here as defined by Futuyma (1986: 550): "Of a population or species, occupying a geographic region different from that of another population or species." Well marked differences in habitat preferences between pairs of allopatric congeners were noted in *Sicalis*. *S. lebruni* was found in open grassy or scrubby coastal steppes on sandy soil. *S. luteola* occurred inland in dense, varied vegetation of grasses and weeds along riverbanks. The two habitats are geographically separated, hence it is not surprising that these two species would be disjunct (see Figs. 37 and 38). However, Peters' (1923) collection of one *S. luteola* and of several *S. lebruni* at Huanuluan (see Fig. 37) suggests sympatry. It would be interesting to know in what habitats Peters (1923) found these birds. In situations where these two species occur relatively near each other, then the habitat differences they show should minimize interactions between them. Furthermore reproductive isolation could be achieved through a combination of other factors including size, color, nest location and vocalizations (see Table 1).

TABLE 1. Differences and similarities between allopatric and sympatric species pairs or triplets in Chubut.

Genus	Species	Size	Color	Nest	Vocalizations	Habitat
Eudromia	*elegans*	similar to *Tinamotis*	no rufous on wings	scrape in ground		
Tinamotis	*ingoufi*	similar to *Eudromia*	rufous on wings	scrape in ground		
Thinocorus	*rumicivorus*	smaller than *orbignyianus*	black line on breast	scrape in ground		open steppe, often sandy plains
Thinocorus	*orbignyianus*	larger than *rumicivorus*	no line on breast	scrape in ground		open steppe, often valley slopes

Genus	Species	Size	Color	Nest	Vocalizations	Habitat
		larger than *cunicularia*		in hole or crevice in rocks		
Geositta		smaller than *rufipennis*		in hole in banks		grassy steppe
Upucerthia	*dumetaria*	larger than *ruficauda* & *Eremobius*	scalloped breast	in hole in banks	trills	shrubsteppes
Upucerthia	*ruficauda*	smaller than *dumetaria*, same as *Eremobius*	streaked breast	in hole or crevice in rocks	trills	shrubsteppes
Eremobius	*phoenicurus*	smaller than *dumetaria*, same as *ruficauda*	streaked breast	stick nest in shrubs	trills	shrubsteppes
Leptasthenura	*platensis*	similar to *aegithaloides*	slightly paler than *aegithaloides*	in tree holes or abandoned nests of other furnariids	trills	monte and shrubsteppes
Leptasthenura	*aegithaloides*	similar to *platensis*	slightly more streaked than *platensis*	often in hole in cliff or road cut	trills	shrubsteppes and semideserts
Asthenes	*patagonica*	similar to *pyrrholeuca*	paler than *pyrrholeuca*	basket with tubular side entrance	trills	slightly more open than *pyrrholeuca*
Asthenes	*pyrrholeuca*	similar to *patagonica*	browner than *patagonica*	basket, more open entrance	trills	slightly denser than *patagonica*
Agriornis	*microptera*	similar to *montana*	very little white on outer tail feathers	often in shrubs		
Agriornis	*montana*	similar to *microptera*	much white in tail	often in holes	whistles	rocks, shrubs, valley slopes
Agriornis	*microptera*		very similar to *murina*	often in shrubs		
Agriornis	*murina*		very similar to *microptera*	in shrubs		
Muscisaxicola	*capistrata*	larger than *maculirostris*	dark facial pattern	often in rodent burrows		
Muscisaxicola	*maculirostris*	smaller than *capistrata*	very plain	under rocks, in crevices		
Mimus	*patagonicus*	larger than *triurus*	less white in tail and wing	in shrubs	less varied than *triurus*	
Mimus	*triurus*	smaller than *patagonicus*	more white in tail and wing	in shrubs	richer than *patagonicus*	
Anthus	*furcatus*	similar to *correndera*	similar to *correndera*	on ground	flight song high pitched	grassy steppe
Anthus	*correndera*	similar to *furcatus*	similar to *furcatus*	on ground	flight song high pitched	grassy steppe
Sicalis	*lebruni*	larger than *luteola*	unstreaked back	in hole in banks	flight song less complex than *luteola*	dry grass or shrubsteppe
Sicalis	*luteola*	smaller than *lebruni*	streaked back	in grass or weeds	trill-like flight song	moister, denser grassy habitats
Phrygilus	*fruticeti*		very similar to *carbonarius*, wing bars well marked	in shrubs		
Phrygilus	*carbonarius*	smaller than *fruticeti*	very similar to *fruticeti*, wing bars less marked	in shrubs	wheezy trill	shrubsteppe

More subtle differences in habitat preferences were noted in four other allopatric species pairs. In the tinamous *Eudromia* and *Tinamotis*, no overlap was detected. *Eudromia* seemed to prefer denser shrubsteppes at lower elevations than *Tinamotis*. Table 1 lists other differences between these two species which could reduce reproductive interactions, should these birds occur in contact elsewhere. In *Thinocorus* and *Muscisaxicola* one species (*T. orbignyianus* and *M. capistrata*, respectively) was found in higher elevation steppes of valley slopes. The other member of the species pair (*T. rumicivorus* and *M. maculirostris*, respectively) occurred in flat, lower elevation steppes. In *Anthus* both species were observed in grassy and scrubby steppes. One of them, *A. furcatus*, was found in coastal areas, whereas *A. correndera* was found in the interior. Although coastal and interior grassy steppes looked very similar to me, further study of these habitats is likely to reveal differences that might help explain better the distribution of these pipits.

Note that, even though I did not observe parapatry or sympatry between species of tinamous, *Thinocorus*, *Muscisaxicola*, and *Anthus*, such contacts can be expected, especially perhaps in areas other than the transect in Chubut. The interspecific interactions that might occur in such cases of contact are unknown. One might speculate that differences in color and crest in tinamous, and in size and male breast pattern (Table 1) between *Thinocorus orbignyianus* and *T. rumicivorus*, could serve as isolating mechanisms. Size and color pattern differences and slight differences in display flights (Table 1) could isolate *Muscisaxicola capistrata* and *M. maculirostris*. Differences in morphology and behavior between *Anthus furcatus* and *A. correndera* seem poorly marked (Table 1), and it would be of great interest to study an area of actual contact between them.

Sympatric or parapatric situations. Sympatric or parapatric situations were observed in several genera. Sympatric is used here as defined by Futuyma (1986: 556): "Of two species or populations, occupying the same geographic locality so that the opportunity to interbreed is presented." Futuyma (1986: 554) defines parapatric as "Populations that have contiguous but non-overlap-ping geographic distributions."

Three kinds of situations were detected along the transect in Chubut: (1) sympatry and habitat overlap, (2) sympatry with little or non-overlap of habitats, and (3) parapatry with similar habitat preferences for the two species in the pair.

(1) Truly sympatric species pairs, where individuals of each species were observed in close proximity of each other in the same habitat, were found in *Upucerthia-Eremobius*, *Asthenes*, *Mimus*, and *Phrygilus*. In these five genera I was able to study instances of habitat overlap, with singing or displaying birds of each species only a few meters from each other.

Upucerthia dumetaria and *Eremobius phoenicurus* were observed side by side in three areas along the transect (Fig. 18). In each they occurred in similar kind of shrubsteppes (Fig. 19, top; Fig. 21, top). Differences between these two species that could minimize their reproductive interactions are given in Table 1.

Sympatry or near sympatry was observed in *Asthenes* in three regions along the transect (Fig. 25). *A. patagonica* and *A. pyrrholeuca* differ in several characters including morphology and nest structure (Table 1). Only in the Paso del Sapo area, however, were the two species seen side by side. They were found in dry thorny shrubs on the floor of the Chubut river valley. In *Asthenes*, color and nest structure (Table 1) may be factors of reproductive isolation. In *Mimus* and *Phrygilus* singing and displaying individuals of each species in the pair were observed at localities with open shrubsteppe (Figs. 34 and 40). Differences in color, size, and vocalizations presumably keep the two species of each pair separate (Table 1).

(2) Sympatry with little or non-overlap of habitat was observed in *Geositta* and *Agriornis*. In *Geositta* the two species differ in size and color (Table 1). Although the vocalizations of both species include trills (Table 1), the sounds emitted are quite different. I found an area near Piedra Parada (see Fig. 16) where both species were neighbors and lived within about 500 m of each other but in very different habitats. *G. cunicularia* occurred in open, flat, grassy steppes with or without shrub cover along the bank of the Río Chubut. *G. rufipennis* foraged in rocky screes with sparse shrubs above the valley floor.

In *Agriornis* I observed *A. microptera* and *A. montana* at the same site near Gastre (Figs. 28

and 29). *A. microptera* foraged by running on the ground in grassy steppe, whereas *A. montana* foraged by flying down from perches on thorny shrubs and basaltic rocks to catch invertebrate prey on the ground. Further differences between these two species include tail pattern and nest location (Table 1).

In both *Geositta* and *Agriornis* a combination of habitat and other characters (listed in Table 1) presumably prevent reproductive interactions between the two species in each pair.

(3) Parapatry with little habitat differentiation was found in *Leptasthenura* and *Agriornis*. *Leptasthenura platensis* and *L. aegithaloides* were observed at sites only a few km from each other in the Península Valdés area and near Paso del Sapo (Figs. 23 and 24). Both species were seen in similarly structured shrubsteppe so that contact between them could be expected. Similarities and differences that could minimize reproductive interactions are listed in Table 1.

In *Agriornis*, parapatry with little habitat differentiation between *A. microptera* and *A. murina* was noted in two coastal areas (Figs. 27 and 29). The main difference that probably minimizes reproductive interactions between these two species is size (Table 1). I observed display flights of only *A. microptera* and hence do not know what behavioral difference, if any, could keep these two species apart.

Prospects for further work

Clearly the ecological and evolutionary study of Patagonian birds in allopatric, sympatric and parapatric situations is a field that is wide open for further exploration. Two major questions are: (1) How can so many similar-looking congeners or closely related species of birds coexist in such a structurally simple and uniformly distributed landscape type as the shrubsteppes of Patagonia? and (2) How did these distribution patterns originate? In order to approach these general problems, answers to more specific questions are needed. A sample of such questions includes:

(1) Is there spatial segregation and exclusion between Patagonian *Eudromia elegans* and *Tinamotis ingoufi*, or between *Thinocorus rumicivorus* and *T. orbignyianus*? To what extent are these two species pairs mutually exclusive in their distribution?

(2) Is there spatial segregation and exclusion, or is there habitat overlap, between Patagonian species of *Anthus*? How different are flight songs and vocalizations among species of *Anthus*? What are their exact breeding habitat requirements? Do they have overlapping territories?

(3) Is there habitat overlap between *Leptasthenura aegithaloides* and *L. platensis*, or is there spatial exclusion? What specific habitat preferences do these two very similar sister species have? Do they have any interspecific interactions? Are there differences in vocalizations?

(4) What behavioral or other mechanisms keep *Mimus triurus* and *M. patagonicus*, and *Phrygilus fruticeti* and *P. carbonarius* apart in their areas of habitat overlap? Do they always have overlapping territories or do they show occasional interspecific territoriality?

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REFERENCES

Bettinelli, M.D., & J.C. Chebez. 1986. Notas sobre aves de la Meseta de Somuncurá, Río Negro, Argentina. Hornero 12: 230—234.

Blondel, J., & J.-P. Choisy. 1983. Biogéographie des peuplements d'oiseaux à différentes échelles de perception: de la théorie à la pratique. Acta Oecologica, Oecol. Gener. 4: 89—110.

Boswall, J., & R.J. Prytherch. 1972. Some notes on the birds of Point Tombo, Argentina. Bull. British Ornith. Club 92: 118—129.

Cody, M.L. 1970. Chilean bird distribution. Ecology 51: 455—464.

Durnford, H. 1877. Notes on some birds observed in the Chuput Valley, Patagonia, and in the neighboring district. Ibis, fourth series, vol. I: 27—46.

Durnford, H. 1878. Notes on the birds of central Patagonia. Ibis, fourth series, vol. II: 389—406.

Fjeldså, J. 1988. Status of birds of steppe habitats of the Andean zone and Patagonia. ICBP Techn. Publ. No. 7: 81—95.

Fjeldså, J. 1991. Biogeographic patterns in birds of high Andean relict woodlands. Acta XX Congr. Internat. Ornithol., pp. 342—353.

Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes. A manual to the birds of the temperate zone of the Andes and Patagonia, South America. Zool. Mus, Univ. Copenhagen, and Apollo Books, Svendburg, Denmark.

Futuyma, D.J. 1986. Evolutionary Biology. Second Edition. Sunderland, Massachusetts.

Gochfeld, M. 1978. Ecological aspects of habitat selection by two sympatric mockingbirds, *Mimus* spp., in Patagonia. Ibis 120: 61—65.

Gochfeld, M. 1979. Interspecific territoriality in Red-breasted Meadowlarks and a method for estimating the mutuality of their participation. Behav. Ecol. Sociobiol. 5: 159—170.

Hueck, K., & P. Seibert. 1972. Vegetationskarte von Südamerika. Gustav Fischer Verlag, Stuttgart.

Maclean, G.L. 1969. A study of seedsnipe in southern South America. Living Bird 8: 33—80.

Meyer de Schauensee, R. 1982. A guide to the birds of South America. 2nd rev. ed. Intercollegiate Press, (no city given).

Nores, M., & S.A. Salvador. 1990. Descripción del nido y huevos del Gaucho chicho (*Agriornis murina*). Hornero 13: 161—162.

Olrog, C.C. 1963. Lista y distribución de las aves Argentinas. Opera Lilloana 9: 1—377.

Olrog, C.C. 1979. Nueva lista de la avifauna Argentina. Opera Lilloana 27: 1—324.

Paynter, R.A., Jr. 1985. Ornithological gazetteer of Argentina. Museum of Comparative Zoology, Harvard University, Cambridge.

Peters, J.L. 1923. Notes on some summer birds of northern Patagonia. Bull. Mus. Comp. Zool. 65: 277—337.

Ridgely, R.S., & G. Tudor. 1989. The birds of South America. Vol. I, The Oscine Passerines. Univ. of Texas Press, Austin.

Root, R.B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317—350.

Rotenberry, J.T., & J.A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228—1250.

Short, L.L. 1968. Sympatry of Red-breasted Meadowlarks in Argentina, and the taxonomy of meadowlarks (Aves: *Leistes*, *Pezites*, and *Sturnella*). Amer. Mus. Novit. No. 2349: 1—30.

Short, L.L. 1975. A zoogeographic analysis of the South American chaco avifauna. Bull. Amer. Mus. Nat. Hist. 154: 163—352.

Vaurie, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). Bull. Amer. Mus. Nat. Hist. 166: 1—357.

Vuilleumier, F. 1967a. Phyletic evolution in modern birds of the Patagonian forests. Nature 215: 247—248.

Vuilleumier, F. 1967b. Mixed species flocks in Patagonian forests, with remarks on interspecies flock formation. Condor 69: 400—404.

Vuilleumier, F. 1971. Generic relationships and speciation patterns in *Ochthoeca*, *Myiotheretes*, *Xolmis*, *Neoxolmis*, *Agriornis*, and *Muscisaxicola*. Bull. Mus. Comp. Zool. 141: 181—232.

Vuilleumier, F. 1972. Bird species diversity in Patagonia (temperate South America). Amer. Nat. 106: 266—271.

Vuilleumier, F. 1985. Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. Pp. 255—304 *in* Buckley, P.A., M.S. Foster, E.S. Morton, R.S. Ridgely & F.G. Buckley (eds.). Neotropical Ornithology. Orn. Monogr. 36. Washington D.C.

Vuilleumier, F. 1991a. A quantitative survey of speciation phenomena in Patagonian birds. Ornit. Neotrop. 2: 5—28.

Vuilleumier, F. 1991b. Speciation in Patagonian birds. Acta XX Congr. Internat. Ornithol., pp. 327—332.

Vuilleumier, F., & J. Kikkawa. 1991. Reconstructing the history of *Nothofagus* forest avifaunas. Acta XX Congr. Internat. Ornithol., pp. 578—586.

Wetmore, A. 1926a. Report on a collection of birds made by J.R. Pemberton in Patagonia. Univ. California Publ. Zool. 24: 395—474.

Wetmore, A. 1926b. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. United States Nat. Mus. Bull. 133: 1—448.

Wiens, J.A., & J.T. Rotenberry. 1980. Bird community structure in cold shrub deserts: competition or chaos? Acta XVII Congr. Internat. Ornithol., pp. 1063—1070.

APPENDIX 1. Discussion of several genera expected along the transect (see Fig. 4) but not encountered.

Tinamous

Besides *Eudromia elegans* and *Tinamotis ingoufi*, two other species of tinamou (*Nothura darwinii* and *N. maculosa*), occur in the transect area but were not encountered, in spite of diligent search. I mention them here because of the possibility that they are much less common today than they were over a hundred years ago (unless I missed them because I looked for them in the wrong habitat). Durnford (1878: 405—406) wrote of *Nothura*: "I obtained specimens in the Chupat [= Chubut] valley, and saw it occasionally in the valleys of the Sengel [= Río Senguerr] and Sengelen [= Río

Chico]." [For nomenclature of place names, see Paynter 1985]. In his 1877 paper, Durnford had written about *Nothura* (pp. 45—46): "Not so common as *Calodromas* [= *Eudromia*] *elegans* but occasionally seen amongst the thick grass and rushes bordering the river. Not seen on the hills." The species mentioned by Durnford in his 1877 paper was *Nothura maculosa*; in his 1878 paper *Nothura perdicaria*. But in a footnote to the 1878 paper, the editors of Ibis stated that the birds collected by Durnford, which they had not seen, were *N. darwinii*. Wetmore (1926b: 33—39) reported only *N. darwinii* from Río Negro (in "alfalfa fields and other green growth near the river"). The habitat given by Olrog (1979: 18) for *N. maculosa* is "estepas húmedas," but that for *N. darwinii* is "estepas áridas."

Cinclodes (Furnariidae)

Not a single *Cinclodes* was seen during the transect. To an ornithologist used to working in other parts of Patagonia, this is surprising. At Huanuluan, Río Negro, Peters (1923: 313—314) found *Cinclodes fuscus* between 6 September and early November. All birds were probably migrants. He collected or saw *C. patagonicus* on 27 November and 2 December. All birds he collected were immature (non-breeders?). Wetmore (1926a: 439) reported *C. fuscus* only from Lago Futalaufquen (Andean zone west of Esquel; winter migrants) and *C. patagonicus* from Lago Futalaufquen (winter birds) and from Huanuluan (male and female, 7 December, i.e., in late spring-early summer). Wetmore (1926a: 439) stated that "the two [*C. patagonicus*] taken at Huanuluan are marked as accompanied with a set of eggs." Bettinelli & Chebez (1986) did not list *Cinclodes* spp. from the Meseta de Somuncurá. Wetmore (1926b) did not mention *Cinclodes* spp. from Patagonia, but *C. fuscus* and *C. oustaleti* from Mendoza. In 1965 I observed *C. fuscus* and *C. patagonicus* in the Bariloche-Lake Nahuel Huapí area. The total absence of *Cinclodes* spp. along the transect is puzzling. Either these birds do not occur in the area I visited or, if they do, in such small numbers as to have remained undetected. I suspect that *Cinclodes* spp. might be only migrants in the transect area, and breed in the Andean region further west (see Peters 1923: 313—314, about *C. fuscus* and *C. patagonicus*), although since Wetmore (1926a: 439) reported two individuals of *C. patagonicus* from Huanuluan (Río Negro) with eggs, breeding of some *Cinclodes* may be expected locally. Further field work in the central-western part of the transect area is necessary, especially at high elevations, to determine the occurence and status of *Cinclodes* spp.

Asthenes (Furnariidae)

Neither *Asthenes modesta*, *A. hudsoni*, nor *A. anthoides* were noted along the transect. Peters (1923) only collected five *A. modesta* and one *A. hudsoni* in several months spent in the Maquinchao-Huanuluan region of Río Negro, to the north of the central part of my transect area in Chubut. Wetmore (1926a: 442) reported one specimen of *A. modesta* collected near Valcheta (eastern Río Negro) and two near Huanuluan, and wrote that *Asthenes* "*modesta* is stated to be of widespread range in Argentina, but must be rarer than one would suppose from published statements, since I failed to secure it there during extended field work in 1920 and 1921." On 13 November 1991 I searched an area of softly rounded hills at about 1350 m near Gastre, with a very sparse cover of low shrubs, that looked suitable for *A. modesta*, but failed to find it. Durnford (1877, 1878) did not mention *Asthenes modesta* at all. Bettinelli & Chebez (1986) reported *A. modesta* from the Somuncurá Plateau in Río Negro. Durnford (1877, 1878) stated that he saw *Asthenes hudsoni* only twice (1878), but in his earlier paper (1877) found it "not uncommon . . . in dry places in the valley." Wetmore (1926b: 273—274) encountered *A. hudsoni* in Buenos Aires Province but did not cite it from either Río Negro or Neuquén. The birds he saw were in "a dense patch of thistles and other weeds on the shore of the Laguna del Monte" and in "marshes grown heavily with *Juncus acutus*, a sharply pointed rush that grew in clumps with little runways between."

Asthenes anthoides was not recorded by Peters (1923) from the central part of a similar transect in Río Negro, but "only encountered near Lake Nahuel Huapí," where I saw it at several localities in 1965 (see also Wetmore 1926a). Durnford (1877, 1878) did not mention *A. anthoides*. I was on the lookout for *A. anthoides* in the transect area, and saw likely habitat (a mixture of relatively dense, grassy and shrubby steppe) at several localities in the western part of the transect (e.g., near Gastre), but did not detect the species there. It is common in parts of southern Patagonia (NW Tierra del Fuego, pers. obs.).

Anairetes (Tyrannidae)

Neither *Anairetes flavirostris* nor *Anairetes parulus* were seen or heard by me, in spite of my having diligently looked for them. *A. parulus* was noted as rare by Durnford (1877, 1878), and two specimens were listed by Wetmore (1926a: 452) from Paja Alta, 7 miles east of Valcheta, eastern Río Negro. Peters (1923: 324—325) unfortunately did not give indications about the relative abundance of *Anairetes parulus* in his study areas, but mentioned six specimens of *A. flavirostris* from San Antonio (coastal Río Negro), stating that "this is the furthest south that this species has been recorded, and also the first record of its appearance on the coast." Bettinelli & Chebez (1986) reported *A. parulus* from the Meseta de Somuncurá area. The complete absence of *Anairetes* from my transect area is hard to explain. I have observed *Anairetes* in other parts of Patagonia. For example, I found *A. parulus* to be fairly common in 1965 around Bariloche in Río Negro.