

Recent ornithological surveys in the Valles region, southern Bolivia

and the possible role of Valles for
the evolution of the Andean avifauna



Centre for Research on the Cultural and Biological
Diversity of Andean Rainforests

The Danish Environmental Research Programme

Front cover: Pictures from Cordillera Carpath

The top ridge, almost constantly wrapped in clouds, is one of the many centres of evolution of endemic biodiversity in the Andes, and this habitat also provides stable water supply for the human population living in the warm and sunny adjacent mountain basin, with the town of Huànuco.

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DIVA, Technical Report no 1

Jon Fjeldså, Zoological Museum,
University of Copenhagen
Sjoerd Mayer, Santa Cruz, Bolivia

Centre for Research on the Cultural and
Biological Diversity of Andean Rainforests (DIVA)
August 1996

Data sheet

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Authors: Jon Fjeldså, Zoological Museum, University of Copenhagen & Sjoerd Mayer, Santa Cruz, Bolivia

Serial title and no: DIVA, Technical Report no 1

Publisher: Centre for Research on Cultural and Biological Diversity of Andean Rainforests (DIVA)

Year of publication: 1996

Technical editor: Jan Bertelsen
Layout: The DIVA secretariat
Figure drawings and water-colour painting: Jon Fjeldså
Photo: Else Bering

Please quote: Fjeldså, J. & Mayer, S. (1996): Recent ornithological surveys in the Valles region, southern Bolivia - and the possible role of Valles for the evolution of the Andean avifauna. Centre for Research on Cultural and biological Diversity of Andean Rainforests, (DIVA), 62 pp. - DIVA, Technical Report no 1

Reproduction permitted only when quoting is evident

Edition closed: October 1995

ISBN: 87-986068-0-8
ISSN: 1396-5581
Key title: Technical report - DIVA

Number of pages: 62
Price: Dkr 50,00

For sale at: The DIVA Secretariat
National Environmental Research Institute
Department of Landscape Ecology
Grenåvej 14, Kalø
DK-8410 Rønde
Denmark
Phone: +45 8920 1700
Fax: +45 8920 1515

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Preface

This report contains an initial survey of the bird fauna in previously unexplored forests in the sub-Andean zone of southern Bolivia, and an analysis of avian biogeographic patterns within the region.

The forests of the Andean slopes accommodate a very high biological diversity caused by complex interactions between geology, climate, history, and human influence. Today, however, highland forest habitats are being burned or logged at an alarming rate to open new roads for colonisation. Unfortunately, the general lack of biological data from the area hinders the development of sound management plans. Therefore, there is an urgent need for detailed information on the distribution of the biodiversity to help develop recommendations for a better land use.

This pilot study lays the foundation for providing the information which is essential for land management plans. Additional studies will be carried out in the area during 1995-1998 by the Centre for Research on the Cultural and Biological Diversity of Andean Rain Forests (DIVA). The studies are part of the general research efforts undertaken by DIVA in the Andean region, and they will cover aspects of anthropology, botany, and include detailed studies of the avian fauna.

It is our hope that this report, and the ones that are to follow, will contribute to the process of making recommendations for a wise and sustainable use of the Andean highland forest habitat.

Lauritz Holm-Nielsen
Chairman of the steering committee

Flemming Skov
Centre coordinator

Centre for Research on the Cultural and Biological Diversity of Andean Rainforests (DIVA)

DIVA is a multidisciplinary research centre funded from 1994 by the Danish Environmental Research Programme. The purpose of the centre is to investigate regional patterns of biodiversity, land use, and human perception of the environment, to improve strategies and to combine the obtained knowledge with recommendations for a balanced and sustainable use of the Andean forest ecosystems and natural resources. The research is carried out in Ecuador, Peru, and Bolivia in close collaborations with local institutions and organisations. The project is divided into eight interconnected and interdisciplinary modules:

1. Establishment of project databases and a Geographical Information System.
2. Mapping environmental constraints.
3. Mapping biodiversity based on present day knowledge and new collections.
4. Development of methodologies for standardised sampling and for modelling biological distributions based on correlations with satellite imagery.
5. Studying environmental perception, local use of natural resources and land-use classification and mapping.
6. Studying the influence of different cultural pressures on biodiversity.
7. Predicting socio-economic scenarios and future development trends.
8. Providing information for better planning.

DIVA involves:

- National Environmental Research Institute, Department of Wildlife Ecology
- University of Aarhus, Department of Systematic Botany of the Institute of Biological Sciences
- Danish National Museum, Department of Ethnography, Copenhagen
- Zoological Museum of the University of Copenhagen
- Several collaborating institutions in Ecuador, Peru and Bolivia

This report is the first publication under the DIVA programme.

Abstract

Results of recent ornithological surveys in the "Valles" of southern Bolivia and a discussion of the role of the "Valles" for the evolution of the Andean avifauna.

- Unexplored parts of the sub-Andean zone of southern Bolivia, including large tracts of deciduous and semi-evergreen forests, were surveyed during several trips in 1991-93. The purpose of these surveys was to improve the knowledge and interpretation of the avian biogeography in this part of the Andes. We here publish 126 new departmental records and several altitudinal records. These include range extensions into Chuquisaca of certain species of the humid cloud forest of the Tropical Andes Region. In general, however, the number of genuine montane-forest birds is low, and this appears to give rise to an ecological release: the few humid-forest birds which are present expand their ecological niches, and lowland birds fill up part of the void by invading the lower part of the semi-evergreen zone, or by settling in semi-humid treeline habitat. Nowhere else in the Andes have lowland birds colonised highland habitat to a similar extent as in the Bolivian valleys. The role of the "Valles" for the evolution of the Andean avifauna is discussed and areas of special importance for the diversification process are indicated.

Jon Fjeldså, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; Sjoerd Mayer, Ter Meulenplantsoen 20, N-7524 CA Enschede, The Netherlands.

1 Introduction

In the research programme of the Centre for Research on Cultural and Biological Diversity of Andean Rainforest (DIVA), the sub-Andean zone of southern Bolivia was selected as one of the principal study areas. This area, known as the Valles ("the valleys", comprising large parts of Departamentos Cochabamba, Chuquisaca, Santa Cruz and Tarija) is a topographical and ecological mosaic. It comprises foothills covered by deciduous forest, arid montane basins, barren high ridges, as well as humidity-capturing scarps with evergreen forests which are isolated from the montane rainforests of the Tropical Andes Region. This latter habitat has its southern limit near the border between Departamentos Cochabamba and Santa Cruz.

Naturally, the habitat mosaic of the Valles has a complex flora and fauna, with high endemism. However, a fairly detailed biological exploration exists only for certain parts of the Cochabamba department. The knowledge about other parts of the region is very fragmentary and the enormous forest tracts known to exist in the Departamento Chuquisaca have remained unexplored. Managing authorities in Bolivia have hardly any information about these areas. At the same time, many highlands suffer from strong land degradation, and the amount of forest destruction accelerates rapidly in the Andean foothills, especially in areas where new roads are being built, resulting in altered patterns of settlements and land use. Enormous areas are being burned every year because the poor sandy soil has lost its fertility after few years of cultivation. No regional plans exist for managing the natural resources.

The DIVA programme (funded for 1994-1999 by the Danish Environmental Research Programme) will assemble data on flora, fauna and land use in the Andes, and correlate these data with features of satellite images in a Geographical Information System. New data will be collected in connection with ethnographic studies and when validating model predictions. The goal of this programme will be to develop regional management plans,

where knowledge based on well-studied areas (notably in Ecuador) is applied in less known areas. The activities are closely linked with those of the Danish Centre for Tropical Biodiversity, where the main objective is to describe and explain patterns of variation in species richness on different geographical scales.

The present paper reports results of preliminary surveys following long transects across several ecological zones, and where the biogeographic patterns were studied using birds as the principal indicator group. The data presented are the first biological data from the enormous forest tracts in the central parts of the Departamento Chuquisaca. Much of this area is virtually uninhabited, and may represent the most virgin habitats that exist today in the Valles.

Using these data, we will analyse the avian distribution patterns in this region and provide a general hypothesis about the biogeographic significance of the Valles. With this we try to demonstrate that the Valles may represent a key area for the evolution of the High Andean biota. Thus, this report tries to combine the presentation of new survey data and interpretations, upon which the planning of more detailed studies can be based.

Little has been published on the distribution of Bolivian birds since the compilation by Bond & Meyer de Schauensee (1942). Remsen *et al.* (1985-7) published no less than 397 new departmental records based mainly on unpublished specimens in North American museums, and Fjeldså & Krabbe (1989) published on the large Andean material collected in 1937-9 by M. Olalla. Although a complex pattern of endemism has long been known to exist in sub-Andean zone (Müller 1973, Cracraft 1985, ICBP 1992), large collecting gaps in the southern departments have so far excluded detailed biogeographic analysis. In Departamentos Santa Cruz, Chuquisaca and Tarija, collecting trips had been made only by M.A. Carriker, Jr. (in the 1930s), K.E. Stager and S.C. Bromley (in 1957) and R. Crossin (in 1972-73) (see locality review in Paynter *et al.* 1975), and some recent observations were published by Nore & Yzurieta (1984), Cabot & Serrano (1988) and

Clarke (1991). Most of the study sites were situated along the few roads in the adjacent lowlands and in the semiarid parts of some montane valleys, and ecotones towards humid forest were reached only at the Cochabamba/Santa Cruz border, near Tomina and Padilla in Chuquisaca, and in southern Tarija. Enormous tracts of uninhabited pre- and submontane forest remained unexplored, the biggest "white spot" being the montane rain-forests of Montes Chapeados (Departamento Chuquisaca), which are isolated by the deep semiarid valleys of Ríos Pilcomayo and Pilaya from similar habitats further north and south (as shown in the ecological map of Bolivia, Unzueta 1975).

The only way to cover these forests would be on foot, from Camargo (on the Potosí-La Quiaca road) to Azurduy (which has road connection to Sucre); this was done by a long trek (400 km in the terrain) in September-October 1991. Later, this was supplemented by some shorter trips in other parts of the Valles, thus good ornithological data now exist along four transects from subtropical foothill forest to semiarid montane basins (Fig. 1). We publish here the most important ornithological records, including at least 126 new departmental records and several altitudinal records. Based on the improved geographical data and the record of birds along the two best-studied altitudinal transects (in Chuquisaca), we will demonstrate here a pattern of altitudinal segregation which differs markedly from that found slightly further north and through most of the Tropical Andes Region.

2 Study areas and methods

Our field surveys focused on the poorly studied zone of extensive deciduous foothill forests and semi-evergreen forests on the higher ridges (Boliviano/Tucumano Forest, see Hueck 1966). Figs 1 and 2 give an overview of the Bolivian Valles, with our study areas shown on three detailed insert maps in Fig. 2. Because vast areas, especially in Chuquisaca, were biologically unexplored, so far, our itinerary (Appendix I) includes fairly detailed habitat descriptions. Our study started with a preliminary survey by SM of the access to central Chuquisaca in August 1991.

Conventions

All geographical names given in the text and in the review list of study sites (Appendix II) exist on the 1:250,000 and 1:50,000 topographic maps of the area. Definitions and descriptions of the ecological zones of Bolivia are given in Unzueta (1975), *Servicio Geológico de Bolivia* (1977) and Montes de Oca (1989); however, the actual life zones may differ considerably from those estimated from climatic and topographic data (see Appendix I), possibly because of anomalies caused by local topographic features and the influence of the vegetation on the climate (see, e.g., Jackson 1989 and Kerfoot 1968). Descriptions and classifications of the forest and woodland types have been given by Hueck (1966) (and Nuñez *et al.* 1991 for northernmost Argentina). The following abbreviations are used in the following text as well as illustrations and appendices: Cerro is abbreviated as C., comminuted as Cmd, Departamento as Dpto, estancia as Eía, hacienda as Hda, rancho as Rcho, serranía as Snía; south, north, etc. as s, n, etc. (also in combinations, s-wards etc.); south of, north of, etc. are abbreviated S, N, etc. Abbreviations in Fig. 4 are made for space considerations; some inconsistency in their construction is made for minimal ambiguity. The names of the present authors are abbreviated JF and SM.

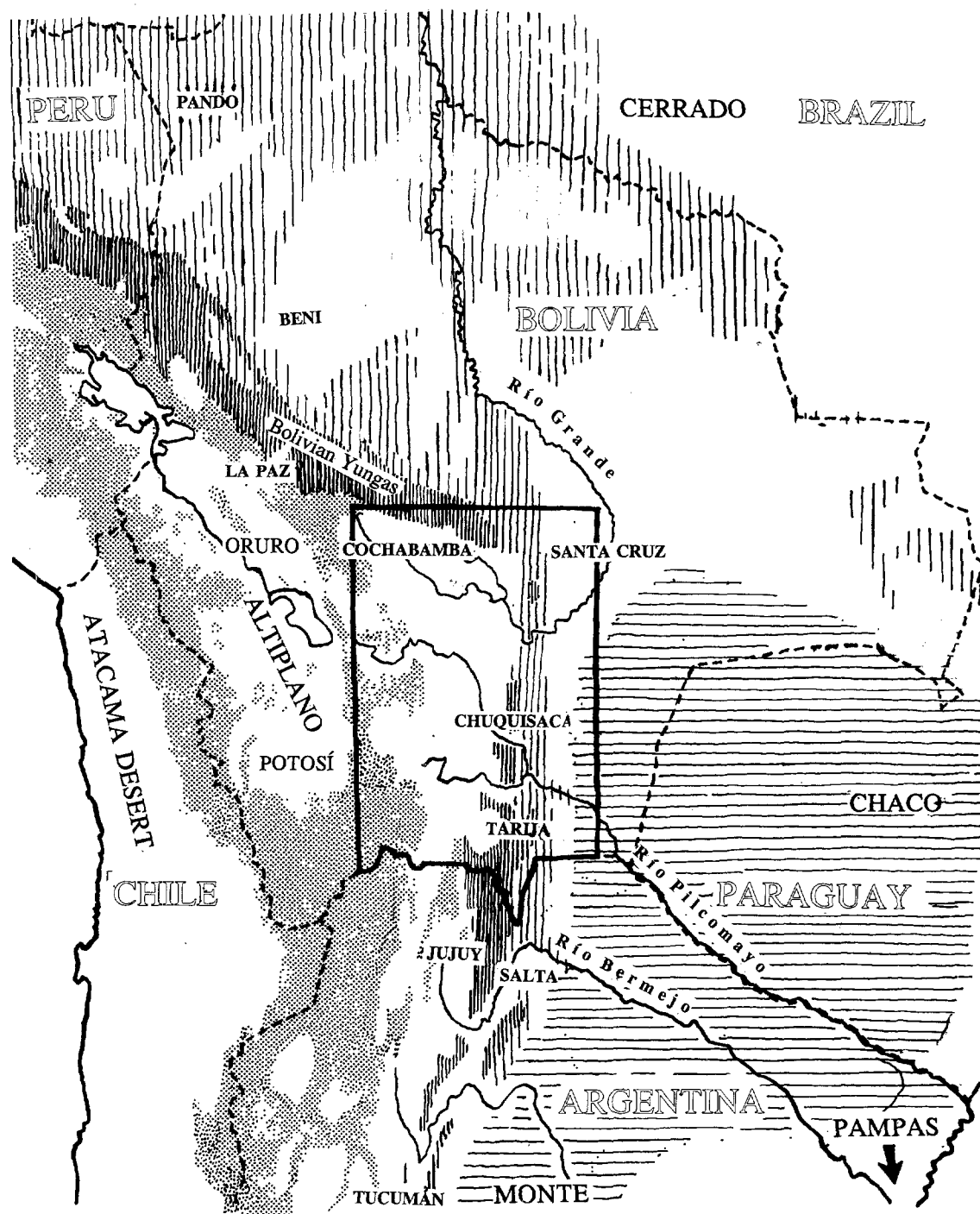


Figure. 1. Review map of Bolivia and adjacent territories. Vertical shading = humid forest, dense shading = montane humid forest. Horizontal shading = Chaco and Monte vegetation of xeric-adapted woodlands and scrubbery, the chaco additionally characterised by extensive seasonal inundations. Stippling = land over 4,000 m. Framed = the area shown in Fig. 2.

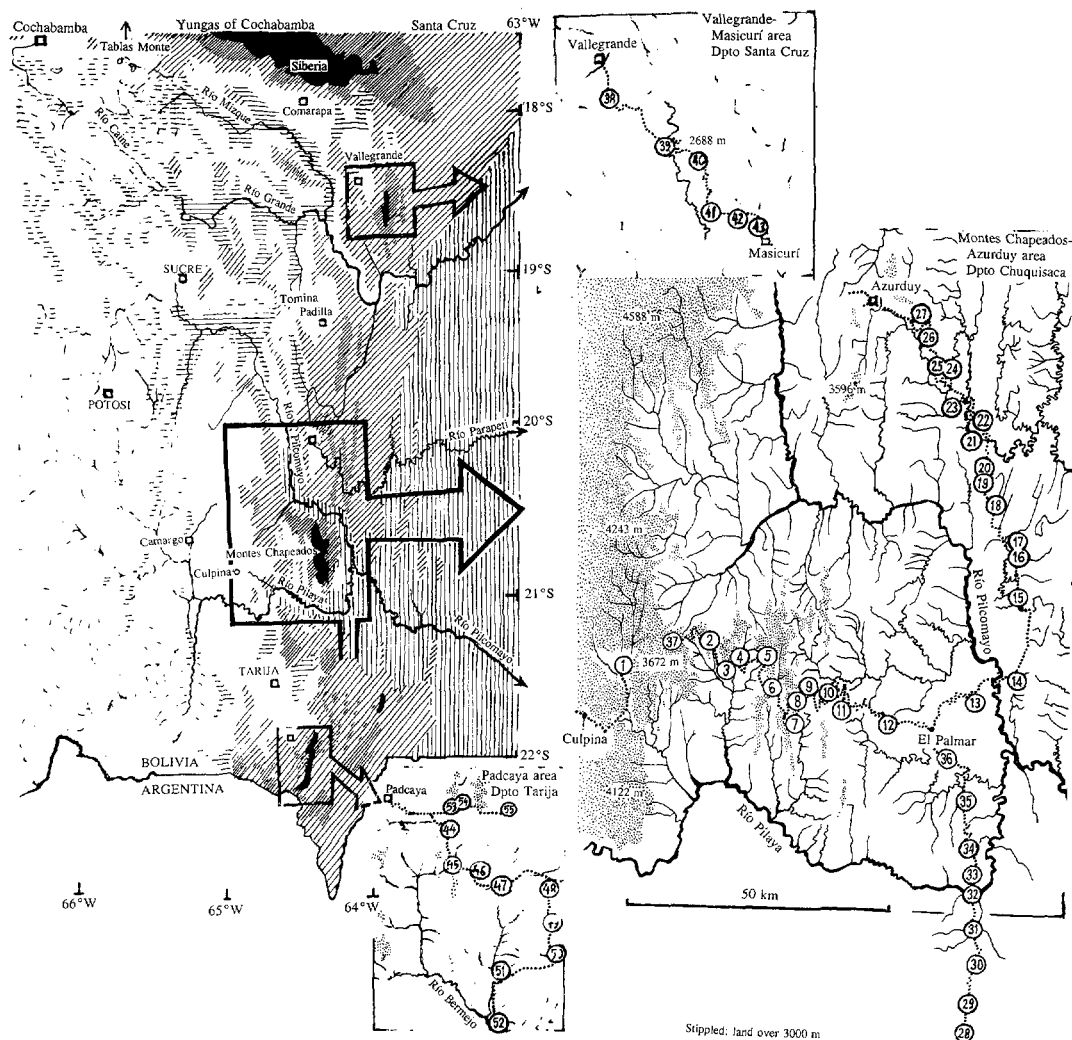


Figure 2. The geography of the Bolivian "Central Valles". The main map of central and southern Bolivia, to the left, shows Bolivian-Tucumán Forest as slanting lines (light: deciduous; dense: semi-evergreen, the most rain-drenched parts black - like the Yungas in the north, at the top of the map). The map also shows xeric woodlands in the lowlands (vertical hatching) and in the montane basins (horizontal hatching). These habitat signatures were primarily derived from the Holdridge Life Zones (as mapped in Unzueta 1975), but were modified where our field studies revealed deviations from the condition estimated from climatic and topographical data. On the three insert maps, areas over 3,000 m are stippled and our routes are shown by dotted lines.

The insert map to the right shows the study area in Chuquisaca, figures showing localities mentioned in the text: 1 Villa Charcas, 2 Abra Portillo, 3 C. San Francisco, 4 Río Lechera, 5 Río Puca Laja, 6 Hda Puca Pampa, 7 Río Puca Pampa, 8 Cerro Cobre Khasa, 9 C. Campamentito, 10 C. Campanarios, 11 C. Campamento area, incl. C. Lagunillas, 12 C. Misión and Bufete, 13 Snía Torobayo, 14 Eía Timboyco, 15 Eía Tacurvite, 16 Añimbo, 17 Uruguay, 18 Cmd Caja Mayu, 19 Cmd Sausi Mayu, 20 C. Alto Despencillus, 21 Río Parapeti, 22 Snía Racete, 23 C. el Tapado, 24 Río Misca Mayu, 25 C. Punta Lajas, 26 C. Hoyadas, 27 Hda Moco Pata and Rcho Monte Grande, 28 Narvaez, 29 Huayco camp, 30 El Tunal camp, 31 San Josecito, 32 Río Pilaya camp, 33 Cañon Verde camp, 34 Río Yahuayhua camp, 35 Río Tuercas camp, 36 Río Nuevo camp and 37 Chirijara.

The small upper insert map shows the Vallegrande-Masicuri study area: 38 Abra Tabla, 39 Río Piraymiri, 40 San Lorenzo, 41 Loma Larga, 42 La Yunga and 43 Dionisios.

The small lower insert map shows the Tariquía area: 44 Oroza, 45 Honduras, 46 Río Escalera, 47 Río Achirales, 48 Pampa Grande, 49 Río Chillaguates, 50 Cambari Chico, 51 Río Emborazú, 52 Cmd Emborazú, 53 Río Alizos, 54 C. Alto de Minas and 53 Río Loraya.

In September-October 1991, both of us made a trek from the Camargo area through Montes Chapeados to El Palmar and then north-wards to Azurduy, and in March 1992 another trek was made (by SM) from Narvaez in the Tarija Department to El Palmar and onwards to Camargo (Figs 3 and 4). The Vallegrande-Masicurí area in Santa Cruz was studied by M. Bohn Christiansen and E. Pitter in November 1991 and (together with SM) 19-25 January 1992, and by SM 2-9 February and 10-15 March 1993. In September-October 1992, SM made three treks in and near the "Reserva Nacional de Flora y Fauna Tariquía" along the humid mountain ridge E and SE Padcaya, Dpto Tarija, near to the Argentinean border. Some comparative studies have also been made by both of us in the adjacent zones of humid Yungas forest in Cochabamba and Santa Cruz. Trip reports from the surveys in 1992 and 1993 are available on request to SM.

Thorough studies were also made in 1991-92 by M.B. Christiansen and E. Pitter (pers. comm.; a brief visit here also by the present authors) in extreme eastern Potosí, on the w bank of Río Caine (upper section of Río Grande, just outside Fig. 2). Reference is also given to observations made on a birding trip in Cochabamba and Santa Cruz in March 1992 by N.P. Dreyer (unpublished report). Data on altitudinal distribution of birds in the corresponding zone in extreme northern Argentina were provided by C. König (in lit.).

Throughout our surveys, birds were recorded by watching and listening, especially near the camp-sites but also as we stopped for one half hour or so as we passed some "interesting" habitat during the walks. Tape recordings were made on several occasions for playback or for careful subsequent scrutiny and comparisons with published sound recordings (Hardy *et al.* 1985, 1991 a,b). In order to document regional variations in community structure, JF made Timed Species Counts (TSC).

The methodology is adapted to the facts that (a) steepness and dense undergrowth often makes it impossible to quietly follow a continuous route, and (b) that the detectability of many (but not all) forest birds drops sharply at 30-50 m distance (Reynolds *et al.* 1980). Records were taken only during ten-minute periods within altogether 35 independent one-hectare plots within each study area. Slow random movement is permitted (where possible) to inspect hidden parts or to follow up unidentified glimpses, but sometimes the terrain is so difficult that the observer must mainly stay at a good vantage point. However, only those birds which were inside a predefined one-hectare area are recorded. This method, which is almost identical to a procedure developed for Afromontane forest by Koen (1988), has been used by JF in a wide diversity of tropical habitats (e.g., Fjeldså 1993; Fjeldså & Rabøl manus). Like all kinds of point counts, the data are biased by interspecific variation in detectability; however, it may represent the most readily applicable semi-quantitative sampling of avian community structure during this kind of rapid survey through difficult terrain and complex habitat.

During the 1991 trek, 1-6 mist nets were used at some camp-sites, mainly for collecting blood-samples (for DNA studies) from live birds, and a few birds were shot. Collected birds are deposited at the Museo Nacional de Historia Natural in La Paz, and blood samples are deposited at the Zoological Museum, University of Copenhagen. Below, species documented by specimens, photos or tape-recordings are marked with S, P and T, respectively. All ornithological records have been entered in databases (BIOPOSER; Dijkhuizen 1993) in the Zoological Museum, University of Copenhagen (ZMUC). The nomenclature and sequence of birds follows Fjeldså & Krabbe (1990).

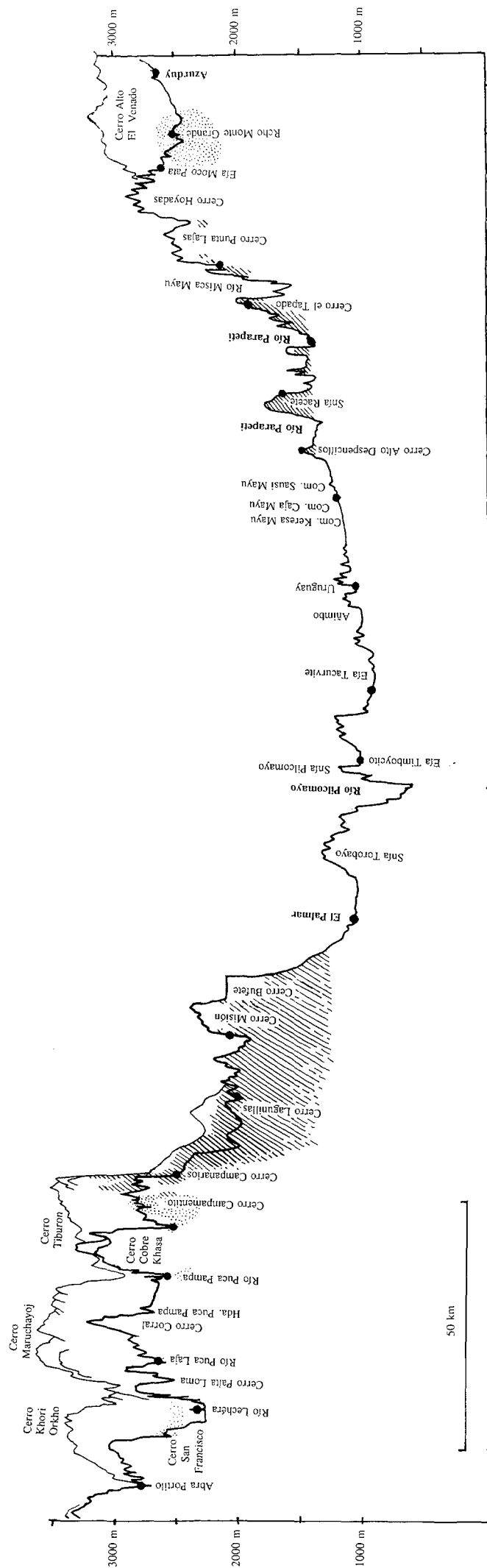


Figure 3. The altitudinal profile of the longest trek, which was walked in September-October 1991 (not including the small zig-zags, which bring the distance up to c. 400 km). Black dots show campsites. The thin line shows the profile of the highest ridges of the water divide. Shading shows the position of the semi evergreen forest, stippling the main tracts of almost pure *Podocarpus* forest.

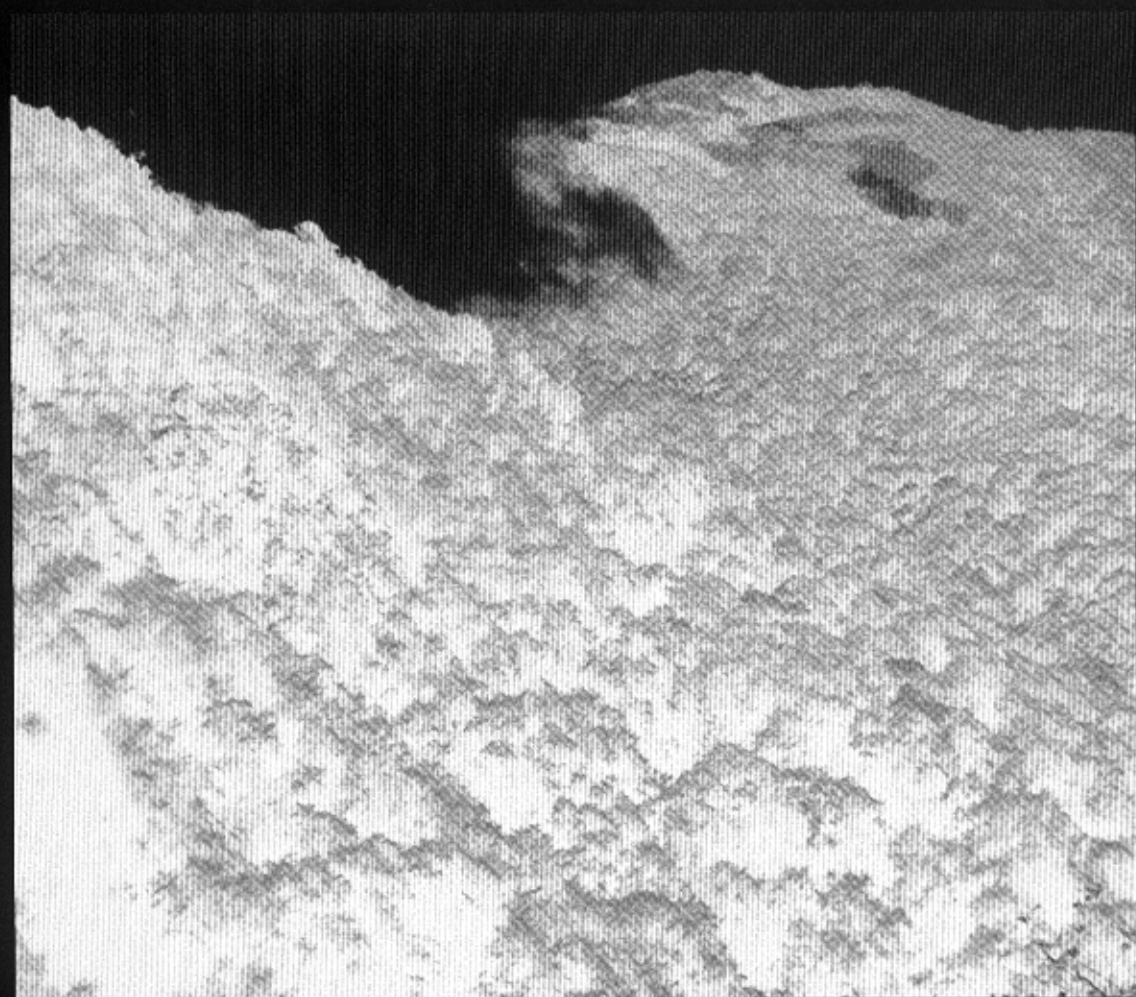


Figure. 4. Habitats in Montes Chapeados. Top: Degraded slopes around 3,000 m in the temporarily humid zone, with remnant woodlands, deciduous *Alnus* shrub in the upper parts and mixed *Eugenia*/*Podocarpus*/*Polylepis* forest in the deeper ravines. Bottom: *Podocarpus* forest near Eia Moco Pata immediately west of the moisture-capturing ridge south of Azurduy.



Figure 4, continued. Top: The grassy plateau at 2,300 m of Cerro Bufete, overlooking the lowlands with El Palmar. Bottom: The interior of tall Growth forest at 2,000 m in the semi-evergreen zone of Montes Chapeados.

3 Results

Altogether 370 bird species were recorded. The distribution of records of all species along the main transects in Chuquisaca is shown in Appendix III; this matrix can be compared with altitude (as shown in Fig. 3) and principal vegetation types (Appendices I and II). The more significant range extensions are specified below, and this will be followed by reviews of the ecological amplitudes of birds inhabiting montane forests in Chuquisaca, and of regional differences in community compositions.

The records specified below comprise 126 or possibly 128 new departmental records, several altitudinal records, and more detailed remarks are given for certain poorly-known species. Most of the new departmental records were expected because the species is common in adjacent departments; others were more surprising. Birds listed for Chuquisaca by Remsen & Traylor (1989) but not recorded by us were mainly waterbirds, strict lowland birds and Nearctic migrants. Species expected in the habitats we visited, but not found by us, were *E. flavogaster* (Yellow-bellied Elaenia), *Fluvicola pica* (Pied Water-tyrant) and *Gnomiopsar chopi* (Chopi Blackbird).

3.1 Comments on individual species

- *Phalacrocorax brasilianus* (Olivaceous Cormorant). 3 October 1991 two on Río Parapeti; 18 March 1992 two on Río Nuevo near El Palmar. First Chuquisaca records of this widespread and adaptable cormorant. Seen on three occasions in Tarija.
- *Syrigma sibilator* (Whistling Heron). Seen several times in the area from Ríos Pilcomayo up to Río Parapeti, up to 1,400 m. First Chuquisaca records of this heron, which is widespread in adjacent lowlands. Also seen at 1,100-1,700 m in Tarija and known up to 1,500 m in nw Argentina.
- *Ardea cocoi* (Cocoi Heron). 28 September 1991 one seen overflying Río Pilcomayo. First Chuquisaca record of this widespread lowland heron.
- *Tigrisoma fasciatum* (Fasciated Tiger-heron).

1 October 1991 one juvenile. seen near Cmd Sausi Mayu; 16 March 1992 one on Río Tueras; 17 March one on a stream near El Palmar; 5 October 1992 two seen in the Río Achirales near Pampa Grande; 8 October 1992 one seen on a stream near Río Cambarí. First Chuquisaca and Tarija records of this widespread but uncommon heron found further n in the Andes (ssp. *salmoni*) and in adjacent nw Argentina (*pallascens*).

- *Coragyps atratus* (Black Vulture). Ubiquitous in the lowlands and foothills (P). Seen 22-24 September 1991 together with other vultures near a grassland fire at 2,850 m on C. Campanarios, and 11-12 October at 2,600-2,700 m around Azurduy. First Chuquisaca records of this vulture, which is widespread in lowland and premontane areas.
- *Sarcoramphus papa* (King Vulture). 24 September 1991 one over C. Campanarios (2,850 m); 25 September three over C. Lagunillas (2,700 m); 30 September one over Eía. Tacurvite (950 m); 17 March 1992 one over Río Tueras; 20 March below C. Bufete (1,500 m). First Chuquisaca records of this widespread vulture of lowland and premontane forest. Also seen in Dptos Santa Cruz and Tarija.
- *Elanoides forficatus* (Swallow-tailed Kite). Seen on several occasions in October 1991 and March 1992 E C. Campanarios and n to Río Parapeti in Chuquisaca, up to 2,200 m. 15 birds were seen mobbing a *Harpyhaliaetus solitarius* (Solitary Eagle) E C. Bufete (T). First Chuquisaca records of this species, which was also seen in Santa Cruz and Tarija, and is widespread in most lowlands and Andean foothills.
- *Elanus caeruleus* (White-tailed Kite). An observation 2 February 1993 near Vallegrande, 2,050 m, is an unusual altitudinal record of this widespread bird of the adjacent lowlands.
- *Harpagus bidentatus* (Double-toothed Kite). 17 and 18 March 1992 a bird was watched on close distance near Río Nuevo. First Chuquisaca record and a s-wards range extension of this widespread tropical bird.
- *Geronaetus melanoleucus* (Black-chested Buzzard-eagle). Seen on several occasions in the highest mountains. Observations near Canaletas (11 March 1992), two near

- Oroza (24 and 25 September 1992) and one near Río Achirales (4 October 1992) represent the first records for Dpto Tarija.
- *Harpyhaliaetus solitarius* (Solitary Eagle). 21 March 1992 one juvenile. was seen at few metres' distance, perched in a low tree E C. Bufete (1,900 m, T). First Chuquisaca record of this rare premontane eagle. 21-22 January 1992 a pair was seen near La Yunga E Vallegrande (possibly breeding).
 - *Buteo leucorrhous* (White-rumped Hawk). 27 September and 2 October 1992 seen circling over forest at 2,000 m at Río Escalera (T). First record for Tarija.
 - *Buteo brachyura* (Short-tailed Hawk). 10 October 1991 one dark-phase bird soared over *Alnus* and *Podocarpus* treeline forest (2,550 m) near Hda Moco Pata and later near Rcho Monte Grande. First Chuquisaca record and a noteworthy altitudinal record of this widespread tropical and subtropical hawk.
 - *Buteo swainsoni* (Swainson's Hawk). 12 March 1993, in the early afternoon, a continuous stream of 10-13,000 birds passed overhead in n-wards direction near Masicurí. There are very few published records of large-scale migration of this raptor between the North American breeding area and the wintering area on the Argentinean Pampas (see Fjeldså & Krabbe 1990).
 - *Spizastur melanoleucus* (Black-and-white Hawk-eagle). 12-13 March 1992 one seen well S El Tunal and 7 October one soared low over Pampa Grande. First Tarija records of this widespread but rare hawk.
 - *Spizaetus ornatus* (Ornate Hawk-eagle). 28 September 1991 perched near our camp N Eía Timboycito. First Chuquisaca record of this widespread bird of tropical lowland forest.
 - *Oroaetus isidori* (Black-and-chestnut Eagle). 23 September 1991 one adult seen over the steep slope W C. Misión (2,100 m). First Chuquisaca record of this uncommon montane forest eagle, known from the Tropical Andes Region s to Santa Cruz (Parker & Bates 1992, and seen at La Yunga E Vallegrande) and in nw Argentina.
 - *Micrastur semitorquatus* (Collared Forest-falcon). 3 October 1991 one adult (tawny phase) seen near the C. Alto Despencillos camp (1,500 m). First Chuquisaca records

of this widespread tropical forest falcon, which was also heard (T) in Tarija.

- *Micrastur ruficollis* (Barred Forest-falcon). This skulking forest falcon is probably common, considering that it was heard on nearly all mornings spent inside forest in Santa Cruz, Chuquisaca (T) and Tarija (T), and in a wide range of forest types up to 2,350 m. SM saw a bird well after it had been driven to a frenzy by playbacking. First Tarija and Chuquisaca records and altitudinal records, but the species is well known (to 1,600 m) in nw Argentina.
- *Penelope dabbeni* (Red-faced Guan). In Chuquisaca seen daily in the 1,700-2,700 m zone, wherever there were forest or woodland patches from Río Lechera and e-wards in Montes Chapeados (SPT) and towards Azurduy (P). A few birds were found in the Vallegrande-Masicurí area (first Santa Cruz records, T). In Tarija, however, only one pair and one single were seen in *Alnus*- and *Polylepis*-clad gullies (Honduras area).

Despite considerable searching in recent years (on lower altitude), there have been no other observations in Bolivia since the early records referred by Bond & Meyer de Schauensee (1943) from Tomina and Río Azero E Padilla and from Piños and 80 km S Tarija. Otherwise this species is known only from the Calilegua and El Rey forests in Jujuy in nw Argentina. We saw it most frequently in the *Podocarpus*-dominated parts and in its transition to the *Alnus* zone, and some observations were in bamboo areas and other second growth. Although one group of c. 25 birds was encountered (in March), most birds were in pairs. Near the campsites, where we could often locate several displaying and calling pairs at dawn, the distances between neighbour pairs/families averaged 4-500 m (corresponding to c. 5 pairs per square kilometer). Estimating the forest area in the relevant altitudinal zone to 1,000 square km, and assuming a somewhat more dispersed occurrence in disturbed forest types, we estimate the population in Montes Chapeados to 3,000 pairs. The total population N Pilcomayo may be of a similar order of magnitude.

Judging from bioacoustic data, we support the judgements of Vaurie (1966) and

Remsen & Cardiff (1990) that this species is not related to *P. montagnii* (Andean Guan) of the Tropical Andes Region, but rather to *P. obscura* (Dusky Guan), which replaces it in adjacent foothills and lowlands (seen by us in the low areas E Río Pilcomayo). *P. montagnii* has its southern limit in Santa Cruz, near the Cochabamba border; its claimed occurrence in the cloudforests of Oran, nw Argentina, [G. Hoy, see Delacour & Amadon 1973] being an error [Narosky & Yzurieta 1987]).

- *Odontophorus speciosus* (Rufous-breasted Wood-quail). Heard calling at La Yunga and Dionisios in the Vallegrande-Masicurí area (T). A s-wards range extension.
- *Aramides cajanea* (Gray-necked Wood-rail). Heard or seen on several occasions , mainly in lowlands, but also near forest creeks as high up as 1700 m. First Chuquisaca records (T) and an altitudinal record for this common woodrail of adjacent lowlands.
- *Porphyryula martinica* (Purple Gallinule). 6 December 1991 seen by S.M. and R. de By on Laguna Alalay (2,550 m), Cochabamba. First Cochabamba record of this widespread and nomadic lowland bird.
- *Oreopholus ruficollis* (Tawny-throated Dotterel). At least 20 seen 25 August 1991 on the shore of a dried-out lake S Culpina. First Chuquisaca record of this peculiar Patagonian and high-Andean plover.
- *Actitis macularia* (Spotted Sandpiper). 28 September 1991 one on bank of Río Pilcomayo; 13 March one on bank of Río Pilaya. First Chuquisaca records of this common Nearctic migrant.
- *Columba fasciata* (Band-tailed Pigeon). In September-October 1991 scattered pairs seen through the semi-evergreen forest zone from N C. Campanarios to C. Misión, and 10 October two birds near Eía Moco Pata. In March 1992 flocks of 15 and 40 seen on C. Campamentito, and two were seen between Ríos Puca Laja and Lechéra in the rainshadow zone. Recorded Tarija. First Chuquisaca and Tarija records, but known from corresponding life zones further n (to Vallegrande-Masicurí area) and in nw Argentina.
- *Columbina talpacoti* (Ruddy Ground-dove). In March 1992 several seen between El Tunal and Cañon Verde and between Río

Nuevo and El Palmar. First Chuquisaca records of this widespread lowland dove. Also recorded in Santa Cruz and Tarija.

- *Metriopelia melanoptera* (Black-winged Ground-dove). In September-October 1992 several parties seen at 2,300-2,800 m in the Padcaya-Pampa Grande area in Tarija, the first records of this highland dove for Tarija.
- *Metriopelia aymara* (Golden-spotted Ground-dove). 17 September 1991 one group seen from the truck between Camargo and Culpina. First Chuquisaca record of this dove, which typically inhabits the arid puna zone of the Andes.
- *Geotrygon frenata* (White-throated Quail-dove). 26 September 1991 heard above El Palmar (1,600 m), and 21-22 March 1992 seen and heard E C. Campanarios (2,200 m). First Chuquisaca records of this dove of montane forests. With records also in the Vallegrande-Masicurí area there is not necessarily any disjunction between ssp. *frenata* of the Tropical Andes Region and ssp. *margaritae* of Tarija and Jujuy.
- *Ara militaris* (Military Macaw). 16 March 1992 seven seen near Río Tueras; 17 March four seen near Río Nuevo; 19 March one pair E C. Bufete. Small flocks and several pairs seen at La Yunga, Dionisios and Abapó in the Vallegrande-Masicurí area (T). There are very few published records of the Bolivian population.
- *Myiopsitta monachus* (Monk Parakeet). 13 September 1991 several found (with nests) at 2,900 m W Río Caine. 27 August 1991 a small flock along the Potosí-Sucre road at c. 19°35'S, 65°15'W. First records for the Potosí department, representing the distinctive form *luchsi*, known so far only from within the Cochabamba Basin.
- *Bolborhynchus aurifrons* (Mountain Parakeet). 25 September 1992 c. 25 birds in *Polylepis* woodland at 2,750 m W La Cumbre. First Tarija record of this highland parakeet.
- *Amazona tucumana* (Alder Parrot). Fairly common on the forested ridge between Vallegrande and Masicurí (T). Small groups seen in several places in Chuquisaca (mainly at 2,000-2,900) in September-October 1991, and in March 1992 at least 900 were seen at a roost near the summit of C. Campamentito, above

2,60 m (T) (a precise count was impossible because low clouds enwrapped the mountain ridges; flocks of 10, 25 and 90-100 birds seen between Río Puca Laja and Río Lechéra may have been flying towards the Campamentito roost). 11-12 March 1992 several flocks of probably this parrot near Narvaez, and September-October 1992 the species was found to be common SE Padcaya (T).

The only previously published Bolivian records of the endemic Boliviano/Tucumano parrot were near Padilla in Chuquisaca and Fortín Campero and Río Lipeo in Tarija (Bond & Meyer de Schauensee 1942). However, the first observations from Santa Cruz were made in 1990 by G. and J. Cox (in lit.). It was also seen *primo* 1991 (Sylvia Estanssoro pers. comm., colour slides shown) W of the road by Río San Antonio N Sopachuy, between Azurduy and Padilla. Our observations and information from locals demonstrate that not all birds spend the arid season in adjacent lowlands, as suggested by Mosa *et al.* (1992) for nw Argentina.

- *Amazona aestiva* (Turquoise-fronted Parrot). Small numbers of this parrot were seen in the lowlands and also passing regularly up and down the Río Caine Valley, Cochabamba/ Potosí border, at c. 1,900 m. 2 February 1992, it was seen near Río Piraymiri, at 1,850. Altitudinal records of this widespread Chaco parrot.
- *Otus ingens* (Rufescent Screech-owl). Songs recorded 5 February 1993 S Loma Grande (1,900 m) and 6 February and 11-12 March 1993 at La Yunga (T). First records for Sta Cruz and a s-wards range extension of this owl of humid premontane forest.
- *Otus hoyi* (König & Straneck 1989; Cloud-forest Screech-owl). This newly described cryptospecies was heard several times and seen once in the light of a lantern during the nights 22-24 September 1991 N C. Campanarios; heard next evening N C. Lagunillas (2200 m, T); 3-4 October heard on Snía Racete; 21-22 March singing NE C. Campanarios (2,000 m, T); 24 March singing in *Podocarpus* forest SW C. Campamentito (T). In September-October 1992 recorded at three locations along the Ríos Escalera and Achirales in Tarija (1,730-2,150 m, T). 3-4 February 1993 sang at San

Lorenzo, Sta Cruz (2,350 m, T). Owls with typical *O. choliba* (Tropical Screech-owl) songs were heard in deciduous woodlands below 1,850 m, and records exist also from drier montane basins in the Valles (ssp. *alilicuco*).

Otus hoyi was not recorded by König & Straneck (1989) for Chuquisaca and Tarija, but two Tarija specimens of *Otus hoyi* have so far been misidentified as *O. choliba*: The Field Museum in Chicago has one bird, collected by R. Crossin 17 February 1973, 67 km E Tarija. One bird, in the Museo Nacional de Historia Natural in La Paz, had been collected 24 September 1986 by J. Salazar B. at Rcho Tambo (2,100 m), 61 rd. km E Tarija (it carried an AMNH label; however, according to F. Vuilleumier [*in lit.*] the American Museum of Natural History does not have additional specimens from Dpto Tarija). This latter bird, and one bird from Salta, in the Field Museum, are of a rufous colour phase not known to König & Straneck (1989) and König (1991 a).

König & Straneck (1989, and *in lit.*) mention *O. hoyi* from several humid scarp forests in nw Argentina (900-2,700 m) and one specimen from Samaipata, Dpto Santa Cruz, Bolivia; thus the records given above are the first for Chuquisaca and Tarija. König & Straneck (1989) knew the wide-ranging *O. choliba* only from more open woodland in the lowland up to the transitory zone at 1,500 m. However, S. Arias (pers. comm.) has heard *O. choliba* songs in the humid Yungas of Cochabamba (as well as in the rainshadow area near Comarapa. Furthermore, the Olalla collection (see Fjeldså & Krabbe 1989) includes *O. choliba* (of very variable morphotypes) from humid Yungas forest in Cochabamba and La Paz. Although a segregation seems to exist in nw Argentina and s Bolivia between *O. hoyi* (humid forest) and *O. choliba* (woodlands), this latter species appears to be ecologically and morphologically variable further n.

- *Pulsatrix perspicillata* (Spectacled Owl). 14 March 1992 heard singing (T) in dry woodland N Cañon Verde (1,150 m). First Chuquisaca record of this widespread tropical owl, known also in the sub-Andean zone of adjacent Argentina.

- *Glaucidium (jardinii) bolivianum* (König 1991 b; Andean Pygmy-owl). 21-22 September 1991 several songs heard S C. Campamiento; 22-24. September and 21-22 March N C. Campanarios; seen 25. September N C. Lagunillas; 5-6 October heard on C. el Tapado (T). 26-27 September 1992 recorded in the Río Escalera area (T). 3-5 February 1993 several songs recorded at San Lorenzo (T). Recorded vocalisations agree well with sonograms of typical songs and introductory long trill and single calls of *bolivianum* (König 1991 b, Abb. 11, 12 and 16); however, other songs correspond to a song of nominate *jardinii* from Venezuela (Hardy *et al.* 1989). First Chuquisaca and Tarija records of montane forest pygmy owls (*G. bolivianum/jardinii* group); however its occurrence was expected because it was known from Sta Cruz (Parker & Bates 1992) and from nw Argentina. *G. brasilianum* (Ferruginous Pygmy-owl) was singing in the foothill zone (T).
- *Ciccaba huhula* (Black-banded Owl). 14, 15 and 16 March 1992 recorded (T) in dry forest near Cañon Verde and near Río Tueras. First Chuquisaca records, but the species is known from the adjacent submontane zones of Santa Cruz and nw Argentina.
- *Ciccaba albitarsus* (Rufous-banded Owl). Well-spaced hoots and a single, short rhythmical series of hoots, heard after sunset 7 October 1991 W Río Misca Mayu (2,100 m), correspond well with those of *C. albitarsus* heard in the subsequent weeks in Cochabamba, Bolivia, and in Ecuador (also in Hardy *et al.* 1989). 21 March 1992 a rather fast series of hoots and loud single replies were heard (T) in humid forest below C. Campanarios (2,200 m). 3-5 February 1993 *C. albitarsus* was recorded at San Lorenzo (T). First Sta Cruz and Chuquisaca records, as the s-most earlier records were in the Yungas of Cochabamba.
- *Speotyto cunicularia* (Burrowing Owl). 22-26 August 1991 seen near Culpina; 18-19 March 1992 two parties on boulder-covered slopes E El Palmar. First Chuquisaca records of this widespread arid-land owl.
- *Nyctibius griseus* (Common Potoo). 14 March 1992 singing near Cañon Verde, inside arid woodland. First Chuquisaca record of this widespread bird.
- *Lurocalis (semitorquatus) rufiventris* (Rufous-bellied Nighthawk). 27 September and 1 October 1992 calls of possibly this species were recorded (T) at 2,000 m in the Río Escalera area. 4 October 1992 calls of possibly this species were heard at 1,730 m at Río Achirales. At dusk 8 October 1992 a nighthawk lacking white wingbar flew back and forth at treetop level along the forested banks of Río Cambarí. The species has not been recorded in Tarija but is known from the Tropical Andes Region and from n-most Argentina (Narosky & Yzurieta 1989).
- *Caprimulgus longirostris* (Band-winged Nightjar). 17 September 1991 after sunset heard singing in Abra Portillo; 20 September heard in Cañon Puca Pampa; 12 October one flushed near Azurduy. 30 September 1992 recorded (T) at Honduras, Tarija. 15-16 October seen several times near Río Alizos (T). First Chuquisaca and Tarija records, most probably a range extension of the puna form *atripunctatus*, although the Argentinean *patagonicus* cannot be ruled out.
- *Uropsalis lyra* (Lyre-tailed Nightjar). Sang during the nights 22-24 September 1991 N C. Campanarios, 2,550 m, and 4 October 1992 at Río Achirales (1,730 m, T). The Chuquisaca record is the only known between the Yungas (ssp. *peruana*, Remsen & Ridgely 1980, Parker & Bates 1992) and Dpto Tarija and n-most Argentina (ssp. *argentina*, Olrog 1975).
- *Cypseloides (fumigatus) rothschildi* (Sooty Swift). 28 September 1991 several swifts corresponding to descriptions of this form appeared together with *Streptoprocne zonaris* (Collared Swift) over the low Snía Torobayo just W Río Pilcomayo. 26 September 1992 a flock of eight near Río Escalera were flying around calling loudly (T); 6 October at least five at Pampa Grande. The probable (but still undocumented) occurrence of this submontane n-Argentinean swift in Bolivia was discussed by Remsen & Ridgely (1980).
- *Chaetura andrei* (Ashy-tailed Swift). 28-30 September 1991 a few flocks were seen in the Pilcomayo-Añimbo area. 18 March

1992 at least 25 near Río Nuevo. In October 1992 several flocks were seen near and above Pampa Grande, Ríos Chillaguatas and Cambarí, Tarija. There are very few published records from Bolivia.

- *Aeronautes montivagus* (White-tipped Swift). 21 March 1992 at least 25 birds swirled over the slopes of C. Bufete (T). 27 March 1992 a single bird in the valley of Río Lechéra (2,600 m). 2 February 1993 adults were seen visiting a nest, probably with large young, and 11 adults wheeled overhead E Abra Tabla in the Vallegrande-Masicurí area; 3 February 1993 at least 5 were seen near Río Piraymiri; 14-15 March 1993 up to 17 were seen at Dionisios. First Chuquisaca record and a s-wards range extension of this montane swift of the Tropical Andes Region.
- *Phaethornis superciliosus* (Long-tailed Hermit). 4 October 1991 seen on Snía Racete (1,400 m) and 5 October on C. el Tapado (1,800 m). First Chuquisaca records and a s-wards range extension.
- *Phaethornis pretrei* (Planalto Hermit). 28 September 1991 one on Snía Torobayo; several 15-19 March 1992 from Río Yahuayhua to E C. Bufete (T). First Chuquisaca records, but known from the foothills further n and s.
- *Colibri serrirostris* (White-vented Violet-ear). 13 March 1992 one near San Josecito (950 m). First Tarija record, but known in the corresponding foothills further n and s.
- *Oreotrochilus estella* (Andean Hillstar). Seen in August 1991 in a ravine near Camargo. First Chuquisaca record of this common high Andean hummingbird.
- *Trogon personatus* (Masked Trogon). 5 October 1991 a female seen inside mossy forest on C. el Tapado. 8 October a pair watched for a long period while feeding inside a remnant cloud-forest patch on C. Punta Lajas. Records of two birds (T) 21 March 1992 inside mossy forest NE C. Campanarios resemble but are not identical to calls of *T. personatus* from Peru (Hardy *et al.* 1987) but correspond to recordings made by SM in Cochabamba and Sta Cruz. First Chuquisaca records, as this bird has been known only from the Tropical Andes Region s to the ecotone near the Cochabamba/Santa Cruz border. It was common in the Vallegrande-Masicurí area.
- *Trogon curucui* (Blue-crowned Trogon). Common in the subtropical zone of Chuquisaca and Tarija, mainly in low-altitude forest between Ríos Pilaya and Pilcomayo and near Río Parapeti, but sometimes up to 1,750 m on the Snía Racete and C. el Tapado (T). First Chuquisaca record of this common lowland bird, and an altitudinal record, although it is seen up to 1,500 m in nw Argentina.
- *Ceryle torquata* (Ringed Kingfisher). 3 October 1991 a male near Río Parapeti (1,350 m). First Chuquisaca record of this widespread lowland kingfisher.
- *Chloroceryle americana* (Green Kingfisher). 3 October glimpsed at Río Parapeti; 7 October at Río Misca Mayu (1,600 m); 12 March near Huayco (1,700 m). First Chuquisaca records of this widespread lowland kingfisher, but altitudinal (stray?) records exist for the temperate zone in Cochabamba (Remsen *et al.* 1986, Fjeldså & Krabbe 1989).
- *Nystalus maculatus* (Spot-backed Puffbird). September 1991 several seen at 2,050 m on the bank S Río Caine. First Potosí record, but it is often found to this altitude, or even higher, in Cochabamba.
- *Aulacorhynchus coeruleicinctis* (Blue-banded Toucanet). In February-March 1993 several seen in the Masicurí area in Santa Cruz (T), which is a s-wards range extension.
- *Ramphastos toco* (Toco Toucan). Seen several times in Chuquisaca and Tarija, up to 16 together, mainly in the area between Ríos Pilaya and Pilcomayo and near Río Parapeti, in bushy and scrubby areas with some large trees, but sometimes in semi-evergreen forest up to 1,750 m below C. Bufete and on Snía Racete up to 1,750 m (T). New for Chuquisaca, with noteworthy altitudinal records for this widespread bird of the Chaco and southern Brazil.
- *Picumnus cirratus* (White-barred Piculet). 20 September 1991 mistnetted at Río Puca Laja (2,700 m, P); 24 September seen N C. Campanarios (2,600 m); 9-10 October in two places SE Azurduy (c. 2,500 m); in February 1993 seen to 2,400 m in the Vallegrande area. These are altitudinal records of the distinctive sub-Andean form *dorbygnianus* of the large *P. cirratus* complex. The mistnetted bird was a typical *dorbygnianus*. Also some birds seen at

lower altitudes in Santa Cruz, Chuquisaca and Tarija may have been this form, but other birds seen at low altitudes were more brown. Short (1975, 1982) attributes the morphological variation in the populations inhabiting the western fringe of the chaco (*thamnophiloides*) to secondary intergradation between *dorbygnianus* and the lowland form *pilcomayensis*. The geographical variation in this part of the range requires clarification (Amperi 1990).

- *Veniliornis fumigatus* (Smoky-brown Woodpecker). 18 September 1991 seen in *Alnus* thickets between Abra Portillo and Río Lechéra (2,700 and 3,000 m); 8 October seen in similar habitat on C. Punta Lajas (c. 2550 m). First Chuquisaca records of this woodpecker, known from humid montane forest and relict cloudforest patches throughout the Tropical Andes Region, and with some records in Dpto Tarija (incl. four observations in 1992) and in Jujuy in n-most Argentina.
- *Veniliornis frontalis* (Dot-fronted Woodpecker). 26 March 1992 two seen at 2,300 m near Río Lechéra, 3 February 1993 a pair at 1,850 m near Río Piraymiri. These are altitudinal records of this endemic sub-Andean woodpecker of Bolivia and nw Argentina. Several seen in the low parts.
- *Colaptes punctigula* (Golden-breasted Woodpecker). Seen at 3,100 m near Liriuni near Cochabamba, to near 3,000 m S Río Caine in Potosí, at 2,400-3,400 in Montes Chapeados and at 2,600-3,050 m in Tarija. These are altitudinal records for the distinctive sub-Andean Argentinean/Bolivian form *melanolaemus* of the southern *melanochloros* group of this woodpecker superspecies which occupies almost the entire cis-Andean lowland (see Short 1975, 1982).
- *Campephilus leucopogon* (Cream-backed Woodpecker). Several records in low-altitude forest (at least to 1,730 m) in Tarija, and 15 March 1992 two birds near Cañon Verde (1,150 m). The latter is the first Chuquisaca record.
- *Xiphocolaptes major* (Great Rufous Woodcreeper). 29 September 1991 seen N Eía Timboycito. In March 1992 seen and heard several times between Cañon Verde and El Palmar, and several times here and below C. Bufete and also in the lowlands

near Río Pilcomayo (T). Probably common, but secretive, calling only once or twice at dawn and dusk. The only earlier Chuquisaca record is 16 km N Monteagudo, 1,500 m (Remsen *et al.* 1986). Several records in Tarija (up to 1,730 m), known from Ele-Ele at c. 1,600 m in Dpto Cochabamba and heard by JF 16 September in a small patch of *Erythrina* trees in a gorge at 2,500 m near Río Jaya Maya N Río Caine. This must be the altitudinal record for this widespread Chaco/Cerrado woodcreeper.

- *Xiphorhynchus ocellatus* (Ocellated Woodcreeper). Calls resembling recordings of this species (Hardy *et al.* 1991 b) were heard on a few occasions in the low hills in the Pilcomayo-Parapeti area. Not listed for Chuquisaca but known from the Vallegrande-Masicurí area (SM; J.V. Remsen, *in lit.*).
- *Lepidocolaptes angustirostris* (Narrow-billed Woodcreeper). Common in woodlands and thickets to 1,550 m. Only earlier records for Chuquisaca are 30 km SE Carandayti and 70 km SE Padilla (Remsen *et al.* 1986). Occurs to above 2,000 m in Potosí (Nores & Yzurieta 1984, and observations S Río Caine) and to 2,100 m near Padcaya, which represent altitudinal records of this widespread Chaco/Cerrado woodcreeper.
- *Lepidocolaptes affinis* (Spot-crowned Woodcreeper). In January 1992 several seen in mixed-species flocks at San Lorenzo and La Yunga in the Vallegrande-Masicurí area. A s-wards range extension, as the s-most earlier records are from the ecotone near the Cochabamba/Santa Cruz border.
- *Geositta rufipennis* (Rufous-banded Miner). 1 October 1992 seen at 2,700 m towards the pass S Honduras. The first Tarija record of this widespread bird of the adjacent puna zone.
- *Geositta tenuirostris* (Slender-billed Miner). Fairly common in the Culpina-Villa Charcas area and seen 20 September on C. Corral. 8 October 1991 one seen at 2,780 m on C. Hoyadas SE Azurduy. Together with an old record from Padilla (Bond & Meyer de Schauensee 1942), this indicates the presence of an isolated population away from the continuous puna habitat of the Andes.
- *Upucerthia jelskii* (Plain-breasted Earth-

creeper). In August 1991 seen running under low shrubs near Camargo, and 17 September one seen shortly W Culpina. First Chuquisaca records of this widespread puna earthcreeper.

- *Upucerthia andaecola* (Rock Earthcreeper). Recorded on several mountain ridges in Chuquisaca from the Villa Charcas area to C. Campamentito and near Azurduy, and also common on the crest of the main ridge SE Padcaya and down to 3,000 m (La Cumbre) and 2,700 m (C. Alto de Minas) (T). These are the first record of this common pre-puna earthcreeper for Tarija.
- *Upucerthia ruficauda* (Straight-billed Earthcreeper). 11-12 October 1991 one bird seen clearly when calling from Puyas on a small rocky hill on the southern edge of the village of Azurduy. This record suggests the existence of an isolated population 150 km E of its typical habitat in the puna zone. The bird appeared to be very uniform ochraceous below the white throat (giving a similar colour contrast as in *U. harterti*, Bolivian Earthcreeper), and may well represent an unnamed subspecies. 24-25 September and 16 October seen at Oroza, Honduras and Río Alizos (T), the first Tarija records of this species.
- *Cinclodes fuscus* (Bar-winged Cinclodes). Found commonly along the ridge SE Padcaya. First Tarija record of this widespread Andean bird.
- *Cinclodes atacamensis* (White-winged Cinclodes). 20 September 1991 and 25 March 1992 along Río Puca Pampa; 7 October 1991 at Río Misca Mayu (at only 1,550 m); 11-12 October 1 km NW Azurduy (S); 11 March several near Canaletas W Narvaez (2,000-2,250 m). First Chuquisaca records and an e-wards range extension for this puna bird. Also recorded SE Padcaya, Tarija.
- *Leptasthenura yanacensis* (Tawny Tit-spinetail). 1 October 1992 one pair at 3,000 m W of La Cumbre, and 17 October common at 2,850-3,100 m W C. Alto de Minas pass, all birds in *Polylepis* trees (T). A slight s-wards range extension, as earlier Tarija records are from the Tupiza area, in the arid zone. M. Kessler (pers. comm.) has seen it NW Azurduy, which is the first Chuquisaca record.
- *Synallaxis azarae*, ssp. *superciliosa* (Buff-

browed Spinetail; see Remsen *et al.* 1988 for taxonomic rank and distribution). Generally present in humid shrubbery in Chuquisaca, mainly at 1,500-2,900 m in regrowth shrub near grassy ridges through the semi-deciduous zone and near Azurduy, and also recorded in many places in Santa Cruz and Tarija (S, T). This wide occurrence was surprising considering the few published records, for Chuquisaca only Río Azuero 25 km E Padilla and 16 km N Monteagudo.

- *Cranioleuca pyrrhophia* (Stripe-crowned Spinetail). Recorded near Río Lechéra, common in the C. Campamentito area (S), C. Misión and in the Azurduy area, mainly in *Alnus* and *Podocarpus* forest. Corresponds to the highland ssp. *striaticeps* (S), which represents a s-wards range extension (from Padilla and Tomina). Also birds seen in the corresponding zone SE Padcaya may have been this form, but birds seen at 1,000-1,200 m in southern Tarija and from Narvaez to Cañon Verde corresponded to the more grey nominate subspecies.
- *Asthenes heterura* (Maquis Canastero). 18 September 1991 seen in a steep ravine with some shrubs and *Polylepis* bushes on C. San Francisco; 20 September seen in low shrub towards C. Corral; 26 September along shrubby borders, mainly *Rubus* and melastome bushes, on C. Misión and Bufete; 25 March 1992 one above Puca Pampa (T); 26 March one near Río Puca Laja (T); 27 March heard W Portillo. 14-16 October 1992 seen near Río Alizos (T). First Chuquisaca and Tarija records of this rare bird, which so far has hardly been recorded outside the intermontane basin of Cochabamba. The observed birds appeared to have a more uniform rufous tail than Cochabamba birds, as the central tail-feathers did not appear to be darker toned than the rest.
- *Asthenes punensis/sclateri* (Puno Canastero). 18 September 1991 seen well on C. San Francisco, and probably glimpsed also on Cs Corral, Campamento, Misión and Hoyadas. 17 October 1992 seen on C. Alto de Minas. First Chuquisaca and Tarija records of representatives of this super-species, which has a patchy distribution in the main cordillera.

- *Asthenes maculicauda* (Scribble-tailed Canastero). 17-18 October 1992 common in dense bunch-grass on the highest ridges of C. Alto de Minas (T). First record between the morphologic-ally distinctive populations (Fjelds  & Krabbe 1990) in Cochabamba and Catamarca, Argentina.
- *Phacellodomus striaticeps* (Streak-fronted Thornbird). Rather common in the montane basins throughout the region. Records (T) on the west slopes of the mountains SE Padcaya are the first for Tarija.
- *Phacellodomus rufifrons* (Rufous-fronted Thornbird). A common birds in shrubby gullies and *Alnus* thickets in a rather narrow ecological zone in the Chapeados mountain, but also seen in the lowlands of the E a Tacurvite area and near R o Perapeti. Thus, this species, which is widespread across the Chaco and Brazilian highland, is also well-established (isolated?) in temporarily humid highland habitat in Chuquisaca. New for Dpto Chuquisaca. The chaco and sub-Andean population, *sincipitalis*, is slightly more rufous than the eastern populations, and judging from our field observations, the highland birds in Montes Chapeados have an even more uniform rufous tail, suggesting additional morphological differentiation.
- *Phacellodomus (striaticollis) maculipectus* (Freckle-breasted Thornbird). Seen in several places in Santa Cruz, Chuquisaca and Tarija (T), at 1,800-3,100 m, which is an altitudinal record of this Boliviano/Tucumano endemic. Inhabits a narrow ecological zone with *Alnus*, some *Podocarpus* trees, *Miconia* bushes and bracken, on the transition between the temporarily humid and semi-evergreen zones.
- *Sclerurus albigularis* (Grey-throated Leafscraper). In February 1993 found to be common at La Yunga, 1,400-1,500 m (T). A s-wards range extension, as the s-most earlier records are from the ecotone near the Cochabamba/Santa Cruz border.
- *Batara cinerea* (Giant Antshrike). 25 September 1991 remains of a dead juvenile bird (S, now in USNM, Washington, D.C.) were found near C. Mis n (2230 m). 4 October seen singing on the transition from subtropical to mossy montane forest, and heard on a bushy ridge higher up, on the slope E C. el Tapado (1,850 and 2,000 m). 15 March 1992 heard in Ca n Verde (1,150 m, T). The only earlier record for Chuquisaca is 60 km SE Padilla, 1,300 m (Remsen et al. 1986). Fairly common (many recordings) in the Vallegrande-Masicur  area, at 1,650-2,050 m (T), and seen by N.P. Dreyer (pers. comm.) as high as 2,700 m in Siberia N Comarapa, which are exceptional altitudinal records. In Tarija it was found only at 1,050-1,730 m (T).
- *Thamnophilus palliatus* (Lined Antshrike). In February 1993 found to be common (T, many recordings) at La Yunga in Santa Cruz, representing a s-wards range extension.
- *Thamnophilus ruficapillus* (Rufous-capped Antshrike) appears to be altitudinally disjunct, since we found the sub-Andean form (*cochabambae*) in the lowlands (850-1,300 m) and (mainly) in *Alnus* coppice and bordering *Myrica* shrub in the treeline zone (1,700-2,850 m, an altitudinal record for this antshrike, T) near the more humid eastern fringe of the temporarily humid zone.
- *Dysithamnus mentalis* (Plain Antwreio). Found in February 1993 inside forest at La Yunga, 1,050-1,600 m (T); probably a s-wards range extension.
- *Pyriglena leuconota* (White-backed Fire-eye). 24 September 1991 a female heard and glimpsed in a humid ravine at 2,200 m N C. Lagunillas. First Chuquisaca record of this widespread tropical and premontane antbird.
- *Myrmorchilus strigilatus* (Stripe-backed Antbird). 29 September seen in tangled *Ziziphus* thickets by E a Timboycito near R o Yairi (1,050 m). First Chuquisaca record (see Remsen et al. 1988 for general discussion).
- *Chamaeza campanisona* (Short-tailed Antthrush). Common at 1,050-2,350 m near San Lorenzo, S Loma Grande and at La Yunga in the Vallegrande-Masicur  area (T). A s-wards range extension, as the s-most earlier records are from the Cochabamba/Santa Cruz ecotone.
- *Grallaria guatemalensis* (Scaled Antpitta). In February 1993 tape-recorded at San Lorenzo, Loma Grande and at La Yunga (1,400-2,350 m) in the Vallegrande-Masicur 

area (T). A s-wards range extension, as the only record for Santa Cruz so far was from the Amboro National Park (T.A. Parker, unpublished).

- *Grallaria albigula* (White-throated Antpitta). Seen on two instances and its two-note plaintive call was heard on numerous occasions in shrubby areas and bamboo (but never in tall-growth forest) throughout the semi-evergreen zones (1,050-2,650 m) from C. Campamentito below C. Bufete and from Río Parapeti to Río Misca Mayu, and at (T). First Chuquisaca or Tarija records of this antpitta, which is known from rather few records further n and s.
- *Scytalopus (femoralis) bolivianus* (Southern White-crowned Tapaculo). 2 October 1991 heard on C. Alto Despencillos (1,380 m). 4 October heard W Snía Racete (c. 1,400 m). 16 March 1992 two singing in a humid ravine on the upper reaches of the Río Yahuaryhua (1,500 m); 22 March two singing near a stream E C. Bufete (1,450-1,500 m, T). Common in dense forest undergrowth near streams at 1,050-1,850 m in the Vallegrande-Masicurí area (T). First Chuquisaca records, and a s-wards range extension of this tapaculo, which was known so far only from the Yungas of s Peru and n Bolivia.
- *Scytalopus (magellanicus) zimmeri* (Andean Tapaculo). Although previously recorded only from two localities in Chuquisaca and Tarija, our studies indicate that this endemic form is widespread at 1,700-3,200 m, although not abundant (T). In Chuquisaca it was found mainly in shady ravines in *Alnus*, mixed *Alnus/Podocarpus* or *Polylepis* woodland in the temporarily humid zone or in ecotones towards the adjacent semi-deciduous zone, but near Río Pucapampa it was found also among small shrubs growing along a stream, in otherwise open habitat, and in Tarija it was common in rocky ravines.
- *Chiroxiphia boliviana* (Yungas Manakin). Common in the narrow altitudinal zone 1,050-1,800 m in the semi-evergreen hills of the Vallegrande area (T), around Río Parapeti (S) and below C. Bufete (T), mainly in places in the forest with edges with dense fruiting melastome bushes and *Rubus*. There is only one earlier record of

this manakin from the Bolivian Valles: 16 km N Monteagudo, Chuquisaca (Remsen *et al.* 1987).

A male collected on C. Alto Despencillos (S) is larger (wing 76.5 mm), its mantle more clear sky-blue and red crest feathers longer (17-18 mm) than 12 examined males from Dptos La Paz and Cochabamba (wings 66.5-72.3 mm, crests 12-16 mm), suggesting a subspecific differentiation.

- *Phyllomyias burmeisteri* (Rough-legged Tyrannulet). 2 October 1991 near Cmd Sausi Mayu (1,380 m). There are only five earlier Bolivian records, including one from Dpto Chuquisaca (Remsen *et al.* 1987, Parker & Rocha 1991).
- *Phyllomyias uropygialis* (Tawny-rumped Tyrannulet). 5 October seen in mossy treeline shrubbery on C. el Tapado (1,950 m), and also seen at 2,000 m W Padcaya. One earlier Chuquisaca record, one for Dpto Tarija (Remsen *et al.* 1987), representing the s-most extreme of the range.
- *Suiriri suiriri* (Suiriri Flycatcher). 3 October a pair seen near Río Parapeti (1,350 m). One earlier Chuquisaca record (Remsen *et al.* 1987). Also seen in arid woodland at 2,800 m near Río Caine (first Potosí record). Thus, this widespread flycatcher of the adjacent lowlands may occur high up in the Bolivian Valles.
- *Mecocerculus hellmayri* (Buff-banded Tyrannulet). Scattered observations in semi-deciduous forest at 1,250-2,500 m in Chuquisaca and Tarija (T). Remsen (1984) lists only 15 localities for *M. hellmayri*, from Puno in Peru to Jujuy in nw Argentina, with only one of these sites in Dpto Chuquisaca.
- *Serpophaga nigricans* (Sooty Tyrannulet). 26-27 September seen near El Palmar; 3-5 October along Río Parapeti and in small side streams. First Chuquisaca records of this tyrannulet, which is widespread in adjacent lowlands. In Dpto Tarija seen at Canaletas (2,050 m) and between Huayco and El Tunal.
- *Anairetes parulus* (Tufted Tit-tyrant). 20 September seen near ridgecrest between Ríos Puca Laja and Puca Pampa and 21. September on C. Cobre Khasa. Seen on several instances in *Polylepis*-clad ravines SE Padcaya (T). First Chuquisaca and

Tarija records of this widespread Andean and Patagonian tit-tyrant.

- *Leptopogon amaurocephalus* (Sepia-capped Flycatcher). Brown-capped birds probably representing this species were rather common at 1,400-1,600 m in La Yunga near Vallegrande (T) and at 1,100-1,500 m in Chuquisaca, indicating that this low-altitude flycatcher here invades the altitudinal zone which is inhabited in the Tropical Andes Region by *L. superciliaris* (Slaty-capped Flycatcher).
- *Phylloscartes ventralis* (Mottle-cheeked Tyrannulet). Several observations at 2,300-2,500 m in Siberia and at San Lorenzo represent a slight altitudinal extension (compare Fjeldså & Krabbe 1990).
- *Ochthoeca leucophrys* (White-browed Chat-tyrant). Scattered observation throughout the seasonally arid zone at c. 2,500-3,000 m. Altogether 11 seen SE Padcaya represent the first records for Tarija (T).
- *Polioptila rufipennis* (Rufous-webbed Tyrant). 18 September 1991 near ridge of C. San Francisco, 21 September on C. Cobre Khasa and 22 September several along top ridges between C. Campamentito and C. Campanarios. First Chuquisaca records and range extension of this flycatcher, which is known mainly from *Polylepis* patches in the puna zone (see Fjeldså 1989).
- *Myiotheretes striaticollis* (Myiotheretes striaticollis). Observations on Cs Campanarios and Bufete and in the Azurduy area are the first records for Chuquisaca. The occurrence of this flycatcher is well documented further n and s.
- *Agriornis andicola* (White-tailed Shrike-tyrant). 11 October 1991 one bird was watched for several minutes when it was perched atop a two meter tall *Puya* above a steep rocky slope with scattered *Polylepis cristagalli* bushes 2 km NW Azurduy. The bird could not be found the following day, but may (like all large *Agriornis* species) be expected to move over a considerable area. First Chuquisaca record of this vanishing shrike-tyrant, known from widely scattered records from Ecuador to nw Argentina (Collar *et al.* 1992). Many of the records appear to be in places with large *Puyas* (see Krabbe 1994).
- *Agriornis microptera* (Gray-bellied Shrike-tyrant). 22-26 August and 17 September 1991 seen near Culpina. First Chuquisaca record of this shrike-tyrant of Patagonia and the arid puna zone. Other Bolivian records are in the western highlands, except for one record in Dpto Cochabamba (Remsen *et al.* 1987).
- *Muscisaxicola maculirostris* (Spot-billed Ground-tyrant). 18 September 1991 seen on puna slopes SE Abra Portillo; 26 March one near Río Puca Laja. First Chuquisaca records of this widespread Andean ground-tyrant.
- *Muscisaxicola capistrata* (Cinnamon-bellied Ground-tyrant). 25 August 1991 several seen near Culpina. First Chuquisaca record of this Patagonian migrant.
- *Muscisaxicola rufivertex* (Rufous-capped Ground-tyrant). 20 September 1991 seen E Río Puca Laja; 22 September and 23-25 March in the C. Campamentito area; 8-12 October on C. Hoyadas and several observations near Azurduy. First Chuquisaca records of this widespread Andean ground-tyrant.
- *Knipolegus hudsoni* (Hudson's Black-tyrant). Seen in many places in Chuquisaca, mainly in rangeland in the lower parts of the area from Río Pilcomayo to N Cmd Sausi Mayu. First Chuquisaca records, but Remsen *et al.* (1987) mentioned several records in adjacent lowlands.
- *Myiarchus tuberculifer* (Dusky-capped Flycatcher). Recorded vocal differences between birds of the montane forest zone (plaintive calls only; ssp. *atricaps?*) and lowlands near Cañon Verde (mainly rapid series of *kee-kew* phrases with plaintive calls interspersed) may indicate a considerable s-wards range extension of the lowland form *tuberculifer* (T).
- *Machetornis rixosus* (Cattle Tyrant). 3 October 1991 one in a large tree on the edge of fields and pasture near Río Parapeti (1,350 m). First Chuquisaca record of this widespread lowland flycatcher.
- *Legatus leucophaius* (Piratic Flycatcher). 9 October 1992 five birds singing near Río Emborozú, c. 900 m. First Tarija record of this widespread lowland flycatcher.
- *Tyrannus melancholicus* (Tropical Kingbird). 27 September 1991 by El Palmar; 30 September-1 October near Uruguay; 11-17 March common from Narvaez to El

Palmar. Apparently the first Chuquisaca record of this ubiquitous Neotropical flycatcher.

- *Casiornis rufa* (Rufous Casiornis). Seen on several occasions especially along Snía Pilcomayo n to Añimbo. First Chuquisaca records of this widespread lowland bird.
- *Progne subis* (Purple Martin). 7 October 1992 a small flock near Pampa Grande. The first Tarija record of this Nearctic migrant.
- *Notiochelidon cyanoleuca* (Blue-and-white Swallow). Seen on several occasions in open terrain from 2,100 to 3,200 m in Montes Chapeados and N Río Parapeti and one near Río Pilcomayo (650 m). First Chuquisaca records of this ubiquitous swallow.
- *Riparia riparia* (Sand Martin). 30 September 1991 one bird near Eía Tacurvite. First Chuquisaca record of this common Nearctic migrant.
- *Hirundo rustica* (Barn Swallow). In August 1991 "quite a few" near Culpina. 30 September 1991 seen near Eía Tacurvite. First Chuquisaca record of this common Nearctic migrant.
- *Cistothorus platensis* (Grass Wren). 7 October 1991 one seen on a recently burned grassy and shrubby slope W Río Misca Mayu (1,950 m). First Chuquisaca record of this rather local bird, but ssp. *tucumanus* is known from northern Bolivia as well as Dpto Tarija (Remsen *et al.* 1987) and nw Argentina.
- *Thryothorus genibarbis* (Moustached Wren). Very common at 1,050-1,900 m SE Vallegrande (T), probably representing the Yungas subspecies *bolivianus*.
- *Cinclus schulzi* (Rufous-throated Dipper). Found to be common along clear streams in wooded terrain at 1,750-2,500 m R ridge SE Padcaya (T). There are just a couple of earlier records from Tarija of this dipper (Remsen *et al.* 1985, M. Blair *in lit.*), previously thought to be endemic to nw Argentina.
- *Myadestes ralloides* (Andean Solitaire). 23 March 1991 heard singing near the river between C. Campanarios and Campamentito, at 2,000 m. First Chuquisaca record and a considerable s-wards extension of this bird of the Tropical Andes Region.
- *Turdus serranus* (Glossy-black Thrush). Common at 1,400-2,800 m in the semievergreen forest zones of Montes Chapeados and from C. Alto Despencillos n-wards (T). First Chuquisaca records, but known from corresponding life zones further s and n, and common in the Vallegrande-Masicurí area. Birds sang much in September-October in Chuquisaca, but not in March.
- *Anthus hellmayri* (Hellmayr's Pipit). Seen 22 September 1991 on a high ridge between C. Campamentito and Campanarios; 26 September seen and collected on C. Bufete (2,230 m, S). Probably this species also on grassy ridges on C. Misión, near el Palmar and S Cmd Caja Mayu in Chuquisaca and on the ridge near Abra Tabla SE Vallegrande (2,200 m) (T). Thus this pipit is present high as well as low. There are very few records from the Boliviano/Tucumano part of the species' range (ssp. *hellmayri*).
- *Anthus bogotensis* (Paramo Pipit). 18 October 1992 two birds on C. Alto de Minas, 3,200 m. First record from southern Bolivia of this widespread but patchily distributed Andean pipit.
- *Scaphidura oryzivora* (Giant Cowbird). 1 October seen S Cmd Caja Mayu and 3 October on descent from C. Alto Despencillos to Río Parapeti. First Chuquisaca records of this widespread tropical and sub-Andean bird.
- *Cacicus chrysopterus* (Golden-winged Cacique). 18 September 1991 seen in a narrow ravine with *Alnus* and *Polylepis* forest and also in scattered *Polylepis* trees on steep, rocky slopes up to 3,000 m between Abra Portillo and C. San Francisco. In September-October 1991 seen in several places in the *Alnus*-dominated zone in the humid parts of Montes Chapeados (2,000-2,800 m, S, T) and SE Azurduy (2,450-2,550), on Snías of the Río Parapeti region (1,450 and 1,650) and in shrubby habitat in the intervening lowlands (S). First Chuquisaca records. Several have also been seen at 2,150-2,350 in Santa Cruz and Tarija, and is also known from similar altitudes in sub-Andean nw Argentina, and widely in adjacent lowlands.
- *Basileuterus signatus* (Pale-legged Warbler). Widespread in semi-ever-green temperate-zone forest at 1,500-2,800 m. First

- Chuquisaca records, but known from corresponding life zones further n and s.
- *Tersina viridis* (Swallow Tanager). 5 October several birds in tops of large trees near Río Parapeti (1,400 m), near high banks and rocks over-hanging the river (potential nestsites). This represents a s-wards range extension for this widespread tropical bird.
 - *Chlorophonia cyanea* (Blue-naped Chlorophonia). 26 September 1991 seen below C. Bufete and 3 October during the ascent to Snía Racete (both times at 1,600 m). First Chuquisaca records; the Andean premontane population is known s to Yungas of Santa Cruz, and the species was found in the Vallegrande-Masicurí area.
 - *Tangara xanthocephala* (Saffron-crowned Tanager). 21 January 1992 and 7 February 1993 seen at La Yunga W Masicurí, a slight s-wards range extension.
 - *Tangara argyrofenges* (Straw-backed Tanager). Altogether four observations at San Lorenzo and La Yunga W Masicurí represent a slight s-wards range extension.
 - *Anisognathus flavinuchus* (Blue-winged Mountain-tanager). 26 September 1991 one male below C. Bufete (S); 19 March one seen here in a mixed flock; seen and heard 3-4 October on Snía Racete (1,500-1,650 m, T). The southernmost published records are in the Yungas of Cochabamba; however, it was found to be common in the Vallegrande-Masicurí area. The male specimen from below C. Bufete was large, with the panel of the primaries Yale blue to Olympic blue, the outer webs of the rectrices Indigo Blue to Dusky Blue, against wing-panel greenish blue (Capri Blue) and sides of tail Blackish Greenblue in 20 examined specimens from La Paz and Cochabamba, indicating a subspecific differentiation.
 - *Piranga leucoptera* (White-winged Tanager). 2 October 1991 on C. Alto Despencillos and 4 October on Snía Racete (1,450 and 1,600 m). First Chuquisaca records, the s-most other records of this premontane forest bird being from Dpto Santa Cruz (Remsen *et al.* 1987, and recorded at La Yunga in the Vallegrande-Masicurí area T).
 - *Ramphocelus carbo* (Silver-beaked Tanager). Seen during all visits at La Yunga SE Vallegrande (c. 1,500 m), which is an exceptional altitudinal record and a slight s-wards range extension.
 - *Hemithraupis guira* (Guira Tanager). 3 and 4 October 1991 seen on Snía Racete (1,700 and 1,800 m). First Chuquisaca record of this tanager, which is widespread in adjacent lowlands and sub-Andean forest zones.
 - *Catamblyrhynchus diadema* (Plush-capped Finch). 21 March 1992 two seen in bamboo and *Polylepis* W C. Bufete (2,500 m). First Chuquisaca record, but widespread in the Tropical Andes Region and also known from nw Argentina.
 - *Saltator rufiventris* (Rufous-bellied Saltator). 19 September 1991 one at Río Lechéra; 20 September at least one at Río Puca Laja; 21 September possibly heard in a large *Alnus* woodland on C. Cobre Khasa; 11-12. October one juv. just outside Azurduy village and at least one pair in a woodland 2 km nw. Not found in Montes Chapeados in March 1992, so the population is probably very small. 17 October 1992 a pair between Río Alizos and C. Alto de Minas SE Padcaya. First Chuquisaca and Tarija records of this threatened bird, known from montane basins from Inquisivi in La Paz (where fairly common; S. Ma•er 1993) to extreme nw Argentina (Remsen *et al.* 1988, Collar *et al.* 1992).
 - *Sporophila caerulescens* (Double-collared Seedeater). Common near Canaletas (2,050-2,250 m); common between Narvaez and Río Yahuaryhua; 26-27 March 1992 several singing near Río Lechéra (2,250 m). Altitudinal and first Chuquisaca records of this widespread seedeater.
 - *Sicalis luteola* (Grassland Yellow-finch). 25-26 August two flocks on the lake shore S Culpina. First Chuquisaca records of this widespread but somewhat local yellow-finch.
 - *Sicalis citrina* (Stripe-tailed Yellow-finch). 19 September 1991 two birds perched in a large tree and 26-27 March 1992 many singing birds near Río Lechéra (T). 26 September 1991 seen well (10 m distance) on the descent from C. Mision to Bufete. 11 March 1992 two birds singing and displaying near Narvaez; 26 March one singing (T) near Río Puca Laja. 12 September 1991 JF saw one 5 km S Clisa, Cochabamba; and S. Arias (verbally) has

seen one in Snía de Huanchaca, Santa Cruz. 2 February and 10 March 1993 one seen singing (T) between Guadalupe and Abra Tabla near Vallegrande. First records for the Andean part of Santa Cruz and for Dptos Chuquisaca, Cochabamba and Tarija, the three earlier Bolivian records of this widespread but very sporadic yellowfinch being from Dptos La Paz, Beni and eastern Santa Cruz (Fjeldsá & Krabbe 1989, Parker & Rocha 1991).

- *Sicalis flaveola* (Saffron Finch). Flocks seen in villages and farms in the lowlands and also at 2,050-3,000 m near Vallegrande, in Azurduy, Culpina, near Río Lechéra and near Canaletas. This indicates that the highland form *koenigi* may be fairly widely distributed in warm basins in the pre-puna zone between the *terra typica* (2,400-4,000 m in nw Argentina; see Hoy 1978) to the Cochabamba Basin (around 2,500 m, large series in the Swedish Natural History Museum corresponding well with the description of *koenigi*, although not compared directly with it; Fjeldsá & Krabbe 1989).
- *Sicalis luteocephala* (Citron-headed Yellowfinch). Outside the core area in the Cochabamba Basin we have seen this restricted-range yellowfinch at Culpina, Villa Charcas and Azurduy. All observations are near farms and villages, usually very dense groups on the ground in the shade of roadside bushes and in eroded creeks. Earlier records outside Cochabamba are from Sucre in Chuquisaca and Oploco in Potosí, and a recent record is from La Quiaca in Jujuy, nw Argentina (M. Pearman).
- *Diuca diuca* (Common Diuca-finch). Fairly common in the Culpina area. First Chuquisaca record, the only other Bolivian record of this Argentinean and Chilean bird being from Oploca, Dpto Potosí (Remsen *et al.* 1987, Ridgely & Tudor 1989).
- *Idiopsar brachyurus* (Short-tailed Finch). 17 October 1992 one or two pairs high up on C. Alto de Minas, at 3,200 m. First Tarija record. This finch has so far been recorded only at high altitudes in Cordillera Real in Puno and La Paz, C. Tunari and Quehuiña Pampa in Cochabamba, and in nw Argentina.
- *Phrygilus unicolor* (Plumbeous Sierra-finch).

Generally distributed on grassy ridges above 2,700 m in Cochabamba, Chuquisaca and SE Padcaya. Previously unrecorded for Tarija.

- *Emberizoides herbicola* (Wedge-tailed Grassfinch). 28 September 1991 one singing in hills N El Palmar (1,300 m). First Chuquisaca record of this bird, which is widespread in adjacent lowlands.
- *Catamenia inornata* (Plain-colored Seedeater). Seen on several occasions on grassy ridges in the high parts of the Chuquisaca study area (Appendix III), and on five occasions SE Padcaya. First Chuquisaca and Tarija records, but the species is common in the corresponding life-zones further n and s.
- *Poospiza boliviana* (Bolivian Warbling-finch). Seen between Abra Portillo and C. San Francisco, near Ríos Lechéra and Puca Laja, along Río Puco Pampa, around Azurduy and also SE Padcaya. Nearly all observations (in Dptos La Paz and Cochabamba as well) were near tall dead herbs (*Viguiera*) in the ecotones between fields and woodland, generally 1-2 pairs in places with a much larger number of *P. hypochondria*. This poorly known Bolivian endemic appears to be restricted to what is core habitat for the more widespread and ecologically tolerant *P. hypochondria* (Rufous-sided Warbling-finch). It could be specialised to use some resources found in small amounts in good *P. hypochondria* habitat, but its precise role is not understood by us.
- *Poospiza (nigrorufa) whitii* (Black-and-rufous Warbling-finch). 12 October 1991 found in a bushy ravine outside Azurduy (S, 2,650 m, an exceptional altitudinal record of this pre-Andean semispecies; however, N.P. Dreyer [pers. comm.] reports seeing this species at 2,700 near Siberia on the Santa Cruz/Cochabamba border).
- *Carduelis atrata* (Black Siskin). In September in the Culpina-Portillo area and in March near Río Pucapampa. First Chuquisaca records of this widespread Andean siskin.

3.2 The southwards reduction in numbers of humid-forest species

Despite the presence of humid forest on many mountain scarps in southern Bolivia and northern Argentina, most Andean cloud-forest have their southern limit south of the Siberia watershed near the Cochabamba/Santa Cruz border in central Bolivia. Of the few species which continue, patchily or more or less continually, further to the south, the majority must be characterised as premontane rather than montane. *Ocreatus underwoodii* (Booted Racket-tail) has been recorded in extreme northern Chuquisaca, and transgression to southern Bolivia is known for *Conopophaga ardesiaca* (Slaty Gnatcatcher) and *Phyllomyias uropygialis*. Some species continue to nw Argentina (*Tigrisoma fasciatum*, *Harpyhaliaetus solitarius*, *Columba fasciata*, *Glaucidium [jardini]* *bolivianum*, *Adelomyia melanogenys* (Speckled Hummingbird), *Colibri thalassinus* (Green Violetear), *Veniliornis fumigatus*, *Piculus rubiginosus* (Golden-olive Woodpecker), *Synallaxis azarae*, the *Scytalopus [magellanicus]* *simonsi/superciliaris/zimmeri* group,

Mecocerculus leucophrys (White-throated Tyrannulet), *Pyrrhomyias cinnamomea* (Cinnamon Flycatcher), *Contopus fumigatus* (Greater Pewee), *Knipolegus signatus* (Plumbeous Tyrant), *Myiodynastes chrysocephalus* (Golden-crowned Flycatcher), *Troglodytes solstitialis* (House Wren), *Turdus serranus*, *Chlorospingus ophthalmicus* (Common Bush-tanager), *Thlypopsis ruficeps* (Rust-and-yellow Tanager), *Catamblyrhynchus diadema* and *Atlapetes torquatus* (Stripe-headed Brush-finch); a few additional species are best characterised as foothill birds (see Appendix III).

Our new data, presented above, expand the list of cloud-forest birds which extend their range south of the Siberia watershed. In the Valleggrande-Macusirí area we recorded *Odontophorus speciosus*, *Otus ingens*, *Aulacorhynchus coeruleicinctus*, *Lepidocolaptes affinis*, *Sclerurus albigularis*, *Dysithamnus mentalis*, *Chamaeza campanisona*, *Grallaria guatemalensis*, *Thryothorus genibarbis*, *Tangara argyrofengens* and *Tangara xanthocephala*. *Piranga leucoptera* was recorded to the Río Parapeti area, and the more surprising

Table I. Number of bird species recorded in humid montane (= temperate) forest habitat in four different areas in Bolivia and northwestern Argentina, classified according to their principal life-zones.

	Yungas of La Paz	Yungas of Cochabamba	Montes Chapeados	Calilegua Scarp
Typical life zone				
Principally in the low-lands	4	4	16	11
Both lowlands and humid Andean	22	22	26	20
Andes, in sub- or premontane zones	52	44	18	12
Humid submontane to montane zones	62	55	16	12
Humid montane zone, incl. elfin forest	49	44	3	4
Boliviano/Tucumano forest	1	2	9	11
Andes basins and high-lands	8	8	6	11
	194	179	94	81

extensions were *Ciccaba albitarsus*, *Aeronautes montivagus*, *Trogon personatus*, *Scytalopus bolivianus*, *Chiroxiphia boliviana*, *Myadestes ralloides*, *Chlorophonia cyanea* and *Anisognathus flavinucha* to Montes Chapeados (all these except *M. ralloides* also seen near Vallegrande).

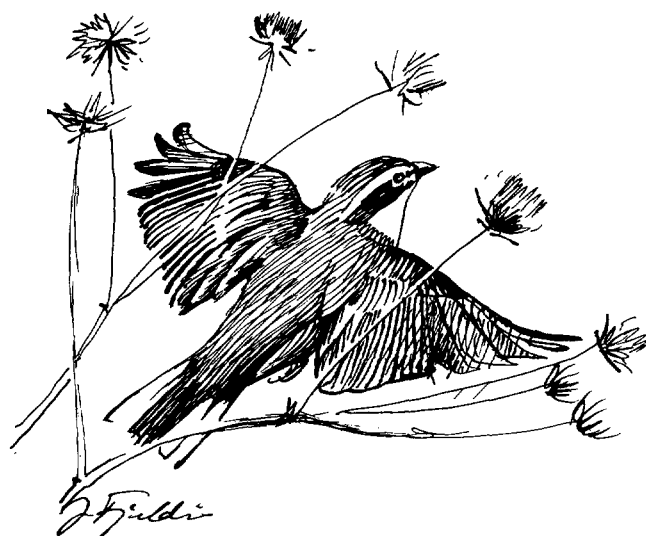
Table I demonstrates the regional variation in number of birds inhabiting humid montane forest habitat, as known presently. Among the c. 250 Andean species which in the Tropical Andes Region can be regarded as typical of the montane forest (2,500-3,800 m; lines 4 and 5 in Table I), 99 reach the Yungas of Cochabamba, 64 of these continue to the cloud forest of the Siberia Watershed N Comarapa in Santa Cruz (Remsen *et al.* 1985-87, Clarke 1991, SM, N. Dreyer pers. comm.). Only 19 of these reach the humid forests in Chuquisaca and 16 reach the Calilegua rainforest in nw Argentina. The decline is most extreme if we consider species which are partial to elfin forests and treeline habitat (line 5 in Table 1).

3.3 Regional differences in ecological amplitudes and niche packing

Table II compares the habitat segregation of the rather few birds which were well established in montane forest habitat in Chuquisaca. Most of these species show a broad ecological amplitude, and this applies even to species which are quite narrowly bound to cloud forest in the Tropical Andes Region: *Mecocerculus leucophrys* was sometimes found in tiny patches of *Alnus* or other deciduous shrubs on barren and degraded slopes (*Veniliornis fumigatus*, a rare species not included in Table II, was found only in *Alnus* thickets in the seasonally humid zone). The habitat selection shown for *Atlapetes torquata* and *Chlorospingus ophthalmicus* is broad compared with their usual occurrence in the Tropical Andes Region. The latter species also has a wide altitudinal range (1,050-2,700 m), while in the Tropical Andes Region, it inhabits mainly the subtropical zone (Graves 1985, Isler & Isler 1987). *Myioborus brunniceps* (Brown-capped Whitestart) and *Atlapetes fulviceps* (Fulvous-headed Brush-finch), southern derivatives of two species groups inhabiting

humid montane shrub in the Tropical Andes Region, also show broad ecological amplitudes in Chuquisaca. Also other endemic taxa of the Boliviano/Tucumano Forest (except *Eriocnemis glaucopoides*, Blue-capped Puff-leg) inhabit deciduous as well as semi-evergreen forest.

Many birds of the lowland deciduous woodlands, scrub habitats and edges of pastures and cultivated land move some distance up along the valleys of Chuquisaca (Table I), and one-third of them can even be found high up in the montane basins, especially so in the semiarid Cochabamba Basin (see above and in Fjelds  1987 and Remsen *et al.* 1986, 1987).



Bolivian Warbling-Finch (*Poospiza boliviana*), an endemic of Bolivian montane basins.

It was even more surprising to find several lowland forms in the semi-evergreen zone on forested sub-Andean ridges or even in fairly unbroken forest on the Andean slope (*Sarcoramphus papa* to 2,850 m, *Elanoides forficatus* to 2,200 m, *Micrastur ruficollis* to 2,350 m, *Aramides cajanea* to 1,700 m, *Caprimulgus rufus* [Rufous Nightjar] to 2,050 m, *Trogon curucui* and *Ramphastos toco* to 1,750 m, *Phaethornis superciliosus* to 1,800 m, *Synallaxis frontalis* [Sooty-fronted Spinetail to 2,750 m, *Pyriglena leuconota* to 2,100 m, two *Cyanocorax* species to 2,300 m, *Parula pitiayumi* [Tropical Parula to 1,850 m, *Basileuterus bivittatus* [Two-banded Warbler] to 2,100 m, *Thraupis sayaca* [Sayaca Tanager] to 2,850 m). Altitudinal records for *Veniliornis frontalis* (2,300 m), *Cychlaris gujanensis* (Rufous-browed Peppershrike, 2,900 m) and *Sporophila caerulescens* (2,250 m) are noteworthy, as well. A fairly abrupt turnover of species is seen at 1,900-2,000 m (Appendix III); above this level there is a fairly stable condensation zone with mossy *Podocarpus*-dominated cloud forest. It is noteworthy that many birds normally associated with lowland habitat have rather isolated populations above this zone, in humid

shrubbery and bracken habitat near the treeline (see Table II). Thus, a bimodal distribution, sometimes with a distinctive altitudinal hiatus, appears to exist between lowland populations and those in ecotones between ever humid and temporarily humid zones. This applied to birds of shrub and grassland (*Rhynchotus rufescens* [Red-winged Tinamou]; *Phacellodomus* [striaticollis] *maculipectus* and *Anthus hellmayri*), woodland (*Accipiter* spp., *Columbina picui* [Picui Grounddove], *Picumnus cirratus*, *Cranioleuca pyrrhophia*, *Thamnophilus ruficapillus*, *Hirundinea ferrugina* [Cliff Flycatcher; known to 3,900 m in Cochabamba] and *Cacicus chrysopterus*) and fairly open habitats (*Colaptes punctigula*, *Furnarius rufus* [Rufous Hornero], *Phacellodomus rufifrons*, *Pitangus sulphuratus* [Great Kiskadee], *Molothrus badius* [Bay-winged Cowbird] and *bonariensis* [Shiny Cowbird; known to 3,350 m in Potosí], *Thraupis sayaca*, *Sicalis flaveola* and *Embernagra platensis* [Great Pampa-finch]).

Table I. Number of bird species recorded in humid montane (= temperate) forest habitat in four different areas in Bolivia and northwestern Argentina, classified according to their principal life-zones.

	Yungas of La Paz	Yungas of Cochabamba	Montes Chapeados	Calilegua Scarp
Typical life zone				
Principally in the low-lands	4	4	16	11
Both lowlands and humid Andean	22	22	26	20
Andes, in sub- or premontane zones	52	44	18	12
Humid submontane to montane zones	62	55	16	12
Humid montane zone, incl. elfin forest	49	44	3	4
Boliviano/Tucumano forest	1	2	9	11
Andes basins and high-lands	8	8	6	11
	194	179	94	81

Table II. Habitat distribution of birds in different types of temperate forest and woodland in Chuquisaca. • = recorded at least once; + = recorded in at least 25% of the observation sites in this habitat category; ■ = ubiquitous. The list includes only species found in at least 25% of the study sites in at least one habitat category. Species marked * are restricted to humid/semihumid Andean forest (BT* = mainly in the Boliviano/Tucumano formation); species marked A inhabit more arid habitats in the Andes; species marked L inhabit mainly lowlands; the remaining species inhabit a broad spectrum of habitats. The habitats are divided in (1) Relict patches in semi-arid, at 2500-3000m: (1) *Alnus*-dominated, (2) quebracho-type (Quebr., 2200-2700 m) and (3) *Podocarpus*-dominated types; humid zone, above 2500 m, (4) *Alnus*-dominated treeline habitat and (5) mossy *Podocarpus*- and *Eugenia*-dominated forest; and habitats at 2000-2500 m, (6) closed forest and (7) edges and more or less open or bushy habitat.

Habitats	Semiarid zone			Humid zone		Humid 2,000-2,500m	
	<i>Alnus</i>	Quebr.	<i>Podocarp.</i>	<i>Alnus</i>	Mossy	Closed	Edges
<i>Penelope dabbeni</i> BT*		•	+	+	+	+	+
<i>Columba fasciata</i> *			+	•	+		+
<i>Leptotila megalura</i> *		+	+	•	+	+	+
<i>Aratinga mitrata</i> *		+	•	•	•	•	•
<i>Pyrrhura molinae</i>		+		•	•	•	•
<i>Amazona tucumana</i> BT*		+	•	+	•	•	•
<i>Adelomyia melanogenys</i> *						•	+
<i>Eriocnemis glauco.</i> BT*			•	+	+	+	+
<i>Sappho sparganura</i> A	+	+	+	+	+		+
<i>Picumnus cirratus</i> L			+	+	•		
<i>Leptasthenura fulig.</i> A	+		+	■	+		
<i>Synallaxis azarae</i> *	•		+	■	+	•	
<i>Cranioleuca pyrrhop.</i>	•	+	■				
<i>Phacell. rufifrons</i> L	+	+	•				
<i>Phacell. striaticol.</i>	+		+	•			
<i>Syndactyla rufosuper.</i>			•	■	■	+	+
<i>Thamnophilus caerul.</i>			•	•	+	•	+
<i>Thamnophilus ruficap.</i>	•		+	+	+		•
<i>Grallaria albigula</i> BT*?				+	•		■
<i>Scytalopus (magell.)</i> *	+		+	+	+		•
<i>Elaenia albiceps</i>	•	•	+	■	■	+	■
<i>Mecocerc. leucoph.</i> *	+	+	+	■	■	+	■
<i>Knipolegus signatus</i> *			•	+	+	+	+
<i>Myiarchus tuberculifer</i>	•		•	+	+	+	+
<i>Troglodytes aedon</i>	+	+	+	+			+
<i>Troglodytes solstitialis</i> *	•	•	+	+	■		+
<i>Turdus chiguanco</i> A	+	•	+	+	•		
<i>Turdus serranus</i> *					+	+	+
<i>Cyclarhis gujanensis</i>	•		•	•	•		+
<i>Cacicus chrysopterus</i> L	•			+			+
<i>Myioborus brunni.</i> BT*	■	+	+	+	+	•	+
<i>Basileuterus signatus</i> *				+	+		+
<i>Chlorospingus ophth.</i> *		+	•	+	+	•	+
<i>Saltator aurantiros.</i>	+	+	+	+	•		•
<i>Atlappetes fulviceps</i> BT*	+	+	+	■	+		•
<i>Atlappetes torquatus</i> *		•		+	+	•	•
<i>Zonotrichia capensis</i>	■	+	+	+	+		•
<i>Pospiza erythro.</i> BT*	•	•	+		+	•	

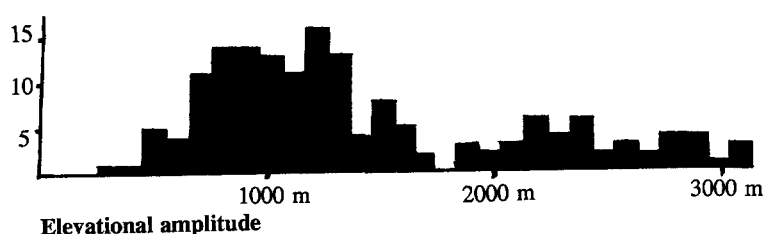


Figure 5. Altitudinal amplitudes of birds recorded along the principal transects in Chuquisaca (species in at least five places; records shown in Appendix III).

However, disjunct altitudinal distributions of *Troglodytes aedon* and *Zonotrichia capensis* [Rufous-collared Sparrow] will be found also in other parts of the Andes. *Syndactyla rufosuperciliaris* [Buff-browed Foliage-gleaner] is continuously distributed from lowlands to treeline in Chuquisaca. For *Batara cinerea* the observations are too few to tell whether the occurrence in the premontane forest is isolated from that in the lowlands.

Altitudinal amplitudes (Fig. 5) were determined by setting the lower limit for birds which are widespread in adjacent lowlands to 500 m, and using data for all species (except open-land birds), recorded in at least five places (Appendix III). The average amplitude is 1,421 m (N=164 species, standard deviation ± 586 m, 23% species spanning 2,000 m or more). For species which do not inhabit adjacent lowlands the average amplitude is 1,179 m (N=82, s.d. ± 462 m, 7.8% of the species spanning 2,000 m or more). The variation in altitudinal amplitudes is bimodal, the main bulk (92 species) at 600-1,200 m, and a smaller group (34 species) at 2,000-2,800 m. Small amplitudes characterise genuine lowland birds and specialists of the uppermost shrub zone, but also *Chiroxiphia boliviana* and *Anisognathus flavinuchus* of the premontane forest (Appendix III). These data can be compared with those (based on mistnetting) from a humid Andean slope in Peru (Terborgh 1971, 1977). The transects in Peru showed a much denser altitudinal packing than in

Chuquisaca, most species spanning 100-1,000 m (mean 741 m for 207 species that did not reach the lowest terminus of the transect, and only 1% spanning 2,000 m or more). However, less detailed studies from isolated tropical mountains with few genuine high-altitude species show some up-hill expansions of premontane species (Bloch *et al.* 1991, Robbins *et al.* 1987, (Terborgh & Weske 1975).

Table III. Population parameters relating to the three studies shown in Fig. 4. As a measure of diversity, we found the Briloin Index (Hurtubia 1973) most suitable, since randomness of the sample is not granted and because this formula describes the actual data rather than estimating the total diversity (as done by the Shannon-Wiener Index).

	Yungas of C- ochabamba	Parapeti region	Montes Chapeados
Total no. of species recorded in each study area (in brackets those covered by the Fig. 4 sample)	72 (52)	62 (39)	56 (39)
% of the species being partial to humid forest	81%	38%	34%
Briloin Index	3.41	2.63	2.73

3.4 Regional differences in community structure

Data on the relative frequency of species in the most humid parts of Montes Chapeados and the Río Parapeti area were compared (Fig. 6, Table III) with data collected near the southern end of the cloud-forest zone of the Tropical Andes Region (data collected 16-20 October 1991 in Tablas Montes near the Cochabamba-Villa Tunari Road, at the upper left of Fig. 2). The three samples are suited for comparison because all were from similar altitudinal zones and covering a variety of habitats within somewhat disturbed areas with mosaics of primary forest, glades and ecotones with dense second-growth shrub.

The Chapeados and Parapeti samples were collected over several days of wandering, whereas the Yungas sample was collected within only two square kilometers. Although the latter sample covered a restricted area, it had a high number of species (Table III). As much as 81% of the recorded Yungas birds were humid forest specialists, compared to only 38 and 34% in the Parapeti and Chapeados samples. There is a corresponding increase of non-specialists, relatively as well as in absolute terms: from 10 species in the Yungas to 22 in the Parapeti forests, 16 in the Chapeados forests (Fig. 6). Thus, non-forest birds fill up part of the void caused by the paucity of genuine humid-forest birds. However, the diversity index drops (Table III; note also the reduced "tails" of the histograms

in Fig. 6). Three of the dominant birds in the Yungas sample are associated with edges and pastured glades (*Elaenia albiceps* [White-crested Elaenia], *Zonotrichia capensis*, *Geotrygon frenata*; also *Buteo magnirostris* [Roadside Hawk] and *Tyrannus melancholicus* were present only near glades). Excluding such opportunists, the Yungas sample represents a forest-bird community of high diversity, with only 1-3 records of most species. In contrasts to this, the forest birds *Mecocerculus leucophrys*, *Syndactyla rufosuperciliaris* and *Myioborus bruniceps* are abundant in Chuquisaca almost anywhere in the semi-evergreen zone (Table II) from tall forest to coppice and shrub.

Compared with the Yungas, the forests of Chuquisaca are characterised by a fauna with only few of those species which typically form mixed feeding parties (see Fjeldså & Krabbe 1990), and by a relative increase in the number of unspecialised and territorial furnarids and tyrannids (compare Thiollay 1991 and Christiansen & Pitter in press). Also an almost total lack of Coeribidae in Chuquisaca is striking; flowerpiercers (*Diglossa*) being recorded on only three instances (Appendix III). Nectarivorous birds were particularly scarce in the lowlands (omitting parrots eating *Tabebuia* flowers). The higher parts of the semi-evergreen zone in Chuquisaca have only five nectarivorous species (and only *Eriocnemis glaucopoides* and *Sappho sparganura* [Red-tailed Comet] were seen in September-October). The corresponding zone in the Yungas has no less than 17 nectarivores.

The Buff-wed Spinetail (*Synallaxis azarae*, ssp. *superciliosa*) is one of the commonest birds in humid montane shrubbery in Chuquisaca.

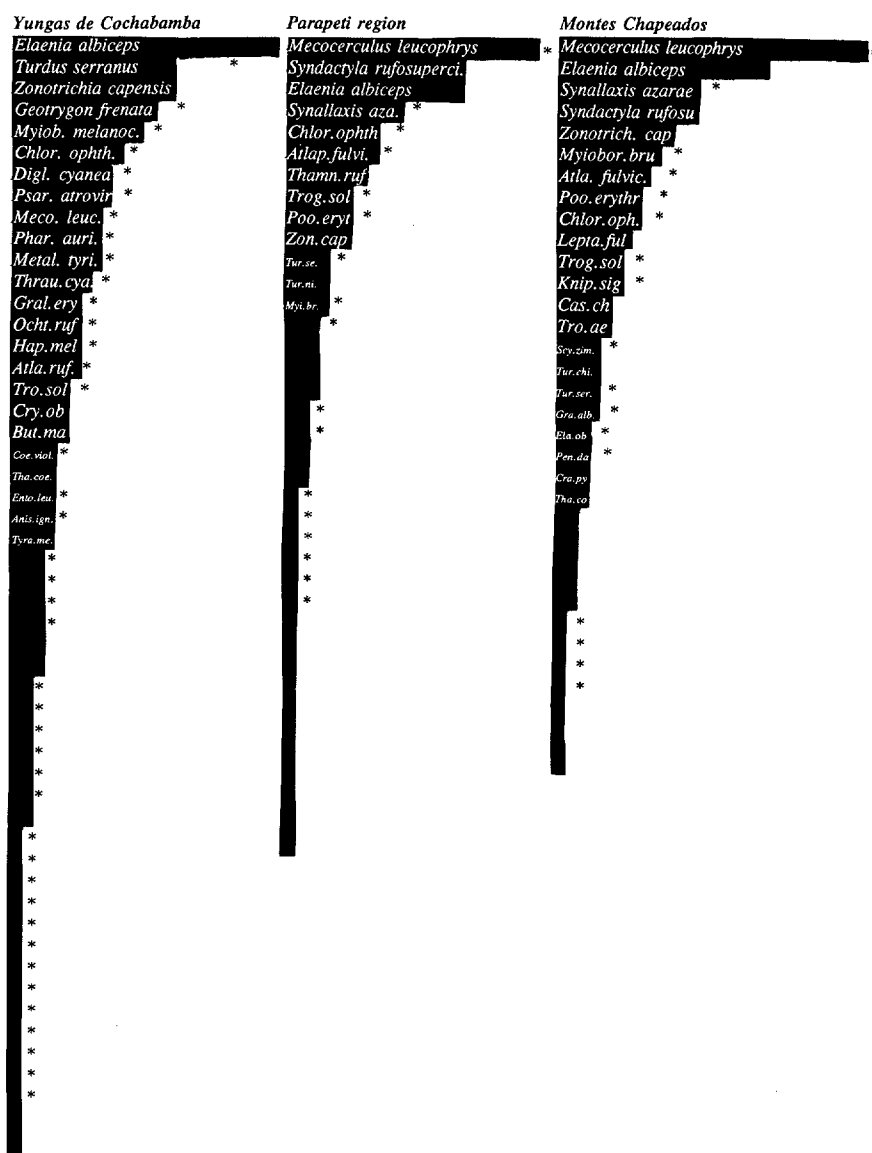
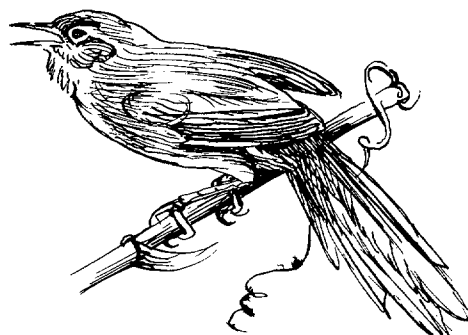


Figure 6. Number of records of individual bird species in three areas: Tablas Montes at 2,600-2,750 m near the Villa Tunari road in the Yungas of Cochabamba, studied 16-20 October 1991; the semievergreen zone of the Parapeti region, at 2,200-2,900 m, studied 4-10 October 1991; and the semievergreen zone in Montes Chapeados, at 2,200-2,900 m, studied 22-26 September 1991. Each of the three histograms sums up all species records made in 35 independent one-hectar plots, each searched for ten minutes (see Materials and Methods for further comments). The diagrams include species names (or abbreviated names) as far as space permits. Species which are partial to humid montane forest are marked with *.

4. Biogeographical patterns

4.1 The southwards reduction of the cloud forest avifauna

The cloud forests of the Tropical Andes Region has an exceedingly rich and complex avifauna, with many vicariance patterns. Several large radiations are endemic to this region (e.g., the hum-mingbird genera *Aglaeactis*, *Coeligena*, *Metallura*, *Heliangelus*; the *Schizoeaca* spinetails; *Grallaricula antpittas*; the flycatchers genus *Myiophobus*; the mount-ain tanagers *Buthraupis/Bangsia* and *Iridosornis* and *Hemispingus* tanagers) or are represented only by one or two species or superspecies outside it (e.g., the hummingbird genus *Eriocnemis*; *Grallaria antpittas*; the flycatchers genera *Ochthoeca/Silvicultrix*; flowerpiercers *Diglossa*; and brushfinches *Atlapetes*). DNA divergence data demonstrate that the diversification of species proceeded explosively during the last few million of years, during the uplift and folding of the northern Andes (Fjelds  1994), when a very complex system of high, humidity-capturing ridges and deep intersecting vallies were formed. At the same time, the species were affected by climatic fluc-tuations of Croll-Milankowitch type, first low amplitude/high frequency oscilla-tions, and during the last 0.9 million years also high-amplitude fluctuations every 100.000 years (e.g., Hooghiemstra *et al.* 1993). The distributions of neoendemic species are correlated with the existence of old taxa with relictual distributions; there-fore, new species may evolve from small populations that survive severe climatic oscillations in places which remained ecologically stable, rather than because of the physical barriers as such (Fjelds  in press).According to this interpretation, the diversification is associated with the existence of certain mountains which have a predictable rainfall, cloud-cover or mist zone (as-sociated with stable atmospheric in-versions) in spite of the global climatic changes.

The radiation of Andean forest birds is assumed to have happened mainly in the northern Andes (Chapman 1926). The few

representatives that live south of the ecotone near the Cochabamba/Santa Cruz border can therefore be regarded as younger derivatives. The claimed sub-species differentiation in *Tigrisoma fasciatum*, *Geotrygon frenata* and *Uropsalis lyra* between the Yungas of Cochabamba and the corresponding habitat in nw Argentina suggests that the gene flow is sporadic. Also the indication of a morphological differentiation of Chuquisaca populations of *Chiroxiphia boliviana* and *Anisognathus flavinuchus* suggests interrupted gene flow. The existence of endemic Boliviano/ Tucumano Forest birds with sister taxa in the Tropical Andes Region (see below) suggests long gene flow breaks in the past. It is worth noting that we found no *Cinclus* species in apparently suitable habitats in Chuquisaca, indicating a considerable disjunction between *C. leucocephalus* (White-capped Dipper) of the Tropical Andes Region and its southern derivate *C. schulzi*.

The distributional data indicate that (apart from the seasonality of the rainfall) the most effective single element of the south Bolivian filter barrier may be the R o Pilaya Canyon. Several species found in Montes Chapeados remain unrecorded in Tarija and in the well studied scarp forests of n-most Argentina.

Most of the humid-forest birds found S 18 S are premontane (subtropical) rather than montane (Table 1). Also within the Tropical Andes Region, premontane birds show less disjunct (and longer) distri-bution ranges and less differentiation than specialists of the montane (temperate-zone) forest (Graves 1985, 1988). The strongest tendency for disjunct distributions and checkerboard and leap-frog variation is shown by the specialised birds of the cool and misty treeline (elfin forest) habitat. It is noteworthy that such species have been unable to colonise or maintain populations in the Boliviano/Tucumano Forest. *Scytalopus* is represented by the same taxon (*zimmeri*) n and s of R o Pilaya, but this treeline bird sometimes survive in rocky ravines with no other vegetation than tall tussockgrass and some shrubs.

4.2 Biogeographic patterns of the birds of Chaco, Cerrado and Paranense Forest, and their invasion of the Andean scene

The numerous sandstone ridges which make up the forested Andean foothills in Bolivia and nw Argentina are erosion remnants of a

land surface that was continuous with the highlands of southern Brazil during the Tertiary. However, a geological subsidence on the Pliocene/ Pleistocene transition led to the formation of wide intervening lowlands, known as the Chaco (Fig. 1). This low-laying area, which now separates the Brazilian and sub-Andean formations, is characterised as low land with xeric-adapted woodlands and

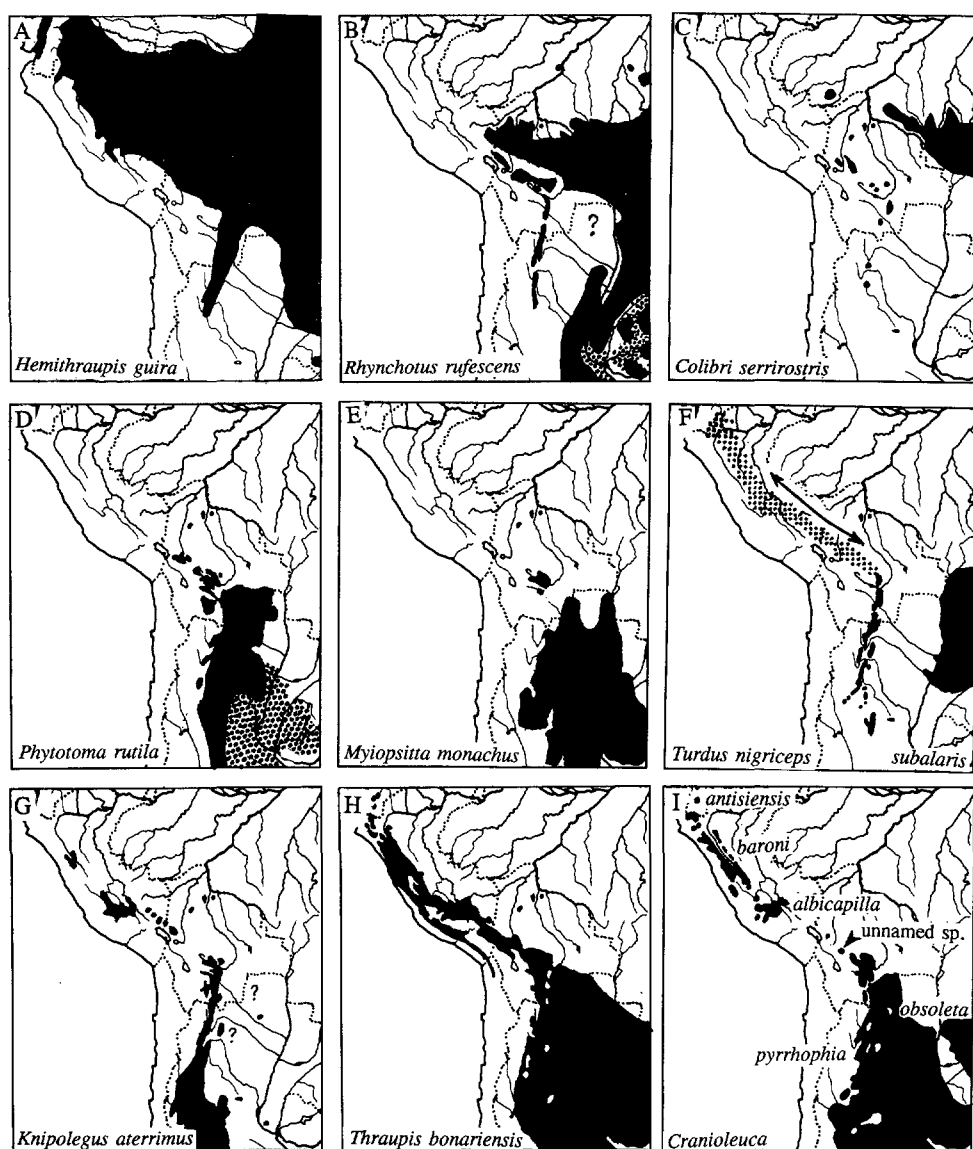


Figure 7. Distributions of selected bird species in central South America. The examples comprise taxa which are widespread in lowlands east of the Andes and enter Andean habitats to variable degrees.

a steady state of habitat alteration caused by extensive seasonal inundations and erratic shifts of the floodwater pattern and only few small erosion remnants of the old plateau (Ramella & Spichiger 1989, Adamoli *et al.* 1990).

The Chaco avifauna is at most mildly distinctive (Short 1975). Probably because of the long- and short-term instability, this area is dominated by adaptable and even opportunistic species representing fairly old lineages (Fjelds  1994). Most of them are shared with the Brazilian savanna and woodland habitats (Cerrado) or with the arid thornscrub habitats (Monte) of central Argentina, and some ubiquitous Neotropical lowland birds.

Despite the dominance of widespread species in the lowlands of Bolivia and northern Argentina, some crude biogeographic categories can be defined, with respect to lowland distributions and Andean colonisations (examples in Fig. 7):

1) Several widespread Chaco and savanna birds extend their ranges a short distance up into the Valles, e.g., to El Palmar or to the rangelands near A imbo and Uruguay, which have chaco-like habitats (see *Syrigma sibilator*, *Cariama cristata* [Black-legged Seriema], *Ara auricollis* [Golden-collared Macaw], *Guira guira* [Guira Cuckoo], *Coryphospingus cucullatus* [Gray-crested Finch]; Appendix III). Certain species extend their ranges a considerable distance up into the arid valleys (*Amazona aestiva*, *Chloroceryle americana*, *Nystalus maculatus*, *Melanerpes cactorum* [White-fronted Woodpecker], *Xiphocolaptes major*, *Lepidocolaptes angustirostris*, *Satrapa icterophrys* [Yellow-browed Tyrant], *Polioptila dumicola* [Masked Gnatcatcher], *Vireo olivaceus* *chivi* [Red-eyed Vireo], *Sporophila caerulescens*; Appendix III; see also Fjelds  1987 and Fjelds  & Krabbe 1990). Some of the widespread low-land birds have colonised Bolivian valleys all the way up to the temperate zone, notably in Cochabamba (*Columbina picui*, *Chlorostilbon aureoventris* [Glittering-bellied Emerald], *Phytotoma rutila* [White-tipped Plantcutter, Fig. 7 D], *Hirundinea ferruginea* [Cliff Flycatcher], *Turdus amaurochalinus* [Creamy-bellied Thrush] and

rufiventris [Rufous-bellied Thrush], *Molothrus bonariensis*, *Thraupis sayaca* and *Poospiza cinerea* [Black-capped Warbling-finch]; Fjelds  & Krabbe 1990). Although not differentiated morphologically, these latter highland populations may be more or less isolated from the lowland stocks under present-day climatic conditions.

2) Some birds which are widespread in wooded lowlands ascend to exceptional altitudes in southern Bolivia and enter semi-evergreen premontane forests (*Crypturellus tataupa* [Tataupa Tinamou], *Micrastur ruficollis*, *Aramides cajanea*, *Caprimulgus rufus*, *Trogon curucui*, *Ramphastos toco*, two *Synallaxis* spp., *Thamnophilus caerulescens* [Variable Antshrike], *Leptopogon amaurocephalus*, *Thraupis sayaca* and *Thlypopsis sordida*) or semi-evergreen habitat on the mountain transitions (*Cyclarhis gujanensis*; see Appendix III).

3) An altitudinal gap separates populations in the lowlands and on the mountain scarps, mainly in ecotones between the semi-evergreen and temporarily humid zones (*Picumnus cirratus*, *Colaptes punctigula*, *Phacellodomus rufifrons* and *P. (striaticollis) maculipectus* and *Thamnophilus ruficapillus*). Also for *Cacicus chrysopterus* and *Veniliornis frontalis* a gap may exist between lowland and highland populations (Appendix III).

Three grassland birds show a similar pattern, with populations in the lowlands and on the fairly humid eastern grassland ridges. The small local populations of *Anthus hellmayri* and *Sicalis citrina* could well have been established in response to relaxed competition, because there is no typical guild of Andean grassland birds (Appendix III). *A. hellmayri* inhabits lowlands from R o de Janeiro to Buenos Aires, and some grasslands along the eastern Andean ecotones from Argentina to southern Peru. *S. citrina* occurs very locally in the Tepuis, eastern Brazil and rather peripheral parts of the Andes. Despite the strong isolation of many populations they are poorly differentiated, which may indicate dispersive habits. We propose that this little-known bird is dispersive and opportunistic, settling in isolated grasslands which are species-poor (= low competition). In

Rhynchotus rufescens (Fig. 7 B) the lowland and high-land populations are well differentiated, morphologically and vocally. (In nw Argentina, an isolated population of *Aimophila strigiceps* [Stripe-capped Sparrow] is found in highland; see Narosky & Uzurietta 1987 and Peris & Alabarce 1990)).

4) A number of widespread Chaco birds are represented in the montane basins in Bolivia by an isolated population which is differentiated, either as a weak subspecies, as a well-marked subspecies (Fig. 7 E) or as an (allo) species. This indicates that expansion/isolation as described under pattern 1 may also have taken place in the more distant past. The number of intermontane forms peaks in the rather closed Cochabamba Basin, but a few extend into Chuquisaca and others even to montane basins and pre-puna habitats in nw Argentina (see further below).

5) The low Chaco Central separates populations of birds inhabiting the forests and woodlands of southern Brazil (Campos Cerrados and Paranense Forests) from those in the sub-Andean forests. Nores (1992) suggests that birds of the Paranense Forests colonised the Andean foothill forests by following strips of riverine forest that developed across the Chaco during more humid climates along the Ríos Pilcomayo and Bermejo (see Sick 1985 for a similar hypothesis). However, most interchange may in fact have been 10-20°S, where c. 25 species are continuously distributed from the Brazilian Highland to the Andes, although they are absent from the Chaco Central (example in Fig. 7 A). Complete disjunctions are shown only by *Aegolius harrisii* (Buff-fronted Owl), *Streptoprocne zonaris* (White-collared Swift), *Phaethornis pretrei* (Fig. 7 B), *Colibri serrirostris*, *Syndactyla rufosuperciliaris*, *Lochmias nematura*, *Batara cinerea*, *Thamnophilus ruficapillus*, *Elaenia obscura* (Slaty Elaenia, *sensu lato*), *Camptostoma obsoleta* (Southern Bearless Tyrannulet), *Phyllomyias burmeisteri* (Rough-legged Tyrannulet), *Pachyramphus validus* (Crested Becard), *Turdus nigriceps* (Slaty Thrush, *sensu lato*, Fig. 7 F), *Euphonia musica* (Blue-hooded Euphonia, *sensu lato*), *Chlorophonia cyanea*, *Pipraeidea melanonota* (Fawn-breasted Tanager) and *Poospiza nigro-rufa* (*sensu lato*). For at least 12 of these cases the separation of Brazilian and

Andean populations could well date back to the time of the subsidence of the Chaco (Silva 1994). Some of these species have a wide but disjunct circum-Amazonian distribution (of a relictual nature in the case of *Aegolius harrisii*), but in other cases the western population segments are restricted to s Bolivia and nw Argentina, where there is little competition from the typical groups of the Tropical Andes Region. It is noteworthy that two of these taxa (*Elaenia obscura* and *Turdus nigriceps*, *sensu stricto*) are tropical migrants which breed only in the Boliviano/Tucumano forest (see Marantz & Remsen 1991 for the first species).

6) It is characteristic of most birds which inhabit southern lowlands (Chaco or Monte habitat) as well as highland habitat, that these populations remain more or less connected in southern Bolivia (examples in Figs 5 D and E; see also distribution maps for *Nothura darwini* [Darwin's Nothura], *Columba maculosa* [Spot-winged Pigeon], *Thamnophilus caerulescens*, *Saltator aurantirostris* [Golden-billed Saltator] and *Carduelis magellanicus* [Hooded Siskin] in Fjeldså & Krabbe 1990). In all these species, a fairly well marked morphological differentiation suggests that highland populations have existed for long periods of time.

7) Certain species groups follow a track comprising lowlands in s Brazil or n Argentina, montane basins in Bolivia, Central Peru and the Pacific slope of Peru (Fjeldså 1992, and Fig. 5 G). This could represent a vicariance pattern formed by fragmentation of a once-widespread Andean ancestor, or it could be the result of dispersal, with taxonomically subordinate populations furthest north (see Fjeldså 1992).

4.3 Possible reasons for expansions of lowland birds to highland habitat in southern Bolivia

Although there are records of lowland birds in several Andean basins (e.g., in the La Paz Canyon in Bolivia and Urubamba Valley in Peru), this tendency may nowhere else be stronger than in the Valles of Bolivia. The tendency is shown by birds of xeromorphic as well as evergreen habitat.

Certain granivorous birds may ascend to the temperate zone because of man-made forest clearing and agriculture, as fallow shifting maintains a habitat mosaic of fields, tall herbs, dense thorny thickets etc. *C. picui* is clearly favoured by human activities and reaches high altitudes in many places, including the city of La Paz (see Fjeldså & Krabbe 1990). On the other hand, the various levels morphological differentiation of highland populations indicates that colonisation of high altitudes has also taken place a thousand, ten thousand or hundred thousand of years ago, long before the human influence started. We suggest that another important factor was the rainshadow effect, causing an almost subtropical heat in the Cochabamba Basin. At the same time, there is an adequate rainfall in the mountain scarps which form the western edge of the basin (see climatic maps in Montes de Oca 1989). This may be caused by local topographic conditions and also by the proximity to the large Bolivian/Peruvian Altiplano, which represents a considerable elevated heat source. An additional positive factor may have been the existence of large Pleistocene wetlands at 2,500 m, near the present city of Cochabamba. These wetlands would have stabilised the local climate and water supply, and created conditions where woodland (notably *Polylepis*) could have persisted continually throughout the coldest and driest climatic periods (see the study of climatic conditions in a semi-closed glacial refuge by Lindroth 1965). The transition towards the Tunari Range is made up of periglacial outwash fans, but woodland may have persisted on the rocky slopes of the moisture-capturing scarp to the west-swards nearly to Río Pilcomayo in Potosí.

Within the Tropical Andes Region, the rainshadow areas are small, and birds of lowland scrub colonised highlands only on a small scale.

The above-mentioned climatic effect cannot explain why lowland birds invade Andean foothill forests or settle on ridges with semi-humid habitat. The occurrence of Chaco birds near the treeline could possibly be a result of simple mechanisms of habitat selection, as the treeline is structurally more similar to the lowland shrubbery than the montane tall-

growth forest. On the other hand, the fact that this colonisation happened in that very part of the cis-Andean zone where typical treeline or elfin-forest birds are lacking (Table I) supports that relaxed competition is the most crucial factor. The wide altitudinal niches of many birds in southern Bolivia (Fig. 5) compared with the Tropical Andes Region is caused, to some extent, by an altitudinal bimodality in certain species. Lowland species may fail to fill up the void caused by the lack of cloud forest birds, because ecological release requires a disposition to make opportunistic responses, well developed only in certain species but slightly in others.

When interpreting the altitudinal patterns, we must bear in mind that the Yungas of northern Bolivia and the humid forests of Chuquisaca are not fully comparable: the latter are semi-evergreen, with more seasonal rainfall. This may explain why elfin-forest specialists cannot live S 18°S. Climatic factors may also explain the reduced diversity of hummingbirds in s Bolivia. Nectarivorous birds may be generally favoured by strongly leached peaty soils, where the lack of nutrients gives the plants a relative energy surplus, permitting them to evolve reproductive strategies where sufficient energy can be allocated to nectar production to attract reliable avian pollinators (Rebello 1991).

It is difficult, in general, to associate the individual colonisations of the evergreen zone with absence of particular temperate-zone specialists. We therefore believe that the altitudinal release is mainly caused by relaxed diffuse competition. However, the specialisation of an endemic guan (*Penelope dabbeni*) related to lowland guans to montane forest could be seen as a specific response to the lack of typical montane forest guans (viz., *P. montagnii*). The presence of populations of *Cacicus chrysopterus* near the treeline could be seen as a specific response to the lack of genuine Andean caciques, namely the similar-sized *C. holosericus* (Yellow-billed Cacique) and the larger *C. leucorhamphus* (Mountain Cacique), which both have their southern limits in the Yungas of Cochabamba.

4.4 Patterns of avian endemism in the sub-Andean basins and prepuna habitats of Bolivia and northern Argentina

The montane basins of Bolivia have an accentuated density of Bolivian endemic and near-endemic birds (Fig. 8A), some of them in pre-puna shrubbery, others inhabiting open terrain, still others subtropical thornforest. The area also has a high plant endemism, including several endemic species of the high-altitude *Polylepis* trees (Kessler in press).

Fig. 8A demonstrates that the peak density of endemic birds is found in the Cochabamba Basin (the upper Río Grande/Caine and Río Mizque drainages), which is isolated by semihumid sub-Andean forest and high ridges from other (climatically similar) basins. However, only a narrow mountain transition near Sucre separates it from similar habitat in the upper Río Pilcomayo Valley. The most narrowly endemic form is *Poospiza garleppi*, which has never been found outside the Cochabamba Basin (Rensen *et al.* 1988, Collar *et al.* 1992; one record in Huaylloma area in the adjacent part of Departamento Oruro by M. Kessler pers. comm.). Other species extend n-wards to La Paz or more or less far s-wards. *Ara rubrogenys* (Red-fronted Macaw) and *Myiopsitta (monachus) luchi* reach the upper part of the Río Pilcomayo valley (Lanning 1991 a,b), but local people in our study area in Chuquisaca did not know them. We did not find *Oreopsar bolivianus* (Bolivian Blackbird) or *Diglossa carbonaria* (Gray-bellied Flowerpiercer) in Chuquisaca. However, *Poospiza t. torquata* extends s-wards to Chuquisaca and *Asthenes heterura* has a local population even in Tarija. Five species reach extreme nw Argentina, while other species have even wider ranges (Fig. 6 A). This s-wards impoverishment supports that the core area for montane basins endemics was in Cochabamba.

Some of the endemics (*Oreotrochilus adela* [Wedge-tailed Hillstar], *Upucerthia andaecola*, *Asthenes heterura*, *Diglossa carbonaria* and *Sicalis luteocephala*, and the more widespread *Sappho sparganura*) represent Andean radiations with no close counterparts in the

lowlands. However, other endemics have their sister taxa in the lowland Chaco (*Upucerthia certhioides/harterti* [Chaco/Bolivian Earthcreepers], *Mimus triurus/dorsalis* [White-banded/Brownbacked Mockingbirds], *Gnorimopsar chopi/Oreopsar boliviana* [Chipí/Bolivian Blackbirds], *Lophospingus pusillus/griseocristatus* [Black-crested/Gray-crested Finches], and several cases with well-marked subspecies). In yet other cases, the sister taxa inhabit forest or scrub in southern Brazil (e.g., three cases in *Poospiza*). Still other patterns are more complex, as the Cochabamba-centered taxon is part of a species group which follows a track extending diagonally from s Brazil to nw Peru (Fig. 5F; Fjeldsø 1992 figs 10, 11 and 14). *Saltator rufiventris* is a very distinctive (old) Bolivian endemic, possibly distantly related to the "greyish" group of *Saltators*, which has the highest diversity in southern Brazil.

Today, many species are fairly continuously distributed from the lowlands and up into the Cochabamba Basin, but the various levels of differentiation of the highland populations indicate that the highland populations were isolated periodically in the past. This could have happened in very cold periods, or in humid periods when the submontane forests formed a dense barrier for birds of thornscrub habitats.

Broad ranges of some of the montane basins birds (Fig. 6A) suggest that, if these species evolved in the Cochabamba Basin, they have gradually become well adapted to the harsh conditions of the pre-puna habitat. The existence of a close counterpart of *Poospiza garleppi* (*P. baeri* [Tucumán Mountain-finch] with more "derived" characters) in nw Argentina, suggests that even for such specialists of densely tangled *Barnadesia* and *Polylepis* shrubbery, opportunities for range expansion have existed in the past (Fjeldsø 1992). Variations between expansion and contractions of the habitat is also supported by the differentiation of *Asthenes dorbygnii/steinbachi* (Creamy-breasted/Chestnut Canasteros, which appear to be partly sympatric today), by the disjunct range of *Picoides lignarius* (Striped Woodpecker, Cochabamba Basin and the Patagonian Andes) and by some close sistergroup

relationships with birds of the Peruvian Andes (Fig. 5F).

Other endemic birds characterise the semi-humid montane forests and the Andean foothill forests of s Bolivia and nw Argentina. These have been divided (in Figs 8B and C) into two groups, according to whether their sister taxa are found in the Tropical Andes Region or in eastern lowlands. In the latter case, the sister taxa are usually isolated on either side of the Chaco, but they may also be in parapatric contact in the foothill zone, indicating that an early separation W and E of the Chaco was followed by secondary expansions of the lowland taxon (*Penelope dabbeni/obscura* and semispecies of the *Picumnus cirratus* and *Colaptes punctigula* groups).

Boliviano/Tucumano forest birds with eastern sister taxa have their peak abundance in Chuquisaca and the Andean slope of extreme nw Argentina. However, many of these species have a wide distribution, which may range far into the Tropical Andes Region (Fig. 8B). Since these species lack close relatives in the Yungas of northern Bolivia, the adaptation to the semi-humid zone may not be constrained strongly by competition. However, *Penelope dabbeni*, *Amazona tucumana* and breeding ranges of *Elaenia strepera* and *Turdus nigriceps* do not extend into the Yungas zone.

A few Boliviano/Tucumano forest birds (Fig. 6C) have their sister taxa in the Tropical Andes Region. Their peak diversity is in nw Argentina. Half of these species are isolated from their sister taxa by considerable geographical gaps, but the other half is in parapatric contact with their northern counterparts. *Grallaria albigula* extends its range n-wards along the sub-Andean ridges into Cochabamba and La Paz (below the northern counterpart *G. erythrotis*). We agree with Nores (1989) that the mountain scarps of extreme nw Argentina probably played a special role for the survival of relict populations of birds from the Tropical Andes Region during the dry climatic episodes. The tremendous altitudinal gradient, from c. 500 m to 5,604 m (C. Cuevas) on the Bolivian/Argentinean border right S Tarija,

and 5,130 m 100 km further S (C. Morado) would probably permit predictable rainfall throughout the coldest parts of the Pleistocene. These slopes have a distinctive condensation zone at 2,000-2,700 m (A. Brown and M. Kessler, pers. comm.). Similar conditions exist also E Sierra del Aconquija (m) in Tucumán, 400 km further s, which could explain the divergence of *Atlapetes fulviceps/citrinelloides* (Fulvous-headed/Yellow-striped Brush-finches) from relictual populations in remnant cloud forests in Calilegua and Aconquija.

The three areas of endemism illustrated in Figs 8A, B and C correspond well with the Endemic Bird Areas B 35 ("Bolivian Andes"), B 34 ("Lower Bolivian Yungas") and B 37 ("North Argentinean Andes") defined by ICBP (1993) by a divisive cluster analysis (Twinspan) of distribution data of restricted-range species on grid squares. Fig. 8 demonstrates that these areas of endemism have distinctive "intensity peaks", and that the biologically most interesting areas are in the Cochabamba Basin and on the mountain scarps of extreme nw Argentina. Our study areas falls slightly outside these "intensity peaks", but on the other hand Departamento Chuquisaca has an outstanding species richness because of the ecological mosaic that exists.



Cloud-forest Screech-owl (*Otus hoyi*) is a newly described endemic of the Boliviano/Tucumano humid forest.

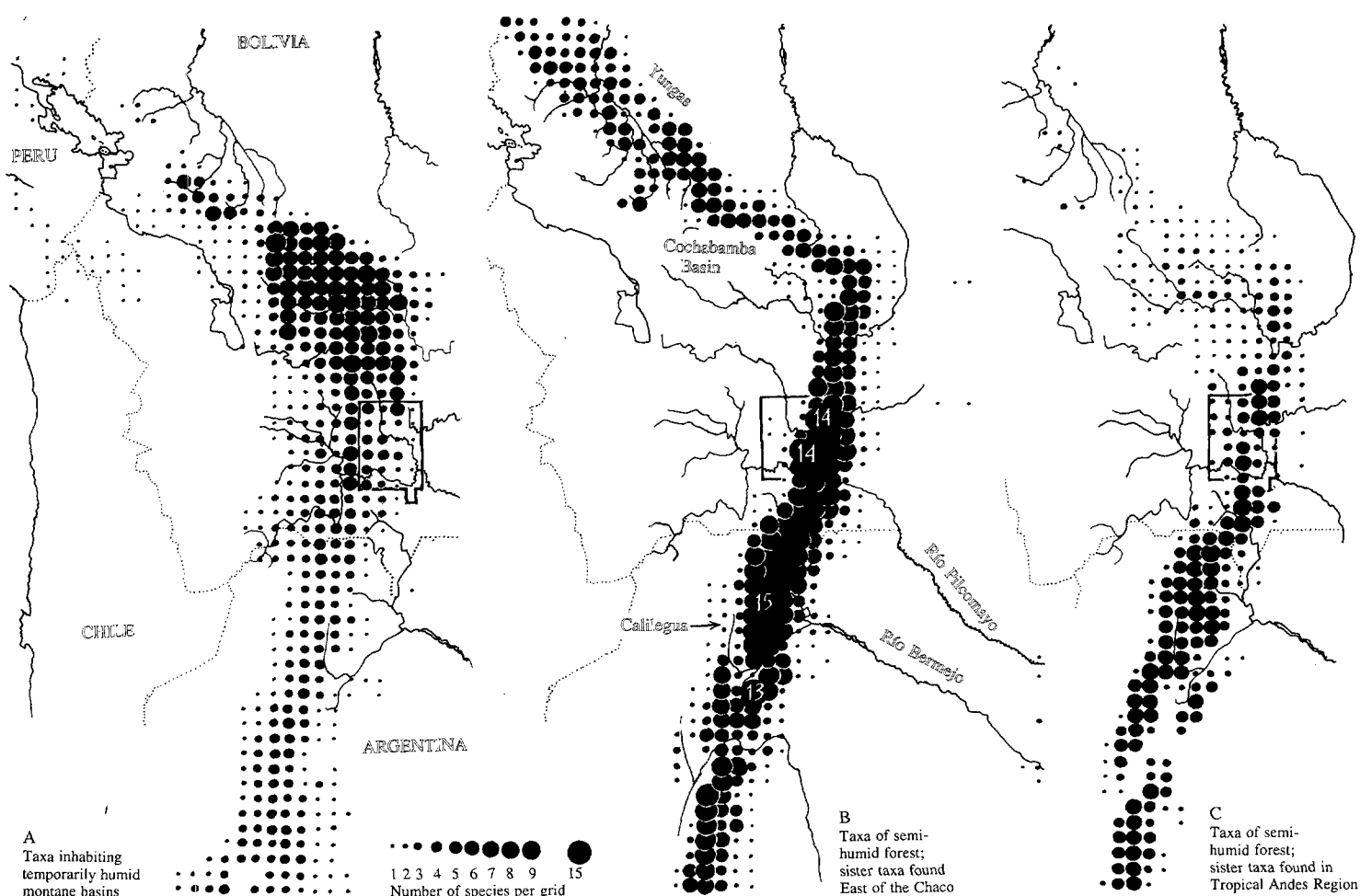


Figure 8. Variations in species richness in Bolivia and adjacent parts of Peru, Chile and Argentina; grid units 25 x 25 km, dot sizes showing the number of species, study area framed. The maps are constructed on the basis of distribution maps of each individual species; such species maps were drawn on the assumption that each species inhabits areas between known records which, judging from available habitat maps and satellite imagery, have suitable habitat, except if the species was searched for in vain in a seemingly suitable place in the intervening area. Map A shows birds of semiarid and temporarily humid montane basins, both those endemic to a small area (*Ara rubrogenys*, *Myiopsitta monachus luchi*, *Oreotrochilus adela*, *Cranioleuca pyrrhophia* (highland subspecies), *Asthenes heterura*, *Oreopsar boliviana*, *Diglossa carbonaria*, *Saltator rufiventris*, *Sicalis luteocephala*, *Poospiza boliviana*, *garleppi* and *baeri*) and those with a wider range (*Bolborhynchus aymara*, *Picoides lignarius*, *Sappho sparganurus*, *Upucerthia andaecola*, *Leptasthenura fuliginiceps*, *Asthenes dorbignyi* [sensu lato; Fjeldså & Krabbe 1990] and *steinbachi*, *Phacellodomus striaticeps*, *Mimus dorsalis*, *Lophospingus griseocristatus*, *Poospiza hypochondria* and *whitii*). Map B shows species of semihumid submontane to montane forest and shrub habitat, whose sister taxa live in southern Brazil or other lowland areas east or south of the Chaco or in some cases more widely in the lowlands (the lowland form included if currently treated as belonging to the same biospecies or superspecies as the Andean form) (*Penelope dabbeni*, *Amazona tucumana*, *Otus hoyi*, *Cypseloides rothschildi*, *Picumnus cirratus*, *Veniliornis frontalis*, *Colaptes punctigula*, *Phacellodomus striaticollis*, *Syndactyla rufosuperciliaris*, *Batara cinerea*, *Thamnophilus caerulescens* and *ruficapilla*, *Melanopareia maximiliani*, *Mecocerculus hellmayri*, *Elaenia strepera* (breeding range) and *E. obscura*, *Phyllomyias burmeisteri*, *Todirostrum plumbeiceps*, *Knipolegus signatus*, *Turdus nigricaps*, *Basileuterus signatus* and *bivittatus*, *Arremon flavirostris*). Map C shows endemics of the Boliviano/Tucumano humid montane forests, forms whose sister taxa are found in the montane forests of the Tropical Andes Region (*Eriocnemis glaucopoides*, *Microstilbon burmeisteri*, *Synallaxis azarae superciliosus*, *Grallaria albigula*, *Scytalopus (magellanicus) zimmeri/superciliaris*, *Cinclus schulzi*, *Myioborus bruniceps*, *Atlappetes fulvipes* and *citrinellus*). Some viewpoints on sister-group relationships of the highland forms have been summarised by Fjeldså (1992, appendix i). (A few species were left out because of uncertainty about their relationships.).

5 Conclusions

1) Despite a fairly unbroken occurrence of forest habitat along the cis-Andean slope from the tropical zone to 27°S in Argentina, the bird groups that radiated mainly in the Tropical Andes Region have a fairly sharp southern limit at 18°S, near the Cochabamba/Santa Cruz border in Bolivia. Probably, the Boliviano/Tucumano Forests could not maintain this humid-forest fauna because they were periodically of a deciduous nature, with semi-evergreen conditions maintained only locally and temporarily during the Pleistocene climatic cycles.

Several generalisations can be drawn from the study of regional differences in ecological amplitudes and community structure:

2) Strong competition in the Tropical Andes Region constrains the vertical distributions of individual species (see Terborgh & Weske 1975), and

3) the quite few birds of the humid subtropical zone which colonise the Boliviano/Tucumano Forest show ecological release and expand their ecological ranges to the zone of seasonal rainfall.

4) Because of the low number of humid-zone specialists, some lowland birds invade the semievergreen zone of the Andean slope, mainly in the premontane forest, but in some cases also by settling in shrubby habitat of semihumid grassland near the treeline. This tendency may be stronger in Chuquisaca than in the more humid zone in s Tarija and extreme nw Argentina.

5) Other lowland birds penetrate Andean valleys and montane basins mainly because of the climatic rain-shadow effect.

6) Using the actualistic principle as a key to the past, we propose that the rainshadow effect and the relaxed competition made the Valles the main area in the Andes where lowland birds establish populations in the large Bolivian/Peruvian highland. Lowland

and highland populations may remain in contact for some time (4.2, pattern 4), but in the course of the Pleistocene climatic fluctuations many populations became temporarily isolated from the lowland stocks in the rainshadow zone of the Cochabamba Basin.

7) In case of vicariance events caused by isolation in forest habitat W and E of the Chaco, the western population often adapted to pre-montane forest or shrub, especially in Chuquisaca; in case of a secondary expansion of the eastern lowland population, a parapatric suture may be established in the foothill zone.

8) During dry climatic periods, some Andean forest birds survived (and diverged to become endemic species) in the semi-evergreen habitat which remained on the high altitudinal gradients (Calilegua and Aconquija) in nw Argentina.

9) The lack of humid-forest endemics in southern Bolivia (other than subspecies) suggests that the large forest tracts in Chuquisaca were too unstable to maintain humid forest continuously for long time periods. However, because of their habitat heterogeneity, with several ecotones, large numbers of species can accumulate here during present-day conditions. The area houses large populations of certain Boliviano/Tucumano endemics (Appendix III), and at the same time some Yungas forms which do not reach nw Argentina, many high-altitude populations of lowland birds, some marginal populations of some Cochabamba-centred endemics and several populations of typical Andean highland birds (Appendix III).

10) Various levels of morphological differentiations of lowland and upland populations and amongst upland populations suggest that, for long geological periods, opportunities for dispersal alternated with periods of isolation; this time's cycle operating

as a "species pump" (see Haffer 1993 for analogous changes in the lowlands).

11) Differentiated while isolated on fairly high altitudes, certain endemic birds became well adapted to highland conditions. Some of these species evolved sufficient ecological tolerance (or even invasive behaviour) to spread to the pre-puna zone of w Argentina, some species also crossing the Altiplano to initiate speciation histories in Peru (Fig. 6A, and see Fjelds  1992).

12) In general, the evolution of new species and new adaptive trends started as small marginal or even relictual populations became isolated in climatically stable places within the regions outside the large biomes such as the Chaco and the humid forests of the Tropical Andes.

Acknowledgements

The fieldwork in September-October 1991 was made possible by a generous grant from the Rockwool Foundation. For obligingness and advice during the preparations, we thank staff members of Instituto Ecol gico and Museo Nacional de Historia Natural in La Paz. Our thanks are also due to J.V. Remsen, Jr., J.M.C. da Silva and N. Krabbe for comments on early drafts of the manuscript, to C. K nig for valuable information about altitudinal distributions in northwestern Argentina, and to M. and P. Isler and M. Kessler for various distributional records used for Fig. 6. M.B. Christiansen and E. Pitter kindly placed data from their studies in Cochabamba and adjacent parts of Santa Cruz at our disposal, and N.P. Dreyer made available, data from a recent birding trip in the same general area, at our disposal. The Royal Natural History Museum in Stockholm kindly provided comparative material as a loan.

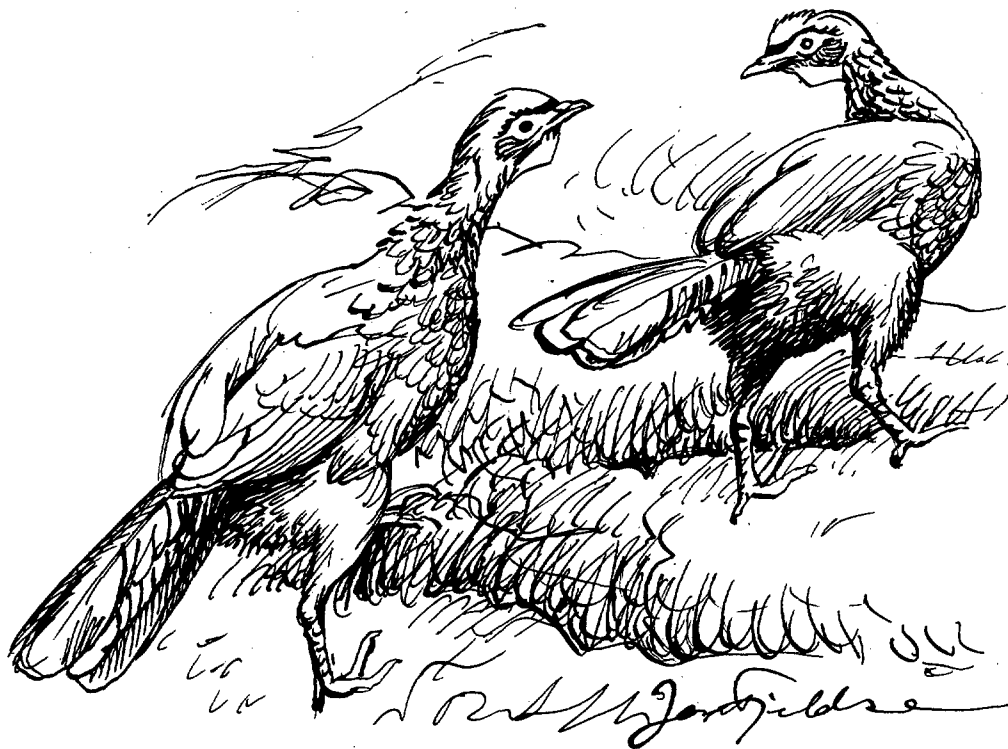
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Central Chuquisaca is the population centre for the restricted-range Red-faced Guan (*Penelope dabbeni*).

Appendix I

Description of surveys made by the authors 1991-93 in southern Bolivia

Surveys in Dpto Chuquisaca (see Figs 1 and 2), with two transects along the ecological and altitudinal gradients from the lowlands to highland rainshadow habitat.

As an initial survey of the accessibility of the large forest, tracts in central Chuquisaca were made by SM in the Camargo-Culpina area in August 1991. We decided to follow what is probably an "Inca" trail, along the southern edge of the Chapeados highland from Abra Portillo (which has connection by a dirt road) to El Palmar, through a high diversity of habitats. Possible survey routes further n or s might give greater altitudinal gradients, but would have brought us through less humid mountain tracts.

The main survey started in Camargo (2,400 m) on 17 September 1991, with trucks to Culpina (2,950), Villa Charcas (3,100) and by a dirt road to Abra Portillo (2,780 m), still in a fairly arid zone. 18-22 September we walked e towards the humidity-capturing eastern scarp of the highland (2,850 m, 8 km S the highest ridge), crossing a number of barren side-ridges of the main range and descending into intervening valleys. Campsites were in the mountain pass Abra Portillo (2,780 m), in deciduous woodland in a side ravine to Valle Río Lechéra (2,350 m); in a small wooded side ravine to Río Puca Laja (2,700 m); in the canyon between Hda Puca Pampa and Cmd Campamiento (at 2,600 m); and in a forested ravine SW C. Campamientito (2,550 m). After passing the eastern scarp we camped 22-24 September N C. Campanarios (at 2,550 m) in the upper fringe of the semi-evergreen forest zone. From this point we over viewed enormous tracts of unbroken tall-growth forest, but proceeded e-wards mainly along a ridge dominated by shrubby treeline vegetation. Campsites were N C. Lagunillas (2,000 m) in the C. Campanarios area and on the ridge towards C. Misión (at 2,350 m). On 26 September we descended from C. Bufete (2,300 m) through the subtropical forest, to reach El Palmar (1,050 m) late in the evening.

On 28 September we walked ne, over plains and low hills, waded across Río Pilcomayo (600 m) and camped N Eía Timboycto. We proceeded n through rangelands and low wooded hills, camping near Eía Tacurvite, near the hamlet Uruguay, between Caja Mayu and Sausi Mayu and finally in humid forest (1,450 m) on C. Alto Despencillos. We crossed Río Parapeti on 3 October, camping in humid forest on the w slope of Snía Racete (1,700 m), passed Río Parapeti a second time to camp above Rcho La Sidra (1,400 m) and two nights in mossy temperate forest near the ridge of C. el Tapado (1,950 m). Río Misca Mayu was crossed S Vallecito. We ascended C. Punto Lajas and proceeded along the ridge at 2,500-2,800 m to Eía Moco Pata, from where Río Misca Mayu was followed to Azurduy, with campsites on the transition between humid shrubbery and steep rocky slopes towards C. Punto Lajas (2,100 m), in the *Alnus* woodland just above Moco Pata (2,600 m) and in mixed *Alnus/Podocarpus* woodlands N Rcho Monto Grande (2,500 m). We stayed in Azurduy 11-12 October, studying remnant shrub and woodland habitats 2,600-2,700 m) and left for the city of Sucre 13 October.

This survey was made at the end of the dry season; however, the weather was unstable with periods of mist, rain and even snow from 23 September. A second survey (by SM) was made in order to get data from the end of the rainy season (March), and in order to improve our data from the largest forest tract W El Palmar. This trek went from the village Narvaez (1,700 m), Dpto Tarija, after a small digression to near Canaletas (2,250 m) further w, proceeding across Río Pilaya and along Cañon Verde to El Palmar, 11-17 March. Campsites were S Huayco (1,750 m), near El Tunal (1,600 m), on the southern bank of Río Pilaya (900 m), in forest habitat N Cañon Verde (1,150 m), at a forest edge near Río Yahuayhua (1,000 m) and in forest habitat near Río Tueras (950 m). Two different campsites were used near El Palmar 17-19 March. From El Palmar the same trail was followed as during the first survey, back to Abra Portillo and Villa Charcas, reached 28 March. Campsites were inside forest E C. Bufete (1,500 m), on the grassy Plateau of C. Bufete (2,300 m), two nights inside cloud forest on C. Lagunillas (2,000 m), two nights in *Podocarpus* woodland on the sw slope of C.

Campamentito (2,700 m), in a shrubby ravine W Pucapampa (2,900 m), in partly cultivated terrain on the bank of Río Lechéra (2,250 m) and in Chirijara (3,150 m).

Studies in the Vallegrande-Masicurí area in Dpto Santa Cruz

Observations were made 5-6 December 1991 and 10-25 January 1992 (by M.B. Christiansen and E. Pitter; only a brief visit by SM) and 2-9 February and 10-15 March 1993 (by SM) on the mountain ridges E of the temporarily humid basin of the town Vallegrande and across the Abra Tabla Pass into the adjacent humid premontane zone towards the village Masicurí, with campsites at Río Piraymiri, near San Lorenzo, Loma Larga, La Yunga and at Dionisios just above Masicurí.

Studies in the Reserva Tariquia in Dpto Tarija

Three treks were made by SM in September-October 1992 and near the "Reserva Nacional de Flora y Fauna Tariquia. The first walk 23-28 September went from the Padcaya area over the ridge (La Cumbre) down the valley of the Río Escalera and back again, with camps near Oroza, at Honduras and two nights at 2,000 m along the Río Escalera. The second walk 30 September-9 October followed the same route but descended further s, near the Argentinean border, to reach Pampa Grande and Emborozú at c. 850 m on the Tarija-Bermejo road. Campsites were Honduras, Río Achirales (two nights at 1,730 m), Pampa Grande (two nights at 1,050 m), near Río Chillaguatas and along the Río Cambari (1,060 m). During the third walk, 14-18 October, the mountain ridge was crossed c. 10 km further n, over C. Alto de Minas (=C. Altomina, 3,350 m) down to 200 m in the deep canyon of Río Lorayo and back, camping at Río Alizos in the *Polylepis*-clad ravine W of the main ridge.

Habitats

The eastern Andean zone of Bolivia consists of numerous parallel n-s-going ridges of

sedimentary rocks, mostly pink and some grey sandstones. The ridges are intersected by the main river valleys, which are warm and arid, and intersect the humid zones which follow high n-s-going ridges.

Very few meteorological data exist from the region. Judging from the state of the vegetation, we have the impression that even the wettest scarp-forests receive little rain during the southern winter. Therefore, zones termed humid forest (*bosque humedo*) and temperate rain-forest (*bosque pluvial montano templado*) by Unzueta (1975) are more correctly characterised as semi-evergreen forest (*bosque semisiempre verde*) (as done by Servicio Geológico de Bolivia 1977). Only in Tarija (and extreme northern Argentina), the eastern Andean slope has truly humid habitat. The western fringes of the shaded zone in Fig. 1 are best described as grass and shrub in temporarily humid environs (*pastos y arbustos en ambiente temporalmente humedo* in Servicio ..., *op. cit.*), and this habitat grades towards semi-desert further w. The lowland of the Central Valley of Tarija, around the town of Tarija, is arid and strongly eroded. Camargo, which is the western endpoint of our main transect, is in a deep valley in the arid pre-puna zone. The valley bottom has a strip of vegetation (*Schinus* trees, orchards and vineyards), but the surroundings have only scattered xeromorphic scrubs and few gnarled *Schinus* trees in the high parts. The Culpina area is an irrigated area on an utterly dry and degraded steppe. Semiarid bunch-grass steppe also characterises the high parts of the mountains surrounding Culpina and Azurduy.

E 64°20'W in Chuquisaca, the semiarid zone is quite abruptly replaced by more permanently humid grassy slopes resembling the "páramo" and "jalca" habitats of the Tropical Andes Region (the signature *pastizal* on the topographic maps). A narrow "páramo" zone also characterises the mountain transitions E Vallegrande ad E Tarija, towards the forested slopes.

Excepting some towns and villages in the montane basins, the entire region is sparsely populated. Nevertheless, because of extensive use of fire to maintain pasture, and fallow-shifting, large portions of the temporarily humid highlands are rather degraded. In Chuquisaca, the high-altitude woodland type

(*Polylepis*) is generally absent, probably because of human activity, but the Tariquia area had numerous moss-covered *Polylepis* forests on the upper eastern slope and also patches of *Polylepis* and bromeliads on the upper part of the drier western slope. The high parts of the Chapeados mountains were barren except for small *Alnus* thickets and patches of composite shrubbery in ravines and hills too steep to be used by man, sometimes up to 3,250 m (Fig. 4, top left). The *Alnus* zone is of a deciduous nature (see Hueck 1966); in September-October it was in its aestival stage, tiny sprouting leaves giving a vague green tinge, and with the first herbs appearing among the withered leaves and brackens underneath. Woodland patches below 2,700 m are evergreen, mainly *Podocarpus parlatorei* mixed with *Eugenia pungens* and *Polylepis hieronymi*, and with some *Escallonia* shrub, but below 2,500 m this zone grades into quebracho type woodland (*Aspidosperma*, *Caesalpina*, *Jacaranda*, *Schinopsis*, *Tipuana*) (e.g., at the Río Lechéra camps). The upper zone has many mistletoes. All woodlands were abundantly covered by lichens, those below 2,700 m also with *Tillandsia usneoides*.

A valley S C. Campamiento has several square kilometres of almost pure *Podocarpus* forest at 2,300-2,800 m, with *Alnus* at the upper fringe. Similar formations are seen also in the Hda Moco Pata (Fig. 4, bottom left) and Rcho Monte Grande SE Azurduy, as well as 40 km N Azurduy. This may be a typical habitat in montane valleys immediately W at the main moisture-capturing ridges.

The treeline is depressed e-wards in Montes Chapeados, as some of the eastern ridge crests have isolated grasslands to below 2,500 m (e.g., on the Plateau of C. Bufete, Fig. 4, top right). The upper fringe of the large forest zone above El Palmar is *Alnus* coppice, often with large amounts of bracken and myrcinaceous and composite shrubs, *Duranta*, *Miconia* and locally bamboo and mimosa-like vegetation. Judging from observations of burning and early succession stages of regrowth, and from the fact that the treeline is above 3,000 m in the least accessible mountains, we believe that the depressed treeline and the shrubby state of the habitat are effects of occasional burning to create pasture.

The semi-evergreen forests of Montes Chapeados cover a continuous area of nearly 1,300 square kilometres. Here, the *Alnus* zone grades through a *Podocarpus*-dominated zone to tall old-growth forest of conifers (*Podocarpus*), mahoganys (*Cedrela boliviana*) and walnuts (*Juglans*) admixed some *Myrcia* and *Tipuana* (Fig. 4, right), and some deciduous trees (*Celtis*, *Erythrina*), and with many *Tabebuia lapacho* in the subtropical zone. The upper (temperate) forest is mossy with some epiphytic ferns, but hardly any bromeliads, the whole terrain being far less laden with wet moss and bromeliads, and the trees generally with smaller leaves, than on similar altitudes in the Yungas of Cochabamba.

The Río Parapeti area further n had similar semi-evergreen habitats as Montes Chapeados, but with many *Citrus* trees in the lower parts. Despite a sparse human settlement, the forest habitats are quite modified and fragmented here, most valley bottoms being mosaics of shrubby areas, pasture and small fields, most hills being in various stages of regrowth, the hilltops converted to grassland, leaving only a narrow zone of old-growth forest (*Podocarpus* and *Myrsiaceae*) in the misty zone at c. 2,000 m.

The submontane zone at 1,000-1,400 m is made up of temporarily humid, wooded hills (*Aspidosperma*, *Caesalpina*, *Bulnesia*, *Schinopsis* and *Tabebuia lapacho*), with vines and strangler figs in the ravines. In Tarija this zone was quite humid with large amounts of vines and bromeliads, but it was sandy and dry in the Río Pilaya area. Some areas N Río Pilcomayo have mainly leguminaceous thorn scrub (*Acacia*, *Prosopis*) and *Prunus* shrubbery on some hills. In many places, this zone is strongly influenced by slash-burning, and many low areas N Río Pilcomayo have well-watered pasture interrupted by coppice of *Tabebuia lapacho* and tangles thickets of *Ziziphus*. The El Palmar area is a large plain with well-watered pasture land and scattered farms with fields and orchards fenced with yucca hedges. However, the hilly areas E El Palmar and N and S Río Pilaya had almost unbroken lowland forest, although sandy and dry in certain places.

Appendix II

Names and coordinates of ornithological study sites from surveys in the Bolivian Valles 1991-1993. Figures (in brackets) behind the locality names refer to locality numbers given in Fig. 1 and Appendix III.

- Abra Portillo* (2), 20°40'S 64°41'W, bushy slopes at 2,750 m. 27-18 September 1991, 28 March 1992
- Abra Tabla* (38), 18°36'S 64°03'W, pass SE Vallegrande at 2,450 m. Several visits
- Añimbo* (16), 20°34'S 64°8'W, rangeland and shrub at 100 m 30 Sep. 1991
- Azurduy*, 20°6'S 64°25'W, village, hills and woodland at 2,500-2,700 m. 10-13 October 1991
- Camargo*, 20°38'S 65°12'W, town in arid valley, 2400 m. August and 17 September 1991, 29 March 1992
- Cañon Verde Camp* (33), 21°06'S 64°14'20"W, in forest at 1,150 m 14-15 March 1992
- C. Alto de Minas* (54), 21°54'S 64°34'20"W, steep grassy slopes at 3,350 m. 17 October 1992
- C. Alto de Minas Camp*, 21°54'S 64°34'40"W, *Polylepis* ravine at 3,050 m. 16-17 October 1992
- C. Alto Despencillos* (20), 20°26'S 64°12'W, forest at 1,500 m. 2-3 October 1992
- C. Bufete Camp 1*, 20°50'S 64°20'W, forest below the scarp at 1,500 m 26 September 1991, 19-20 March 1992
- C. Bufete Camp 2* (12), 20°51'S 64°22'W, grassy plateau, 2,300 m. 26 September 1991, 20-21 March 1992
- C. Campamentito camps* (9), 20°48'20"S 64°32'W, *Podocarpus* forest at 2,600 m. 21-22 September 1991 and 23-25 March 1992
- C. Campanarios* (10), 20°48'S 64°29'W, forest at 2,100-2,600 m. 22-24 September 1991, 22 March 1992
- C. Corral*, 20°46'S 64°36'W, barren mountains to 3,200 m. 20 September 1991 and 26 March 1992
- C. Cobre Khasa* (8), 20°47'S 64°34'W, barren terrain to 3,200 m. 21 September 1991, 26 March 1992
- C. el Tapado* (23), 20°15'S 64°16'W, humid forest to 1,950 m. 5-7 October 1992
- C. Hoyadas* (26), 20°11'S 64°18'W, shrub and barren terrain to 2,800 m. 8 October 1991
- C. Lagunillas Camp* (11), 20°48'S 64°28'W, forest at 2,000 m. 24-25 September 1991, 21-23 March 1992
- C. Mision* (12), 20°49'S 64°24'W, sharp ridge with forest and shrub at 2350 m. 25-26 September 1991, 20 March 1992
- C. Punta Lajas* (25), 20°12'S 64°18'W, thickets and barrens to 2,550 m. 8 October 1992
- C. San Francisco* (3), 20°45'S 64°41'W, barren terrain to 3,000 m. 18 September -01, 27 March 1992
- Chirijara* (37) 20°40'S 63°48'W, barren land at 3150 m. 27-28 March 1992
- Cmd Caja Mayu* (18), 20°26'S 64°11'W, thickets at 1,200 m. 1 October 1991
- Cmd Campamiento* (7), 20°54'S 64°31'W. Mentioned in the Itinerary
- Cmd Sausi Mayu* (19), 20°24'S 64°12'W, thickets at 1,380 m. 2 October 1991
- Culpina*, 20°50'S 64°12'W, village and irrigated orchard-areas on barren semiarid steppe at 3,000 m. 22-26 August and 17 September 1991 and 29 March 1992
- El Palmar*, 20°51'S 64°15'W, pasture at 1,100-1,200 m. 26-28 September 1991, 18-19 March 1992
- El Tunal camp* (30), 21°15'20"S 65°15'W, meadows and forest at 1,600 m. 12-13 March 1992
- Eía Moco Pata* (27), 20°8'S 64°20'W, woodland around 2,600 m. 9 October 1991
- Eía Tacurvite* (15), 20°37'S 64°9'W, rangeland and woodlands at 900 m. 30 September 1991
- Eía Timboycito* (14), 20°45'S 64°8'W, rangeland and woodland at 1,050 m. 28-29 September 1991
- Honduras* (45), 21°58'30"S 64°37'30"W, fields and *Polylepis*, 2,450-2,800 m. Ult. September 1992
- Huayco camp* (29), 21°21'S 64°16'W, woodland at 1,750 m. 11-12 March 1992
- La Cumbre*, 22°00'S 64°36'25"W, pass with *Polylepis* at 3,020 m. 25 September 1992
- La Yunga* (42), 18°47'S 63°51'W, secondary forest towards Masicurí, at 1,450 m. Several visits
- Liriuni*, 17°17'S 66°18'W, semiarid valley with *Polylepis* patches W Cochabamba town, at 2,900-3,800 m. Studies by S. Arias, and visit by SM
- Loma Larga* (41), 18°46'S 63°53'W, degraded forest above Masicurí, at 1,900 m. Several

- visits
- Masicurí*, 18°48'S 64°47'30"W, forest at Dionisios, 1,050 m, above the village. Several visits
- Narvaez* (28), 21°27'S 64°18'W, village at 1,700 m
- Oroza* (44), 21°M56'S 64°M37-38'W, degraded slopes at 2,000-2,150 m. Sep-October 1992
- Padcaya*, 21°58'S 64°39'W, town at 2,000 m in a rainshadow basin. Sep-October 1992
- Pampa Grande* (48), 22°02'20"S 64°26'W, village and bushy terrain at 1,050 m. 5-7 October 1992
- Puca Pampa* (6), 20°45'S 64°36'20"W, mountains at 2,900 m. 20 September 1991 and 25-26 March 1992
- Rcho Monte Grande* (27), 20°8'S 64°22'W, woodland at 2,500 m. 10 October 1991
- Río Alizos* (53), 21°54'50"S 64°35'50"S, scrub and *Polylepis* at 2,600 m. 14-16 October 1992
- Río Achirales* (47), 22°02'S 64°33'40"W, slightly disturbed forest at 1,730 m. 3-5 October 1992
- Río Caine*, S bank towards Torotoro, arid woodland and mountainous areas at 1,900-3,000 m, in Sucusuma, extreme ne Dpto Potosí. Studies by M.B. Christiansen and E. Pitter (and visit by JF and SM) 1991-1992
- Río Cambarí* (50), 22°09'25"S 64°25'55", in forest at 1,060 m. 8-9 October 1992
- Río Chillaguitas* (49), 22°06'00-35"S 64°25'00-25"W, tall forest at 1,200 m. 7-8 October 1992
- Río Escalera* (46), 22°00'S 64°34-35'W, forest at 2000-2700 m. 25-28 September, 1-3 October 1992
- Río Lechéra camps* (4), 20°44'S 64°40'W, woodland, 2,300 m. 18-19 September 1991, 26-27 March 1992
- Río Lorayo* (53), 21°54'30"S 64°32'W, deep canyon in wet zone, 2,000-2,150 m. 17-18 October 1992
- Río Misca Mayu* (24) crossed at 20°15S 64°17'W, shrub at 1,550 m. 7 October 1991
- Río Nuevo camp* (36), 20°53'50"S 64°17'30"W, woodland at 1,100 m. 17-18 March 1992
- Río Piraymiri* (39), camp at 18°38'S 63°59'30"W, in woodland at 1,850 m. Several visits
- Río Parapeti* (21), crossed 20°17'+21'S and 64°11'+15'W, at 1,350 and 1,400 m, in zone of fragmented forest. 3 and 5 October 1991
- Río Pilaya camp* (32), at 21°07'S 64°14'W, sandy plain with shrubs at 900 m. 13-14 Mar
- Río Pilcomayo* crossed at 20°45'S 64°11'W, in woodland at 600 m. 28 September 1991
- Río Puca Laja camp* (5), 20°48'S 64°35'W, bushy gorge, 2,600 m. 20 September 1991, 26 March 1992
- Río Tueras camp* (35), 21°57'S 64°15'W, in woodland at 950 m. 16-17 March 1992
- Río Yahuayhua camp* (34), 21°02'S 64°13'W, in woodland at 1,000 m. 15-16 March 1992
- San Josecito* (31), 21°09'S 64°14'W, dry woodland at 950 m. 13 March 1992
- San Lorenzo* (40), 18°39'30"S 63°55'30"W, montane forest and open areas, 2,300-2,500 m. Several visits
- Siberia*, watershed right N Comarapa, 17°45'S 64°40'W, cloud forest near the Cochabamba/Santa Cruz border. Visits by SM 1992 (and by N. Dreyer, Remsen *et al.* 1985-7, Clarke 1991 and others)
- Snía Pilcomayo*, 20°45'S 64°10'W, forest at 1,200 m. 28 September 1991
- Snía Racete* (22), 20°19'S 64°13'W, cloud-forest 1,750 m. 3-4 October 1991
- Snía Torobayo* (13), 30°46'S 64°12'W, woodland to 1,350 m. 28 September 1991
- Tablas Montes*, 17°15'S 65°10'W, in cloud-forest at 2,600-2,750 m near the Cochabamba-Villa Tunari Road. Studies by S. Arias and by JF in 1983 and 16-20 October 1991
- Uruguay* (17), 20°31'S 64°9'W, rangeland and bushy hills at 1,050-1,200 m. 30 September-1 October 1991
- Vallegrande*, 18°29'S 64°06'W, wide seasonally humid valley at 2,050 m. Several visits 1991-3
- Villa Charcas* (1), 20°44'S 21°52'W, plains at 3,000 m. 17 September 1991 and 28 March 1992.

Appendix III

Birds recorded during surveys in Chuquisaca in September-October 1991 and in March 1992. The records are distributed along the routes walked and on an altitudinal gradient. Most localities along the transects are referred to by numbers given in Fig. 1.

The code given to the right tells the principal distribution of each species: A = Andean, mainly barren highlands; AF = Andean humid forest; B = forest in southern Brazil or adjacent Argentina (ev. in combination with AF or BT, in case of a disjunctly distributed species [or superspecies]); BT = Boliviano/Tucumano forest; M = migrant visitor; O = other; PP = prepuna basins, mainly in Bolivia; U = ubiquitous (high and low, but sometimes with a disjunct or patchy occurrence); + means some occurrence in other zones (this mark is not used, however, for lowland birds which ascend to the temperate zone in southern Bolivia but not elsewhere in the Andes).

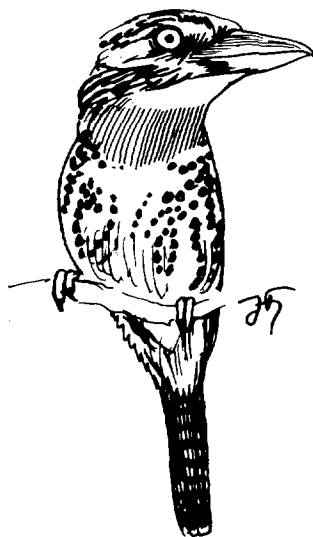
	1000 m	2000 m	3000 m	Azurdury	Monte Grande	C. Hoyadas	C. Puntalajas	C. El Tapado	Río Parapetí	Santa Racete	Río Parapetí	C. Alto Desp.	Com. SausiMayu	Com. CajasMayu	Uruguay	Añimbo	Eña Tacurvite	Río Pilcomayo	El Palmar	Cerro Bufete	Cerro Misión	N. C. Lagunillas	C. Campanarios	C. Campanento	C. Cobre Klasa	Río Puca Pampa	Río Puca Laja	Río Lechéra	Abra Portillo	Culpina	Camargo	
<i>Crypturellus tataupa</i>	+																		+													
<i>Rhynchotus rufescens</i>																			+													
<i>Nothoprocta pentlandi</i>				+++																												
<i>Phalacrocorax olivac.</i>																																
<i>Bubulcus ibis</i>																																
<i>Nycticorax nycticorax</i>																																
<i>Syrigma sibilator</i>																																
<i>Tigrisoma fasciatum</i>																																
<i>Ardea cocoi</i>																																
<i>Theristicus caudatus</i>																																
<i>Coragyps atratus</i>																																
<i>Cathartes aura</i>				+++																												
<i>Cathartes melambrotos</i>																																
<i>Vultur gryphus</i>																																
<i>Sarcoramphus papa</i>																																
<i>Elanoides forficatus</i>																																
<i>Elanus leucurus</i>																																
<i>Ictinia plumbea</i>																																
<i>Circus cinereus</i>																																
<i>Accipiter striatus</i>																																
<i>Accipiter bicolor</i>																																
<i>Oroaetus isidori</i>																																
<i>Spizaetus ornatus</i>																																
<i>Geranoaetus melanoleuc.</i>	+																															
<i>Buteo magnirostris</i>																																
<i>cf. Buteo albigularis</i>																																
<i>Buteo polyosoma</i>	+																															
<i>Phalcoboenus megalopt.</i>	+																															
<i>Polyborus plancus</i>																																
<i>cf. Micrastur ruficollis</i>																																
<i>Micrastur semitorquatus</i>																																
<i>Falco sparverius</i>	+																															
<i>Falco femoralis</i>																																
<i>Merganetta armata</i>																																
<i>Penelope dabbeni</i>																																
<i>Penelope obscura</i>																																
<i>Cariama cristata</i>																																
<i>Aramides cajanea</i>																																
<i>Vanellus chilensis</i>																																
<i>Vanellus resplendens</i>	+																															
<i>Pluvialis dominica</i>	?																															
<i>Oreopholus ruficollis</i>	+																															
<i>Actitis macularia</i>																																
<i>Columba fasciata</i>																																
<i>Columba livia</i>	•	+																														
<i>Zenaida auricularia</i>	•	•																														
<i>Columbina picui</i>	++																															
<i>Claravis pretiosa</i>																																
<i>Metriopelia ceciliae</i>	•	•																														
<i>Metriopelia melanoptera</i>	++	++																														
<i>Metriopelia aymara</i>	+																															

	1000 m	2000 m	3000 m	
<i>Leptotilla verreauxi</i>				Lep.ver.
<i>Leptotilla megalura</i>				Lep.meg.
<i>Geotrygon frenata</i>				Geotfre.
<i>Ara auricollis</i>				Ara aur.
<i>Aratinga acuticaudata</i>				Aratacu.
<i>Aratinga mitrata</i>				Aramit.
<i>Pyrrhura molinae</i>				Pyrrmol.
<i>Bolborhynchus ayмара</i>				Bolbay.
<i>Brotogeris versicolor.</i>				Bro.ver.
<i>Pionus maximiliana</i>				Pio.max.
<i>Amazona tucumana</i>				Amaztuc.
<i>Amazona aestiva</i>				Amazaes.
<i>Piaya cayana</i>				Piaycay.
<i>Crotophaga ani</i>				Crot.ani
<i>Guir guira</i>				Gui.gui.
<i>Tyto alba</i>				Tyr.alb.
<i>Onus choliba</i>				Onuscho.
<i>Onus hoyi</i>				Onushoyi
<i>Bubo virginianus</i>				Bubovir.
<i>Glaucidium bolivianum</i>				Glaubol.
cf. <i>Ciccaba albitarsus</i>				Cic.alb.
<i>Speotyto cunicularia</i>				Spe.cun.
cf. <i>Lurocalis rufiventris</i>				Lur.ruf.
<i>Nyctidromus albicollis</i>				Nyc.alb.
<i>Caprimulgus rufus</i>				Cap.ruf.
<i>Caprimulgus longirostris</i>				Cap.lon.
<i>Uropsalis lyra</i>				Uro.lyra
<i>Streptoprocne zonaris</i>				Str.zon.
<i>Chaetura andrei</i>				Chaeand.
cf. <i>Cypseloides rotschil.</i>				Cyp.rot.
<i>Aeronautes andecolus</i>				Aer.and.
<i>Phaethornis pretrei</i>				Phaepr.
<i>Phaethornis superciliaris</i>				Phaesup.
<i>Chlorostilbon aureoventris</i>				Chl.aur.
cf. <i>Hylocharis chrysura</i>				Hyl.chr.
cf. <i>Heliortyx baroti</i>				Hel.bar.
<i>Amazilia chionogaster</i>				Ama.chi.
<i>Thalurania furcata</i>				Tha.fur.
<i>Adelomyia melanogenys</i>				Ade.mel.
<i>Oreotrochilus adela</i>				Ore.ade.
<i>Patagona gigas</i>				inf. Pat.gig.
<i>Eriocnemis glaucopoides</i>				Eri.gla.
<i>Sappho sparganura</i>				Sap.spa.
<i>Microstilbon burmeisteri</i>				Micbur.
<i>Trogon personatus</i>				Trogper.
<i>Trogon curucui</i>				Trogcur.
<i>Ceryle torquata</i>				Cerytor.
<i>Chloroceryle americana</i>				Chl.ame.
<i>Momotus momota</i>				Mom.mom.
<i>Nystalus maculatus</i>				Nys.mac.
<i>Ramphastus tocius</i>				Ram.toc.
<i>Picumnus cirratus</i>				Picumci.
<i>Veniliornis frontalis</i>				Ven.fro.
<i>Veniliornis fumigatus</i>				Ven.fum.
<i>Piculus rubiginosus</i>				Piculru.
<i>Colaptes melanochlorus</i>				Col.mel.
<i>Campephilus melanoleuc.</i>				Campmel.
<i>Sittasomus griseicapil.</i>				Sit.gri.
<i>Xiphocolaptes major</i>				Xiphmaj.
<i>Lepidocolaptes angusti.</i>				Lepiang.
<i>Geositta rufipennis</i>				Geosruf.
<i>Geositta tenuirostris</i>				Geosten.
<i>Upucerthia jelskii</i>				Upu.jel.
<i>Upucerthia andaeicola</i>				++ Upu.and.
<i>Upucerthia ruficauda</i>				Upu.ruf.
<i>Cinclodes fuscus</i>				++ Cinfus.
<i>Cinclodes atacamensis</i>				Cincata.
<i>Furnarius rufus</i>				Fur.ruf.
<i>Leptasthenura fuligini.</i>				Leptful.
<i>Leptasthenura aegithal.</i>				Leptaeg.
<i>Synallaxis azarae</i>				Synaaza.
<i>Synallaxis frontalis</i>				Synafo.

	1000 m	2000 m	3000 m	Azurdury	Monte Grande	C. Hoyadas	C. Puntalajas	C. El Tapado	Río Parapei	Snia Racete	Río Parapei	C. Alto Desp.	Com. SausMayu	Com. Caja Mayu	Uruguay	Añimbo	Eia Tacurvite	Río Pilcomayo	El Palmar	Cerro Bufete	Cerro Misión	N C. Lagunillas	C. Campanarios	C. Campanario	C. Cobre Khasa	Río Puca Pampa	Río Puca Laja	Río Lechera	Abra Portillo	Culpina	Canargo
<i>Synallaxis scutatus</i>				Synascu.																											
cf. <i>Synallaxis albescens</i>				Synaalb.																											
<i>Cranioleuca pyrrhophia</i>				Cra.pyr.																											
<i>Asthenes dorbignyi</i>				Ast.dor.																											
<i>Asthenes heterura</i>				Ast.het.																											
<i>Asthenes punensis/sclat.</i>				Ast.pun.																											
<i>Phacelodomus rufifrons</i>				Phacruf.																											
<i>Phacelodomus striaticeps</i>				Phac.s-ps																											
<i>Phacelodomus striatocollis</i>				Phac.s-is																											
<i>Syndactyla rufosupercil.</i>				Syndruf.																											
cf. <i>Philydor rufus</i>				Phi.ruf.																											
<i>Xenops rutilans</i>				Xen.rut.																											
<i>Lochmias nematura</i>				Loc.nem.																											
<i>Thamnophilus caerulescens</i>				Tha.cae.																											
<i>Thamnophilus ruficapillus</i>				Tha.ruf.																											
<i>Batara cinerea</i>				Bat.cin.																											
<i>Taraba major</i>				Tar.maj.																											
<i>Myrmorchilus strigilatus</i>				Myr.str.																											
<i>Formicivora melanogaster</i>				For.mel.																											
<i>Pyriglena leuconota</i>				Pyrileu.																											
<i>Grallaria albigula</i>				Gra.alb.																											
<i>Scytalopus (magell.) zimmeri</i>				Scy.zi.																											
<i>Chiroxiphia boliviana</i>				Chi.bol.																											
<i>Phyllomyias sclateri</i>				Phy.scl.																											
<i>Phyllomyias uropygialis</i>				Phy.uro.																											
<i>Phyllomyias burmeisteri</i>				Phy.bur.																											
<i>Phaeomyias murina</i>				Phaemur.																											
<i>Campostoma obsoletum</i>				Campobs.																											
<i>Elaenia albiceps</i>				Ela.alb.																											
cf. <i>Elaenia parvirostris</i>				Ela.par.																											
<i>Elaenia obscura</i>				Ela.obs.																											
cf. <i>Elaenia palatangae</i>				Ela.pal.																											
<i>Myiopagis caniceps</i>				Myi.can.																											
<i>Mecocerculus leucophrys</i>				Mec.leu.																											
<i>Mecocerculus hellmayri</i>				Mec.hel.																											
<i>Serpophaga munda</i>				Ser.mun.																											
<i>Serpophaga subcristata</i>				Ser.sub.																											
<i>Serpophaga nigricans</i>				Ser.nig.																											
<i>Stigmatura budyoides</i>				Sti.bud.																											
<i>Anairetes flavirostris</i>				Anaifla.																											
<i>Anairetes parulus</i>				Anaipar.																											
<i>Leptopogon amaurocephal.</i>				Lep.ama.																											
<i>Phylloscartes ventralis</i>				Phy.ven.																											
<i>Todirostrum plumbeiceps</i>				Tod.plu.																											
<i>Todirostrum margaritaceiv.</i>				Tod.mar.																											
<i>Tolmomyias sulphurescens</i>				Tol.sul.																											
<i>Myiophobus fasciatus</i>				Myi.fas.																											
<i>Contopus fumigatus</i>				Con.fum.																											
<i>Cnemotriccus fuscatus</i>				Cne.fus.																											
<i>Sayornis nigricans</i>				Say.nig.																											
<i>Ochthoeca oenanthoides</i>				Och.oen.																											
<i>Ochthoeca leucophrys</i>				Och.leu.																											
<i>Polioxolmis rufipennis</i>				Pol.ruf.																											
<i>Myiotheretes striatcol.</i>				Myi.str.																											
<i>Pyrocephalus rubinus</i>				Pyr.rub.																											
<i>Xolmis irupero</i>				Xol.iru.																											
<i>Agriornis montana</i>				Agr.mon.																											
<i>Agriornis andicola</i>				Agr.and.																											
<i>Agriornis microptera</i>				Agr.mic.																											
<i>Muscisaxicola maculirost.</i>				M.mac.																											
<i>Muscisaxicola rufivertex</i>				Muscruf.																											
<i>Muscisaxicola cinerea</i>				M.cin.																											
<i>Lessonia oreas</i>				Les.ore.																											
<i>Knipolegus signatus</i>				Kni.sig.																											
<i>Knipolegus aterrimus</i>				Kni.ate.																											
<i>Knipolegus hudsoni</i>				Kni.hud.																											
<i>Satrapa icterophrys</i>				Sat.ict.																											
<i>Hirundinea ferruginea</i>				Hir.fer.																											
<i>Suiriri suiriri</i>				Sui.sui.																											
<i>Myiarchus tuberculifer</i>				Myi.tub.																											
<i>Myiarchus tyranninus</i>				Myi.tyr.																											
<i>Myiarchus swainsoni</i>				Myi.swa.																											

	1000 m	2000 m	3000 m	Azurduty	Monte Grande	C. Hoyadas	C. Puntalajas	C. El Tapado	Río Parapei	Santa Racete	Río Parapei	C. Alto Desp	Com. SausilMayu	Com. Caja Mayu	Uruguay	Añimbo	Elá Tacurvite	Río Pilcomayo	El Palmar	Cerro Bufete	Cerro Misión	N C. Lagunillas	C. Campanarios	C. Campanito	C. Cobre Khasa	Río Puca Pampa	Río Puca Laja	Río Lechéra	Abra Portillo	Culpina	Camargo
<i>Pitangus sulphuratus</i>	+			Pit.sul.																											
<i>Myiodynastes maculatus</i>				Myi.mac.																											
<i>Machaetornis rixosus</i>				Mac.rix.																											
<i>Tyrannus melancholicus</i>				Tyr.mel.																											
<i>Xenopsaris albinucha</i>				Xen.alb.																											
<i>Casiornis rufa</i>				Cas.ruf.																											
<i>cf. Pachyramphus viridis</i>				Pac.vir.																											
<i>Pachyramphus polychopt.</i>				Pac.pol.																											
<i>Pachyramphus validus</i>				Pac.val.																											
<i>Notiochelidon cyanoleuca</i>				Not.cya.																											
<i>Hirundo rustica</i>				Hir.rus.																											
<i>Riparia riparia</i>				Rip.rip.																											
<i>Petrochelidon pyrrhonota</i>				Pet.pyr.																											
<i>Petrochelidon andecola</i>				Pet.and.																											
<i>Cyanocorax chrysops</i>				Cya.chr.																											
<i>Cyanocorax cyanomelas</i>				Cya.cya.																											
<i>Cistothorus platensis</i>				Cis.pla.																											
<i>Troglodytes aedon</i>				Tro.aed.																											
<i>Troglodytes solstitialis</i>				Tro.sol.																											
<i>Mimus dorsalis</i>				Mim.dor.																											
<i>Catharus dryas</i>				Cat.dry.																											
<i>Turdus chiguanco</i>				Turdchi.																											
<i>Turdus serranus</i>				Turdser.																											
<i>Turdus rufiventris</i>				Turdruf.																											
<i>Turdus amaurochalinus</i>				Turdama.																											
<i>Turdus albicollis</i>				Turdalb.																											
<i>Turdus nigriceps</i>				Turdnig.																											
<i>Anthus hellmayri</i>				Ant.hel.																											
<i>Cyclaris gujanensis</i>				Cyc.guj.																											
<i>Vireo (olivaceus) chivi</i>				Vir.chi.																											
<i>Molothrus bonariensis</i>				Mol.bon.																											
<i>Molothrus badius</i>				Mol.bad.																											
<i>Psarocolius decumanus</i>				Psa.dec.																											
<i>Cacicus chrysopterus</i>				Cac.chr.																											
<i>Scaphidura oryzivorus</i>				Scapory.																											
<i>Icterus cayenensis</i>				Ict.cay.																											
<i>Parula pitayumi</i>				Par.pit.																											
<i>Myioborus bruniceps</i>				Myiob.br.																											
<i>Basileuterus signatus</i>				Bas.sig.																											
<i>Basileuterus bivittatus</i>				Bas.biv.																											
<i>Conirostrum speciosum</i>				Conispe.																											
<i>Diglossa sittoides</i>				Dig.sit.																											
<i>Tersinia viridis</i>				Ter.vir.																											
<i>Chlorophonia cyanea</i>				Chl.cya.																											
<i>Euphonia musica</i>				Euphmus.																											
<i>Pipraeidea melanonota</i>				Pip.mel.																											
<i>Anisognathus flavinuchus</i>				Ani.fla.																											
<i>Thraupis bonariensis</i>				Thr.bon.																											
<i>Thraupis sayaca</i>				Thr.say.																											
<i>Piranga leucoptera</i>				Pir.leu.																											
<i>Hemithraupis guira</i>				Hem.gui.																											
<i>Trichothraupis melanops</i>				Tri.mel.																											
<i>Thlypopsis sordida</i>				Thl.sor.																											
<i>Chlorospingus ophthalmic.</i>				Chl.oph.																											
<i>Salpator aurantirostris</i>				Sal.aur.																											
<i>Salpator rufiventris</i>				Sal.ruf.																											
<i>Pheucticus aureoventris</i>				Phe.aur.																											
<i>Cyanocompsa brissonii</i>				Cya.bri.																											
<i>Volatinia jacarina</i>				Vol.jac.																											
<i>Catamenia analis</i>				Cat.ana.																											
<i>Catamenia inornata</i>				Cat.ino.																											
<i>Ammodramus humeralis</i>				Ammodram.																											
<i>Sicalis citrina</i>				Sic.cit.																											
<i>Sicalis luteocephala</i>				Sic.lut.																											
<i>Sicalis olivascens</i>				Sic.oli.																											
<i>Sicalis flaveola</i>				Sic.fla.																											
<i>Diuca diuca</i>				Diu.diu.																											
<i>Phrygilus atriceps</i>				Phr.atr.																											
<i>Phrygilus fruticeti</i>				Phr.fru.																											
<i>Phrygilus unicolor</i>				Phr.uni.																											
<i>Phrygilus plebejus</i>				Phr.ple.																											
<i>Phrygilus alaudinus</i>				Phr.ala.																											

	1000 m	2000 m	3000 m
<i>Lophospingus griseocrist.</i> +			
<i>Coryphospingus cucullat.</i>			
<i>Atlapetes fulviceps</i>			
<i>Atlapetes torquatus</i>			
<i>Arremon flavirostris</i>			
<i>Zonotrichia capensis</i>			
<i>Emberizoides herbicola</i>			
<i>Poospiza boliviana</i>			
<i>Poospiza hypochondria</i>			
<i>Poospiza torquata</i>			
<i>Poospiza cinerea</i>			
<i>Poospiza (nigroru.) whittii</i>			
<i>Poospiza erythrophrys</i>			
<i>Embernagra platensis</i>			
<i>Carduelis magellanica</i>			
<i>Carduelis atrata</i>			
<i>Passer domesticus</i>			
<i>Lop.gri.</i>			
<i>Corycuc.</i>			
<i>Atl.ful.</i>			
<i>Atl.tor.</i>			
<i>Arr.fla.</i>			
<i>Zon.cap.</i>			
<i>Emb.her.</i>			
<i>Poo.bol.</i>			
<i>Poo.hyp.</i>			
<i>Poo.tor.</i>			
<i>Poo.cin.</i>			
<i>Poo.whi.</i>			
<i>Poo.ery.</i>			
<i>Emb.pla.</i>			
<i>Car.mag.</i>			
<i>Car.atr.</i>			
<i>Pas.dom.</i>			
Azurduy			
Monte Grande			
C. Hoyadas			
C. Puntalajas			
C. El Tapado			
Río Parapetí			
Suía Racete			
Río Parapetí			
C. Alto Desp			
Com. SausiMayu			
Com. Caja Mayu			
Uruguay			
Añimbo			
Eña Tacurvíte			
Río Pilcomayo			
El Palmar			
Cerro Bufete			
Cerro Misión			
N C. Lagunillas			
C. Campanarios			
C. Campamento			
C. Cobre Klasa			
Río Puca Pampa			
Río Puca Laja			
Río Lechéra			
Abra Portillo			
Culpina			
Canmargo			



Spot-backed Puffbird (*Nyastalus maculatus*)

