PRELIMINARY CLIMATIC OVERVIEW OF MIGRATION PATTERNS IN SOUTH AMERICAN AUSTRAL MIGRANT PASSERINES

Leo Joseph
Laboratorio de Evolución, Facultad de Ciencias, Tristán Narvaja 1674, Montevideo 11200, Uruguay

Resumen. Un examen preliminar de 92 paseiriformes de migración austral sugiere que a pesar de que ellos se solapan ampliamente en verano en el sur templado de Sudamérica, se separan después de la migración de post-nidificación en dos grupos diferentes: uno en áreas cálidas y húmedas con temperaturas diarias promedio mayores que aproximadamente 20°C, y otro en áreas de temperaturas diarias promedios menores de aproximadamente 20°C. Dos especies son difíciles de ubicar en cualquiera de estos grupos, indicando que la distinción no es absoluta. El área limitada por la zona entre las isothermas de 16°C y 20°C separan esencialmente los dos grupos de migrantes en invierno, aunque existe cierto solapamiento. Se necesita una revisión más extensa de los patrones de distribución ecológica basados en estudios de campo y museo. Sin embargo, se argumenta la existencia de un sistema de migración templado-tropical en Sudamérica, el cual ha sido indicado por muchos autores, que debería ser claramente reconocido junto con la complejidad del resto de migración austral. El reconocimiento de estos patrones debería promover un mejor entendimiento de los procesos que han operado en la ecología y evolución de los migrantes australes.

Abstract. A preliminary survey of 92 austral migrant passerines suggests that although they overlap widely in summer in the temperate southern cone of South America they divide after post-breeding migration into two distinct groups: one in warm humid areas with daily mean temperatures greater than approximately 20°C, and the other in areas with daily mean temperatures lower than approximately 20°C. Two migrants difficult to place in either group show that this distinction is not absolute. The area bounded by the 16°C and 20°C daily mean temperature isotherms essentially separates the two groups of migrants in winter though there is overlap. More extensive reviews of seasonal distribution patterns based on field and museum study and bioclimatic analyses are needed. Nonetheless, it is argued that the existence of a South American temperate-tropical migration system, which has been indicated by many authors, should be clearly recognized along with the complexity of all other austral migration entirely within cooler climates of South America. The recognition of these patterns should promote a better understanding of the processes that have operated in the evolution and ecology of austral migrants. Accepted 28 December 1996.

Key words: Austral migration, migration, temperature, passerines, temperate-tropical migration, Neotropical migrants.

INTRODUCTION

Migrations of birds that breed in southern South America, often for simplicity described as austral migration, have been little studied in their entirety (e.g., Chesser 1994, Sick 1983, Zimmer 1938) though many authors have discussed the migrations of individual species (e.g., Belton 1994, Gore & Gepp 1978, Hayes 1995a, Hayes et al. 1994, Nores et al. 1983, Short 1975, Wetmore 1926, Willis 1988). The prevailing view of austral migration patterns has combined elements of climate and latitude and was embodied by Chesser (1994), in a pioneering review of the subject, who defined austral migrants as "species that breed in temperate areas of South America [climatic and latitudinal elements - LJ] and migrate north, towards or into, Amazonia [a latitudinal element - LJ], for the southern winter".

Some authors, however, have decoupled climatic and latitudinal elements when discussing these same birds' migration patterns. In purely climatic terms, two broad migration patterns have long been recognized. Wermore (1926), Zimmer (1938), Gore & Gepp (1978), Narosky & Yzurieta (1993), Chesser (1994) and Hayes et al. (1994) all recognized these patterns. One is characterized by species with non-breeding distributions in warm humid lowland tropical zones and a clear example is the migration of Swainson's Flycatcher Myiarchus swainsoni (for details see Lanyon 1978). The other involves birds with non-breeding distributions in climatically temperate and/or cooler regions, some of which may lie well into tropical latitudes; these regions variously include the high Andes (e.g., all migratory ground tyrants Muscisaxicola spp.; see Ridgely & Tudor 1994)

Present address: Department of Ornithology, Academy of Natural Sciences, 19th and Parkway, Philadelphia, 19103, U.S.A.
and the northern parts of the so-called southern cone of South America (e.g., Rufous-chested Dotterel Charadrius modestus; see Belton 1994). Conversely, Hayes (1995b) adopted an extreme, latitudinal approach, defining “Austral migration” as the migration of any migratory birds breeding anywhere in the southern hemisphere, nor just in South America, and then undergoing a northward migration of any extent.

Nonetheless, knowledge of the seasonal distributions of most South American/Austral migrants is still rudimentary. There is a pressing need for detailed reviews of the kind published for Myiarchus swainsoni by Lanyon (1978), the Slaty Elaenia Elaenia strepera (Marantz & Remsen 1991), and the Patagonian Tyrant Colorhamphus parvirrostris (Chesser & Marín 1994) for all Austral migrants. Here, I do not attempt such reviews. Instead, I ask whether an exploratory overview of the maps assembled in Ridgely & Tudor (1989, 1994) for South American passerines might indicate the worth of such future reviews relating Austral migration patterns to climatic factors. I approach my aim by discussing whether correlations are apparent between daily mean temperatures in the breeding and non-breeding seasons and seasonal changes in distribution patterns of the austral migrants themselves. Having based this preliminary survey on the distribution maps in Ridgely & Tudor (1989, 1994), I restrict its scope to passerines.

METHODS

I examined the maps in Ridgely & Tudor (1989, 1994) and noted where different species were indicated as sharing distributional limits in summer and winter. I then tried to correlate the estimated shared distributional limits with maps of daily mean temperature (DMT, °C) isotherms in January and July derived primarily from Hoffman (1975) but also from Martyn (1992) and Prohaska (1976). I chose July because that is when Austral migrants can be expected to have reached their winter destinations, and January because that is when they can be expected to be well into their breeding cycle either with young in the nest or feeding fledged young. One may criticize the maps in Ridgely & Tudor (1989, 1994) and my procedure by saying that the indicated limits reflect the biases of the compiler(s) of the maps rather than real limits. While it is perhaps impossible to dismiss this objection, the maps were compiled by drawing lines around locations of museum specimens and reliable published records and they show summer breeding ranges and winter distribution as far as could be discerned (R. Ridgely, pers. comm.). Until more detailed distributional reviews are available, it is with due caution worth looking for trends in the maps. Equally, I acknowledge and stress that many of the maps are first attempts to summarize distributions. I further consider limitations of the maps in the discussion. The maps were not prepared, however, to show southern limits in winter. Therefore, the northern part of the summer, breeding range shown on the maps may include the southern part of the wintering range. This problem was usually obviated by reference to the text of Ridgely & Tudor (1989, 1994) or by reference to papers dealing with particular species (e.g., Chesser & Marín 1994, Lanyon 1978, Marantz & Remsen 1991, da Silva 1995, Straneck 1993) and regions (Narosky & Giacomo 1993, Short 1975, Zotta 1944). Appendix I lists the 92 migrants for which maps in Ridgely & Tudor (1989, 1994) were used to look for patterns in seasonal distributions among austral migrants.

RESULTS

Distributions of birds. The maps show twenty-seven Austral migrant passerines distributed in winter in the warm, humid lowland tropics and sharing part or all of a common western limit in a zone orientated north-west to south-east in lowland Amazonian Peru and Bolivia (Fig. 1, Appendix 1 - Group 1a). Three of these, Red-eyed Vireo Vireo olivaceus, Bran-coloured Flycatcher Myiopodus fasciatus and Euler’s Flycatcher Lathotriccus euleri, each have two Austral migrant subspecies but whether both winter in south-western Amazonia in each case is unclear. Fourteen other migrants are also shown as wintering in lowland tropical areas but do not reach south-western Amazonia (Appendix 1 - Group 1b). Group 1 (a and b, 44 migrant taxa) is dominated by tyrannids and hirundinids.

Most of the other Austral migrant passerines studied winter either west of south-western Amazonia, in the high altitudes of the Andes, or south of a narrow zone running diagonally through the chaco of Bolivia and Paraguay, virtually bisecting the latter country, and which then inflects north-eastwards into Brazil (Fig. 1, Appendix 1 - Group 2, 46 migrants). Those in the Andes are characterized by the ground tyrants Muscicarpus spp. such that a disjunction
occurs between Groups 1a and 2 along the zone referred to in south-western Amazonia. The continuation of this zone in Paraguay also marks the indicated northern winter limit of Group 2 migrants such as the Sharp-billed Canastero Asbhenes pyrrholecus, Lesser Shrike-Tyrant Agriornis murina, Grey-bellied Shrike-Tyrant Agriornis m. micropterus, Black-crowned Monjita Xolmis coronata, and the Chilean Swallow Tachycineta leucopyga. A few other Group 2 migrants are shown as occurring in winter a little beyond this zone to northernmost Paraguay (e.g., Spectacled Tyrant Hymenops p. perspicillatus, Hudson’s Black-Tyrant Knipolegus hudsoni, White-banded Mockingbird Mimus triurus). Conversely, most of the Group 1a and 1b migrants are shown generally north of the zone. A few Group 1 migrants, however, are shown south of the zone in winter (e.g., Cliff Flycatcher Hirundinea ferruginea bellica, Creamy-bellied Thrush Turdus amaurochalinus, Grassland Yellow Finch Sicalis lutola lutiventris). Despite this minor overlap, a disjunction broadly separating Groups 1 (a and b) and 2 again appears.

Maps for several Group 2 migrants in winter share inflections north-eastwards into south-eastern Brazil, some ranging as far as the Brazilian states of Paraná and São Paulo and others only as far as that of Rio Grande do Sul (e.g., Many-coloured Rush-Tyrant Tachuris rubrigaster, Hymenops perspicillatus, Coppery Pipit Anthus corentini, Mimus triurus). Again, the maps for Group 1 migrants in lowland tropical areas in winter suggest little overlap with Group 2 migrants, which are generally further to the south. One of the Group 1 migrants, Tropical Kingbird Tyrannus m. melancholicus, does have a southern limit along a similarly placed inflection. A disjunction between Group 1 (a and b) and Group 2 is again indicated (Fig. 1).

At least two species cannot readily be placed in either group. The Blue-billed Black-Tyrant Knipolegus cyanirostris and Eastern Slaty-Thrush Turdus subalaris are largely south-eastern Brazilian species that migrate roughly westwards towards Paraguay (see also comments on Sporophila spp. in discussion and Appendix).

In summer, the maps indicate a broad zone of overlap between Groups 1 and 2, mainly in central-northern Argentina. Group 1 ranges south in summer mostly as far into north-eastern Argentina, south-eastern Paraguay, Uruguay and south-eastern Brazil in the northernmost part of the temperate zone. A subset of 19 of that group (asterisked in Appendix 1) shares a common western limit along a zone that runs roughly north-south in central-northern Argentina and another subset of eight of these extends further to the south to an eventual limit running east-west in northern Chubut (Fig. 2). The White-crested Elaenia Elaenia albiceps chilensis is exceptional in ranging still further south during summer. Group 2 is mostly in or south of central Argentina and Chile in summer.

Climatic correlates: temperature. In January, the 20°C DMT isotherm correlates with the indicated western and southern limits in summer of the 19 southernmost migrants of Group 1 (except Elaenia albiceps chilensis, which ranges even further to the south and west; Fig. 2). These migrants are marked with an asterisk in the Appendix. In July, the shape and

**FIG. 1.** Map of South America showing location of an arc-shaped zone in winter here suggested as broadly separating the non-breeding season distributions of 44 migrant passerines that are then mostly widespread in lowland tropics (temperate breeding-tropical wintering group – Groups 1a and 1b in Appendix) and 46 that then collectively remain mostly south of the zone (temperate-temperate zone group – Group 2 in Appendix). Arrows indicate approximate limits.
FIG. 2. Maps of South America showing location of, top left, the 20°C daily mean temperature isotherm in January (summer) and, top right, the zone between the 16°C and 20°C isotherms in July (winter) (simplified from Martyn 1992). To facilitate orientation, only relevant international boundaries are shown. In January, most of the 44 temperate-tropical migrants discussed in the text (see Group 1 in the Appendix) are suggested to be east and north of the central 20°C isotherm, which correlates well with the apparent southern and western limits of a subset of 19 of the group. These 19 are indicated with an asterisk in the Appendix. Only Elaenia albiceps chilenis extends substantially to the south and west of this isotherm in summer (see Joseph, in press). In July, note the correlation between the location of the 16°C–20°C zone and the zone shown in Figure 1 as marking a likely distributional disjunction between Group 1 (a and b) and Group 2 migrants, especially in south-western Amazonia. Distribution maps, from Ridgely & Tudor (1989, 1994), of several austral migrants are shown (striped is summer breeding range, black lines enclose winter limits) (maps from The Birds of South America Volumes 1 and 2, 1989, 1994, reproduced by permission of Oxford University Press and R. Ridgely). Note the various correlations between the summer and winter limits and the isotherms in both seasons. See text for further discussion.
location of the zone between the 16°C and 20°C DMT isotherms correlate broadly, and in south-western Amazonia sharply, with the zones described above that separate the winter distributions of Groups 1 and 2 (Fig. 2). Within the zone, the 19°C DMT isotherm, which also runs diagonally through Paraguay in July (Prohaska 1976), correlates with the northern, winter limits shown on the maps in Ridgely & Tudor (1989, 1994) for members of Group 2 such as Xolmis coronata and Anthus c. correndera (see Fig. 2). Similarly, the 16°C DMT isotherm inflects north-eastwards into Brazil in July and so correlates with the north-eastwards inflections shown in the winter distributions of Group 2 migrants such as Anthus c. correndera and in the southern limit of the Group 1 migrant Tyrannus m. melancholicus. Finally, the areas where in summer migratory high Andean species of Muscisaxicola ground-tyrants breed have temperatures at that time of the year typically less than 15°C. In winter, DMTs in these areas fall to 0°C or less and the birds migrate north to areas, some as far away as Ecuador in the case of the White-browed Ground-Tyrant M. albifrons, where DMTs are at 15°C or less all year.

DISCUSSION

The aim of this exploratory survey has been to determine whether later descriptions of migration patterns of Austral migrants based on detailed field and museum specimen data might usefully be analysed in terms of climatic correlates. Stressing that the study has been based on maps that are often first attempts to summarize distributions for the birds involved, I state the key finding of this study as follows: that in the non-breeding season passerine Austral migrants separate into two groups, depending on whether they are in areas with July DMTs greater than or less than approximately 20°C. The present finding affirms and refines the long held view, which is effectively based solely on climate (see introduction), that there are two main migration patterns among austral migrants, here represented by Groups 1 and 2, but which might best be considered as two extremes of a climatically defined spectrum of long- and short-distance migration patterns among these species. Inaccuracies in the maps of Ridgely & Tudor (1989, 1994) will most profoundly affect this conclusion if they are at a very broad geographical scale showing, for example, an Austral migrant as not occurring in the warm, humid tropics in its non-breeding season when in fact it does or vice-versa.

The migration pattern of Group 1 (a and b) is a "temperate zone breeding-warm, humid tropical zone wintering" pattern. In winter these birds are mostly north and east of the distributional disjunction shown in Fig. 1. More specifically, in July they are mostly in areas with DMTs greater than 16°C–20°C whereas in January they are in areas with DMTs in that month of greater than 20°C. Zimmer (1938) alluded to the value of temperature in understanding the migration pattern of this group of birds. Among them are 44 passerines dominated by tyrannids and hirundinids (for non-passerine examples see the northern Austral migrants in Hayes et al. 1994).

The migration pattern of Group 2 is a "temperate zone breeding-temperate wintering" pattern although it is almost certainly a complex of migration patterns or migration subsystems. In winter these birds are mostly south and west of the distributional disjunction shown in Fig. 1. Some range well into tropical latitudes in winter but the DMTs in July of the areas where they winter are less than 20°C. Among this group there are 46 passerines (again, for non-passerine examples see the southern Austral migrants of Hayes et al. 1994).

The likely complexity of migration patterns shown by all Austral migrants within cool and/or temperate climates of South America, therefore, can most easily be seen when one compares the migrations of, for example, a) species such as Knipolegus cyanrostris and Turdus subalaris, which migrate more east-west than north-south, b) the migrations of strictly Andean passerines such as the migratory Muscisaxicola ground-tyrants and the Andean Slaty-Thrush Turdus nigriceps, c) migrations of birds along the Atlantic littoral although this involves non-passerines such as the Royal Tern Sterna maxima (Escalante 1985), d) migrations of many tyrannids that in winter extend northwards into Paraguay and southern Brazil, and e) the altitudinal migrations of many south-east Brazilian and central Argentinian birds.

Some of this complexity has been referred to earlier. Sick (1983) described trans-Andean crossings of individuals of Hymenops perspicillatus and of Euphonia albiceps and Willis (1988) discussed the complex movements of birds in the São Paulo region. Altitudinal migration has been discussed by numerous authors (Belton 1994, Nores et al. 1983, Ridgely &
Tudor 1989, 1994, Willis 1988). This complexity of migration patterns in South American cool and/or climates needs to be studied further. Furthermore, the migrations of species in group a) above and indeed the altitudinal migrants in group c) may better be considered as intraregional migrations. Intraregional migration is an increasingly clear phenomenon among tropical birds such as the Resplendent Quetzal Phaethon mocinno and Lesson’s Seedee Pharomachrus bouvronides (see Powell & Bjock 1994 and Ridgley & Tudor 1989 respectively) and still more Austral migrants may also best be regarded as intraregional migrants when more data are available on their movements. Possible examples are the Strange-tailed Tyrant Alectrurus rivoso (see Pacheco & Gonzaga 1994) and the Sporophila seedeaters. I stress, however, that such intraregional migration often involves altitudinal movements or east-west patterns of movements with little clear correlation to seasonal changes in temperature such as I have discussed (Antas 1994, Belton 1984-85, Willis 1988). Presumably, these movements will be found to correlate more strongly with other environmental stimuli.

Also to emerge in this study have been issues for further field and museum study to address among Austral migrants and these include the gradation between short- and long-distance migration and the presence in migratory species of resident and migrant individuals. The distinction between short-distance intraregional migrants and long-distance migrants is often not clear and species such as the Chestnut Seedee Pharomachrus cinnamomea, Marsh Seedee Pharomachrus palustris and Black-bellied S. melanogaster have migration patterns difficult to place in either category on present knowledge (see Ridgely & Tudor 1989; Appendix). This is not surprising given the number of times that migration has evolved and the short time during which new directions of migration can evolve (Berthold et al. 1992). Similarly, the distinction between resident and migrant individuals is also blurred. At least in some tropical species, resident individuals have homed to their point of origin in translocation experiments and in tropical and temperate species they have shown the same physiological and behavioral changes that conspecific migrants undergo prior to migration (Chan 1994, 1995; Ramos 1988; Ramos & Rappole 1994).

Sporophila seedeaters collectively demonstrate the potential intricacy of these problems among austral migrants. Davis (1993) found that the Black and Tawny, Ruddy-breasted, Dark-throated, and Rufous-rumped Seedeaters, (S. nigrorufa, S. minuta, S. rufo-occili, and S. hypochroma, respectively), were each recorded once in a two year study period in September or November and again, though questionably so, once in March or April. These observations could be consistent with long distance temperate-tropical migration, intraregional migration, local wandering or with several of these categories applying to the same individuals or populations over several years. A full understanding of Austral migrants will need to consider the possibility of such variation within species and between years.

Conclusion. Climatic correlates of the migration patterns of Austral migrants might usefully be sought when the migration patterns themselves are better defined with detailed field and museum study. Ultimately, Austral migration patterns might be described not just in terms of latitude, longitude and altitude but also in terms of bioclimate envelopes generated from statistical distributions of bioclimatic variables measured throughout the distribution of each migrant (for examples of the approach see Nix 1976 and Root 1988). The use of temperature in the present study is a first step in this direction and Geographic Information Systems (GIS) are ideal for developing it (Shaw & Atkinson 1990, Star & Estes 1990). Elsewhere, I have explored some ecological and evolutionary ramifications of these conclusions (Joseph 1996) and offered a more detailed climatic approach for nine Austral migrants (Joseph, in press) to complement this initial overview.

ACKNOWLEDGEMENTS

For helpful criticisms and encouraging comments I thank J. Bates, K. Burns, E. Danulat, S. Davis, G. D’Elia, F. Hayes, E. Lessa, W. Magnusson, A.L. Por-zechanski, R. Prum, M. Ramos, J. Rappole, R. Ridgely, M. Rouges, K.-L. Schuchmann, T. Schulenburg, D. Storz and an anonymous reviewer of an earlier draft, though I am responsible for the views expressed. Dr. J. Navas and Sra G. Crispo (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires) and Dr. J. Cuello (Museo Nacional de Historia Natural, Montevideo) allowed me to examine museum specimens in their care in order to better familiarize myself with some finer points of Austral migration and my wife Domitilia and G. D’Elia helped in this respect. For help with literature I especially thank J. Bates, J.P. Cuello, S. Degnan,
F. Hayes, J. Lyons, J. García-Moreno, J.F. Pacheco, R. Slade, M.F. Smith and F.G. Stiles. J. Bates and S. Degnan critically commented on a draft and E. Lessa provided conditions in which to work and also commented on a draft. A.L. Porzecanski and I. Tomasco helped with the Spanish abstract. Financial support was from the Programa de Desarrollo de las Ciencias Basicas (PEDECIBA) and the Consejo Nacional de Investigacion Científica y Tecnológica (CONICYT), Montevideo and the Third World Academy of Sciences (TWAS), Trieste, Italy. Finally, I acknowledge the important contributions of R. Rüdgel and G. Tudor in producing their 1989 and 1994 books on which I have largely based this analysis, T. Chesser for writing a stimulating review of Austral migration and J.T. Zimmer's foreshadowing in 1938 of many of the ideas I have elaborated many years later (but before reading his paper!).

APPENDIX

Austral migrant passerine species and subspecies studied in the present analysis and arranged in groups presented in Results above. In addition, Turdus subalaris and Knipeleus cyanirostris were included but could not readily be placed in either of the two main groups listed below. All breed in temperate South America and on present evidence undergo a post-breeding migration followed by a regular return to breeding grounds, though this may not involve all populations of each species or subspecies. Clearly, a full analysis of migration by birds breeding in southern South America will need clarification of the migratory status of all species through more field work and complete surveys of literature and museum sources.

1. Temperate-tropical migrants suggested here to be migrating between breeding and non-breeding areas with January and July, respectively, daily mean temperatures greater than or equal to approximately 16°C–20°C. Those migrants marked with an asterisk have southern and western range limits in summer that correlate with the location of the 20°C isotherm in that season.


b. Other species or subspecies with winter ranges mostly in lowland tropics: Olivaceous Eulaenia Eulaenia mesoleuca, Lesser Eulaenia Eulaenia chiquiquensis, Slaty Eulaenia Eulaenia strepera* (winners in hilly country in northern Venezuela – Marantz & Remsen 1991), Hirundinea ferruginea felicosa (also H. f. pallidior), Yellow-browed Tyrant Saccapua icterophyrs*, Rufous-tailed Antilla Antilla phoenicurus, Myiarchus s. swainsoni, Piratic Flycatcher Legatus l. leucophatus, Swallow-tailed Cotinga Phibalura flavirostris, Bare-throated Bellbird Procnias nudicollis, Tawny-headed Swallow Stegiodoptyx fuscata*, Turdus amaurochalinus*, Hepatic Tanager Piranga flava flava, Sicalis luteola luteiventris*.

2. Cool temperate zone migrants in which winter are in areas with July daily mean temperatures generally less than 20°C

Short-billed Miner Geositta antarctica, Scale-throated Earthcreeper Upucerthia d. dumetaria, Bar-winged Cinclodes Cinclodes f. fuscescens, Cordoba Cinclodes Cinclodes mochochegonis, Asthenes pyrohela, White-bellied Tyrant Serpophaga munda, Gray-crowned Tyrannulet Serpophaga griseiceps (see Straneck 1993), Warbling Dorado Pseudocolopetrix flaviiventris, Dinelli’s Dorado Pseudocolopetrix dinellianus, Tufted Tit-Tyrant Anairetes parulus patagonicus, Yellow-billed Tit-Tyrant Anairetes f. flavirostris, Patagonian Tyrant Coloramphus parvirostris, Tachy-

REFERENCES


