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TOWARDS A BROADER VIEW OF NEOTROPICAL MIGRANTS: CONSEQUENCES OF A RE-EXAMINATION OF AUSTRAL MIGRATION

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Resumen. La evolución de la migración de aves Neárticas-Neotropicales templada-tropical es examinada brevemente. Orígenes tropicales o subtropicales son considerados presentemente más plausibles que orígenes templados. Lo mismo se concluye para los orígenes del sistema migratorio templado-tropical Sud Americano descripto en un artículo que acompaña a este. El reconocimiento de dos sistemas migratorios templado-tropicales en las Américas sugiere a su vez una clasificación de los principales patrones migratorios de las Américas: un Sistema Migratorio del Nuevo Mundo, Sistemas Migratorios Templado-Tropicales Neartico-Neotropical (NETT) y Sud Americano (SATT), y Sistemas Migratorios Templado Fríos Sud Americano (SACT) y Norte Americano (NACT). Varias aves migratorias, en especial las de migración intraregional, poseen patrones de migración que son dificiles de asignar a alguno de los sistemas descriptos. Sin embargo, el reconocimiento de estos patrones principales permitiría avanzar en el estudio de los procesos involucrados en la evolución y ecología de la migración de las aves americanas. A modo de ejemplo, se propone una hipótesis filogenética resultante del reconocer la existencia de dos sistemas migratorios templado-tropicales.

Abstract. The evolution of Nearctic-Neotropical temperate-tropical bird migration is briefly reviewed. Tropical or subtropical origins are at present as plausible or more plausible than temperate origins. A similar conclusion is drawn for the origins of the South American temperate-tropical migration system identified in an accompanying paper. Recognition of two temperate-tropical migration systems in the Americas in turn suggests a classification of major migration patterns in the Americas: a Pan New World Migration System, Nearctic-Neotropical Temperate-Tropical (NETT) and South American Temperate-Tropical (SATT) Migration Systems, and South American Cool Temperate (SACT) and North American Cool Temperate (NACT) Migration Systems. Migration patterns of some migrants, especially intraregional ones, cannot readily be placed in either system. Nonetheless, recognition of these main patterns should facilitate further study of the processes involved in the evolution and ecology of bird migration in the Americas. As an example, a phylogenetic hypothesis arising from the recognition of two temperate-tropical migration systems is proposed. *Accepted 17 June 1996.*

Key words: Temperate-tropical migration, Austral migration, Neotropical migrants, migration systems.

INTRODUCTION

The existence of two main migration patterns among South American austral migrant birds has long been recognized (Wetmore 1926, Zimmer 1938, Gore & Gepp 1978, Narosky & Yzurieta 1993, Hayes *et al.* 1994, Chesser 1994). Elsewhere (Joseph, submitted) I have examined the migration patterns of austral migrants in more detail and concluded that ornithologists should abandon the concept of a single Austral migration system among Austral migrants in favour of a more bioclimatically orientated view. By that view, we would explicitly recognize both the existence of a South American temperate-warm, humid tropical system, hereafter for simplicity termed temperate-tropical, and the complexity of all other Austral migration.

Though in part due to plainly acknowledged semantic difficulties, it is ironic that Austral migrants, some of which undergo migrations of more than a thousand kilometres within the Neotropical region, have been excluded from some recent major reviews of Neotropical migrants (e. g., DeGraaf & Rappole 1995, Hagan & Johnston 1992, Keast & Morton 1980) though the review of Chesser (1994) in Morton *et al.* (1994) rectified this. In this essay I continue attempts to place Austral migration in a broader context of Neotropical migration by examining some evolutionary and ecological relationships between Austral migrants and bird migration in the Americas generally.

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EVOLUTION OF TEMPERATE-TROPICAL MIGRATION: THE NEARCTIC-NEOTROPICAL SYSTEM

I contend that a key to an ecological and evolutionary perspective on Austral migrants lies in beginning with a consideration of the evolution of the Nearctic-Neotropical migration system, especially its strictly temperate-tropical component. This involves birds that breed in temperate North America and winter in the tropics of Central and South America and the Caribbean (see DeGraaf & Rappole 1995, Hagan & Johnston 1992, Keast & Morton 1980, Terborgh 1989). Accordingly, the evolutionary question I consider first is whether the Nearctic-Neotropical temperate-tropical migrants originated in North American temperate climates and evolved migration southwards to the tropics ("northern home" hypothesis) or in tropical American climates and evolved migration northward to the temperate zone ("southern home" hypothesis).

Gauthreaux (1982) briefly reviewed debate on this point. He noted that evidence in support of one hypothesis does not disprove the other and that direction of migration and the capacity to migrate can both evolve rapidly (see also Berthold *et al.* 1992). The southern home hypothesis, however, has recently gained increasing support. This has come mainly from ecological standpoints (see Keast 1980, DeGraaf & Rappole 1995, Fretwell 1980, Levey & Stiles 1992, Rappole & Tipton 1992, and papers cited therein). Cox (1985), formulated the southern home hypothesis precisely in terms of tropical origins followed by evolution of migration covering ever greater distances north into the temperate zone. He tested it for the migratory parulines and rejected it in favour of an alternative that these and other temperate-tropical migrants evolved from resident ancestors in a staging area in the strongly seasonal, essentially wet-dry monsoonal, environments of the Mexican plateau in northernmost Mexico and southern Arizona. Terborgh (1992) later considered the two hypotheses equally plausible. He too noted the possible importance of the Mexican plateau region in support of a southern home hypothesis. He cited as likely support for the hypothesis the number of species that are otherwise permanent residents in tropical and subtropical regions but which show migratory behaviour only in the Mexican plateau region.

Parulines deserve further attention here because they are numerically dominant among Nearctic-Neotropical temperate-tropical migrants yet exceptional in some respects. Levey & Stiles (1992) proposed that dependency on resources supplied by plant reproduction and/or life in highly seasonal habitats is positively associated with seasonal movements and that species most prone to seasonal movements within the tropics were predisposed to migrate out of the tropics. They found that most long distance temperate-tropical migrants supported their scheme but that the parulines and fluvicoline flycatchers were notable exceptions. They suggested that the lack of fit of parulines may reflect their supposed northern origin and, more specifically, their association more with seasonal habitat than with diet. Indeed, the hypothesis that these birds had evolved from ancestors in North American tropical environments that were much more seasonal and dry than in Central America had been suggested by Lonnberg (1927) and Mayr (1946). Among the similarly exceptional fluvicolines, Levey & Stiles (1992) noted that *Empidonax* does contain examples of a link between diet and movement. The lack of fit of the highly insectivorous genus *Contopus* remained inexplicable.

EVOLUTION OF TEMPERATE-TROPICAL MIGRATION: THE SOUTH AMERICAN SYSTEM

The next evolutionary questions to ask therefore concern the origins of the South American temperate-tropical system identified elsewhere (Joseph, submitted). That is, should the birds involved be thought to have evolved from tropical or temperate ancestors (or both) and did their migrations evolve southwards or northwards (or both), respectively?

The passerines among the group are mostly tyrannids and hirundinids. An hypothesis of tropical origins for the tyrannids, which are most diverse in tropical Central and South America, seems simple and reasonable. DNA-DNA hybridization studies suggest that the hirundinids involved are at least New World in origin (Sheldon

& Winkler 1993) though whether their origins were tropical, subtropical or temperate remains unclear. This question obviously requires further study. At present, I conclude that for temperate-tropical migrants hypotheses of origins from resident or locally wandering ancestors in tropical or subtropical regions followed by evolution of northwards and southwards migration to North American and South American temperate zones, respectively, are as likely as any other at present and, in some cases, are to be preferred. It is worth noting that Safriel (1995) similarly concluded that origins from tropical or subtropical ancestors are most likely for Palearctic-African migrants, i. e., those birds that migrate between temperate breeding grounds in the Palaearctic and non-breeding grounds in tropical or subtropical Africa.

TOWARDS A BROADER VIEW OF NEOTROPICAL MIGRANTS

In view of the above discussion, I suggest that a broader and predictive outlook on temperate-tropical bird migration in the Americas can come from recognizing that what has evolved are two geographically sister temperate-tropical systems. One of these systems has species breeding in temperate North America and is dominated by parulines, and the other has species breeding in temperate South America and is dominated by tyrannids (Fig. 1).

This view of the *patterns* of temperate-tropical migration is useful in that it immediately brings into focus questions relating to evolutionary *processes* such as the relative roles of history and ecology in determining why, among passerines, parulines should be numerically dominant in the northern arm and tyrannids in the southern arm. Taking the approach of Levey & Stiles (1992), one might rephrase this question as: what has been the relative importance of biogeographic origins on one hand and plant resources in strongly seasonal wet dry tropical and subtropical environments on the other in the evolution of the two temperate-tropical migration systems?

Viewing temperate-tropical migration in the Americas as comprising two geographically sister temperate-tropical migration systems both with tropical or subtropical origins may also be considered as a phylogenetic hypothesis for species that have populations in both systems. In the Plumbeous Kite *Ictinea plumbea* (Accipitridae), Red-eyed Vireo *Vireo olivaceus* (Vireonidae), Vermillion Flycatcher *Pyrocephalus rubinus*, Piratic Flycatcher *Legatus leucophaius*, Tropical Kingbird *Tyrannus melancholicus* and Scissor-tailed Flycatcher *Tyrannus savanna* (Tyrannidae) complexes (see Ridgely & Tudor 1989, 1994; Hoyo *et al.* 1994), there are three groups of populations: migratory populations breeding in North or Central America and at least some of which migrate to or towards Amazonia in the boreal winter and so belonging to the northern system, populations breeding in southern South America and migrating to Amazonia for the austral winter and so belonging to the southern system, and breeding resident tropical populations widespread in tropical South America. Various patterns of phylogenetic relationships between these three groups are possible. However, that of the two groups of migrant populations being each other's closest relatives is specifically excluded by the hypothesis that they evolved from resident tropical ancestors. They could only be closest relatives if, for example, one migrant population was founded by individuals of the other migratory population that overshot their destinations. Multiple origins of migration would also further complicate the picture. For the *Vireo olivaceus* complex some allozyme data relevant to this hypothesis are available (Johnson & Zink 1985, Johnson *et al.* 1988). Though consistent with the hypothesis of tropical origins, the need for further study was also clearly indicated in these papers and the possibility of *Vireo olivaceus diversus* being a cryptic species was raised.

The concept of sister temperate-tropical migration systems in the Americas leads to further suggestions for what is essentially a reclassification of the patterns of long distance bird migration in the Americas. Again, I suggest that such a reclassification of the various migration systems operating in the Americas can offer broader and useful perspectives on the processes involved in their ecology and evolution. This is analagous to a systematist suggesting that ecological and evolutionary relationships among closely related species can best be understood when it is appreciated that what has been considered as one or two species should be viewed as several. That is, patterns in long distance bird migration in the

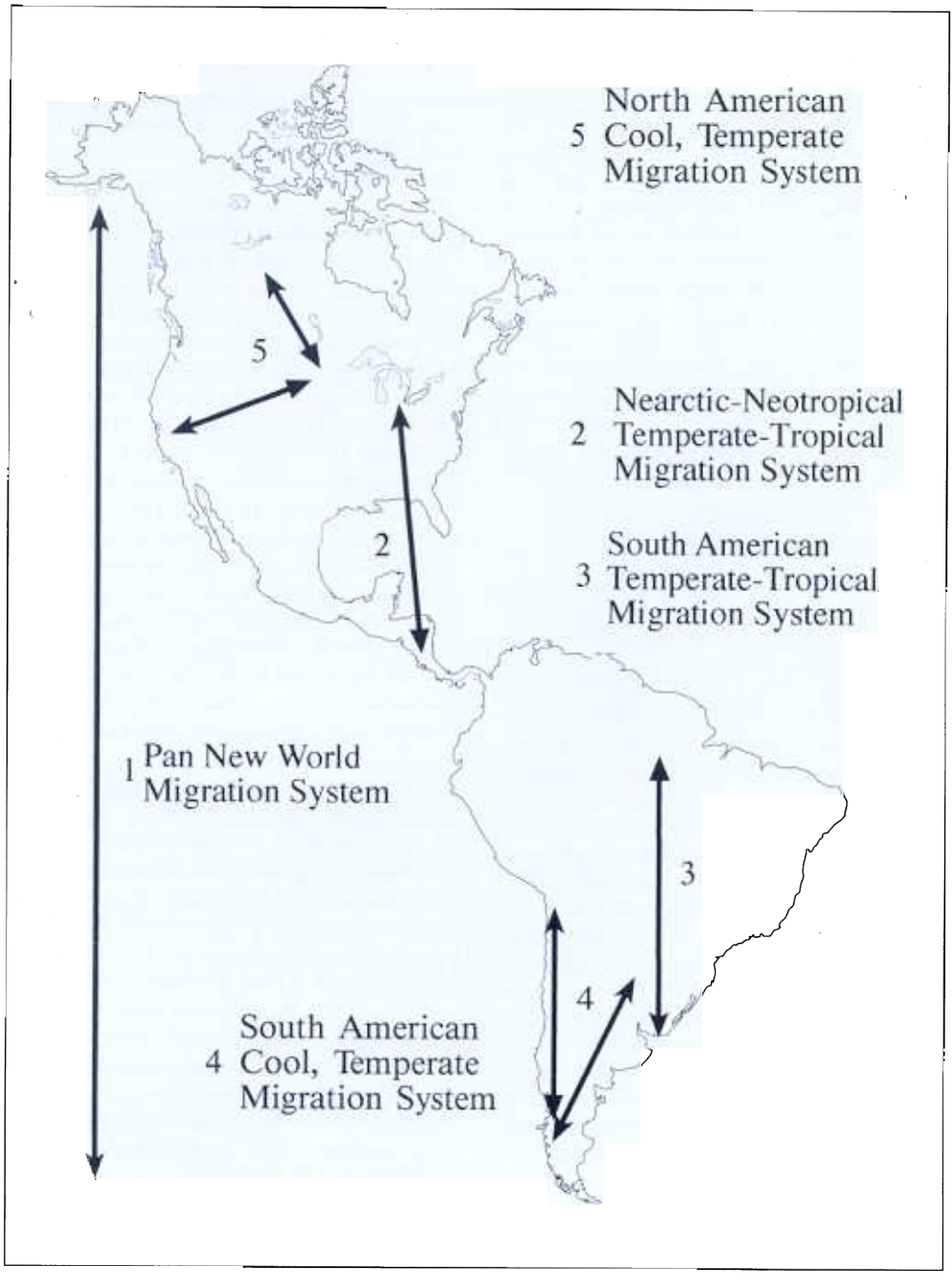

FIG. 1. Schematic diagram to illustrate the classification suggested here of major patterns of long distance bird migration in the Americas. The arrows are intended to indicate only the general bioclimatic patterns shown by the species in the respective migration systems or complexes and not precise migration routes. Shorter distance intraregional migrations blur the distinctions between the main long distance patterns (see text).

Americas might be broken down as follows (Fig.1):

1. *Pan New World Migration System* possibly warranting subdivision and comprising species that winter and summer widely between the geographical extremes of the South and North American continents such as shorebirds, birds of prey, some swallows (e. g., Bank Swallow *Riparia riparia*) and other passerines (e. g., Bobolink *Dolichonyx oryzivorus*) that are not found only in the warm humid tropics when in the Neotropics.

2. *Nearctic-Neotropical Temperate-Tropical* (NETT) *Migration System* with species breeding in temperate North America and migrating to the warm humid tropics and dominated by parulines.

3. *South American Temperate-Tropical* (SATT) *Migration System* with species breeding in temperate South America and migrating to the continent's warm humid regions and dominated by tyrannids. This system includes Hayes *et al.*'s (1994) northern Austral migrants.

4. *South American Cool, Temperate* (SACT) *Migration System*, which has been discussed in more detail elsewhere (Joseph, submitted) and which includes Hayes *et al.*'s (1994) southern Austral migrants and groups such as migratory groundtyrants *Muscisaxicola* spp.. This is most likely a complex of migration subsystems.

5. *North American Cool, Temperate* (NACT) *Migration System*, which, like the South American Cool, Temperate System, has complex patterns of migration and would include most or all of the 95 migratory species referred to by Keast (1980) as not occurring south of the United States in winter. Species with only a very small proportion of their non-breeding distributions south of the Tropic of Cancer such as Mountain Plover *Charadrius montanus*, Lesser Snow Goose *Chen caerulescens* and Field Sparrow *Spizella pusilla* would most reasonably be placed in this category. DeGraaf & Rappole (1995), however, listed these and many others with similarly small proportions of their ranges south of the Tropic of Cancer as Neotropical migrants in the sense of NETT migrants above.

Blurring the distinctions between the Temperate-Tropical and Temperate Migration Systems of long-distance migration patterns are birds that undergo short to medium distance intraregional migrations within and between tropical and/or temperate regions (e. g., South America: Snail Kite *Rostrhamus sociabilis* — Hoyo *et al.* 1994, Lesson's Seedeater *Sporophila bouvronides* — Ridgely & Tudor 1989, the "caatinga" population of Lined Seedeater *Sporophila lineola* — da Silva 1995; North America: Gray Vireo *Vireo vicinior* — Bates 1992). Their migration patterns are intermediate between those characterizing the remaining migration systems. That there are no sharp divisions between long-distance migration systems should not be considered surprising in view of how often migration has evolved and how rapidly the direction of migration can change (Berthold *et al.* 1992).

This "taxonomy" of bird migration in the Americas, which may be seen as a finer level of the hierarchical view recently proposed by Hayes (1995), is a bioclimatic hypothesis and not an evolutionary one though it may lead to a clearer understanding of evolutionary origins of the migration patterns involved as in the example above. To test it, the distributions of the species in each group could be described as bioclimatic profiles. This could determine whether each migration system has its own characteristic bioclimatic profile and, possibly, though as a separate question, evolutionary origins. I suggest that the names used here of "South American Temperate-Tropical Migration System" and "South American Cool, Temperate Migration System", for the "northern Austral migrants" and "southern Austral migrants", respectively, of Hayes *et al.* (1994) are preferable because they avoid the word "austral", the usage of which has contributed to retarding our understanding of bird migration patterns in South America. Also, I have tried to show that the proposed names better place these migration systems in ecological and evolutionary contexts. I hope that these views will contribute to the broader view of Neotropical migrants that Levey (1994) has urged.

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