

## EVOLUTION OF OLD AND NEW WORLD MIGRATION SYSTEMS

JOHN H. RAPPOLE<sup>1</sup> & PETER JONES<sup>2</sup>

Rappole J.H. & P. Jones 2002. Evolution of old and new world migration systems. In: Both C. & T. Piersma (eds) *The avian calendar: exploring biological hurdles in the annual cycle*. Proc. 3rd Conf. European Orn. Union, Groningen, August 2001. *Ardea* 90(3) special issue: 525-537.



The apparent nomadism of Palearctic migrant birds during the wintering period in Afrotropical savannah resulted in their characterisation as wandering interlopers, subordinate to Tropical residents, forced to subsist on temporary resource concentrations in marginal habitats. These ideas persist, and, indeed, provide the theoretical basis for many modern studies of migrant evolution. However, recent studies have established that migrant ecology is more complex, with many migrants using stable resources and demonstrating site fidelity to a broad range of Tropical habitats, both within and between wintering seasons. Furthermore, intra-Tropical movements are now known to occur in a number of Tropical resident species as well as migrants, and appear related to resource and habitat seasonality. These findings, plus extensive taxonomic evidence, indicate that most long-distance migrants to temperate and boreal breeding sites are derived from Tropical-breeding resident birds, emphasising the critical importance of taking into account selective factors and evolution occurring during the non-breeding portion of the life cycle. The three principal Holarctic migration systems are similar in these and many other aspects, but differ in that, while roughly one third of the Nearctic/Neotropical and eastern Palearctic/Asian Tropical migrants winter in forest, almost none of European/Afrotropical migrants do so. We propose that habitats connecting Holarctic and Tropical regions serve as a filter for potential migrants to the Holarctic, and that absence of forest from northern Africa has limited exploitation of European forests by Afrotropical species.

Key-words: Migratory bird evolution - Old World migration systems - New World migration systems

<sup>1</sup>Smithsonian Conservation & Research Centre, 1500 Remount Road, Front Royal, Virginia 22630, USA; E-mail jrappole@crc.si.edu; <sup>2</sup>Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, Scotland, UK.

### INTRODUCTION

Many of the ideas and controversies regarding the origin, evolution, and significance of avian migration derive from investigations of Old World migrants wintering in the European subtropics and central African Tropics. One of the critically important studies in the development of these ideas was the work by Morel & Bourlière (1962) on migratory bird ecology in Senegal, from which they concluded that migrants as a class were sub-

ordinate to Tropical resident species, constituting a floating population (*population flottante*) of wandering consumers taking advantage of the seasonal surplus existing in their wintering areas. MacArthur (1972) elaborated on these observations, using wintering migrants as examples of 'fugitive species,' i.e., 'species that are able to survive by their relatively quick and temporary occupancy of suitable new habitats as these first become available.' (MacArthur & Wilson 1967). Several studies in both the African and New

World Tropics have presented data in support of this hypothesis (Willis 1966; Morse 1971; Karr 1976; Leisler 1990). Their observations are consistent with an evolutionary scenario in which migrants, derived principally from temperate and boreal resident populations, are pushed into complex Tropical communities by climatic factors, where they are forced to compete with Tropical resident species. These studies provided a framework in which the non-breeding portion of the life cycle did not have to be taken into account in studies of speciation among migrants, following the reasoning that if migrants do not occupy distinctive niches in tropical environments, then their morphological characteristics could be attributed principally to selection on the breeding grounds. Several modern investigations of migrant evolution and/or speciation appear to be based on this assumption, since non-breeding season distribution and selection pressures are given no relevance (Bermingham *et al.* 1992; Richman & Price 1992; Price *et al.* 1997; Cicero & Johnson 1998).

In contrast, Lack (1944, 1968), Salomonsen (1955), and Rappole (1995) proposed that the non-breeding portion of the migrant life cycle must affect migrant evolution and speciation, and recent studies of migratory bird ecology support this view. These studies have expanded our understanding of migrant non-breeding season biology, providing a different perspective on the role of migrants in Tropical communities, and new insights into the possible origins of avian migration in which many migrant species are seen as having evolved from Tropical residents (Rappole & Tipton 1992). In this paper, we review information on the ecology of migrants along with its relevance to understanding migrant origin and evolution, and consider how these data and ideas could help to explain some of the similarities and differences between the world's principal migration systems, particularly the lack of forest-wintering species in the Palearctic-Aftropical migration system.

## ECOLOGICAL CHARACTERISTICS OF WINTERING MIGRANTS

The 'migrants as fugitive species' hypothesis was based on three main categories of data: 1) Site Fidelity - Wintering migrants did not appear to show fidelity to particular wintering sites, rather populations seemed to move from site to site at random over the course of the season, i.e., pursuing a 'nomadic' or 'wandering' habit of Tropical resource and habitat exploitation; 2) Habitat Use - Wintering migrants did not appear to use primary habitat types in the Tropics, most notably lowland rain forest. They seemed to be excluded from use of such habitats by resident 'ecological counterparts' (MacArthur 1972), and forced to use secondary, marginal, or disturbed habitats; 3) Resource Use - Wintering migrants appeared to be prevented from using the stable resources of Tropical communities by Tropical residents to whom they were subordinate, and forced to subsist on temporary concentrations (i.e., 'superabundant resources'), e.g., fruits, seeds, nectar, or insect swarms. We examine and discuss each of these characteristics below in the light of more recent studies suggesting that migrant ecology is more complex than early investigations had indicated.

### Site Fidelity

The concept of migrants as nomadic wanderers pursuing a strategy of random, intra-Tropical movements over the course of the wintering period derived from two main types of circumstances: Palearctic migrants in Aftropical savannas; and Nearctic migrants at resource concentrations such as fruiting trees. Lack of migrant site fidelity under each situation is well-documented (Morel & Bourlière 1962; Leck 1972; Karr 1976; Leisler 1990; Petit *et al.* 1995). However, under different circumstances, wintering migrants have been found to demonstrate within-season site fidelity in a variety of Tropical habitats and localities (Blake & Loiselle 1992, Rappole *et al.* 1992; Staicer 1992; Herremans *et al.* 1995; Salewski *et al.* 2000) and return rates to Tropical wintering sites comparable to return rates to temperate breeding sites

(Rappole & Warner 1980; Holmes & Sherry 1992). Furthermore, recurrence in winter quarters based on band returns has been demonstrated for a wide spectrum of migrant taxa and in all of the major geographical wintering areas for migrants around the world (Southeast Asia: Nisbet & Medway 1972; McClure 1974; Africa: Moreau, 1972; Curry-Lindahl 1981; Neotropics: Rappole 1995: Table 4.1). These findings show that nomadism is not a characteristic of migrants as a class or even for migrants within a particular geographical migration system.

Nevertheless, movement during the wintering season (Nov-Mar), is typical for many migrant species exploiting Afrotropical savanna habitats, a group that constitutes as much as 20% of the savanna avian community (Jones 1998). The majority of these species are insectivores that arrive in the northern Afrotropics between August and October at the end of the rainy season. Within two to three months, these habitats become very dry, and many of the migrants then undertake a second southward migration to less arid dry season conditions in broadleaved savannas closer to the equator or to southern African savannas where the local rains are just beginning. These mid-winter movements, called 'itinerancy' by Moreau (1972) and 'step migration' by Curry-Lindahl (1981) are now well documented throughout Africa (Jones 1985, 1995, 1998; Pearson 1990; Pearson & Lack 1992; Elgood *et al.* 1994). However, 40% of Afrotropical savanna avian 'resident' species appear to perform similar, intra-Tropical migrations. Although the precise timing of these movements varies by species, departure by many Afrotropical birds from northern Tropical savannas to wetter southern localities roughly corresponds with the arrival of migrants from the Palearctic (Jones 1985, 1995, 1998; Elgood *et al.* 1994). For both Palearctic migrants and Afrotropical species, this behaviour is determined by the sequence of alternating wet and dry seasons caused by the annual north-south movements of the Inter-Tropical Convergence Zone (ITCZ). The ITCZ and most Afrotropical migrants move northwards in the first half of the calendar year and southwards

in the latter half. Palearctic migrants are obliged to do likewise during the time they spend in Africa, and for the same reasons. The apparent lack of site fidelity over a wintering season is not a characteristic of migrants, but rather is a function of the types of resources exploited and the changing availability of those resources over time. Indeed, itinerancy does not itself preclude site fidelity. Itinerant Garden Warblers *Sylvia borin* occupied territories in Uganda for about six weeks until departing in December, but then returned in February to exactly the same territories they had occupied two months earlier (Curry-Lindahl 1981). Furthermore, Garden Warblers show strong recurrence between years in southern Africa (Herremans 1997), suggesting a strategy in which individuals may retrace their step migration year after year, revisiting the same places in strict sequence and remaining at each for as long as necessary before moving on to the next. Intra-seasonal, intra-Tropical movements have been reported for Nearctic migrants wintering in the Neotropics as well. Levey & Stiles (1992) proposed that intra-Tropical movements represent a strategy for exploitation of particular types of patchily-distributed resources rather than a characteristic of Nearctic migrants as opposed to Neotropical residents. In fact, such movements are typical for many of the birds exploiting fruit and nectar resources, whether they are Nearctic migrants, like the Eastern Kingbird *Tyrannis tyrannis* (Morton 1971) or Neotropical-breeding birds, like the Resplendent Quetzal *Pharomachrus mocinno* (Powell & Bjork 1994).

### Habitat Use

Two observations regarding habitat use shaped early concepts regarding the role of migrants in the Tropics: First, that no Palearctic migrants winter in Afrotropical rain forest, and, in fact, only five species are restricted to Afrotropical, closed-canopy, broad-leaved habitats (Moreau 1972; Mönkkönen *et al.* 1992; Baumann 1999; Bijlsma, *in press*); Second, that migrants often predominate in both diversity and numbers over Tropical residents in disturbed, secondary habitats

while the reverse is often true in undisturbed, primary habitats (Petit *et al.* 1995). These observations, based on excellent field data collected by many different researchers, have led to the conclusion that migrants are prohibited by superior Tropical-breeding competitors from occupying niches in stable, Tropical habitats (Robinson *et al.* 1988). We know now, however, that migrants winter in nearly every Tropical habitat type, primary as well as secondary, undisturbed as well as disturbed (Moreau 1972; McClure 1974; Rappole 1995), though the relative numbers of migrants and residents in Tropical primary and secondary environments may vary in different regions and situations. We also now know that, with the exception of the Afrotropical forests, which we discuss as a special case below, wintering migrants use forested habitats extensively, including rain forests. For example, 20 species of Nearctic migrants arrive in undisturbed Neotropical rain forest in Mexico in September and October, establish individual territories, remain on these territories until departure in April northward on spring migration, and often return to these territories in subsequent years (Rappole & Warner 1980).

If migrants are present in nearly all Tropical habitat types, it follows that they are not being excluded by residents from such habitats. But what accounts for the general predominance of migrants over residents in secondary, disturbed, or marginal habitats? We see two possible explanations that are not mutually exclusive: 1) Tropical species that exploit ephemeral habitats or resources might be predisposed to becoming migrants (Rappole & Warner 1980; Levey & Stiles 1992), so that migrants are likely to form a disproportionate number of the species found in these communities; 2) If winter habitat is limiting for migratory species (as opposed to breeding, post-breeding, or stop-over habitat) then more individuals are likely to be produced than can be supported by available winter habitat, and many individuals will be forced to use marginal habitats on arrival at the wintering grounds (Fretwell 1972; Rappole & McDonald 1994, 1998).

### Resource Use

The idea that migrants are prevented from using the stable resources in Tropical communities (i.e., those resources on which an individual can depend for prolonged periods e.g. an entire season) by resident species, and are thereby forced to depend upon temporarily superabundant resources for which they do not have to compete, derives mainly from migrant-resident interactions observed in the Neotropics at army ant swarms (Willis 1966), fruiting trees (Leck 1972), flowering plants (DesGranges & Grant 1980), and interspecific aggression among ground-feeding birds in Africa (Leisler 1990). Despite these observations of interactions, there are no data to indicate that migrants actually are prevented from using the stable resources of Tropical communities on a long-term basis, or that interactions with residents have an effect on migrant survivorship. Detailed observations of the ecology of migrants in the non-breeding season indicate that a broad range of resource-use patterns exists, comparable to the range observed in Tropical-breeding species. This diversity of patterns, and the comparable diversity in sociality evolved to exploit resources, seem to be related to the requirements of each species and the distribution of critical resources in the environment (Brown 1964), rather than to a particular pattern of resource use peculiar to migrants as a group. For instance, a number of field studies document that individuals of many migrant species remain successfully on small plots of ground in Tropical habitats throughout the wintering period, defending these sites as individual territories, and even returning to the same sites in subsequent years (Snow & Snow 1960; Schwartz 1964; Rappole 1995: Table 3.3), indicating that critical, stable resources are available and defensible. Other species, while still apparently solitary during the wintering period, do not appear to defend territories, perhaps because they are forced to be more mobile to find patchily distributed food, obtained by a narrower range of feeding behaviours and foraging substrates (Salewski *et al.* 2002). Staicer (1992) observed a broad range of sociality/resource-use patterns for three species of

migrant parulids wintering in Puerto Rico (Northern Parula *Parula americana*, Cape May Warbler *Dendroica tigrina*, Prairie Warbler *Dendroica discolor*), from site-specific territoriality, to solitary foraging, to loose, single-species flocks, many of whose members demonstrated both within- and between season site fidelity.

Many migrants as well as Tropical-breeding birds participate in mixed-species foraging flocks through the wintering period. Such flocks can be quite stable in both membership and home range, and have been observed in a wide variety of Tropical localities in the New World, Hawaii, and Southeast Asia (Harrison 1962; Powell 1985, King & Rappole 2000, 2001; Hart 2001). In some of these mixed-species flocks, single individuals of migrant species appear to defend the flock itself, preventing other conspecifics from joining, and demonstrating both within- and between-season site fidelity (Powell 1980). Others contain more than one individual of a particular migrant species, although the actual number of conspecific flock participants may still be determined by a combination of resource availability and intraspecific competition (King & Rappole 2000).

Large, single-species flocks also are common for some species of both migrants and Tropical-breeding birds that exploit widely dispersed patches of resources, e.g., rice fields, flowering or fruiting trees, exposed tidal flats (Ffrench 1967; Ward & Zahavi 1973; Piersma *et al.* 1992; Levey & Stiles 1992). Interestingly, close investigation of some wintering flocks of migrants in the Tropics has revealed within- and between-season site fidelity to particular feeding sites, even though the birds may move to a number of different sites over the course of the season (Johnston & Downing 1968).

As noted above, migrants often have been observed to use temporary resource concentrations in disturbed or marginal habitats in much greater numbers of both species and individuals relative to Tropical-breeding species (Willis 1966; Karr 1976). Some migrants as well as some Tropical-breeding species apparently are well-adapted to locate and exploit relatively stable resources in

habitats of this type, showing long-term site fidelity within and between seasons, e.g., Least Flycatchers *Empidonax minimus* in overgrown Veracruz pastures (Rappole & Warner 1980). However, members of other migrant species obviously are searching for, and depending upon, temporary resource concentrations (Willis 1966; Karr 1976; Rappole & Morton 1985; Rappole *et al.* 1989). These birds tend to show higher turnover rates and disproportionate declines in total numbers over the course of the winter season relative to members of the same species in other habitat types, indicating that the habitat is indeed marginal (Rappole *et al.* 1989). We propose that this pattern of resource use is caused by production of more young by members of these species of migrants than can be accommodated in 'preferred' Tropical wintering habitats (i.e., habitats in which survivorship would be higher). Concentrations of these species of migrants in marginal Tropical habitats essentially represent dispersing individuals in the process of trying to relocate to better quality habitats (Rappole *et al.* 1989; Rappole & McDonald 1994; Winker *et al.* 1995).

#### ORIGIN AND EVOLUTION OF TROPICAL-HOLARCTIC MIGRATION

Numerous theories have been proposed for the origin and evolution of migration (summarised in Rappole 1995), most of which focus on species' breeding distributions (Mengel 1964; Cohen 1967; Snow 1978; Cox 1985). However, MacArthur (1972) and others recognised that both the breeding and non-breeding portions of the migrant life cycle were important in understanding migrant origins. An explanation for the ability of an avifauna composed of hundreds of species and millions of individuals to invade Tropical habitats each year in competition with Tropical-breeding species is a required part of any theory of migrant evolution. Accordingly, they proposed the 'fugitive species' hypothesis as a solution in which migrants do not actually join Tropical communities, but essentially harvest excess resources



through a process of random movements. This explanation may be appropriate for migrations seen in some species, e.g., weather-induced irruptions by European parids. However, it is now known that many species of migrants arrive in the Tropics during times when resources are decreasing ('Moreau's Paradox': Fry 1992) or are already at a low ebb (DesGranges & Grant 1980), enter primary Tropical communities like rain forest, cloud forest, pine-oak, savannah, grassland, and marshland (Rappole 1995: Table 2.1, Rappole *et al.* 2000), live there for six or seven months of the year, evidently competing successfully with specialised Tropical residents for the stable resources of the community (Rappole & Warner 1980), depart, and often return to the same winter site in subsequent years (Rappole 1995: Table 4.1). These and similar observations regarding the obvious integration of many migrant species into Tropical communities are not consistent with a 'fugitive species' hypothesis. Accordingly, we have developed an alternative explanation for the origin and evolution of Tropical-Holarctic migration that explains the paradox of successful migrant invasion of Tropical communities. We propose that migrants are able to exploit stable Tropical niches because they originated in the Tropics and evolved a migratory habit to capitalise on seasonally abundant resources in the temperate and boreal regions, where fewer competitors and predators allow for considerable increase in production of offspring over what is possible in Tropical habitats. These ideas complement and expand upon those of Rappole *et al.* (1983); Rappole & Tipton (1992); and Rappole (1995) for the Neotropics and Safrieli (1995), who proposed a similar southern origin for Holarctic-Tropical migrants based on the relative costs and benefits of long-distance dispersal by tropical-breeding species, and used the Palearctic-African system as an example. Our hypothesis involves the following steps in the evolution of a migratory habit:

1. Long-distance migrants from Tropical to temperate regions originate as sedentary, Tropical-breeding residents.
2. Each year, despite intense competition and predation, more young are produced by these birds than available, Tropical habitat can support.
3. Thus, young of the year are forced to disperse to find available breeding habitat.
4. The process of dispersal favours evolution of adaptations for undertaking successful movements in search of suitable habitat, e.g., hyperphagia on discovery of resource concentrations, subcutaneous fat storage, navigation, and homing.
5. Some species are adapted to use of niches common to many different habitat types, e.g., gleaning insects from leaves, which allows them the option of exploiting resources in different habitats or regions.
6. Increased food availability along with reduced competition and predation in seasonal temperate habitats during summer allow much higher reproductive rates in temperate populations relative to Tropical populations of the same species.
7. These fitness rewards favour rapid (in an evolutionary sense) invasion of relatively depauperate temperate habitats by those Tropical species capable of exploiting them.

A logical question deriving from this scenario is, 'If temperate migrants evolved from tropical residents, where are those source populations now?' We propose two answers to this question. First, as discussed below, for 23% (Afrotropics) – 48% (Neotropics) the source populations are conspecifics with breeding populations in the Tropics. Second, for those species in which the source population has disappeared, the reason is the same as for the disappearance of any other trait, namely natural selection in which members of the migratory population are favored over those of the resident.

We have presented data in support of the steps in this theory elsewhere (Rappole *et al.* 1983; Rappole & Tipton 1992; Rappole 1995), as has Safrieli (1995). In addition, recent experimental evidence on Blackcaps *Sylvia atricapilla* demonstrates the

rapidity with which migrants can colonise new temperate wintering habitat (Helbig 1996). Nevertheless, the principal evidence in support of this hypothesis for evolution of migrants from Tropical species is phylogenetic. Consider for instance that of the 338 species of migratory birds that breed in temperate and boreal North America, 162 (48%) have conspecifics and 78% have congeners that breed in the Neotropics; for the Asian migration system, the numbers are comparable: 106 (31%) of 338 species of migrants have conspecific populations that breed in the Tropics while 262 species (78%) have congeners; for the Palearctic-African migration system: 42 of 185 species of migrants (23%) have conspecific populations that breed in the Tropics while 139 (75%) have Tropical-breeding congeners. These numbers are highly suggestive that most of the birds that breed in the Nearctic and Palearctic region are Tropical in origin, although several groups (e.g., *Phylloscopus*, *Dendroica*, *Vermivora*, *Empidonax*, *Vireo*, and *Myiarchus*) clearly have undergone radiation subsequent to evolution of a migratory habit (Rappole 1995). They live in temperate or boreal regions only during the time of year when these regions are like the Tropics.

Despite the extensive evidence indicating Tropical origin and the critical importance of Tropical environments for many migratory species, several recent treatments of evolution in temperate-breeding migrants that winter in the Tropics have ignored the Tropical portion of the life cycle, attributing observed patterns of breeding distribution and morphological characteristics entirely to breeding ground factors (e.g., Bermingham *et al.* 1992; Richman & Price 1992; Cicero & Johnson 1998; Price *et al.* 1997). Whether stated or not, these treatments are based conceptually on the 'fugitive species' hypothesis in which migrants are pushed southward annually by seasonal climatic change into the Tropics where they fail to occupy distinctive niches in Tropical habitats. In addition to ignoring the extensive information now available to indicate that migrants do hold distinctive niches in Tropical habitats, and are thus subject, presumably, to selection shaping

morphology, behaviour, and physiology (Bairlein 1993), these studies ignore three additional factors: First, that 23%-48% of migrants that breed in temperate regions have breeding populations in the Tropics as well, including some of those whose speciation has been attributed to Pleistocene effects on Nearctic habitats (e.g., *Vireo plumbeus* and *V. cassinii*) (Cicero & Johnson 1998); Second, that invasion of temperate habitats by a tropical-breeding species is a dynamic process that can occur over a matter of years rather than millennia, e.g., the case of the Cattle Egret *Bubulcus ibis* in North America (Rappole *et al.* 1983); Third, that broad changes in breeding distribution also can occur in a matter of years e.g., the case of the Blackcap in the British Isles (Helbig 1996). A complete understanding of migrant phylogeny and evolution will have to take into account the dynamic nature of the process and the importance of non-breeding season selection in addition to breeding-season selection factors.

### OLD WORLD VERSUS NEW WORLD MIGRATION SYSTEMS

There are three major Holarctic migration systems: 1) the Nearctic-Neotropical in which birds migrate between the Neotropics and Nearctic breeding grounds; 2) the Palearctic-African in which birds migrate between the African Tropics and Europe and western Asia; and 3) the Palearctic-Asian in which birds migrate between the Asian Tropics and the temperate and boreal regions of eastern Asia. Comparison of the numbers of migrant species by family for these different migration systems reveals some striking similarities and differences (Table 1). First, despite the fact that several different families are involved, the overall size of the Palearctic-Asian and New World migration systems are quite similar (about 338 species for both) while the Palearctic-Tropical African system is much smaller (185 species - excluding coastal migrants). Closer examination of the table shows that the Palearctic-African system is depauperate relative to the other systems in

**Table 1.** Numbers of species by family for the three main migration systems of the Northern Hemisphere (from Rappole 1995). <sup>1</sup>N/A = Not Applicable - family does not occur in the region.

Family	Migration System		
	Nearctic/ Neotropical	Palaearctic/ Afrotropical	Palaearctic/ Asian Tropical
Podicipedidae	4	0	0
Pelecanidae	2	0	2
Phalacrocoracidae	2	0	1
Anhingidae	1	0	0
Ardeidae	12	8	16
Threskiornithidae	4	3	4
Ciconiidae	1	2	6
Anatidae	20	11	19
Cathartidae	2	N/A <sup>1</sup>	N/A
Accipitridae	11	17	23
Falconidae	4	8	6
Phasianidae	0	1	1
Rallidae	7	5	8
Gruidae	2	2	2
Jacaniidae	0	0	1
Rostratulidae	N/A	0	1
Burhinidae	0	1	1
Glareolidae	N/A	2	1
Charadriidae	8	7	11
Haematopodidae	1	0	1
Recurvirostridae	2	2	2
Scolopacidae	30	20	38
Laridae	21	5	17
Columbidae	5	1	2
Cuculidae	3	3	9
Strigidae	3	2	2
Caprimulgidae	5	3	1
Apodidae	4	4	4
Trochilidae	13	N/A	N/A
Trogonidae	1	0	0
Upupidae	N/A	1	2
Alcedinidae	1	0	2
Meropidae	N/A	1	2
Coraciidae	N/A	1	1
Picidae	3	1	1
Tyrannidae	32	N/A	N/A
Alaudidae	0	2	2
Hirundinidae	8	5	5
Troglodytidae	3	0	0
Campephagidae	N/A	0	5
Pycnonotidae	N/A	0	1
Dicruridae	N/A	0	4
Oriolidae	N/A	1	4
Muscicapidae	12	50	97



(Table 1. continued)

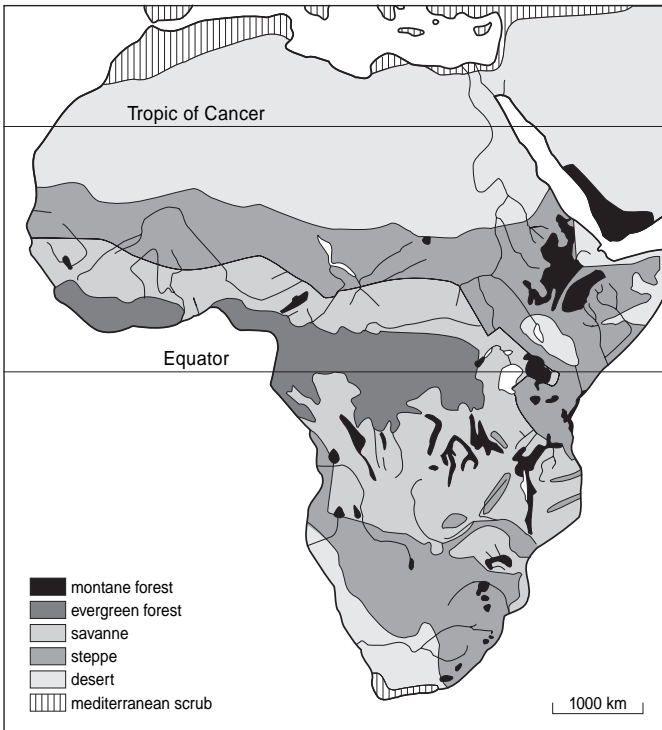
Family	Migration System		
	Nearctic/ Neotropical	Palaearctic/ Afrotropical	Palaearctic/ Asian Tropical
Mimidae	2	N/A	N/A
Motacillidae	2	6	12
Bombycillidae	1	0	0
Laniidae	1	6	3
Sturnidae	0	0	6
Zosteropidae	N/A	0	2
Vireonidae	11	N/A	N/A
Parulidae	50	N/A	N/A
Thraupidae	4	N/A	N/A
Icteridae	13	N/A	N/A
Emberizidae	25	3	6
Fringillidae	2	0	4
Ploceidae	0	1	0
Total	338	185	338

one major class of migrants, namely birds using forest habitats. Moreau (1972) listed 48 species of migrants as breeding in Palaearctic forest while about 112 species breed in Nearctic forests and 107 in east Asian forests (Rappole 1995). However, while nearly all of the Asian and Nearctic species that breed in forests also winter in some type of forest, only five Palaearctic migrants winter in African Tropical forests (European Honey-buzzard *Pernis apivorus*, Golden Oriole *Oriolus oriolus*, Pied Flycatcher *Ficedula hypoleuca*, Collared Flycatcher *F. albicollis*, and Wood Warbler *Phylloscopus sibilatrix*) (Mönkkönen *et al.* 1992; Baumann 1999; Bijlsma *in press*).

We believe that these differences in avifaunal composition for forest-related birds in the different migration systems provide an insight into the processes by which migration evolves. If most migrants evolved from Tropical or subtropical ancestors, as we have suggested, those ancestors would have had to use habitats to which they were adapted to sustain movements north to exploit the temporary resource flushes associated with temperate and boreal summers. The habitats intervening between the Holarctic region and Tropical

source habitats for migrants will therefore act as a filter, screening out any whose habitats are absent and preventing them from completing the journey. In both eastern Asia and the New World there are extensive forests as well as other major habitat types that connect temperate and Tropical regions for both eastern Asia and the New World (Bailey 1989). In contrast, any forest-dependent Afrotropical species would confront thousands of kilometres of desert and salt water to make such a journey to the Palaearctic (Fig 1).

But surely the filter could act in either way - that is, it could prevent boreal woodland species from invading the tropics just as well as prevent Tropical woodland species from invading the boreal region. Certainly that is true, but the following facts argue against a boreal origin. First, the much smaller size of the European migrant avifauna as compared with both Asia and New World. We contend that this smaller size of the Palaearctic-African migrant avifauna is a result of more Tropical species being prevented from invading the temperate zone. Second, the very small number (only five species) of European migrants that appear dependent on forest during



**Fig.1.** Principal African habitats. Data are from Bailey (1989) and Moreau (1972).

both summer and winter. In contrast, there are 48 species that use European temperate and boreal forests in summer, but use open habitats in winter. We would argue that these birds that breed in forest but winter in savannah are evolved from Tropical and subtropical open habitat species that use temperate and boreal woodlands in summer because there is very little competition, i.e., few forest species, and abundant resources. In addition, of course, extensive evidence of taxonomic relationship to Tropical resident species detailed above exists for Palearctic-African migrants (75% with Tropical-resident congeners) just as for migrant species from the other migration systems.

In summary, we hypothesise that the majority of species in all of the world's migration systems, New World, Palearctic/African, Asian, and so forth, evolved in the same way, with dispersing individuals spreading out from Tropical-breeding areas seasonally to locate under-exploited resources that would allow them to produce more

offspring than their sedentary relatives. The types of species involved depend on the diversity of the Tropical source populations, the availability of intervening stopover habitats, and the types of seasonally available temperate and boreal habitats.

#### ACKNOWLEDGEMENTS

We thank Theunis Piersma, Rudi Drent, and other organisers of the Third European Ornithologists' Union meetings in August, 2001, in Haren/Groningen, The Netherlands for the opportunity to attend and present this paper.

## REFERENCES

- Bailey R.G. 1989. Ecoregions of the world. U.S. Department of Agriculture, Washington, D.C.
- Bairlein F. 1993. Ecophysiological problems of Arctic migrants in the hot tropics. *Proc. Pan-African Orn. Congr.* 8: 571-578.
- Baumann S. 1999. Zur Zugphänologie und zum Ueberwinterungsgebiet des Europäischen Pirols (*Oriolus o. oriolus*) in Afrika. *Vogelwarte* 40: 63-79.
- Birmingham E., S. Rohwer, S. Freeman & C. Wood 1992. Vicariance biogeography in the Pleistocene and speciation in North American wood warblers: A test of Mengel's model. *Proc. Natl. Acad. Sci. USA* 89: 6624-6628.
- Bijlsma R.G. *in press*. Ecology of Honey Buzzards *Perisoreus apivorus* wintering in Africa. *Vogelwarte* 41.
- Blake J.G. & B.A. Loiselle 1992. Habitat use by migrants at La Selva Biological Station and Braulio Carrillo National Park, Costa Rica. In: Hagan III J.M. & D.W. Johnston (eds) *Ecology and conservation of Neotropical migrant landbirds: 257-272*. Smithsonian Inst. Press, Washington, D.C.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.
- Cicero C. & N.K. Johnson 1998. Molecular phylogeny and ecological diversification in a clade of New World songbirds (genus *Vireo*). *Mol. Ecol.* 7: 1359-1370.
- Cohen D. 1967. Optimization of seasonal migratory behavior. *Am. Nat.* 101: 5-18.
- Cox G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *Am. Nat.* 126: 451-474.
- Curry-Lindahl, K. 1981. *Bird migration in Africa*. Acad. Press, London.
- DesGranges J-L. & P. Grant 1980. Migrant hummingbirds' accommodation into Tropical communities. In: Keast A. & E.S. Morton (eds) *Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation: 395-409*. Smithsonian Inst. Press, Washington, D.C.
- Elgood J.H., J.B. Heighman, A.M. Moore, A.M. Nason, R.E. Sharland & N.J. Skinner 1994. *The birds of Nigeria*. 2nd edition, British Ornithologists' Union Checklist No. 4, British Ornithologists' Union, Tring.
- Ffrench R.P. 1967. The Dickcissel on its wintering grounds in Trinidad. *Living Bird* 6: 123-140.
- Fretwell S.D. 1972. *Populations in a seasonal environment*. Princeton Univ. Press, Princeton, New Jersey.
- Fry C.H. 1992. The Moreau ecological overview. *Ibis* 134 Suppl.: 3-6.
- Harrison J.L. 1962. Distribution of feeding habits among animals in a Tropical forest. *J. Anim. Ecol.* 31: 53-63.
- Hart P.J. 2001. Demographic comparisons between high and low density populations of Hawaii 'Akepa. *Studies in Avian Biology* 22: 185-193.
- Helbig A.J. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in Palearctic warblers (Aves: Sylviidae). *J. Exp. Biol.* 199: 49-55.
- Herremans M. 1997. Garden Warbler *Sylvia borin*. In: Harrison J.A., D.G. Allan, L.G. Underhill, M. Herremans, A.J. Tree, V. Parker & C.J. Brown (eds). *The atlas of southern African birds: 225*. BirdLife South Africa, Johannesburg.
- Herremans M., D. Herremans-Tonnoeyr & W.D. Borello 1995. Non-breeding site-fidelity of Red-backed Shrikes *Lanius collurio* in Botswana. *Ostrich* 66: 145-147.
- Holmes R.T. & T.W. Sherry 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. In: Hagan III J.M. & D.W. Johnston (eds). *Ecology and conservation of Neotropical migrant landbirds: 563-575*. Smithsonian Inst. Press, Washington, D.C.
- Johnston D.W. & A.C. Downer 1968. Migratory features of the Indigo Bunting in Jamaica and Florida. *Bird-Banding* 39: 277-293.
- Jones P. 1985. The migration strategies of Palearctic passerines in West Africa. In: McDonald A. & P. Goriup (eds) *Migratory birds: Problems and prospects in Africa*. Report of the 14th Conference of the European Continental Section, ICBP, 1983: 9-21. International Council for Bird Preservation, Cambridge.
- Jones P. 1995. Migration strategies of Palearctic passerines in Africa. *Israel J. Zool.* 41: 393-406.
- Jones P. 1998. Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change. In: Newberry D.M., H.H.T. Prins & N.D. Brown (eds) *37th Symposium of the British Ecol. Soc.: 421-447*. Blackwell Science, London.
- Karr J.R. 1976. On the relative abundance of migrants from the North Temperate Zone in Tropical habitats. *Wilson Bull.* 88: 433-458.
- King D.I. & J.H. Rappole 2000. Factors affecting avian flock formation in pine-oak habitat in Middle America. *Condor* 102: 664-672.
- King D.I. & J.H. Rappole 2001. Mixed-species bird flocks in dipterocarp forest of north-central Burma (Myanmar). *Ibis* 143: 380-390.
- Lack D. 1944. Ecological aspects of species formation in passerine birds. *Ibis* 86: 260-286.

- Lack D. 1968. Bird migration and natural selection. *Oikos* 19: 1-9.
- Leck C.F. 1972. The impact of some North American migrants at fruiting trees in Panama. *Auk* 89: 842-850.
- Leisler B. 1990. Selection and use of habitat of wintering migrants. In: Gwinner E. (ed.) *Bird migration: physiology and ecophysiology*: 156-174. Springer-Verlag, Berlin.
- Levey D.J. & F.G. Stiles 1992. Evolutionary precursors of long-distance migration: Resource availability and movement patterns of Neotropical landbirds. *Am. Nat.* 140: 467-491.
- MacArthur R.H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.
- MacArthur R.H. & E.O. Wilson 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton.
- McClure H.E. 1974. *Migration and survival of the birds of Asia*. U.S. Army Medical Component, Southeast Asia Treaty Organization (SEATO), Bangkok, Thailand.
- Mengel R.M. 1964. The probable history of species formation in some Northern Wood Warblers. *Living Bird* 3: 9-44.
- Mönkkönen M., P. Helle & D. Welsh 1992. Perspectives on Palaearctic and Nearctic bird migration: Comparisons and overview of life-history and ecology of migrant passerines. *Ibis* 134 Suppl. 1: 7-13.
- Moreau R. 1972. *The Palaearctic-African bird migration system*. Academic Press, New York.
- Morel G. & F. Bourlière 1962. [Ecological relations of the sedentary and migratory avifauna in a Sahel savanna of lower Senegal.] *Terre et Vie* 4: 371-393.
- Morse D.H. 1971. The insectivorous bird as an adaptive strategy. *Ann. Rev. Ecol. Syst.* 2: 177-200.
- Morton E.S. 1971. Food and migration habits of the Eastern Kingbird in Panama. *Auk* 88: 925-926.
- Nisbet I.C.T. & L. Medway 1972. Dispersion, population ecology and migration of eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114: 451-494.
- Pearson D.J. 1990. Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements. In: Gwinner E. (ed.) *Bird migration: physiology and ecophysiology*: 156-174. Springer-Verlag, Berlin.
- Pearson D.J. & P.C. Lack 1992. Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. *Ibis* 134 suppl.: 89-98.
- Petit D.R., J.F. Lynch, R.L. Hutto, J.G. Blake & R.B. Waide 1995. Habitat use and conservation during winter in the Neotropics. In: Martin T. & D. Finch (eds) *Status and management of Neotropical migratory birds: A synthesis and review of the critical issues*: 145-219. Oxford Univ. Press, Oxford.
- Piersma T., P. Prokosch & D. Bredin 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. *Wader Study Group Bull.* 64 suppl.: 52-63.
- Powell G.V.N. 1980. Migrant participation in Neotropical mixed species flocks. In: Keast A. & E.S. Morton (eds) *Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation*: 477-483. Smithsonian Institution Press, Washington, D.C.
- Powell G.V.N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Orn. Monogr.* 36: 713-372.
- Powell G.V.N. & R. Bjork 1994. Implications of altitudinal migration for conservation strategies to protect biodiversity: A case study at Monteverde, Costa Rica. *Bird Conserv. Intern.* 4: 161-174.
- Richman A.D. & T.D. Price 1992. The evolution of ecological differences in the Old World Leaf Warblers: roles of history and adaptation. *Nature* 355: 817-821.
- Rappole J.H. 1995. *The ecology of migrant birds: a Neotropical perspective*. Smithsonian Inst. Press, Washington, D.C.
- Rappole J.H., D.I. King & P. Leimgruber 2000. Winter habitat and distribution of the endangered Golden-cheeked Warbler. *Anim. Conserv.* 2: 45-59.
- Rappole J.H. & M.V. McDonald 1994. Cause and effect in migratory bird population changes. *Auk* 111: 652-660.
- Rappole J.H. & M.V. McDonald 1998. A response to Latta and Baltz. *Auk* 115: 246-251.
- Rappole J.H. & E.S. Morton 1985. Effects of habitat alteration on a tropical forest avian community. *Orn. Monogr.* 36: 1013-1021.
- Rappole J.H., E.S. Morton, T.E. Lovejoy & J.S. Ruos 1983. *Nearctic avian migrants in the Neotropics*. U.S. Fish & Wildlife Service, Washington, D.C.
- Rappole J.H., E.S. Morton & M.A. Ramos 1992. Density, philopatry, and population estimates for songbird migrants wintering in Veracruz. In: Hagan III J.M. & D.W. Johnston (eds) *Ecology and conservation of Neotropical migrant landbirds*: 337-344. Smithsonian Inst. Press, Washington, D.C.
- Rappole J.H., M.A. Ramos & K. Winker 1989. Movements and mortality in wood thrushes wintering in southern Veracruz. *Auk* 106: 402-410.
- Rappole J.H. & A.R. Tipton 1992. The evolution of avian migration in the Neotropics. *Orn. Neotropical* 3: 45-56.
- Rappole J.H. & D.W. Warner 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. In: Keast A. & E.S. Morton (eds) *Migrant birds in the Neotropics: Ecology, behavior, distribution, and*

- conservation: 353-393. Smithsonian Inst. Press, Washington, D.C.
- Robinson S.K., J. Terborgh & J.W. Fitzpatrick 1988. Habitat selection and relative abundance of migrants in southeastern Peru. Proc. 19 Intern. Ornithol. Congr.: 2298-2307.
- Safriel U.N. 1995. The evolution of palearctic migration - the case for southern ancestry. Israel. J. Zool. 41: 417-431.
- Salewski V., F. Bairlein & B. Leisler 2000. Site fidelity of Palearctic migrants in the Northern Guinea savanna zone, West Africa. Vogelwarte 40: 298-301.
- Salewski V., F. Bairlein & B. Leisler 2002. Different wintering strategies of two Palearctic migrants in West Africa - a consequence of foraging strategies? Ibis 144: 85-93.
- Salomonsen F. 1955. Evolution and bird migration. Proc. 11 Int. Ornithol. Congr.: 337-339.
- Schwartz P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3: 169-184.
- Snow D.W. 1978. Relationships between the European and African avifaunas. Bird Study 25: 134-148.
- Snow D.W. & B.K. Snow 1960. Northern Waterthrush returning to same winter quarters in successive winters. Auk 77: 351-352.
- Staicer C.A. 1992. Social behavior of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth in southwestern Puerto Rico. In: Hagan III J.M. & D.W. Johnston (eds) Ecology and conservation of Neotropical migrant landbirds: 308- 320. Smithsonian Inst Press, Washington, D.C.
- Ward P. & A. Zahavi 1973. The importance of certain assemblages of birds as 'information- centres' for food finding. Ibis 115: 517-534.
- Willis E. 1966. The role of migrant birds at swarms of army ants. Living Bird 5: 187-231.
- Winker K., J.H. Rappole & M.A. Ramos 1995. The use of movement data as an assay of habitat quality. *Oecologia* 101: 211-216.

## SAMENVATTING

Het schijnbaar nomadische voorkomen van Palearctische trekvogels tijdens de winter in het Afrotropische savannegebied heeft geleid tot de gedachte dat het zwervende beunhazen zijn, die ondergeschikt aan de tropische standvogels, worden gedwongen om te leven van tijdelijke voedselbronnen in marginale habitats. Dit idee is hardnekkig en verschaft de theoretische basis voor veel van de huidige studies naar de evolutie van vogeltrek. Recente onderzoeken tonen echter aan dat de ecologie van vogeltrek veel complexer is: veel trekvogels maken in de winter gebruik van stabiele voedselbronnen en vertonen in veel habitats zowel binnen als tussen winters een sterke plaatstrouw daaraan. Tegelijkertijd weten we nu van een aantal tropische standvogels dat ze zich over vrij grote afstanden verplaatsen, bewegingen die waarschijnlijk te maken hebben met seizoenveranderingen in hun voedsel en habitat. Deze bevindingen leiden, samen met de uitgebreide taxonomische kennis, tot de conclusie dat langeafstandstrekken die in de gematigde en boreale gebieden broeden, hun oorsprong hebben in tropische broedvogels. Dit idee benadrukt het cruciale belang van onderzoek buiten het broedseizoen om de selectie op en evolutie van langeafstandstrek te begrijpen. De drie belangrijkste Holarctische treksystemen hebben een tropische oorsprong van langeafstandstrek met elkaar gemeen, maar verschillen in het feit dat ongeveer eenderde van de Nearctisch-Neotropische en oostelijke Palearctisch-tropisch Aziatische trekvogels in bossen overwinteren, terwijl vrijwel geen enkele Europees-Afrotropische trekvogel dit doet. De auteurs maken zich sterk voor het idee dat dit komt doordat de habitats tussen de Holarctische en tropische regionen fungeren als een filter voor potentiële trekvogels met een tropische oorsprong, zodat de afwezigheid van bossen in Noord-Afrika een belangrijke beperking is geweest voor bosvogels uit tropisch Afrika om naar het noorden te trekken en de Europese bossen te koloniseren. CB)

